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Assessing relationships between red spruce radial growth and pollution critical load exceedance values

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ABSTRACT

Acidic sulfur (S) and nitrogen (N) deposition depletes cations such as calcium (Ca) from forest soils and has been linked to increases in foliar winter injury that led to the decline of red spruce (*Picea rubens* Sarg.) in the northeastern United States. We used results from a 30 m resolution steady-state S and N critical load exceedance model for New England to better understand the spatial connections between Ca depletion and red spruce productivity. Atmospheric deposition and other inputs were estimated for a 5-year period (1984–1988) in order to smooth year-to-year variations in climate and patterns of atmospheric transport. Deposition levels prior to the reductions that followed the 1990 Amendments to the Clean Air Act were used because tree health and productivity declines were expected to be most responsive to high acid loading. We examined how radial growth (basal area increment) of 441 dominant and co-dominant red spruce trees from 37 sites across Vermont and New Hampshire was related to modeled estimates of S and N critical load exceedance. We assessed growth using statistical models with exceedance as a source of variation, but which also included “year” and “elevation class” (to help account for climatic variability) and interactions among factors. As expected, yearly climate-related sources of variation accounted for most of the differences in growth. However, exceedance was significantly and negatively associated with mean growth for the study period (1951–2010) overall, and particularly for the 1980s and 2000s – periods of numerous and/or severe foliar winter injury events. Because high winter injury reflects the convergence of predisposing (cation depletion) and inciting (weather) factors, exceedance alone appears insufficient to define associated patterns of growth reduction. Significant interactions indicated that exceedance had little influence on growth at low elevations (where intrinsic conditions for growth were generally good) or high elevations (where growth was uniformly poor), whereas exceedance was significantly associated with reduced growth at mid elevations over long periods of time. Exceedance was also linked to reduced growth rebounds following a region-wide foliar winter injury event in 2003. Overall, our analyses suggest that modeled S and N critical load exceedance can help account for red spruce growth and rebound from injury in the field. Interestingly, recent growth for red spruce is above average for the 20th to 21st century dendrochronological record – indicating that the factors shaping growth may be changing. The influence of reduced pollution inputs on this recent growth surge is under investigation.

1. Introduction

Anthropogenic processes, primarily pollutant additions of sulfur (S) and nitrogen (N) compounds that form acid deposition, disrupt nutrient cycles and lead to the leaching loss and depletion of base cations from eastern United States (US) forests (Driscoll et al., 2001). Although cation depletion can have numerous important effects on ecosystem function, calcium (Ca) loss, in particular, poses a unique threat to forest ecosystem health (Schaberg et al., 2001). Ca is highly vulnerable to leaching loss (DeHayes et al., 1999), and is a component of biochemical pathways that regulate carbon (C) metabolism and allow plants to sense and respond to environmental stress (Marschner, 2002). Particularly when the

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latter role of Ca is compromised, it can leave trees more vulnerable to inadequate stress response following exposure to a range of abiotic and biotic stressors (Schaberg et al., 2010). Although acidic deposition inputs have decreased significantly since their regional peaks in the 1960s and 1970s (Driscoll et al., 2001; Lawrence et al., 2012), the net leaching of base cations remains an ongoing problem (Talhelm et al., 2012; Greaver et al., 2012).

The mechanism whereby acid deposition-induced Ca depletion alters the stress physiology of red spruce (*Picea rubens* Sarg.) and predisposes trees to decline is particularly well-established (e.g., DeHayes et al., 1999; Hawley et al., 2006; Halman et al., 2008; Schaberg et al., 2011a). Red spruce foliage is barely cold tolerant enough to escape freezing injury under ambient winter temperatures, and this limited cold tolerance is further reduced by acid-induced Ca depletion (DeHayes et al., 1999). As a consequence, exposure to acid deposition increases the likelihood of winter injury and foliar losses that instigate growth declines and tree mortality (Schaberg and DeHayes, 2000).

Numerous studies have provided evidence that Ca depletion has been detrimental to the health and productivity of multiple tree species (e.g., Hawley et al., 2006; Huggett et al., 2007; Halman et al., 2011; Battles et al., 2014). However, the current patchwork of localized studies has been insufficient to define the broader threat posed by Ca depletion across the landscape. One solution to providing a more broadly applicable and spatially explicit estimate of the vulnerability of sites to acid deposition-induced Ca depletion is through the use of critical load exceedance models and associated maps. The critical load with respect to S- and N-induced Ca leaching, is a quantitative estimate of the amount of pollution deposition below which there is no harmful effect (e.g., net Ca leaching loss; Schaberg et al., 2010). When a site's threshold for pollution loading (critical load) is subtracted from the estimated amount of incoming dry and wet acidic deposition at that site, the exceedance of the critical load is determined. Sites with positive exceedance values are predicted to become vulnerable to pollution-induced reductions in health and productivity as Ca reserves are depleted over time. Past work has shown that tree growth is sensitive to soil pH and Ca levels and postulated that Ca losses due to acid deposition in exceedance of critical loads would increase the incidence of tree decline (e.g., Ouimet et al., 2001; Watmough, 2002).

One pollution critical load exceedance model grew out of the Conference of New England Governors and Eastern Canadian Premiers Forest Mapping Group (NEG/ECP, 2001). The NEG/ECP S and N steady-state critical load model estimates the various inputs and outputs that influence cation cycling at a particular site to determine nutrient levels and cycling that are the basis for critical load estimates (NEG/ECP, 2001). For each point on the landscape, this model integrates various site factors that influence cation cycling (e.g., forest type, climate, hydrology, soil mineral weathering, etc.) to produce a critical load estimate that is subtracted from modeled pollution inputs to generate the projected exceedance (an estimate of whether or not pollutant inputs lead to net cation depletion). Preliminary field tests of the NEG/ECP model have shown promise (Schaberg et al., 2010). While some previous studies have tested other regional critical load exceedance models with plot-based growth data, interest in doing so has grown in recent years. Ouimet et al. (2001), using a similar critical load exceedance model developed for Quebec, Canada, found significantly lower growth at both hardwood and conifer sites that were in exceedance compared to non-exceedance sites. Duarte et al. (2013) developed critical load exceedance estimates for over 4000 plots in the northeastern US. They found significant negative correlations between exceedance and growth for many tree species, but data were limited to the mid-1990s so that long-term trends, including periods after known stress events, were not evaluated.

