

## TREE PHYSIOLOGY REVIEW

# Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data

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**Summary** The response of tree growth to a change in temperature may differ in predictable ways. Trees with conservative growth strategies may have little ability to respond to a changing climate. In addition, high latitude and altitude tree growth may be temperature-limited and thus benefit from some degree of warming, as opposed to warm-adapted species. Using data from 63 studies, we examined whether trees from different functional groups and thermal niches differed in their growth response to a change in growth temperature. We also investigated whether responses predicted for a change in growth temperature (both reduced and elevated) were similar for increased temperatures by repeating the analysis on the subset of raised temperature data to confirm the validity of our results for use in a climate-warming scenario. Using both the temperature-change response and the warming response, we found that elevated temperatures enhanced growth (measured as shoot height, stem diameter and biomass) in deciduous species more than in evergreen trees. Tropical species were indeed more susceptible to warming-induced growth declines than temperate or boreal trees in both analyses. More carbon may be available to allocate to growth at high temperatures because respiration acclimated more strongly than photosynthesis, increasing carbon assimilation but moderating carbon losses. Trees that developed at elevated temperatures did not simply accelerate growth but followed different developmental trajectories than unwarmed trees, allocating more biomass to leaves and less to roots and growing taller for a given stem diameter. While there were insufficient data to analyze trends for particular species, we generated equations to describe general trends in tree growth to temperature changes and to warming for use at large spatial scales or where data are lacking. We discuss the implications of these results in the context of a changing climate and highlight the areas of greatest uncertainty regarding temperature and tree growth where future research is needed.

*Keywords:* carbon balance, climate change, development, global warming, thermal acclimation.

## Introduction

Rising greenhouse gases and changes in the reflective properties of the earth's surface are predicted to raise global temperatures 1.1–6.4 °C by 2100, and high-latitude forest regions may warm by almost 10 °C (Christensen et al. 2007). While forests cover 30% of the terrestrial biosphere and store approximately 1640 Pg C (Sabine et al. 2004), there is little consensus on how trees will respond to the changing environment. Responses in tree growth to climate warming will likely depend on many factors, including water and nutrient availability, the timing of the warming, rising atmospheric CO<sub>2</sub>, the ability of species to acclimate to new growing conditions and how close trees already are to their thermal optimum for growth.

One way to project how trees may respond in the future is to look at past responses. Dendrochronology studies have often found increased growth during warmer growing seasons (e.g., McKenzie et al. 2001, Bunn et al. 2005), leading to a positive relationship between growing season temperature and growth in northern forests (D'Arrigo et al. 2008). However, while early 20th century warming promoted growth (e.g., increased tree ring density and width), increasing temperatures since 1950 have generally had a lower than expected effect in many Northern Hemisphere species (Briffa et al. 1998, Lloyd and Fastie 2002, D'Arrigo et al. 2004, D'Arrigo et al. 2008). This switch in growth response to temperature is known as the divergence problem in tree ring studies. One postulated cause for the divergence from earlier relationships between summer temperatures and tree growth is increased drought stress: for example, in the Sierra Nevada of California, increased mortality of fir and pine trees between 1980 and 2004 correlated with increasing temperatures, but no compensating increase in precipitation (van Mantgem and Stephenson 2007). Other possible explanations for the divergence problem are shorter growing seasons caused by increased snowfall and therefore later snowmelt (Vaganov et al. 1999) (although earlier snowmelts in warm years can

also reduce forest carbon sequestration (Monson et al. 2002)), decreasing stratospheric ozone levels or changes in solar intensity (Briffa et al. 2004, D'Arrigo et al. 2008). Another potential explanation is that summer temperatures are now exceeding the thermal optimum for growth. D'Arrigo et al. (2004) found that the switch in growth response for white spruce (*Picea glauca* (Moench) Voss) correlated with a threshold summer temperature of 7.8 °C, with recent summers regularly exceeding this temperature. If such thresholds are common, rising temperatures may stimulate growth below the thermal optimum but lead to reduced growth as temperatures continue to rise.

