Sapling growth responses to warmer temperatures 'cooled' by browse pressure

NICHOLAS FISICHELLI*, LEE E. FRELICH* and PETER B. REICH*†
*Department of Forest Resources, University of Minnesota, 1530 Cleveland Avenue North, St. Paul, MN 55108, USA,
†Hawksbury Institute for the Environment, University of Western Sydney, Penrith, NSW 2753, Australia

Abstract

Rising temperatures are predicted to cause temperate tree species to expand north into currently boreal dominated forests. Other factors, such as overabundant deer, may hinder temperate expansion. We examined how interactions among temperature, browse pressure, light availability, and initial size impact height and radial growth of naturally regenerated, competing temperate and boreal saplings across their overlapping range limits in central North America. In 9 of 10 growth model comparisons, the inclusion of mean summer temperature and browse damage as explanatory variables strongly improved model performance over the base model with only initial size and light availability as parameters. Potential growth reductions due to browse damage and temperature limitation were similar in magnitude (up to ~50%). Temperate sapling growth increased and boreal growth decreased with temperature across a regional summer temperature gradient (2.3 °C), causing a rank reversal in growth rates, and suggesting that temperature is a key driver of sapling performance and range boundaries. However, under high browse pressure positive temperate responses to temperature were eliminated, essentially pushing the crossover point in growth between temperate and boreal species further south. These results highlight the importance of interactions among global change agents and potential impediments for tree species to track a rapidly changing climate.

Keywords: browse pressure, climate change, competition, ecotone, herbivory, range limits, sapling growth, temperate-boreal transition zone, tree migration

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Introduction

Global change agents and their interactions and inter-relationships with local environmental conditions will drive the future trajectory of forest ecosystems (Chapin *et al.*, 1997; Dietze & Moorcroft, 2011). Forest overstory composition is determined in large part by performance at the younger seedling and sapling stages where survival and growth rates have been shown to be excellent predictors of canopy layer composition (Kobe, 1996; Pacala *et al.*, 1996; Wyckoff & Clark, 2002). Sapling performance in the understory is primarily driven by light availability, with responses partially dependent upon nutrients, moisture availability, and competitive dynamics (Canham *et al.*, 1996; Walters & Reich, 1997; Coomes & Grubb, 2000; Kobe, 2006; Montgomery *et al.*, 2010). In addition, global change agents such as rising temperatures and overabundant herbivores may select for differing suites of species, especially near range boundaries (Post & Pedersen, 2008; Olofsson *et al.*, 2009; Speed *et al.*, 2011). Given

Correspondence: N. Fisichelli, Department of Silviculture and Forest Ecology of the Temperate Zone, Georg-August-Universität, Büsgenweg 1, 37077 Göttingen, Germany, tel. + 49 551 393 667, fax + 49 551 393 270, email: nfisichelli@gmail.com
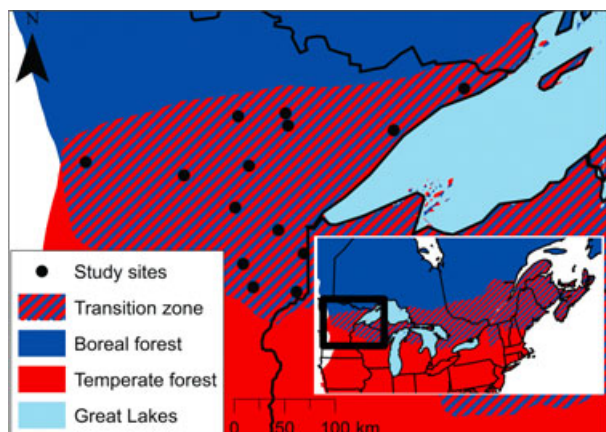
the often stressful growing conditions in the forest understory, including potentially intense browse pressure, tree regeneration responses to warming may be inhibited, creating an extended time lag to climate change.

