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## Temperature and leaf nitrogen affect performance of plant species at range overlap

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**Abstract.** Plant growth and survival near range limits are likely sensitive to small changes in environmental conditions. Warming temperatures are causing range shifts and thus changes in species composition within range-edge ecotones; however, it is often not clear how temperature alters performance. Through an observational field study, we assessed temperature and nitrogen effects on survival and growth of co-occurring temperate (*Acer saccharum*) and boreal (*Abies balsamea*) saplings across their overlapping range limits in the Great Lakes region, USA. Across sampled ranges of soil texture, soil pH, and precipitation, it appears that temperature affects leaf nitrogen for *A. saccharum* near its northern range limit ( $R^2 = 0.64$ ), whereas there was no significant leaf N ~ temperature relationship for *A. balsamea*. Higher *A. saccharum* leaf N at warm sites was associated with increased survival and growth. *Abies balsamea* survival and growth were best modeled with summer temperature (negative relationship); performance at warm sites depended upon light availability, suggesting the shade-tolerance of this species near its southern range limits may be mediated by temperature. The ranges of these two tree species overlap across millions of hectares, and temperature and temperature-mediated nitrogen likely play important roles in their relative performance.

**Key words:** *Abies balsamea*; *Acer saccharum*; acid deposition; climate change; ecotone; global change; herbivory; nutrients; shade tolerance; temperate-boreal transition zone.

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### INTRODUCTION

Species' range limits change with changing conditions. Paleorecords show species-specific shifts in direction and rate of range expansions and contractions, resulting in ephemeral plant community assemblages (Davis 1983, Williams et al. 2004). These changes are due to differences in migration rates and may also be due to species responses to differing limiting factors and to differing rates of change in limiting factors. Latitudinal or elevational range limits are often tied to temperature, and recent range shifts

across the globe are commensurate with warming trends (Parmesan and Yohe 2003); however, it is often not clear how temperature mediates these changes. Nitrogen is typically a limiting nutrient in temperate and boreal forests (Vitousek and Howarth 1991). Much research has focused on temperature effects where these forest types overlap (Beckage et al. 2008, Fisichelli et al. 2014a, Reich et al. 2015); however, whether temperature-related changes in plant nitrogen status play a role in ecotone dynamics is unknown, to our knowledge.

Ecosystems are being altered by multiple

global change agents including climate change and pollution (Vitousek 1994). Warmer temperatures directly impact phenology, growth, and survival of plant species (Parmesan and Yohe 2003, Fisichelli et al. 2014b). Other changes in plant performance can occur due to temperature-mediated changes in nutrient cycling and availability (Reich et al. 1995, Walters and Reich 1997). Additionally, anthropogenic processes account for roughly twice as much N input into ecosystems as natural processes and in many areas local deposition rates have increased 10 fold (Galloway et al. 2008). Depending on N deposition rates and intrinsic N supply rates, plant responses can be positive or negative. Soil acidification and cation depletion under high deposition cause negative responses in plants, including decreased seedling survival (Aber et al. 2001, Catovsky and Bazzaz 2002). Modest increases in N, generally a limiting nutrient, can increase growth and survival of overstory trees (Aber et al. 2001, Dietze and Moorcroft 2011). Thus, the effects of warming temperatures in many systems may be altered or limited by nutrient availability (Porter et al. 2012).

The temperate-boreal transition zone stretches across North America from Minnesota and Ontario in the west to the Atlantic coast in the east (Appendix: Fig. A1). Small changes or differences in temperature relate to detectable changes in the performance of temperate and boreal species (Beckage et al. 2008, Fisichelli et al. 2012, 2014a, Reich et al. 2015). Prior studies showed contrasting sensitivities to relatively modest climate variation in northern Minnesota between temperate *Acer saccharum* (sugar maple) and boreal *Abies balsamea* (balsam fir)—along just a 2.3°C spatial gradient, the growth ranking of saplings of the two species reversed (with *A. saccharum* outperforming *A. balsamea* at the warmer sites; Fisichelli et al. 2012), while a +3.4°C field warming experiment showed *A. saccharum* photosynthesis and growth to be positively influenced by warming, with *A. balsamea* negatively influenced (Reich et al. 2015). However, mechanisms for these responses remain uncertain. Both *A. saccharum* and *A. balsamea* have been shown to respond positively to modest gradients of soil resources in shaded understory habitats in the Great Lakes region (Walters and Reich 1997, 2000, Machado et al.