While growth at high latitudes or altitudes may be temperature-limited and thus show at least an initial positive response to warming, trees from warmer climates are less likely to benefit from increasing temperatures. In the tropics, tree growth across a wide range of species shows a negative correlation with minimum daily temperatures (Clark et al. 2003, 2010, Feeley et al. 2007). Other studies have indicated that tropical tree species may be near a high temperature threshold for photosynthesis that, if exceeded, will greatly reduce CO<sub>2</sub> assimilation and thereby growth (Doughty and Goulden 2008). Taken together, these findings suggest that trees from colder environments may benefit from some degree of climate warming, but species from warmer environments will not (Figure 1). We would also expect greater variation in the response of high latitude and altitude trees to a given temperature increase than we do for tropical or warm-adapted species. Trees from cold environments may show either large positive or negative growth responses to warming depending on both inherent acclimation potential and other potentially limiting factors (such as water and nutrients), but trees from warm locales may not benefit from increased temperatures, even if conditions are otherwise ideal (Figure 1).

Different functional types often differ in the strength of their response to environmental changes. For example, in re-

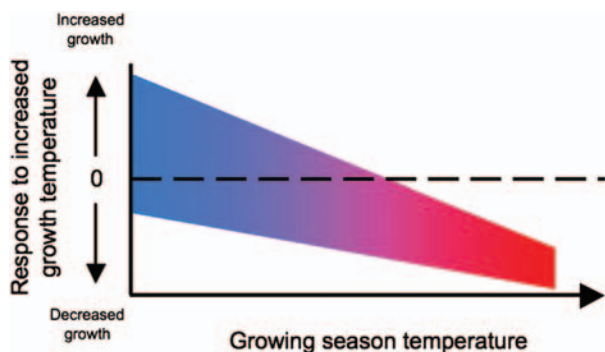


Figure 1. Hypothetical response of trees from different thermal environments to an increase in growth temperature. The colored region indicates the range of responses possible. Species from colder environments (in blue) would generally show a positive growth response to warming but could show reduced growth if water or nutrients were limiting. Species from warmer environments (in red) would always experience decreased growth, with less variation between individuals or species.

sponse to elevated CO<sub>2</sub>, woody plants show less acclimation of stomatal conductance than crops or grasses, and light-saturated photosynthetic rates are stimulated more strongly in trees than in other functional groups (Ainsworth and Rogers 2007). Within trees, stomatal conductance in evergreen conifers is less responsive to elevated CO<sub>2</sub> than in broad-leaved trees (Medlyn et al. 2001). Similarly, there is also the possibility that different functional groups will show different growth responses to climate warming. In a provenance trial estimating the growth response of 10 temperate forest trees to a 4 °C temperature increase, two of five deciduous, broad-leaved species showed a positive response to warming, none of the evergreen conifers did and neither did the sole deciduous conifer (Carter 1996). In contrast, thermal acclimation of respiration in seedlings was weaker in broad-leaved boreal species than in conifers (Tjoelker et al. 1999). While there are still too few studies regarding how functional groups respond to growth temperature, Campbell et al. (2007) found no difference in the level of thermal acclimation for either photosynthesis or respiration between grasses, forbs and woody plants. Indeed, Saxe et al. (2001) concluded that tree responses to warming would likely fall out along fine-scale divisions, such as species or provenance, rather than at broader functional categorizations, but this supposition was based on results from only two studies.

To address whether the response to a change in growth temperature varies between trees from different thermal environments or functional groups, we can use data from multiple types of studies, all of which have inherent strengths and weaknesses. While providing the most realistic scenario, establishing how natural inter-annual variation in temperature affects growth is complicated by the many factors that covary with temperature in the field: air vapor pressure deficit (VPD) increases exponentially with a linear increase in temperature, and drier summers are often associated with higher VPDs (Oishi et al., 2010). Field chamber studies around intact trees provide data on how tree growth responds to a change in temperature with natural seasonal fluctuations in light and moisture, but these are usually established on trees that have already grown at common conditions (which may limit the ability to respond to the new temperature) or on small individuals that may not be generalizable to large trees. Chamber and greenhouse studies in pots allow for more controlled and extreme changes in growth temperature but are limited by space to seedlings and saplings.