Trees growing near their range limits are likely most sensitive to climate change and apt to exhibit growth responses to small variations in climate (Fritts, 1976; Parmesan *et al.*, 2005; Reich & Oleksyn, 2008). Furthermore, juvenile stages may have narrower climate thresholds than adult stages and thus be more responsive to climate change (Grubb, 1977; Jackson *et al.*, 2009; Van Mantgem *et al.*, 2009). In addition to shifts in germination and early survival, warming temperatures may shift competitive interactions among saplings in favor of those species with more positive growth increases (Woodward, 1987). Differential growth responses to temperature are likely greatest where northern and southern range limits of competing species overlap, such as within the temperate-boreal transition zone (Fig. 1). Temperate species near their northern range limits are predicted to exhibit strong positive growth responses to increases in temperature, whereas growth responses of boreal species near southern limits are less certain, with evidence for positive, flat, and negative responses, depending on species

Fig. 1 Overlapping range limits of temperate and boreal species define the temperate-boreal transition zone. Fourteen study sites located across a 2.3 °C summer temperature gradient where boreal (*Abies balsamea* and *Picea glauca*) and temperate (*Acer rubrum*, *Acer saccharum*, and *Quercus rubra*) species occur together as advance regeneration. Range limits of study species modified from Little (1971).

and location (Schenk, 1996; Loehle, 1998; Reich & Oleksyn, 2008).

Other global change agents, such as overabundant herbivore populations, are also likely to play important roles in determining future forest composition and may facilitate or inhibit climate-mediated forest changes. Within the temperate-boreal transition zone in the Great Lakes region of North America, white-tailed deer (*Odocoileus virginianus*) densities are roughly 2.5–5 times higher than prior to European settlement (Rooney & Waller, 2003). Interspecific differences in palatability can lead to large differences in browse damage and potentially to shifts in understory composition toward dominance by less palatable species, such as boreal *Picea glauca* (Potvin *et al.*, 2003; Côté *et al.*, 2004). Recent studies at alpine tree line and within tundra systems indicate that vegetation responses to temperature may be sharply limited by browse pressure (Post & Pedersen, 2008; Olofsson *et al.*, 2009; Speed *et al.*, 2011). Similar trends are likely within forest systems such as the temperate-boreal transition zone, where sensitivities to temperature and browse pressure likely vary widely among tree species.

The primary objective of this research was to examine how interactions among temperature, browse pressure, light availability, and sapling size influence the growth of temperate and boreal saplings across their overlapping range limits. We hypothesized that temperate tree species will exhibit stronger positive growth responses to temperature than the boreal species. Temperate species will also have more negative responses to browse pressure due to higher palatability and thus

higher rates of severe browse damage. The strengths of these drivers and their interactions will influence competitive interactions and thus impact migration potential and future forest composition.

Materials and methods

Field and laboratory

This study included 14 research sites, which span the temperate-boreal transition zone in Minnesota, USA (Fig. 1). Potential upland mesic stands with an overstory mixture of temperate and boreal tree species were identified from GIS vegetation layers. Final site selection was based on presence of advance regeneration and inclusion of sites to maximize the temperature gradient. Mean annual temperature varies from 3.0 to 5.5 °C, mean summer temperature (JJA) from 16.2 to 19.1 °C, and annual precipitation from 683 to 835 mm (1978–2007 period) across the transition zone (Daly *et al.*, 2008).

Sapling growth rates were studied for five mid to very shade-tolerant species, including two boreal conifers, *Abies balsamea* and *Picea glauca*, and three temperate broadleaf species, *Acer rubrum*, *Acer saccharum*, and *Quercus rubra*, commonly found growing together as advance regeneration in mixed temperate-boreal stands (Table S1). Each study site contained between two and five species and each was present at 7–14 sites. We conducted a stratified random sample of saplings in four height classes (20–50, 50–100, 100–200, and 200–450 cm) and attempted to include only saplings that appeared to have established from seed (multistemmed basal sprouts were avoided). Plots within sites were randomly located and a subset or all saplings of a species and size class combination (depending on abundance) were sampled within 15 m of plot center. Our goal for each species was to include ~10 stems per size class at each site, although due to varying abundances, sample size varied between 1 and 15 stems per size class (Table S2).

For each individual stem, in the field we recorded browse damage and light availability. Browse pressure to each sapling was scored on a scale from 0 to 10 based on the percentage of branches with browse damage (0 = no damage, 1 = 10% of branches damaged, 2 = 20% of branches damaged, 10 = 100% of branches with browsed tips) (Frelich & Lorimer, 1985). The temperate broadleaf species generally experienced much higher browse pressure than the boreal conifers (Table 1). The majority of browse damage was due to white-tailed deer (*Odocoileus virginianus*), with moose (*Alcesalces*) and snowshoe hare (*Lepusamericanus*) accounting for a very low percentage of observed damage. Although deer densities are regionally very high, we were able to exploit local scale variability in browse pressure, likely due in part to winter deer yarding behavior and local hunting regulations. Only one deer exclosure at a single site was utilized and these stems only accounted for 1% of the overall sample size. The light environment (percent canopy openness) at the top of each sapling (or at 3 m above ground level for saplings >3 m in height) was measured with a LI-COR LAI-2000 plant canopy analyzer (LI-COR Inc., Lincoln, Nebraska) under uniform overcast conditions.