2003), although it is unclear whether temperature plays a role in these responses.

The primary objective of this observational field study was to examine how temperature and plant nitrogen status relate to performance of co-occurring temperate (*A. saccharum*) and boreal (*A. balsamea*) saplings across their overlapping range limits and whether these species are responding to the same factors. We examined leaf nitrogen content and sapling survival rates across the temperate-boreal transition zone and extend previous research on sapling growth rates (Fisichelli et al. 2012) by adding leaf nitrogen as a potential explanatory variable. Understanding how nitrogen and temperature may impact species near range limits will facilitate better projections of likely future ecosystem shifts.

## METHODS

### *Study area, conditions, and sapling performance*

This study included 14 research sites, which span the temperate-boreal transition zone in Minnesota, USA (Appendix: Fig. A1). Each site included a mix of temperate (*Acer rubrum*, *Acer saccharum*, and *Quercus rubra*) and boreal (*Abies balsamea*, *Betula papyrifera*, *Picea glauca*, and *Populus tremuloides*) tree species in the overstory. Long-term mean annual temperature varies from 3.0°C to 5.5°C, mean summer temperature (JJA) from 16.2°C to 19.1°C, and annual precipitation from 683 to 835 mm (1978–2007 period) across the study sites (Daly et al. 2008). Nitrogen wet deposition ( $\text{NO}_3^- + \text{NH}_4^+$ ) varied narrowly across sites, from 3.8–5.1 kg/ha/yr (10 year average, 1999–2008; NADP 2007).

For sapling survival, naturally established, co-occurring *Acer saccharum* and *Abies balsamea*, two common and very shade-tolerant tree species (Burns and Honkala 1990), were sampled from the understory within plots at five study sites (Appendix: Fig. A1). The study included 253 *A. balsamea* and 283 *A. saccharum* stems in 26 plots; sapling height varied from 15–140 cm (median = 48 cm), and canopy openness varied from <1% to 25% (median = 7%, mean = 8.6%, sd = 3.5%). The light environment (percent canopy openness) at the top of each sapling was measured with a LI-COR LAI-2000 plant canopy analyzer (LI-COR, Lincoln, Nebraska, USA) under uniform overcast conditions. Browse damage of

each sapling was scored as the percentage of branches with evidence of browse. Plots within sites were randomly located and plot samples of the upper 20 cm of mineral soil were collected. Soil pH was measured using a water:soil suspension and sand particle fraction was determined with the hydrometer method. Mean summer temperature (June–August) and annual precipitation for each site during the study period were obtained from PRISM 4 km resolution gridded climate data (Daly et al. 2008). Stem-level survival was followed over 4 growing seasons (2010–2013). Maple leaves and fir needles (first- and second-year needles) were collected mid-growing season (2010) to assess leaf nitrogen content (leaf N %). Species leaf samples were combined at the plot level. Leaves were ground and analyzed for tissue nitrogen concentration with a C-N Analyzer (ECS 4010; COSTECH Analytical Technologies, Valencia, California, USA). Lab analyses were done at the Ecosystems Analysis Lab, University of Nebraska, Lincoln, USA.

Sapling growth data used here are the same as reported in Fisichelli et al. (2012) with the addition of leaf N data collected at all 14 study sites. Environmental variables were measured as above for survival. In this separate dataset from survival analyses, there were a total of 506 *A. balsamea* saplings (19–48 per site) and 532 *A. saccharum* stems (19–62 per site), and height varied from 20 to 450 cm. Height growth (annual terminal shoot extension, 2007–2008) and annual radial growth (2005–2009) were measured on each sapling.