Here, we synthesize existing data from field, greenhouse and chamber studies to determine how an imposed change in temperature affects tree growth. Although most current research focuses on the effects of warming, there is a long history of studies examining how changes in temperature (both increases and decreases) affect tree growth (Hellmers and Sundahl 1959, Brix 1971). We therefore sought to develop general relationships between a change in temperature and tree growth because this larger data set increases our ability to detect trends of thermal acclimation beyond what is possible with the smaller set of studies where temperatures are ele-

vated. However, to ensure that our results also accurately represent the effects of warming on tree growth, we repeat our analysis using only data where growth temperatures were increased and compare results from both approaches. Lastly, we discuss our results and compare them with those from tree ring and provenance studies where natural variation in temperature alters tree growth. The specific goals of this review are to: (i) characterize how a change in growth temperature affects growth, biomass allocation and physiological characteristics in trees; (ii) assess how well the relationship between growth and a change in temperature represents the growth response to warming; (iii) determine whether cold-adapted trees show a more positive response to increasing growth temperatures than warm-adapted trees (as in Figure 1); (iv) examine whether different functional groups (such as deciduous and evergreen species) vary in their responsiveness to a change in growth temperature; (v) link physiological changes to growth temperature with larger scale growth patterns; and (vi) identify key research areas where more information is needed.

### Experimental changes in growth temperature—a synthesis

#### Methods

*Effects on growth, photosynthesis and respiration* To investigate how temperature affects tree growth, we analyzed the results of studies where a change of temperature was imposed experimentally. We searched the Institute for Scientific Information (ISI) Web of Science for studies that imposed a growth temperature treatment on a tree species and then measured biomass, anatomical, hydraulic, photosynthetic or respiratory changes. For photosynthetic variables ( $V_{\text{cmax}}$ , the maximum rate of carboxylation of Rubisco, and  $J_{\text{max}}$ , the maximum rate of electron transport), we also used studies where temperature varied seasonally in the field due to the low number of studies meeting our requirements. Because the ability to acclimate respiration to temperature varies between new and pre-existing leaves (Campbell et al. 2007), the respiration data set was constrained to studies where the growth temperature change was imposed experimentally and measured leaves developed at the new growth temperature.

For studies that explicitly grew trees at a temperature representative of their current range and then imposed a change, we used the native temperature as the control treatment. For all other studies, we chose one of the growth treatments as the control. Because temperatures and water availability in June are often conducive to growth, we used June temperatures for field sites (for field experiments) or for seed source locations (for pot experiments) as the basis for assigning control temperatures where needed. Online databases for climate norms were used to find average June maximum and minimum temperatures (December temperatures for Southern Hemisphere sites and species) to represent typical day and night temperatures for each species in each study. For field studies, measurements from unwarmed plots were used as

controls; for pot studies, the temperature treatment closest to the species' native June maximum/minimum temperatures was used as the control. All other growth temperatures were designated as treatments for comparison.

The response to a change in growth temperature for each variable (e.g., height or biomass) was calculated by dividing the treatment value by the control value. A response of 1 indicates no change between different growth temperatures, a response  $<1$  means that the change in temperature reduced the measured variable relative to the control, and a response  $>1$  means that the variable was increased compared with the control treatment.

To determine how a change in growth temperature altered tree growth and physiology, we ran general linear models (GLMs) with each growth and physiological variable (e.g., shoot height, biomass,  $V_{\text{cmax}}$ ) as the dependent variable. We included explanatory variables from three broad categories: (1) changes in growth temperature; (2) experimental conditions; and (3) species and species range traits. In category 1, we included changes in day and night temperature (both continuous variables) and the interaction between them. The second category provided information on whether differences in experimental methods affected how a change in temperature alters growth. We considered (i) air moisture control (categorical variable: no control, constant relative humidity or constant VPD) since VPD increases with rising temperature and also affects stomatal conductance and transpiration; (ii) pot versus field studies (categorical variable), since pot size has been found to be a significant factor in the response of elevated  $\text{CO}_2$  studies (Curtis and Wang 1998) and field studies usually expose trees to greater diurnal and seasonal variability in light, precipitation and other environmental factors than chamber experiments; and (iii) experiment length in days (continuous variable) to assess whether short-term experiments produce similar results to long-term studies. The third category addressed whether species from different groups and thermal niches have similar responses to a change in growth temperature. We considered: (i) whether the species was a conifer or an angiosperm (categorical variable), a division reflecting deep evolutionary differences in anatomy and physiology; (ii) whether the species was evergreen or deciduous (categorical variable), reflecting differences in life history strategy that span both conifers and broad-leaved trees (see review in Givnish 2002); (iii) June day temperature (continuous variable) as a fine-scale indicator of growing season temperature and, therefore, thermal niche; and (iv) biome (categorical variable: boreal, temperate or tropical/subtropical) as a broader categorization of thermal niche. Differences in the response of each dependent variable to these explanatory variables are presented in Tables 2 and 4; significant  $P$  values indicate a significant difference between groups within that explanatory variable.