Table 1 Summary information for explanatory variables used in sapling radial and height growth models. Browse pressure is based on the proportion of branches on individual stems with evidence of browse damage. Mean summer temperature is based on the months of June–August, 2005–2009 (Daly *et al.*, 2008)

Species	Initial radius (mm)			Initial height (cm)			Light (canopy openness%)			Browse pressure (0–10 scale)			Summer Temp (JJA, °C)	
	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Min	Max
Abies balsamea	6.2 (4.2)	0	22.3	124.9 (76.9)	3.2	366.7	9.4 (7.8)	0.8	39.7	0.7 (1.7)	0	9	17.0	19.3
Picea glauca	7.7 (5.8)	0	31.3	126.6 (76.1)	0	382.5	8.6 (7.1)	0.7	39.8	0 (0.1)	0	1	17.0	19.3
Acer rubrum	3.4 (2.4)	0	13.0	126.6 (101.6)	0	454.4	12.5 (10.2)	1.5	39.2	3.0 (3.2)	0	9	17.0	18.7
Acer saccharum	3.8 (2.7)	0	18.4	146.5 (105.5)	2.4	453.0	8.2 (5.5)	0.5	30.5	2.7 (2.9)	0	9	17.0	19.3
Quercus rubra	3.5 (2.3)	0	11.1	112.4 (93.9)	8.6	403.7	11.6 (8.1)	1.3	37.3	3.4 (3.4)	0	9	17.0	19.3

Finally, samples of the upper 20 cm of mineral soil were collected at each plot. Soil pH was measured using a water:soil suspension and sand particle fraction was determined with the hydrometer method.

We assessed the performance of saplings through measures of both height and radial growth. Although the broadleaf and conifer species in this study have somewhat differing life history strategies, height and radial growth are integrated measures of plant performance and growth responses to varying understory conditions reflect shifts in overall fitness. Furthermore, direct comparisons of height growth are warranted as competition for light, typically the main limiting resource in the forest understory, is asymmetric with faster growing individuals overtopping competitors and usurping the resource (Pacala *et al.*, 1994). Plots were sampled in 2009 and 2010. Terminal leader annual stem elongation (height growth) was determined for up to 6 years (2005–2010) by measuring the distance between terminal bud scars. Saplings were harvested at 10 cm above ground level and a basal cross-section collected. These were then dried and sanded (up to 1200 grit), and age and ring width measurements, to the nearest 0.01 mm, were made along the radial line that bisected the angle between the longest and shortest radii using a stereomicroscope and a Velmex sliding-stage measuring system (Velmex, East Bloomfield, NY, USA).

Statistical analyses

To model sapling growth, we utilized linear mixed-effects models with transformed growth, initial size, and light data, a Gaussian error distribution, and site as a random effect. Although other modeling of sapling growth has used nonlinear Michaelis-Menten functions (Pacala *et al.*, 1994; Kobe, 1996; Wright *et al.*, 1998), ~95% of saplings in this study were growing in <20% full sunlight. Thus asymptotic growth rates were rarely achieved and biplots indicated reasonably linear relationships between response and explanatory variables (Fig. S1). We calculated mean annual radial growth from the 5 year period 2005–2009 and mean annual height growth from

2007 to 2008. Height growth for the full 5 year period (2005–2009) could not be accurately measured on heavily browsed stems because it was difficult to identify stem lengths going back more than a couple of years. In addition, as many stems were harvested at the end of the 2009 growing season and most browse damage occurs during winter months, 2008 was the most recent year of shoot growth to experience a full year of browse pressure. Mean summer temperature (June–August) for these years was obtained from PRISM (Daly *et al.*, 2008) 4 km resolution gridded climate data. As understory conditions can change over relatively short periods, such as light levels due to canopy gaps forming and closing, interannual variability in growth response to climate variables is difficult to detect in understory saplings. Thus, we use differences among sites to model responses to temperature. Present and past temperatures across the transition zone are compared with future predictions of Kling *et al.* (2003). Preliminary analyses found soil variables (texture and pH) and precipitation to be poor predictors of growth, likely due to insufficient variation in these variables (data not shown), and thus these predictors were dropped from further analyses.