Although prior field-testing of the NEG/ECP model has involved multiple tree species at a more limited geographic scale, red spruce serves as an ideal test species for broader regional analysis because of its known sensitivity to Ca depletion. Furthermore, in comparison to various measurements that reflect health and productivity conditions for a limited date/duration, the examination of xylem increment cores provide a high resolution record of woody growth over the life of the tree, supplying a unique and powerful tool for evaluating the impacts of Ca depletion over long time periods, including before, during and after peaks of acidic loading and other stress events.

In this study, we examined if spatially explicit, steady-state critical load exceedance estimates were associated with long-term reductions in red spruce growth and an altered rebound in growth following a severe winter injury event. We hypothesized that critical load exceedance would be associated with reduced growth overall and a more muted growth rebound following winter injury. We further hypothesized that the influence of critical load exceedance could vary over time and space as deposition patterns change. This evaluation is unique in its fine geographic scale (critical load exceedance modeled at a 30 m × 30 m resolution), which was assessed across a geologically and topographically complex landscape (37 plots throughout Vermont [VT] and New Hampshire [NH]), and analyzed over a long temporal scale (growth over 60 years). The results of this research provide insight into long-term trends in red spruce growth, including rebounds following a major stress event, and illuminate the potential for exceedance mapping to help account for tree health and productivity at a fine geographic scale in complex terrain. Although this work focused on red spruce in the northeastern US, the approach should, at a minimum, also be appropriate for evaluating other sensitive tree species (e.g., sugar maple – *Acer saccharum* Marsh.; Schaberg et al., 2001) in regions that have experienced high pollutant loading.

2. Materials and methods

2.1. Critical load and exceedance estimates

The NEG/ECP steady-state model (NEG/ECP, 2001; Schaberg et al., 2010) provides 30 m × 30 m estimates of critical load (Fig. 1a) and exceedance (Fig. 1b), the latter of which we evaluated relative to red spruce xylem radial growth. Exceedance estimates ranged from −4 to +4 keq ha^{-1} y^{-1} for the broader region. Within the NEG/ECP model, a steady-state ecosystem process model was coupled to extensive spatial databases to create maps with quantitative representations of the degree of potential Ca depletion (NEG/ECP, 2001). The model incorporates many factors that influence critical load including forest type, timber extraction intensity, prior land-use, atmospheric deposition rates, and site factors including climate, hydrology, and soil mineral weathering rates (NEG/ECP, 2001). Extensive field and modeling work was required to develop the spatial data layers needed to apply this model to New England. Weathering, one of the most important determinants of critical load, was estimated through bedrock composition, glacial redistribution of material and additional specific landscape information (e.g., precipitation, mean annual temperature). Direct cation loss through timber harvest was estimated based on harvesting records averaged by county and by ownership type (public vs. private) from combinations of state and federal sources. Atmospheric deposition of S, N (nitrate and ammonium), chloride (Cl), Ca, magnesium (Mg), sodium (Na), and potassium (K) were estimated for a 5-year period (1984–1988) in order to provide smoothing of year-to-year variations in climate and patterns of atmospheric transport. While the NEG/ECP model provides exceedance products based on two different time periods (1984–1988 and 1999–2003),

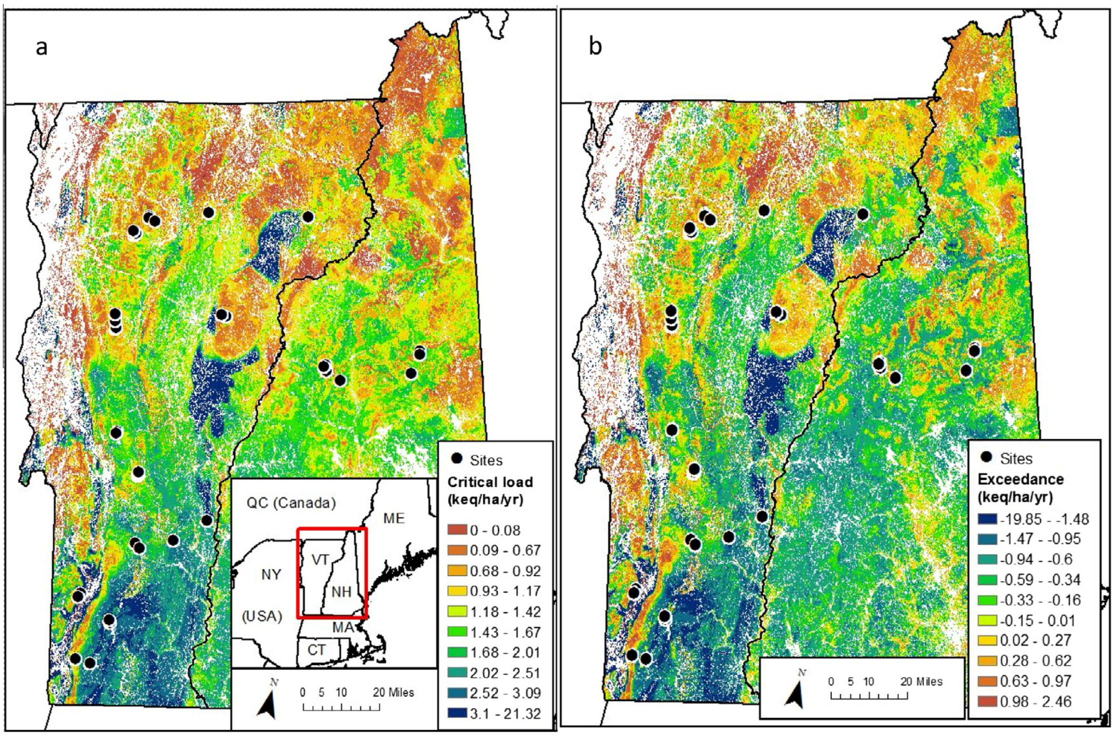

Fig. 1. Map of modeled critical load (a) and exceedance (b) of 1984–1988 sulfur and nitrogen deposition for forests in Vermont and New Hampshire (NEG/ECP, 2001). Yellow to red areas indicate areas with low critical load (a) or high exceedance (b), while green to blue areas indicate increasing critical loads (a) and decreasing exceedance (b). Red spruce (*Picea rubens* Sarg.) sample sites in those states are indicated by black circles. Some sites in close proximity appear to be overlapping in this representation.