### Statistical analyses

To assess the relationship between plant nitrogen status and environmental conditions for each species, site level leaf N (%) was regressed on summer temperature, annual precipitation, soil pH, soil sand fraction (%), overstory conifer relative basal area (a proxy for litter nutrient quality), and N deposition ( $\text{NO}_3^- + \text{NH}_4^+$ ) using simple linear regression.

Sapling survival over the duration of the study was modeled using generalized linear mixed-effects models, a binomial error distribution, and plot nested in site as the random effect. Explanatory variables included initial size (square root transformed height), light availability (natural

log transformed % canopy openness), browse damage, summer temperature (JJA 2010–2013, °C), and leaf N (%). We used existing growth models for these species (Fisichelli et al. 2012) as a basis for initial assessment of survival, in order to examine whether the same factors driving growth are driving survival. As with the previous growth study, other environmental variables (soil pH, soil sand fraction, and annual precipitation) were assessed during preliminary analyses; however, none was a strong predictor of survival and thus all were omitted from further analyses. For each species, we fit models of varying complexity from a simple model only including size and light as explanatory variables to a model with four main effects and associated two-way interactions. Model parameters were fit using maximum likelihood estimation which finds the set of parameter values that maximize agreement with the observed data. We evaluated models through comparisons of small sample corrected Akaike information criteria ( $\text{AIC}_c$ ), which assesses model performance based on goodness of fit and a penalty for the number of model parameters (Burnham and Anderson 2002). For each species, we present results from the model with lowest  $\text{AIC}_c$ .

Sapling height and radial growth were modeled using linear mixed-effects models, a Gaussian error distribution, and plot nested in site as the random effect. The top performing model based on small sample corrected Akaike information criteria ( $\text{AIC}_c$ ) from Fisichelli et al. (2012) for each species and growth metric was included as the initial model ('Temp model'). Nitrogen was added to the initial model to assess whether model fit improved (change in  $\text{AIC}_c$ ). Nitrogen was included as an additive effect ('T+N model') and as a replacement for temperature ('N model'). Data were analyzed using the 'lme4' package (v. 1.1-7; Bates et al. 2014) in R (v. 3.1.1; R Core Team 2014).

## RESULTS

### Leaf nitrogen

Leaf N (%) was more variable for *A. saccharum* (mean 1.35, min–max 0.96–1.91) than *A. balsamea* (mean 1.22, min–max 1.04–1.44). Leaf N was positively related to summer temperature for *A. saccharum* ( $-4.35 + 0.32 \times \text{summer temperature}$ ,  $P$

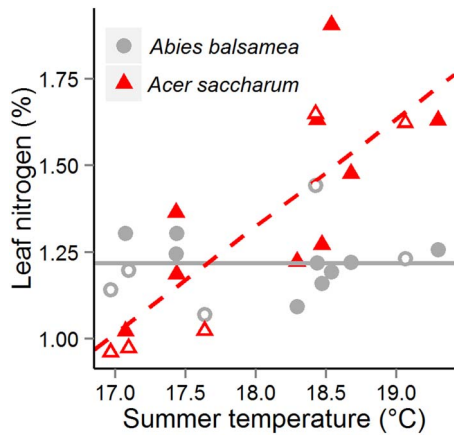


Fig. 1. Leaf nitrogen relationship to study site mean (JJA) summer temperature (simple linear regression) for two tree species found growing together across their overlapping range limits. *Abies balsamea* (gray circles, solid gray line) is at/near its southern range limit and *Acer saccharum* (red triangles, dashed red line) is at/near its northern range limit. Open symbols denote growth and survival study sites, closed symbols denote growth study sites.