Our final set of potential predictors included initial size (natural log transformed radius in 2004, square root transformed height prior to 2007), light availability (natural log transformed % canopy openness), browse damage (0–10 index, treated as a continuous variable), and summer temperature (JJA, °C) (Table 1). In addition to these main effects we examined five *a priori* selected two-way browse and temperature interactions: size by browse, light by browse, browse by temperature, size by temperature, and light by temperature. Because *Picea glauca* received essentially zero browse pressure, only combinations of three main effects and two interactions were possible for this species.

For each species, we fit models of varying complexity from a simple model only including size as a predictor to a model with all four main effects and five interactions. Model parameters were fit using maximum likelihood estimation which finds the set of parameter values that make the observed data most likely to have occurred. We evaluated models through

comparisons of small sample corrected Akaike information criteria (AIC_c), which assesses model performance based on goodness of fit and a penalty for the number of model parameters (Burnham & Anderson, 2002). Correlations among predictors were weak ($-0.3 < r < 0.3$) and variance inflation factors (VIFs) for variables in final models were <2 indicating a lack of multicollinearity (Zuur *et al.*, 2009). For each species, we present results from the model with lowest AIC_c (see Tables S3 and S4 for comparisons among models via ΔAIC_c, and Fig. S2 for top model residual plots). Parameter estimates of top models were assessed via t values and prediction intervals calculated through model fitting. Data were analyzed using the 'nlme' package (v. 3.1) (Pinheiro *et al.*, 2009) in R (v. 2.12) (R Development Core Team, 2008). Figures depicting interactions display the interacting variable at low (20th percentile) and high (80th percentile) values defined by the data for each species.

Results

The inclusion of temperature, browse, and interactions as explanatory variables strongly improved sapling growth model performance over simpler models with only initial size and light in 9 of 10 modeling comparisons ($\Delta AIC_c > 9$) (Tables S3 and S4). Browse interactions were included in top performing height and radial growth models for each of the four browsed species and temperature or temperature interactions in 9 of 10 top growth models for the five study species (Fig. 2, Tables S5 and S6). The *P. glauca* radial growth model was the only instance where summer temperature was not supported as a predictor. Radial and height growth model parameters and the strength and direction of coefficients were generally similar within species. For example, the top *Quercus rubra* height and radial growth models included identical parameters with comparable coefficients.

Responses to temperature or temperature interactions were detected for all species over the 2.3 °C summer temperature gradient (Figs 2 and 3). Growth declined with temperature for the two boreal conifers, with the reduction in growth more pronounced for *Abies balsamea* than *P. glauca* (Fig. 3a–d). All three temperate broadleaf species exhibited neutral to positive growth responses to temperature, depending on the level of the interacting variable (Fig. 3e–j, interacting variable shown at low, 20th percentile, and high, 80th percentile, values). We observed strong positive *Acer rubrum* height growth and *Acer saccharum* height and radial growth responses to temperature when browse pressure was low, but increasing browse pressure strongly reduced these positive growth responses. Heavily browsed stems displayed essentially no growth response to temperature, and at warm sites this pressure resulted in growth reduction of ~50%
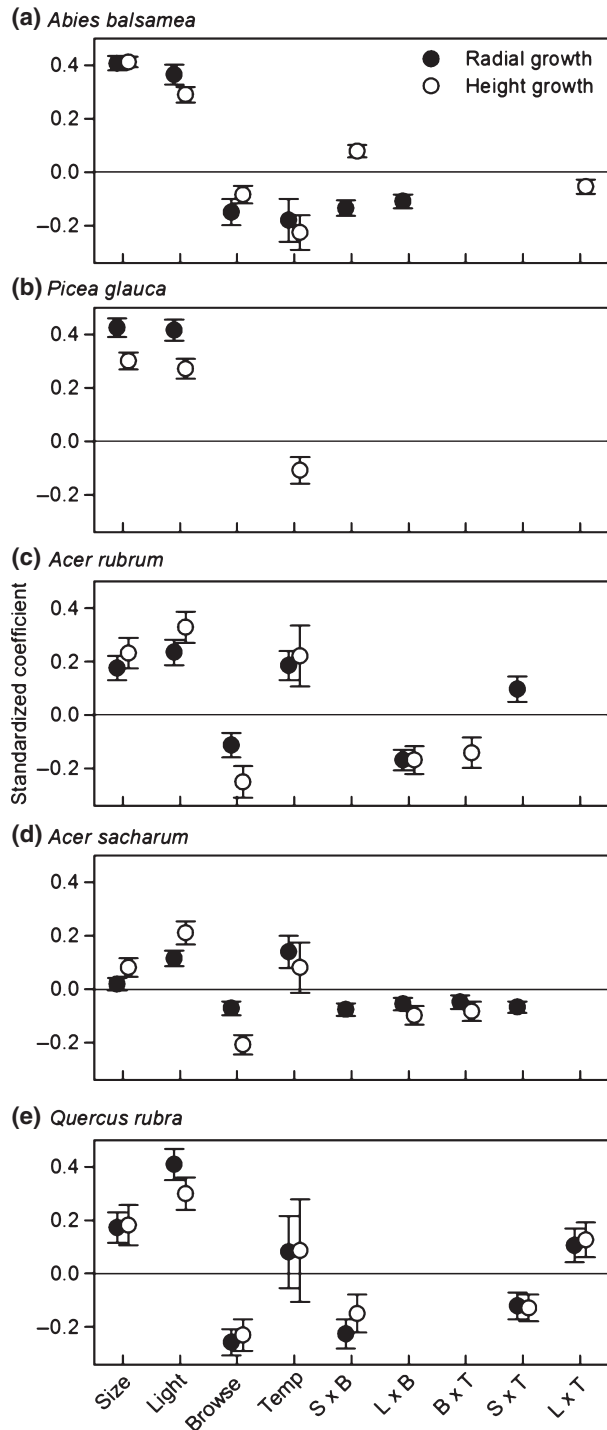