we chose to assess the 1984–1988 period because it was prior to deposition reductions that followed the 1990 Amendments to the Clean Air Act, and thus should relate more strongly to the growth impacts of high acid loading and associated cation leaching. Total deposition (including precipitation, cloud droplet interception, and dry deposition) was estimated using atmospheric chemistry data from the US NADP, CASTNet, and NOAA-AirMon deposition monitoring networks and Ecosystems Research Group, Ltd.'s High-Resolution Deposition Model (NEG/ECP, 2001). More information on NEG/ECP critical load and exceedance models is available online (http://www.ecosystems-research.com/fmi/VT-NF-Forest-Sensitivity-Report.pdf) and in Schaberg et al. (2010).

2.2. Site selection

In order to maximize the sample size and range of exceedance values assessed, this study utilized a large set of both preexisting (Weverka, 2012; Kosiba et al., 2013, 2014) and newly collected red spruce xylem increment cores from VT and NH (Table 1; Fig. 1), for a total of 441 trees at 37 sites. These sites included 23 plots chosen to reflect a broad range of red spruce forest conditions (Weverka, 2012; Kosiba et al., 2013, 2014) and 14 new plots that were selected using the following NEG/ECP model criteria to identify areas where: (1) red spruce were predicted to occur in the forest type module of the NEG/ECP model, (2) located on state and federal lands to streamline the issuance of collection permits, and (3) at locations where modeled exceedance values approach the positive and negative limits for the study area (-2 and $+2$ keq ha^{-1} y^{-1}) to extend and balance the range of values assessed. This resulted in a range of exceedance values from -1.52 to $+1.68$ keq ha^{-1} y^{-1} across all sites included in this analysis. Atmospheric deposition of S and N exceeded the critical load at 20 sites, with the remaining 17 sites exhibiting negative exceedance (non-exceedance sites).

Due to spatial uncertainty associated with common and unavoidable geo-referencing error in complex terrain, exceedance estimates for a site were determined based on the mean exceedance value for a 5 × 5 pixel window (150 m × 150 m), surrounding the sample plot center. This scale was determined based on field-testing of the NEG/ECP model conducted in Massachusetts (E.K. Miller, unpublished results), as well as the results of a preliminary analysis using increment core data collected by Kosiba et al. (2013). Candidate sampling sites were further filtered to minimize variability in exceedance values within the 5 × 5 pixel window by including only plots where the standard deviation of the mean exceedance <0.2 keq ha^{-1} y^{-1} within the 5 × 5 pixel window. Field plots contained approximately 12 mature dominant or codominant red spruce trees within an area roughly equal to one pixel (30 m × 30 m).

2.3. Tree growth

For all sites, tree growth was measured using xylem increment cores that were collected from an average of 12 mature red spruce trees following standard collection, processing and analysis procedures (Stokes and Smiley, 1968). Two cores per tree were collected at breast height (1.37 m above ground level) with a 5 mm increment borer. Cores were taken at 180° to each other and perpendicular to the dominant slope to improve crossdating and avoid compression wood (Speer, 2010). Cores were mounted in grooved wooden blocks, sanded, and crossdated using the list method (Yamaguchi, 1991). Annual 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). The computer program COFECHA (Version 6.06P) was used to detect and correct potential crossdating errors in tree-ring series (Holmes, 1983). Dendrochronological statistics such as series intercorrelation, autocorrelation, and

Table 1

Dendrochronological statistics for red spruce (*Picea rubens* Sarg.) radial xylem increment measurements from 37 sites (441 total trees) in Vermont (VT) and New Hampshire (NH). The year listed in parentheses beside expressed population signal (EPS) values indicates the last year when it was below 0.85 at that site (Speer, 2010).