For figures where an explanatory variable significantly affected the growth response to temperature (as determined by the GLMs), we present regressions to provide an overall response to changes in tree growth with changing temperature.

Table 1. Breakdown of the number of data points (contrasts) and studies for analysis based on leaf type, pot vs field study and air moisture control (none, constant relative humidity (RH) or constant vapor pressure deficit (VPD)). Note that there were 63 studies used, but five examined both deciduous and evergreen species.

	Broad-leaf	Conifer	Pot	Field	No control	Constant RH	Constant VPD	Total
<b>Contrasts</b>								
Deciduous	110	10	87	33	55	19	46	120
Evergreen	118	196	273	41	186	34	94	314
<b>Studies</b>								
Deciduous	22	3	14	10	14	4	6	25
Evergreen	9	34	26	17	25	4	14	43

We selected the most parsimonious regressions to describe the relationship between temperature and growth based on three criteria: (i) confirming that there was no pattern to the residuals; (ii) ensuring that the regression was statistically significant (using an ANOVA); and (iii) when linear, polynomial and exponential functions equally met the first two criteria, choosing the function with the highest  $r^2$  and lowest root mean square error. Where there was no significant effect of either day or night temperature on a growth variable, we present the mean value and indicate whether it is significantly different than 1. Statistics were performed using JMP (v 7.0.1; SAS, Cary, NC).

**Ontogenetic trajectories** We also determined whether the trajectory of tree growth was altered by growth temperature or whether growth was simply accelerated along the same trajectory as control trees. We used data from two groups: control trees grown at their native temperature conditions and warmed trees where the day temperature was increased by at least 3 °C and the night temperature either was not altered or was increased above the control temperature. Because most of the field studies were initiated on older trees that had already accumulated significant biomass that might obscure shifts in allometry, we excluded field studies from this analysis. To determine whether warmed trees followed a significantly different developmental trajectory than control trees, we first tested whether stem, root or leaf mass and their ratios changed by running GLMs with leaf, stem and root mass as the dependent variables and group (categorical variable: control or warmed), total biomass (continuous variable) and the interaction between group and total biomass as the dependent variables; biomass variables were log-transformed where necessary. We also looked at changes in stem allometry by running GLMs with either stem mass or shoot height as the dependent variable and group (categorical variable: control or warmed), stem diameter (continuous variable) and the interaction between group and stem diameter as dependent variables. Analyses were performed using JMP (v 7.0.1).

## Results

**Effects on growth, photosynthesis and respiration** Our analysis consisted of 434 contrasts from 63 studies, spanning 58

tree species. The breakdown of leaf types, pot versus field, and humidity control across the data point contrasts and studies are listed in Table 1. Results are presented as box plots for data binned into 5 °C bins (with the median, 10th, 25th, 75th and 90th percentiles), while the regression lines were fitted to the continuous (non-binned) data and are thus slightly offset from the boxplot data (e.g., Figure 2). We fit regression lines to a maximum of a 13 °C increase in growth temperature because no climate models that we are aware of predict increases above this and because we had few points above this temperature. While there was considerable variation in the growth response of trees to changes in temperature (Figure 2), these regressions allow us to evaluate overall cross-species and cross-study trends and to provide estimates of tree growth for modeling exercises across large spatial scales.

Within the first category of explanatory variables (temperature change), we found that growth was suppressed by temperatures below normal but often enhanced by increasing growth temperatures by up to approximately 13 °C, with many growth variables responding exponentially across the range of temperatures (Figure 2). There are few data on growth temperatures above 13 °C, but growth was usually reduced at these high temperatures. Some variables responded more strongly to daytime growth temperature (such as height), while other variables (such as stem diameter) were better explained by nocturnal temperatures; results are plotted against the temperature that best explained the variable in the analysis (Table 2).

The second category of variable addressed experimental design issues between studies. In general, the same response was seen whether a tree was grown in a pot or in the field and regardless of the duration of the experiment, indicating that differences in these experimental factors had little effect on the results (Table 2). While the level of humidity control in the experiment significantly contributed to the response of tree height, stem diameter and some mass measurements (Table 2), we found no generalized trends between studies that maintained a constant relative humidity or VPD and those that did not.