= 0.0006,  $R^2 = 0.64$ ) but not for *A. balsamea* ( $P = 0.75$ ; Fig. 1). Leaf N showed no relationship to annual precipitation, soil pH, or soil sand fraction for either species ( $P \gg 0.05$ ), and was also not related to overstory conifer relative basal area ( $P \gg 0.05$ ), though conifers made up less than 20% of basal area at all sites. Leaf N had a weak relationship to N deposition for *A. saccharum* ( $0.02 + 0.30 \times \text{N deposition}$ ,  $P = 0.09$ ,  $R^2 = 0.22$ ) but not *A. balsamea* ( $P = 0.51$ ).

**Sapling survival and growth**

Overall survival for the four growing seasons was high and very similar between the two species (*A. saccharum* 87.3%, *A. balsamea* 87.0%). The inclusion of nitrogen as an explanatory variable for sapling survival was supported for *A. saccharum* while temperature and interactions were supported for *A. balsamea* (Table 1; Appendix: Table A1). The best model (lowest AIC<sub>c</sub> score) for *A. saccharum* included the main effects of size, light, and leaf N; more complex models with interactions did not improve model fit. Nitrogen was the only significant explanatory variable, with proportion of stems surviving positively related to higher leaf N (Fig. 2a). The

Table 1. Survival, radial, and height growth model rankings based on Akaike information criteria (AIC<sub>c</sub>). For survival, ‘Temp (height)’ and ‘Temp (radial)’ models are based on the best fit growth model parameters (‘Temp model’) from Fisichelli et al. (2012). For growth, nitrogen was included as an additive effect (‘T + N model’) and as a replacement for temperature (‘N model’). Symbols: S = initial size, L = canopy openness (light), B = browse pressure, T = mean summer temperature (JJA °C), N = leaf N. Two letter combinations are two-way interactions.

Species, variable, and model	Model parameters	ΔAIC <sub>c</sub>
<i>Acer saccharum</i>		
Survival		
<b>N model</b>	S + L + N	0
N + browse	S + L + N + B	1.29
Temperature	S + L + T	8.33
Base	S + L	8.56
Temp (height)	S + L + B + T + LB + BT	12.41
Temp (radial)	S + L + B + T + SB + LB + BT + ST	13.27
Radial growth		
<b>N model</b>	S + L + B + N + SB + LB + BN + SN	0
T + N model	S + L + B + T + N + SB + LB + BT + ST	11.94
Temp model	S + L + B + T + SB + LB + BT + ST	21.52
Height growth		
<b>N model</b>	S + L + B + N + LB + BN	0
T + N model	S + L + B + T + N + LB + BT	7.87
Temp model	S + L + B + T + LB + BT	13.14
<i>Abies balsamea</i>		
Survival		
<b>Temp (height)</b>	S + L + B + T + SB + LT	0
Temp (radial)	S + L + B + T + SB + LB	7.74
Temperature	S + L + T	19.89
Base	S + L	22.01
N model	S + L + N	22.44
Radial growth		
T + N model	S + L + B + T + N + SB + LB	0
<b>Temp model</b>	S + L + B + T + SB + LB	0.56
N model	S + L + B + N + SB + LB	3.42
Height growth		
<b>Temp model</b>	S + L + B + T + SB + LT	0
T + N model	S + L + B + T + N + SB + LT	0.26
N model	S + L + B + N + SB + LN	4.36

best model for *A. balsamea* survival included four main effects and two interactions. *Abies balsamea* survival decreased with increasing temperature, but only under low light levels, suggesting a potential relationship between shade-tolerance and temperature for this species near its southern range limit (Fig. 2b). Survival for *A. balsamea* also