Location	State	Elevation (m)	Critical load (keq/ha/yr)	Exceedance (keq/ha/yr)	N trees	Length of chronology	Series inter-correlation[a]	Average mean sensitivity[a]	Expressed population signal[b]
Bald Mtn.	VT	727	0.01	1.68	12	1912–2012	0.652	0.248	0.957 (1920)
Bartlett Exper. For.	NH	775	1.33	−0.27	9	1759–2010	0.623	0.276	0.937 (1786)
Bartlett Exper. For.	NH	682	1.57	−0.59	10	1859–2010	0.631	0.227	0.945 (1866)
Burke Mtn.	VT	840	2.40	−1.28	10	1759–2010	0.555	0.267	0.926 (1880)
Burnt Mtn.	VT	950	1.57	−0.23	10	1920–2010	0.603	0.241	0.938 (1948)
Burnt Mtn.	VT	601	0.47	0.49	10	1891–2010	0.485	0.236	0.904 (1923)
General Stark Mtn.	VT	880	1.28	0.15	20	1927–2010	0.649	0.239	0.949 (1930)
Hedgehog Mtn.	NH	710	1.27	−0.22	12	1854–2010	0.665	0.212	0.960 (1909)
Hubbard Brook Exper. For.	NH	771	1.66	−0.59	24	1895–2010	0.577	0.286	0.970 (1913)
Killington Mtn.	VT	1147	1.06	0.58	22	1798–2010	0.502	0.285	0.917 (1873)
Killington Mtn.	VT	1028	1.18	0.32	13	1793–2010	0.491	0.260	0.926 (1881)
Killington Mtn.	VT	919	1.38	1.09	11	1827–2010	0.493	0.249	0.915 (1901)
Killington Mtn.	VT	808	1.08	0.99	10	1861–2010	0.445	0.266	0.889 (1924)
Camel's Hump Mtn.	VT	856	1.84	−0.44	10	1906–2010	0.552	0.267	0.925 (1927)
Mt. Ascutney	VT	836	2.36	−0.81	12	1862–2012	0.606	0.222	0.949 (1920)
Mt. Carmel	VT	996	0.91	0.82	11	1905–2010	0.562	0.339	0.934 (1920)
Mt. Carmel	VT	775	1.46	−0.06	10	1795–2010	0.506	0.251	0.911 (1851)
Mt. Ellen	VT	1045	0.68	1.09	11	1825–2010	0.602	0.242	0.943 (1917)
Mt. Ellen	VT	930	1.18	0.29	10	1919–2010	0.453	0.289	0.892 (1934)
Mt. Equinox	VT	1150	2.69	0.07	11	1920–2010	0.672	0.308	0.958 (1923)
Mt. Equinox	VT	962	1.01	0.92	12	1857–2010	0.551	0.277	0.936 (1879)
Mt. Mansfield	VT	910	0.74	0.75	11	1890–2012	0.604	0.230	0.944 (1917)
Mt. Mansfield	VT	986	0.69	0.93	11	1908–2012	0.608	0.219	0.945 (1920)
Mt. Mansfield	VT	915	0.69	0.78	17	1922–2012	0.616	0.233	0.965 (1926)
Mt. Moosilauke	NH	736	0.58	0.50	10	1923–2010	0.448	0.192	0.890 (1937)
Mt. Moosilauke	NH	1172	0.89	1.07	10	1760–2010	0.599	0.258	0.937 (1904)
Mt. Moosilauke	NH	967	0.94	0.45	11	1890–2010	0.450	0.278	0.900 (1919)
Proctor-Piper State Park	VT	490	2.86	−1.40	10	1897–2012	0.671	0.221	0.953 (1911)
Sterling/Whiteface Mtn.	VT	1052	0.63	1.12	12	1825–2012	0.610	0.267	0.949 (1914)
Sterling/Whiteface Mtn.	VT	960	0.97	0.63	11	1899–2012	0.583	0.257	0.939 (1915)
Sterling/Whiteface Mtn.	VT	532	1.51	−0.43	10	1910–2012	0.588	0.232	0.935 (1871)
Stratton Mtn.	VT	685	3.15	−1.52	11	1906–2012	0.577	0.186	0.938 (1920)
Stratton Mtn.	VT	685	3.00	−1.38	12	1912–2012	0.562	0.200	0.939 (1913)
Weston	VT	573	2.41	−0.92	11	1862–2012	0.575	0.213	0.937 (1872)
Weston	VT	487	2.62	−1.13	12	1886–2012	0.620	0.207	0.951 (1890)
Wolcott Res. For.	VT	372	1.22	−0.17	10	1912–2010	0.539	0.223	0.921 (1937)
Woodford	VT	789	2.53	−0.74	12	1897–2012	0.566	0.221	0.940 (1909)

[a] From COFECHA output (Holmes, 1983).

[b] EPS = $(t * r_{bt})/(t * r_{bt} + (1 - r_{bt}))$, where t is average number of trees in the series and r_{bt} is the mean series intercorrelation (Wigley et al., 1984).

average mean sensitivity were calculated in COFECHA and used to calculate the expressed population signal (EPS) based on the equation presented by Wigley et al. (1984). EPS values were used to determine the time period over which all of our plot chronologies maintained a robust stand-wide signal.

Raw ring widths were converted to basal area increments (BAI, $cm^2\ year^{-1}$) assuming a circular outline of stem cross sections (Cook and Kairiukstis, 1990). BAI is considered a more meaningful indicator of tree growth since it standardizes annual increments relative to basal area and does not necessarily decline as diameter increases (West, 1980; Hornbeck and Smith, 1985). This is the preferred standardization technique for this study because it accounts for growth in ring width while preserving long-term trends that may relate to acid deposition and soil Ca depletion (Duchesne et al., 2002).

2.4. Statistical analyses

Plot-level mean BAI was compared to modeled site-specific exceedance values based on deposition estimates from 1984 to 1988. This period was chosen to reflect the period of high acid loading. As the recovery of tree vigor following peak acid exposure has likely been slow and minimal, plots with high exceedance may be the most relevant in influencing tree growth during and following this period of high S and N loading. In addition, using deposition and exceedance values for a period of near maximum pollution loading would help to evaluate how much these high loading levels resulted in a legacy of altered growth. This 1984–1988 period of deposition estimates was also roughly central to the period for which growth was examined (1951–2010).

Growth parameters of interest included BAI trends over the full 60-year chronology, as well as decadal periods, and the period of rebound in growth following a severe region-wide foliar winter injury event in 2003 (Lazarus et al., 2004; Schaberg et al., 2011b; Kosiba et al., 2013). Annual growth rates were evaluated as BAI plot averages over the full 60-year chronology and as individual decades. Winter injury growth rebound was calculated as a ratio of mean plot growth in a specific year and growth for the same plot in the two years preceding the winter injury event (2001–2002, "pre-injury growth"). This helped standardize growth relative to plot conditions and is consistent with the work of Kosiba et al. (2013), who chose those two baseline years because they were likely unaffected by other major stress events. Because growth in 2001 was generally lower than in 2002, this provides a more conservative analysis than using only a single pre-injury growth year as a baseline.

Differences in growth parameters as they relate to exceedance were assessed through analyses of variance (ANOVA) models for the full 60-year chronology, each decade of the chronology, and for overall and yearly growth after the 2003 injury event. ANOVA models used “exceedance”, “year” and “elevation” as primary sources of variation to both target the possible influence of exceedance on growth, while also accounting for annual variability (presumably climate-related) that could mask the influence of exceedance. This study was not designed to assess the influence of specific climatic drivers on growth, or to assess the influence of various site factors (e.g., stocking and land use history) that can also alter growth.