Within the third category of variables were differences in functional group and thermal niche. We used the native June temperature of the tree to determine if high latitude or altitude trees showed a different response than trees from warmer environments, but this was not a significant predictor of how



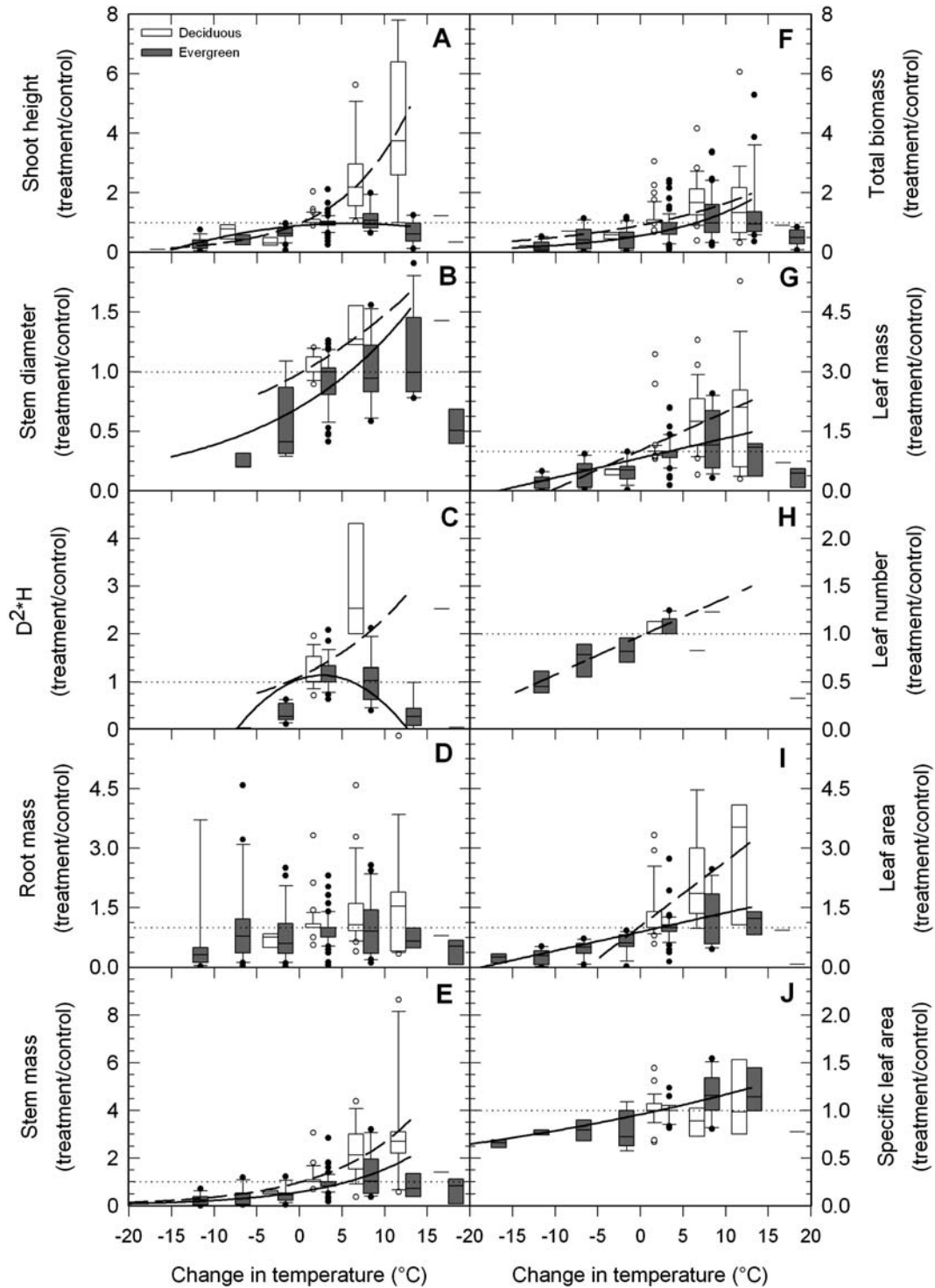


Figure 2. Increasing growth temperatures increase tree growth more strongly in deciduous (open symbols, dashed lines) than evergreen species (filled symbols, solid lines). The response of (A) shoot height; (B) stem diameter; (C) diameter<sup>2</sup> × height ( $D^2H$ ); (D) root mass; (E) stem mass; (F) biomass; (G) leaf mass; (H) leaf number; (I) leaf area and (J) specific leaf area to changes in growth temperature. Shoot height,  $D^2H$ , stem mass and all leaf variables are plotted against day temperature changes; stem diameter, root mass and total biomass against night temperature changes. Graphs are box plots for data binned into 5 °C bins (showing median, 10th, 25th, 75th and 90th percentiles); regressions lines are fit to the raw (non-binned) data and are thus offset from the box plots. Details of all regression lines are in Table 3.