Fig. 2 Fixed effects parameter standardized coefficient estimates (mean ± standard error) for top performing sapling height (cm × yr^{-1}) and radial (mm × yr^{-1}) growth models for (a) *Abies balsamea*, (b) *Picea glauca*, (c) *Acer rubrum*, (d) *Acer saccharum*, and (e) *Quercus rubra*. Letter abbreviations shown for interactions: S = initial Size, L = Light availability, B = Browse damage, T = mean summer Temperature.
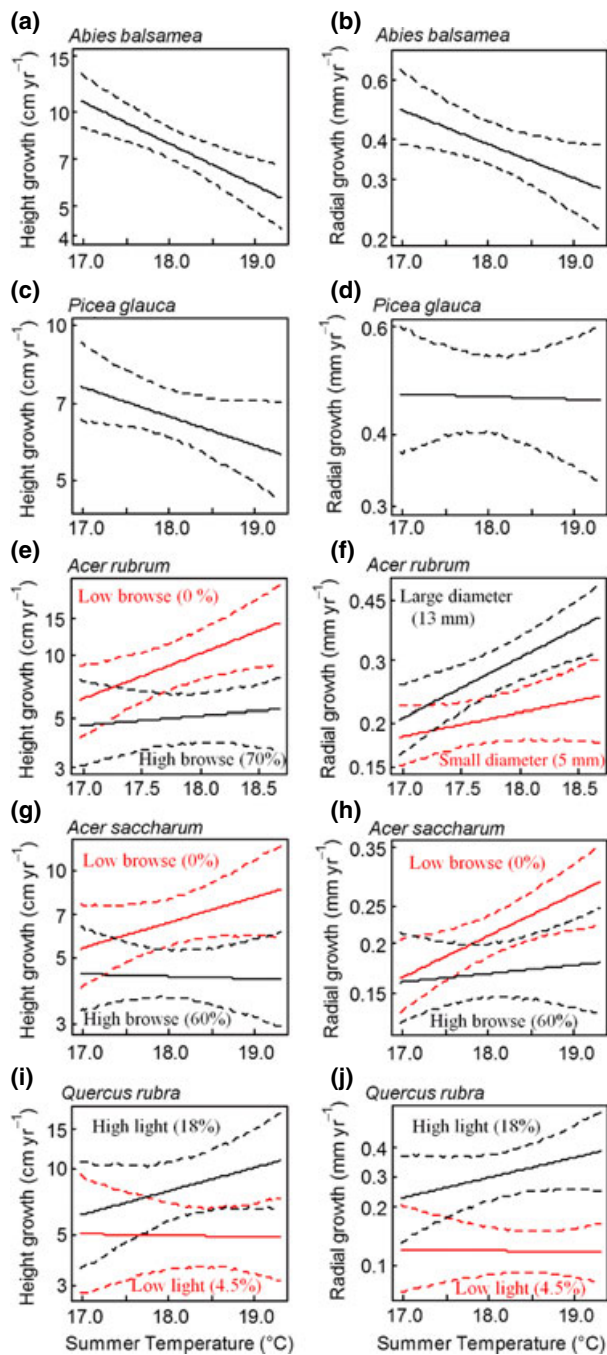
Fig. 3 Height (a, c, e, g, i) and radial (b, d, f, h, j) growth responses to mean summer temperature and temperature interactions across the temperate-boreal transition zone. The boreal conifer species *Abies balsamea* (a, b) and *Picea glauca* (c, d) are growing near their southern range limits, whereas temperate broadleaf species *Acer rubrum* (e, f), *Acer saccharum* (g, h), and *Quercus rubra* (i, j) are near their northern range limits. Low (red) and high (black) values of interacting factors are assigned their 20th and 80th percentile values, respectively. Dashed lines represent approximate 95% prediction intervals.