As in other studies, modeled exceedance was considered a categorical parameter (e.g., De Vries et al., 1994, 2000; Posch et al., 1997); here where sites were separated by whether they were in exceedance (>0 keq ha^{-1} y^{-1}; calculated to have experienced net cation depletion due to S and N deposition) or non-exceedance (<0 keq ha^{-1} y^{-1}; not calculated to have experienced net cation depletion) (Ouimet et al., 2001; Schaberg et al., 2010; Duarte et al., 2013; Kluge et al., 2013). Many components of the modeling process lead to uncertainties in critical load and exceedance estimates (see review by Skeffington, 2006). In addition to exceedance, “year” was included as a categorical source of variation to capture the influence of climate in year-to-year differences in growth. “Elevation” was also included as a categorical source of variation because of the established differences in climate, growth and winter injury along elevational gradients (Kosiba et al., 2013). Plot elevation was converted to a categorical variable based on established ecotones (Siccama et al., 1982; Kosiba et al., 2013): low elevation, <765 m; mid-elevation, 765–920 m; and high elevation, >920 m. ANOVA models for BAI growth were evaluated with exceedance, year, elevation and the interactions of these sources of variation. However, because no interactions with year were significant, these interactions were removed as sources of variation in final analyses. Because environmental factors that influence growth can vary with elevation, we were particularly interested in testing for possible exceedance × elevation interactions. The ANOVA model for BAI growth rebound also incorporated elevation, exceedance and the interaction of these as sources of variation. However, because there was no significant interaction between elevation and exceedance for the rebound period, this interaction was dropped from the final model. One benefit of the ANOVA model used was that it helped to separate exceedance-related influences from other environmental factors (e.g., temperature, precipitation, etc.) that vary across elevations, while also assessing how exceedance and elevation may interact to influence growth. The statistical package JMP 9 (SAS Institute, Inc., Cary, NC) was used for all statistical analyses and results were considered significant if $P \leqslant 0.05$.

3. Results and discussion

3.1. General growth trends

The overall mean BAI over the 60 years from 1951 to 2010 was 8.80 ± 0.09 cm^2 for the 441 red spruce trees at 37 plots. Dendrochronological statistics (Table 1) indicate that the red spruce trees used in this analysis were sensitive to environmental influences and had a coherent stand-level signal (Speer, 2010). Specifically, the values for average mean sensitivity (a measure of relative change in ring width) and series intercorrelation (a measure of the strength of the signal that is common to all trees in a given stand) fell within the accepted range for red spruce chronologies (0.08–0.32 and 0.42–0.68, respectively) (NOAA National Climatic Data Center, 2008). Measures of EPS were used to establish a synchronous chronology start date when all 37 plots showed consistent stand-level responses to the environment. EPS is a measure of the common variability in a chronology and is dependent on sample size: when it falls below a predetermined value – usually 0.85, the chronology is a less reliable indicator of a coherent stand-level signal (Speer, 2010: Wigley et al., 1984). For this study, the earliest year for which all stands had an EPS > 0.85 was 1948 (Table 1), so we chose to begin the chronology in 1951 to allow for six decades of growth assessments (Fig. 2).

In general, there was a high degree of year-to-year variability in growth over the length of the chronology (Fig. 2). Two of the more noticeable features of the chronology were the growth decrease in 2003 associated with a severe region-wide winter injury event, as well as the subsequent region-wide upturn in growth beginning in 2007 (Kosiba et al., 2013). In 2003, 90% of red spruce in VT, NH, Massachusetts, and New York were damaged by winter injury, with an estimated 65% of current-year foliage and 56% of buds killed on dominant and co-dominant trees (Lazarus et al., 2004). This injury resulted in growth reductions lasting three to four years (Kosiba et al., 2013), which is consistent with our updated chronology (Fig. 2). Initial analysis of the rebound in growth following the 2003 injury event showed uncharacteristically high growth from 2007 through 2010 (the last year in that chronology) (Kosiba et al., 2013). We extended the chronology through 2012 at 14 sites beyond those used by Kosiba et al. (2013). For the 174 trees at these 14 sites, high growth continued through 2012 (Fig. 2). Since 1951, the four years of greatest growth occurred from 2009 to 2012, and eight of the ten greatest growth years occurred since 2000. The rebound in growth that occurred from 2007 to 2012 was approximately 50–100% greater than the mean BAI from 1951 to 2010.

3.2. Growth relative to exceedance, elevation and year

The ANOVA of BAI growth over the 60-year chronology detected significant main effects for year ($P = 0.0001$), elevation ($P = 0.0001$), and exceedance ($P = 0.0019$). Trees on plots where S and N deposition exceeded the critical load exhibited significantly reduced growth over the 60-years relative to trees on plots where the critical load was not exceeded (Fig. 3). This suggests a persistent negative influence of high pollution loading on red spruce radial growth consistent with cation depletion. However, the influence of exceedance on growth was not consistent across elevational zones: there was a significant interaction between exceedance and elevation ($P < 0.0001$). The exceedance × elevation interaction reflected little influence of exceedance at low elevations (where growth was consistently good) or high elevations (where growth was consistently poor), but reduced growth with exceedance at

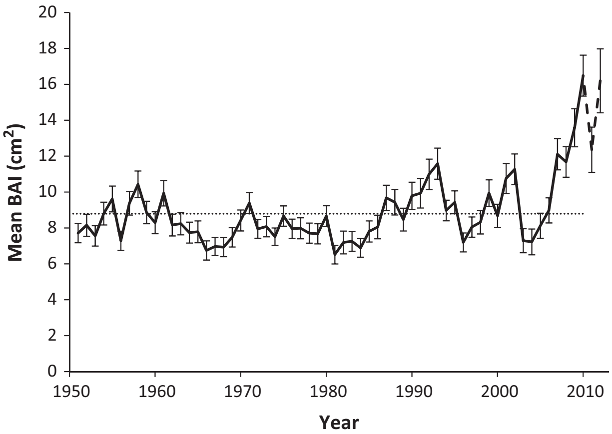

Fig. 2. Overall growth chronology. Mean (±SE) basal area increment (BAI) for 37 red spruce (*Picea rubens* Sarg.) sites in Vermont and New Hampshire from 1951 to 2010. The solid straight line represents the mean BAI from 1951 to 2010 (8.80 cm^2). The dashed portion of the chronology from 2011 to 2012 represents the mean (±SE) BAI for 14 sites for which data was available for those years.