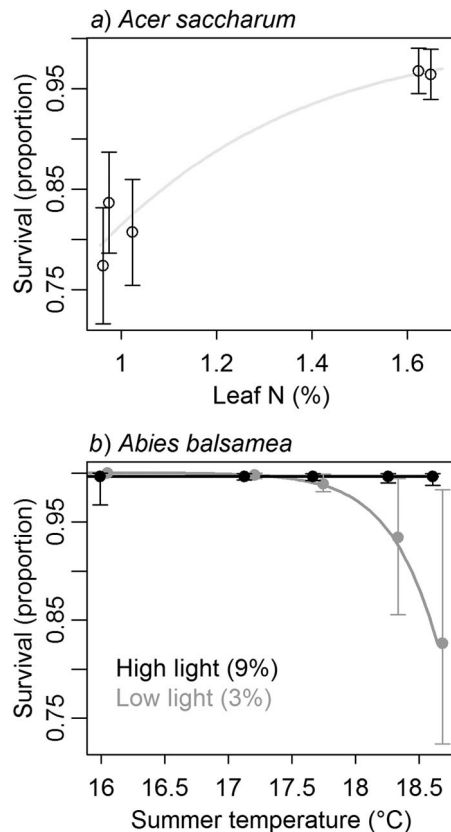


Fig. 2. Sapling survival responses of (A) *Acer saccharum* to leaf N and (B) *Abies balsamea* to summer temperature by light interaction (10th percentile [3%] and 80th percentile [9%] light values shown). Error bars are 95% prediction intervals.

increased with stem size, though this was greater under low than high browse pressure (Appendix: Fig. A2).

Across their overlapping range limits, growth of *A. saccharum* was most influenced by leaf N, whereas temperature most influenced *A. balsamea* (Table 1, Fig. 3; Appendix: Fig. A3). Leaf N improved radial and height growth models, compared to models that included temperature, for *A. saccharum* but not *A. balsamea* (Table 1). The parsimonious model for *A. balsamea* radial and height growth remained the temperature model, as inclusion of nitrogen either resulted in a higher AIC<sub>c</sub> score (height growth) or a similar score but a more complex model (radial growth,  $\Delta\text{AIC}_c = 0.56$ ). Thus, survival and growth were both best fit by models with nitrogen for *A. saccharum* and by models with temperature for *A. balsamea*.

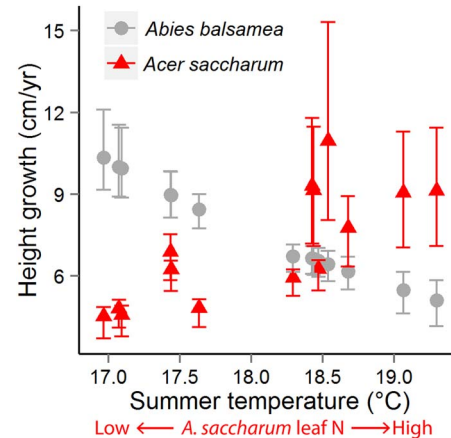


Fig. 3. Height growth trends for *Acer saccharum* and *Abies balsamea* across the temperate-boreal transition zone. Point locations on x-axis are based on site temperature. Growth for *A. balsamea* modeled with site-level summer temperature, growth for *A. saccharum* modeled with leaf N (leaf N ~ temperature relationship shown in Fig. 1). 95% prediction intervals shown for 1 m tall stems.

## DISCUSSION

Sapling performance of co-occurring temperate and boreal species across their overlapping range limits is driven in part by temperature and nitrogen and their interactions with other factors (e.g., light availability and browse pressure). Locations of ecotones are often related to temperature or nutrient gradients (Pastor and Mladenoff 1992, Bigelow and Canham 2002) and this observational field study suggests the temperate-boreal ecotone may be related to temperature and temperature-mediated nitrogen status of these dominant tree species. The positive relationship between leaf N and temperature and enhanced performance of *A. saccharum* at warm sites suggest greater supply of N and/or improved ability of this species to compete for soil N under warmer conditions. A narrower range of leaf N, no positive relationship between leaf N and temperature, and decreasing growth and survival with increasing temperature appear to make *A. balsamea* an inferior performer at warmer sites. These two tree species co-occur across millions of hectares and temperature and nitrogen appear to play influential roles in their dynamics.