compared with unbrowsed stems. *Acer rubrum* radial growth response to temperature also increased with stem size. For moderately shade-tolerant *Quercus rubra*, height and radial growth responses to temperature were detectable under high light availability. Thus, at warmer sites, growth of higher light *Q. rubra* stems was approximately twice as great as low light stems, whereas there was no difference in growth by light levels at cooler sites.

In addition to the browse by temperature interactions, the effects of browse pressure also varied with size and light availability (Figs 2 and S1). Heavy browse damage reduced height and radial growth by ~50% or more for potentially fast growing stems of all four browsed species. Although browse damage was generally low for *A. balsamea* (mean browse index <1), growth was strongly reduced where browse damage was high. Browse pressure also strongly negated height and radial growth responses to increasing light levels for both *A. rubrum* and *A. saccharum* and more negatively impacted height and radial growth of large than small *Q. rubra* stems.

Interspecific variations in palatability and thus level of browse damage as well as differing responses to temperature resulted in strong shifts in relative performance across the temperate-boreal transition zone (Fig. 4). Under low browse pressure (index = 0), height growth was generally greater for the boreal conifers than temperate broadleaf species at cool sites while temperate species exhibited relatively higher growth rates at warm sites, resulting in a rank reversal of growth rates (Fig. 4a). However, under high browse pressure (each species assigned its 80th percentile browse rating) temperate species height growth was uniformly low and as a result lower than that of boreal conifers at all, but the warmest sites (Fig. 4b). These growth patterns from across the current temperate-boreal transition zone are shown with temperature changes over the past five decades (+0.5 °C) and predicted warming over the next three decades (+1.7 °C) (Kling *et al.*, 2003) for these same sites (Fig. 4c).

Discussion

The results of this research underscore the importance of interactions among global change agents in driving forest composition and potential response rates to climate change. Eventual overstory composition is the result of species level performance and competitive interactions at multiple early life stages (Pacala *et al.*, 1996; Poorter, 2007). Radial and height growth are integrated measures of plant performance and inclusion of temperature and browse as strong explanatory variables in both sets of analyses bolsters the evidence
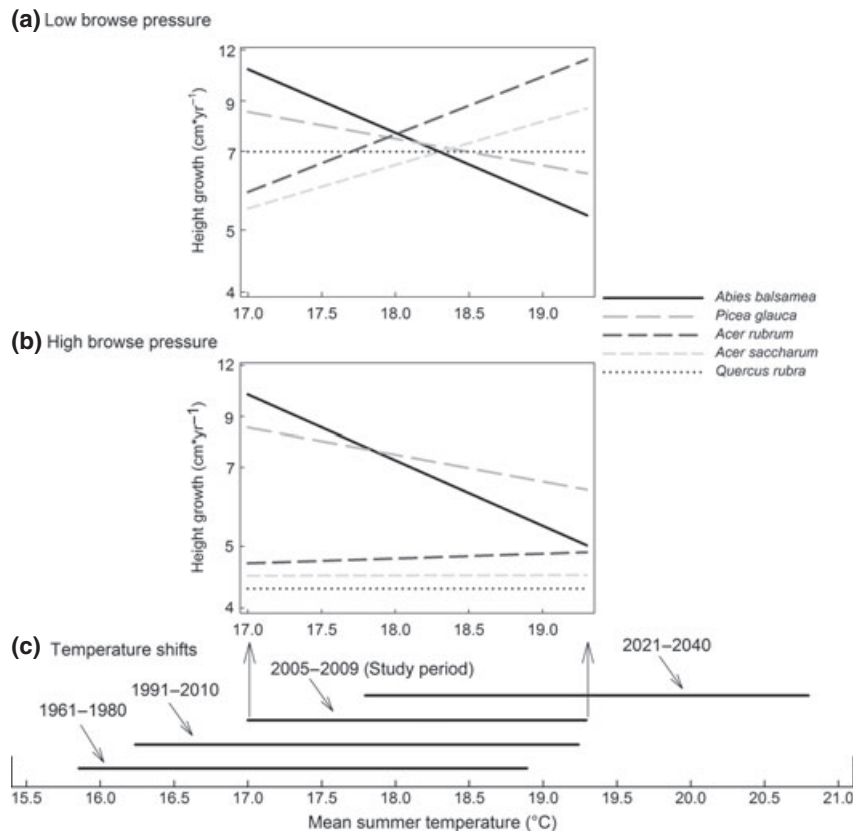
Fig. 4 Height growth responses to temperature of all five species at (a) low and (b) high browse pressure. (c) Comparisons of recent past and predicted future temperatures (Kling *et al.*, 2003) across the temperate-boreal transition zone. Low and high browse pressure for each species were determined based on 20th and 80th percentile values, respectively.