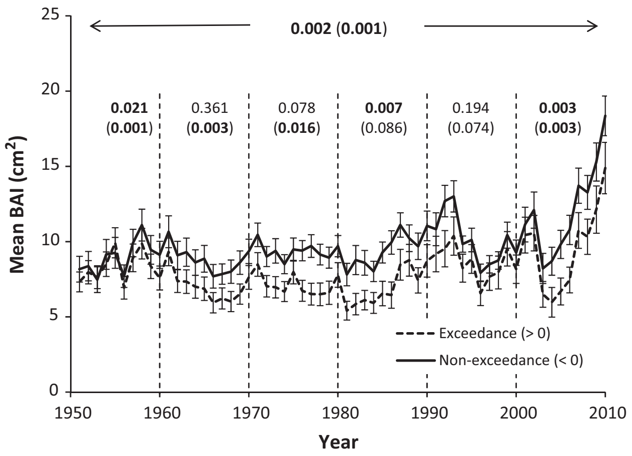

Fig. 3. Growth by sulfur and nitrogen critical load exceedance category. Mean (±SE) basal area increment (BAI) of red spruce (*Picea rubens* Sarg.) at 37 sites in Vermont and New Hampshire that were exceeding or not exceeding modeled critical loads. The values displayed at the top of this figure are *P*-values for the influence of exceedance and the interaction between exceedance and elevation (within parenthesis), with bolded numbers indicating significant values ($P \leqslant 0.05$) tested using an ANOVA with year, elevation, exceedance and the interaction of elevation and exceedance as sources of variation. The model was run for the 1951–2010 period overall, and for each decade therein. The solid line represents the mean (±SE) annual BAI for sites where exceedance <0 keq ha^{-1} yr^{-1}, while the dashed line represents the mean (±SE) for sites where exceedance >0 keq ha^{-1} yr^{-1}.

mid elevations (Fig. 4). Our *a priori* expectations were that moderate climates and low acid loading at low elevations would favor elevated growth and low winter injury there, whereas harsher climates and higher acid loading at high elevations would generally reduce growth and increase the number and severity of winter injury events. Results of the exceedance × elevation interaction (Fig. 4) were consistent with these expectations. In contrast, mid elevations plots were expected to be at more of a threshold where the negative influences of acid loading were more likely to influence winter injury and limit growth in conjunction with climatic drivers. We hypothesize that spruce at mid elevations may also experience fewer climatological limitations to growth as the climate warms – especially a reduction in the frequency, intensity and duration of low winter temperature periods (Hayhoe et al., 2007) that incite winter injury and constrain yearly photosynthetic gains (Schaberg and DeHayes, 2000). Whether the result of reduced pollution loading, increasing temperatures, or some combination thereof, the unique responsiveness of trees at mid elevations was evident after the 2003 winter injury event in particular, when the relative rebound in growth after injury occurred earlier and was greatest for trees there relative to trees at low and high elevations (Kosiba et al., 2013).

To further explore how climate, elevation and exceedance influenced growth, and how that influence may have changed over time, we ran the same form of ANOVA model that was run for the full chronology for each constituent decade (Fig. 3). For the decade models, “year” was a significant source of variation in every decade except for 1971–1980, when interannual growth was uniformly stable and below the long-term mean growth rate. The elevation effect was also significant in every decade, with lower elevation sites having higher growth, with the exception of 2001–2010 – a period that included major growth reductions due to foliar winter injury that were then reversed by a substantial growth rebound at mid-elevations (Kosiba et al., 2013). Exceedance was associated with a significant reduction in growth during the 1980s and 2000s (Fig. 3) – periods with frequent (1980s) or severe (2000s) winter injury events (Johnson et al., 1988; Peart et al., 1991; Lazarus et al., 2004). This pattern of decadal influence highlights the well-established mechanism through which pollutant inputs predispose red spruce to foliar winter injury (e.g., DeHayes et al., 1999) and result in reduced woody growth (e.g., Kosiba et al., 2013). Because extensive winter injury is associated with the combined effects of Ca depletion that increases foliar sensitivity to freezing damage (Hawley et al., 2006) and weather phenomenon (e.g., winter low temperature events; Schaberg et al., 2011b) that then induce injury, the temporal pattern highlighted in the decadal analysis underlines the need to integrate predisposing and inciting contributors to account for injury expression over time.

As with the 60-year chronology, there were significant interactions of exceedance and elevation in the 1960s, 1970s and 2000s (Fig. 3). The nature of these interactions also reflected the patterns noted for the overall chronology. Higher exceedance was associated with reduced growth at mid elevations, but not at low or high elevations where growth was more consistently good or poor, respectively.

One surprising finding detected in the decadal analysis was a significant positive exceedance and exceedance × elevation effect in the 1950s. ANOVA-calculated least square mean growth for exceedance plots (8.5 cm^2) was significantly higher ($P = 0.021$) than growth for non-exceedance plots (7.3 cm^2) when the influence of elevation was accounted for (which is not depicted in Fig. 3). This was especially evident at high elevations where growth in exceedance plots was much higher (8.3 cm^2) than growth in non-exceedance plots (3.4 cm^2) ($P = 0.001$). Although this is consistent with an initial surge of cation release (a fertilizer effect) with early acid loading (Likens et al., 1996), interpretation of this observation awaits further specific analysis. This effect would be most likely at high elevations where acid inputs are greatest (Mohnen, 1992) and soils are thin and nutrient-poor (Fernandez, 1992).