Variation in *A. saccharum* leaf N could not be explained by ranges of soil texture, soil pH, precipitation, or litter quality; only summer temperature was related to *A. saccharum* leaf N ( $R^2 = 0.64$ ). Increased soil temperature can lead to increased N mineralization and nitrification rates (Melillo et al. 2002). Lower leaf N at cooler sites could be due to lower availability, weaker nutrient demand by slower growing tissues (Körner 1998), or reduced ability to compete for soil nutrients by a species at its northern limit. Higher leaf N results in stronger net photosynthesis increases for broadleaf than conifer species (Reich et al. 1995) and thus may explain increased survival and growth and the high density of *A. saccharum* seedlings within boreal forest neighborhoods at warm sites (Fisichelli et al. 2014a). The strong *A. saccharum* leaf N to temperature relationship suggests further research and controlled experiments are needed to tease apart temperature effects on nitrogen supply, demand, and uptake in this system.

This study was from the western end of the temperate-boreal transition zone, and the strong *A. saccharum* relationship between leaf N and temperature may not hold across the entire transition zone. Leaf N values found here for *A. saccharum* are at the low end of concentrations for this species compared with samples in the northeast U.S. (NERC 2013), where N deposition rates have historically been much higher. A lack of response of *A. saccharum* performance to N in numerous studies in the northeast (Finzi and Canham 2000, Bigelow and Canham 2002, Catovsky and Bazzazz 2002) suggests that N supply may be greater than demand within that region (Aber et al. 2003). In contrast, the present study and prior work (e.g., Walters and Reich 1997, 2000) show *A. saccharum* to respond positively to higher levels of nitrogen supply or leaf N status, within the natural range of variability. Nitrogen deposition rates are relatively low in the study region and the weak relationship between deposition and leaf N may indirectly reflect temperature, as pollution sources (i.e., agriculture and developed areas) are located closer to warmer (southern) than cooler (northern) sites.

The rapid rate of climate change raises concern over the ability of species to track shifting conditions. *Acer saccharum* may be able to quickly

take advantage of warming temperatures if this response is contingent, in part, on soil nitrogen. N mineralization and soil respiration rates fluctuate greatly across days to weeks within individual growing seasons in response to temperature variations (Zogg et al. 1996), and thus may be able to track longer-term shifting mean temperatures across years. Of course, range expansions will be driven by multiple factors, including dispersal ability, trophic interactions, and disease (Fisichelli et al. 2013, Brown and Vellend 2014) that could slow range expansions in response to temperature and nitrogen.

In addition to survival and growth, analyses also revealed that *A. balsamea* shade tolerance, an important trait for this species that typically establishes beneath intact forest canopies, appears to vary with temperature. As other factors that influence plant carbon balance (e.g., moisture, nutrients, plant size) reduce shade tolerance when carbon balance is negatively impacted, it is not surprising that this may be true for temperature as well. Thus, persistence of this species near its southern range limits may depend on canopy gap dynamics and light availability. Disjunct southern populations of the species are often found in open sites such as around wetlands, further suggesting that increased photosynthesis may be needed to match increased respiratory demands at warm sites.

Relative magnitudes of global change drivers across the temperature-boreal transition zone will determine the rate and direction of species' range shifts. At least at the western end of the transition zone, temperature and nitrogen appear to be important drivers of ecotonal dynamics. These findings are from an observational field study but a realistic open-air warming experiment also found divergent response to warming by temperate and boreal species, including the same species studied herein (Reich et al. 2015). The apparent consistency of these different responses suggests that future studies are needed to shed further light on the mechanistic underpinnings of this shifting ecotone.

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## SUPPLEMENTAL MATERIAL

### ECOLOGICAL ARCHIVES

The Appendix is available online: <http://dx.doi.org/10.1890/ES15-00115.1.sm>