that these factors are important drivers of plant productivity and forest dynamics. Decreasing growth by both temperate and boreal saplings as they approach their range limits suggests that temperature-mediated competitive dynamics are a key driver of sapling performance, forest composition, and range boundaries across the temperate-boreal transition zone. However, heavy browse pressure can eliminate increased growth of temperate broadleaf species at warmer sites and tilt growth rates in favor of less palatable boreal species. This 'cooling' effect of selective browsing may manifest in reduced northward expansion rates for temperate species and the persistence of boreal trailing edge populations due to reduced competition. Comparable reductions in growth due to browse damage and temperature limitations indicate that the potential impacts of both factors are currently similar in magnitude across the study region. Thus, successional trajectories could lead in multiple directions, depending on the relative strengths and variability in drivers over space and time (Rodenhouse *et al.*, 2009).

Notable recent studies have found indications that many tree species are not exhibiting northward expan-

sions (Zhu *et al.*, 2012) and have shown that other factors, such as competition, likely play a bigger role than climate variation (Clark *et al.*, 2011; Xu *et al.*, 2012). By focusing our research on the temperate-boreal transition zone, we were able to detect temperature-mediated rank reversals in growth, suggesting that at least near range limits the outcome of competition is tightly linked to climate. Secondly, by measuring browse pressure and its interactions with temperature we were able to quantify the impacts of a potential causal mechanism for failed migration.

Decreasing growth with increasing temperature for the two boreal conifers indicated that not only are these species unable to keep pace with the growth of temperate species but they are also more stressed as they approach their southern range limits. These results suggest that abiotic stressors at least partially determine southern range limits for boreal conifers in the advance regeneration layer. A study of several western North American shade-tolerant conifers found similar results with higher low light growth in the coolest climatic regions (Wright *et al.*, 1998). In Europe, *Pinus sylvestris* in the southern part of its range showed decreased

growth and survival with modest warming in transplant experiments (Reich & Oleksyn, 2008). These results may reflect a tradeoff between photosynthetic rates and respiration costs with varying temperature and light regimes (Adams & Loucks, 1971; Tjoelker *et al.*, 1998), or the increased frequency of drought and/or heat stress events (Reich & Oleksyn, 2008), or both. If warming is accompanied by reduced soil moisture, then drought-intolerant species such as *Abies balsamea* may exhibit particularly strong negative responses. For example, the greater decline in growth at warm sites by *A. balsamea* stems in higher light suggests that lower soil moisture and higher respiration rates within warm, sunny gaps may have swamped any potential benefit of higher understory light levels. Similarly, the lack of response to temperature differences by low light *Quercus rubra* stems may also indicate that increasing respiratory costs with increasing temperature were not met by low light photosynthetic rates for this mid-shade-tolerant species.

Continued summer warming for the region (up to 1.7 °C by 2030) (Kling *et al.*, 2003) suggests that temperature-mediated shifts in relative performance among temperate and boreal species will intensify in the coming decades, depending on browse levels (Fig. 3). Summer warming of the magnitude predicted for the end of the 21st Century, 3–8 °C (Kling *et al.*, 2003; IPCC, 2007) will eventually cause the relative performance of boreal saplings to be much poorer than temperate species across most if not all of the current temperate-boreal transition zone, regardless of browse intensity. As temperatures continue to increase across this region, the influence of browse pressure will shift from facilitating the resilience of boreal conifers to driving competitive interactions among expanding temperate species. As deer are likely to also respond to climate change by expanding northward (Côté *et al.*, 2004), the importance of future deer-sapling growth interactions at and beyond the current northern limit of the temperate-boreal transition zone will depend in part on the direction and rate of changing climatic conditions, with summer temperatures influencing plant growth rates and winter conditions driving browse pressure levels (Rodenhouse *et al.*, 2009).