Decadal relationships between growth and exceedance are interesting because the modeled critical load exceedance values are steady-state estimates that have no temporal resolution (i.e., they indicate *whether* pollution inputs exceed the inherent capability of a site to replenish nutrient supplies if deposition remained constant indefinitely at a particular level (here 1984–1988 rates), not *when* biologically relevant nutrient depletion will be reached). The time when a biologically compromised state is reached and where growth or health problems might be observed depends on

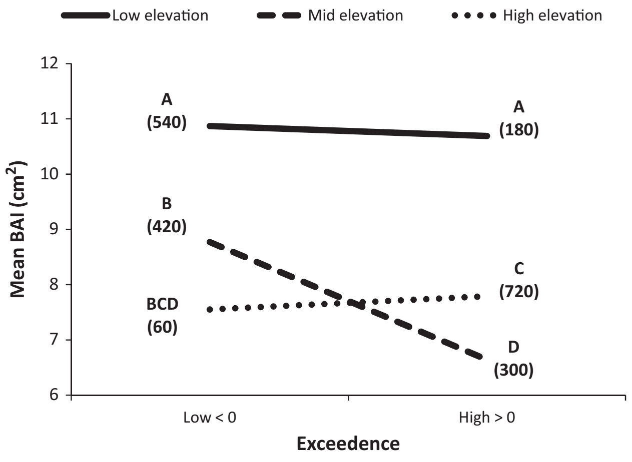

Fig. 4. Depiction of the interaction between sulfur and nitrogen critical load exceedance and elevation for the 60-year chronology (1951–2010). This interaction was a significant source of variation in BAI growth ($P = 0.0001$). Means with different letters are significantly different (Tukey HSD test). Sample sizes (number of years in the chronology for that elevation and exceedance level) are listed within parentheses.

the magnitude of the exceedance and the size of the labile Ca pool when exceedance commences. Thus, not all sites with positive exceedance values are expected to show immediate or current growth and health effects, particularly at low elevations where deeper soils are common, labile Ca pools are generally larger, and climatic limitations to growth are less pervasive. Sites with positive exceedance with respect to 1984–1988 deposition loads are also likely to have been in exceedance for many years due to temporal stability in the broad pattern of atmospheric deposition in the northeastern US prior to pollution reductions mandated by the 1990 Amendments to the Clean Air Act (Likens et al., 1996; Driscoll et al., 2001). Sites with negative exceedance values based on 1984–1988 (near peak) S and N deposition rates are not likely to be experiencing Ca-depletion, and thus, would not be anticipated to exhibit Ca-mediated health effects. Sites with only slightly negative exceedance relative to 1984–1988 deposition loads are likely in an early stage of recovery from previously higher deposition loads that would have produced a negative mass balance for Ca.

Although there is some evidence of a recent rebound in soil pH and reduction in soil Al availability in the northeastern US as pollution loading has decreased, there is little evidence of an associated improvement in soil Ca within regional red spruce forests (Lawrence et al., 2012). Similarly, the fact that exceedance was a significant source of variation in growth through the 2000s (Fig. 3) suggests that acid loading continues to negatively impact red spruce in the region, which is consistent with modeled projections that acid impacts are likely to persist over time (e.g., Driscoll et al., 2001). The influence of exceedance was greatest during periods of frequent and/or severe winter injury events (the 1980s and 2000s; Fig. 3) and at mid elevations (Fig 4.). Considering this, we expect that any improvements in red spruce growth associated with pollution reduction would be preferentially evident: (1) when winter injury levels were low (possibly as winter temperatures moderate) and, (2) at mid elevations where exceedance appears to be more of a limiting factor.

There was a greater than 2-fold variation in mean BAI growth over the 60-year chronology overall and since the 2003 winter injury event. The ANOVA model accounted for 28% of the total variation in annual BAI growth over the 60-year chronology. The low proportion of variation accounted for by our model was not surprising because growth is influenced by a wide range of factors (e.g., stocking, past land use, etc.) that likely varied greatly among the 37 sites in two states that we assessed. Although land use history was a component of the of the NEG/ECP model, the scale of this data was large compared to the plot-level focus of this study. Despite all the factors that could influence growth, exceedance was a significant source of variation in growth for this period overall, during the 1980s and 2000s for all elevations and for the 1960s, 1970s and 2000s at mid elevations. However, exceedance accounted for only a fraction of the variation in growth overall. Partitioning the variance within the 60-year ANOVA model revealed that exceedance and the interaction of exceedance with elevation accounted for only about 1.3% of the total variation in growth over the 60-year chronology. Even at its peak association in the 2000s, exceedance and the interaction of exceedance with elevation accounted for 4% of the variation in growth. While this may seem like a low proportion of variability, it is not uncommon in models of complex ecophysiological processes such as tree growth to exhibit low contributions of variability for significant variables. The strength of ANOVA analysis is the ability to identify significant relationships associated with sources of variation in spite of potentially muted responses. In this case, the contribution of critical load exceedance likely only captured the influence of factors that predispose red spruce to winter injury (cation depletion), rather than the combined influences of predisposing and inciting (e.g., weather) factors.

Even the proxy variables for weather impacts (year and elevation) were only able to account for approximately 16% and 7.5% of the variation in growth over the full 60-year chronology, respectively. Climate is well-recognized as the factor that most influences the distribution and productivity of trees (e.g., Woodward et al., 2004; Fritz, 2012). Thus, as expected, "climate" (as a direct or indirect influence) appeared to be a prominent driver of growth variation within our 60-year chronology. Accordingly, our group is now conducting a more detailed, direct assessment of the influences of various climate metrics on red spruce radial growth – including possible connections to the species' high recent (2008–2012) productivity.

3.3. 2003 winter injury and growth rebound

To better understand the relationship of exceedance with winter injury and tree recovery from this injury, we examined the growth response to the well-documented and severe 2003 winter injury event in which 96% of all dominant and co-dominant red spruce trees assessed across the region were injured, 65% of the newest needle cohort lost and 56% of buds killed (Lazarus et al., 2004). An ANOVA for 2003 only revealed that the severe decline in growth that year (see Figs. 2 and 5) was not significantly different across either elevation or exceedance categories. All sample plots experienced major winter injury and subsequent decline in growth during 2003. Interestingly, exceedance was significantly related to the dramatic rebound in growth after 2004, with trees located at non-exceedance sites exhibiting higher average growth following injury relative to trees on exceedance sites (Fig. 5). Elevation was not a significant source of variation in growth rebound despite the documented elevational variation in severity of winter injury during the 2003 event (Lazarus et al., 2004). This may indicate that a higher Ca status (as implied by non-exceedance) was a prerequisite for red spruce weakened by a major winter injury event (and loss of foliar photosynthetic capacity) to take advantage of favorable conditions that existed across all elevations (Fig. 3). However, it is likely that standardizing growth relative to the 2001–2002 pre-injury growth of trees by plot effectively removed normal differences in growth due to elevation, so that the resulting

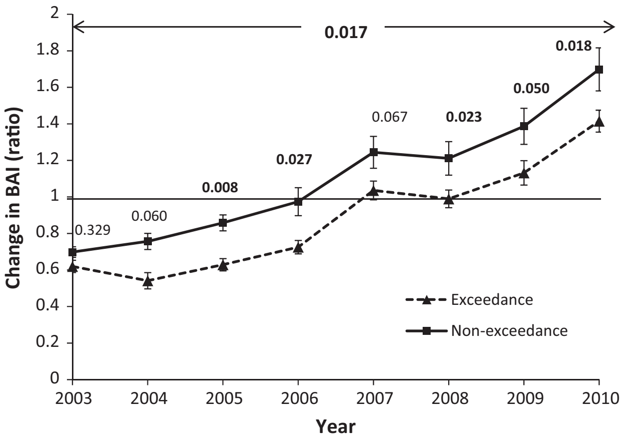

Fig. 5. Growth rebound by sulfur and nitrogen critical load exceedance category. Mean (±SE) basal area increment (BAI) rebound for red spruce (*Picea rubens* Sarg.) at 37 sites in Vermont and New Hampshire following a winter injury event in 2003. The values displayed at the top of this figure are *P*-values for the influence of exceedance for the period overall (top, middle) and each year, with bolded numbers indicating significant values ($P \leqslant 0.05$) tested using ANOVAs with elevation and exceedance as sources of variation. Growth was standardized based on mean growth at each site in 2001–2002 (Kosiba et al., 2013), with values below 1 indicating decreased growth from that period, and values above 1 indicating growth exceeding pre-injury levels.

site-specific rebound in growth was significantly linked with exceedance but not elevation.

Examining recovery on an annual basis, exceedance was a significant source of variation in growth rebound for every year after 2005 except 2007 (Fig. 5). Overall, this indicates that rebound following the 2003 winter injury event appeared to be strongly tied to exceedance, but that this trend was not evident until several years after the 2003 event. Past work has shown that it took at least three years for red spruce to rebound in growth after the 2003 winter injury event (Kosiba et al., 2013), but that analysis did not explore the possible influence of pollution loading on the recovery process. Results here suggest that this rebound can be quicker when sites are not in exceedance.

3.4. Conclusions

ANOVA analyses indicated that exceedance was significantly associated with reduced growth for the overall chronology, and during the 1980s and 2000s. High winter injury reflects the combined influences of predisposing factors (e.g., cation depletion) that increase the susceptibility of trees to injury and inciting (weather) factors that then induce damage (Schaberg et al., 2011b). Critical load exceedance reflects just one of these – cation depletion. Reductions in growth during periods of repeated and/or severe winter injury events in the region are consistent with well-established evidence that acid deposition leaches Ca and predisposes red spruce to winter injury (DeHayes et al., 1999), and that foliar loss from winter injury leads to prolonged reductions in tree growth (Kosiba et al., 2013). The persistence of exceedance based on 1984–1988 deposition rates as a significant influence on growth into the 2000s suggests that the broad effect of deposition loading during the 1980s remained pertinent even as acid loading declined following enforcement of the Clean Air Act and its Amendments. However, the particular sensitivity of trees at mid elevations to exceedance indicates that the influence of exceedance was not uniform. At high elevations exceedance values are often positive, but other factors (notably short growing seasons, poorer soils, and low winter temperatures) result in uniformly low growth. Although not evident at this time, it is possible that exceedance may better account for differences in growth at high elevations if continued reductions in pollution inputs allow for rebounds in Ca nutrition there. At low elevations, more favorable growing conditions allow for better growth whether or not sites are in exceedance. In contrast, red spruce at mid elevations may experience both climatic limitations to growth (e.g., changing lengths of growing seasons and differential exposure to winter temperature lows that can incite winter injury) and the influence of exceedance on Ca levels that alter tree response to climate. As such, in the near-term we expect that red spruce at mid elevations would be most responsive to both changes in climate and pollution loading over time.

Our findings that exceedance was associated with reduced growth may be particularly pertinent considering that the trees in our study were the remnants that survived the regional decline and mortality of red spruce that was ultimately attributed to acid deposition-induced Ca depletion and resulting foliar winter injury (e.g., DeHayes et al., 1999; Schaberg et al., 2010). Reduced growth and increased mortality were hallmarks of acid deposition-induced red spruce decline (Hornbeck and Smith, 1985; DeHayes et al., 1999; Driscoll et al., 2001). One potential consequence of the wave of mortality in the 1970s and 1980s is that surviving trees might have experienced a growth release as nearby competitors died. There was an increase in growth for the trees we sampled that began in the mid-1980s (Fig. 3). However, because growth trends appear similar for both exceedance (where acid deposition-associated mortality would have been higher) and non-exceedance plots, it is unclear how differential mortality might have influenced growth across the landscape. All plots exhibited a temporally synchronous “growth release”. However, plots where the critical load was not exceeded, and Ca availability is projected to be higher, grew more than those where the critical load had been exceeded.

In contrast to trees that died subsequent to high acid loading, the living trees evaluated here were likely less impacted by acidic inputs and would be expected to exhibit a more muted association between growth and pollutant exceedance. Despite this unavoidable sampling constraint and uncertainties in critical load and exceedance estimates (Skeffington, 2006), exceedance was associated with lower growth, especially following the 2003 winter injury event. Our finding that plot-based critical load exceedance data does have relevance to tree growth in the field underscores the potential utility of exceedance data to managers and policy makers trying to understand and project the growth of sensitive tree species under historic and changing pollutant deposition loads.

Relative to the long-term average across the chronology, the red spruce in our study were experiencing superlative growth in the most recent years samples (2007–2012). Additional analysis is needed to assess, (1) the spatial extent of this growth surge (e.g., is it range-wide, region-wide, primarily restricted to montane populations, etc.) and, (2) what factors are most closely associated with recent growth increases. Although reduced pollutant inputs could well contribute to increased recent growth, the possible influences of changing climate, rising atmospheric CO_2 concentrations and other factors must also be considered.

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