Our research revealed natural spatial heterogeneity in browse pressure across the landscape that is sufficient to modify sapling growth trends of all browsed species and thus potentially influence the temporal and spatial patterning of temperate tree expansion. Chronic browse pressure can delay ascension above the browse layer for decades (Vila *et al.*, 2003), and thus delay temperature-mediated shifts in species composition (Rodenhouse *et al.*, 2009). At the northern, cool end of the transition zone, high browse pressure will inhibit the ability of temperate species to expand in those areas. On the other hand, low browse pressure sites, such as those located in the lake-effect snowbelt near Lake Superior, may facilitate temperate expansion. Deer avoid the deep snows of this area during winter when most browse damage occurs (Frelich & Lorimer, 1985), thus minimizing growth loss and improving the relative performance of more palatable broadleaf temperate species.

In addition to growth, mortality rates are an important driver of understory dynamics (Pacala *et al.*, 1994; Wyckoff & Clark, 2002). Although we did not directly measure mortality rates, probability of mortality increases with decreasing growth, especially at very low growth rates (Kobe, 1996; Wyckoff & Clark, 2002). Slow growing stems (small size, low light, high browse pressure, or near temperature limits) surviving near their physiological limits likely have higher mortality rates. Thus, differences in relative performance based solely on growth rates may underestimate actual fitness differences among species growing near their range limits. Furthermore, slight increases in stressors, for example, increased browse damage at northern range limits for temperate species and warmer temperatures at the southern range limits of boreal species, may have nonlinear impacts on mortality rates that are not reflected in minor growth shifts for already slow growing individuals.

All saplings in this observational study were naturally established advance regeneration growing in typical forest understory conditions and these results demonstrate that natural variation in drivers across the narrow temperate-boreal transition zone can cause detectable changes in growth rates and relative performance of competing saplings. Although warming temperatures are predicted to result in large potential habitat shifts (Iverson *et al.*, 2008), the outcome of competitive interactions among saplings will depend on multiple interacting factors including browse pressure, understory light levels, and even sapling size. Enhanced growth by temperate species in response to temperature was most detectable under favorable growing conditions, including low browse pressure and high light. Thus, models of future forest composition as well as management efforts at facilitating forest compositional changes will need to address these interactions, especially the 'cooling' effect of browse pressure.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Bivariate relationships between (a) radial growth and initial size, (b) radial growth and canopy openness, (c) height growth and initial size, (d) height growth and canopy openness for saplings of all five study species.

Figure S2. Height (a, c, e, g) and radial (b, d, f, h) growth model residual plots. See Tables S5 and S6 for model parameters.

Figure S3. Height (a, c, e, g) and radial (b, d, f, h) growth responses to browse interactions. Browse damage index (0–10) was based on the percentage of browse damaged branches on individual saplings (0 = 0%, 10 = 100%). Low (red) and high (black) values of interacting factors are assigned their 20th and 80th percentile values, respectively. Dashed lines represent approximate 95% prediction intervals.

Table S1. Summary data for the two boreal conifer and three temperate broadleaf study species. Species selected were common as advance regeneration in temperate-boreal transition zone forests. Stem age and radial growth were determined from basal cross-sections harvested 10 cm above ground level.

Table S2. Species level stem counts by size class and site. Sites are arranged by mean summer temperature [June–August 2005–2009 (Daly *et al.*, 2008)].

Table S3. Height growth model rankings based on AICc. Top models (<2 ΔAICc), base (size + light), browse (size + light + browse), temperature (size + light + temperature), and additive (size + light + browse + temperature) models are shown for comparison. Model parameter symbols: S = initial size, L = canopy openness (light), B = browse pressure, T = mean summer temperature (JJA, °C 2007–2008). Two letters combined represent two-way interactions.

Table S4. Radial growth model rankings based on AICc. Top models (<2 ΔAICc), base (size + light), browse (size + light + browse), temperature (size + light + temperature), and additive (size + light + browse + temperature) models are shown for comparison. Model parameter symbols: S = initial size, L = canopy openness (light), B = browse pressure, T = mean summer temperature (JJA, °C 2005–2009). Two letters combined represent two-way interactions.

Table S5. Fixed effects parameter estimates from linear mixed-effects models of sapling height growth for each of the five study species. r^2 is the squared correlation coefficient between observed and modeled values.

Table S6. Fixed effects parameter estimates from linear mixed-effects models of sapling radial growth for each of the five study species. r^2 is the squared correlation coefficient between observed and modeled values.

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