Table 2. Results of a least-squares model of the response of growth variables against growth temperature changes, species traits and experimental design. Bold indicates  $P < 0.05$ . Tday, change in day temperature from control; Tnight, change in night temperature from control; Evergreen, evergreen or deciduous; Conifer, conifer or broad-leaf; June temp, June day temperature; Biome, boreal, temperate or tropical; Pot, pot or field experiment; Water, humidity control; Expt length, experiment length; SLA, specific leaf area;  $R:S$ , root-to-shoot ratio;  $D^2H$ , stem diameter squared times height;  $D/H$ , stem diameter divided by height; LA/stem area, leaf area divided by stem area;  $V_{\text{cmax}}$ , maximum carboxylation rate of Rubisco;  $J_{\text{max}}$ , maximum electron transport rate;  $R_{\text{dark}}$ , dark respiration rate;  $T_{\text{common}}$ , common measurement temperature;  $T_{\text{leaf}}$ , measured at leaf temperature.

	Tday	Tnight	Tday × Tnight	Evergreen	Conifer	June temp	Biome	Pot	Water	Expt length	$R^2$	$n$
Height	<b>&lt;0.0001</b>	<b>0.0038</b>	0.23	<b>&lt;0.0002</b>	0.64	0.45	0.53	<b>0.004</b>	<b>0.001</b>	0.13	0.45	212
Stem diameter	0.67	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.026</b>	0.44	0.14	<b>0.043</b>	0.27	<b>0.0012</b>	0.47	0.55	116
Leaf area	<b>0.035</b>	<b>0.033</b>	0.66	0.37	<b>0.0004</b>	0.31	<b>&lt;0.0001</b>	0.053	<b>0.0033</b>	<b>0.012</b>	0.56	147
Leaf number	0.16	0.51	<b>0.0038</b>	0.59	–	0.62	0.51	0.57	0.85	0.57	0.53	39
SLA	0.12	0.25	0.094	0.085	0.13	0.78	0.29	0.91	0.054	0.38	0.32	105
Total mass	<b>0.0106</b>	<b>&lt;0.0001</b>	<b>0.0044</b>	<b>&lt;0.0001</b>	0.078	<b>0.036</b>	<b>&lt;0.0001</b>	0.33	0.12	0.48	0.33	307
Leaf mass	<b>0.0004</b>	0.72	<b>0.0003</b>	<b>0.0025</b>	0.18	0.12	<b>0.0085</b>	<b>0.049</b>	0.20	0.35	0.41	192
Stem mass	<b>0.0017</b>	0.29	0.13	<b>0.013</b>	<b>0.0027</b>	0.81	0.20	0.11	0.61	0.10	0.42	179
Shoot mass	0.58	<b>&lt;0.0001</b>	<b>0.0001</b>	<b>0.022</b>	0.088	0.21	<b>0.0015</b>	<b>0.032</b>	<b>0.30</b>	0.14	0.40	237
Root mass	0.43	<b>0.055</b>	0.63	0.10	0.66	0.72	0.36	0.96	0.46	0.98	0.08	224
$R:S$	0.11	<b>0.0046</b>	<b>&lt;0.0001</b>	0.18	<b>0.003</b>	0.35	0.23	0.18	0.058	0.35	0.24	30
$D^2H$	0.11	0.46	<b>0.0026</b>	<b>0.046</b>	0.68	0.54	<b>0.011</b>	0.18	<b>0.012</b>	0.36	0.49	80
$D/H$	0.10	0.52	<b>0.0002</b>	0.053	0.90	0.81	<b>0.03</b>	0.16	<b>0.012</b>	0.30	0.49	80
LA/stem area	0.48	–	<b>0.023</b>	0.31	0.064	0.22	0.063	0.11	<b>0.033</b>	0.093	0.54	30
$V_{\text{cmax}}$ at 25 °C	0.25			0.47	0.79	0.66	0.66	0.71	0.70		0.26	22
$J_{\text{max}}$ at 25 °C	0.86			0.26	0.87	0.94	0.38	0.62	0.75		0.39	22
$R_{\text{dark}}$ at $T_{\text{common}}$	<b>0.021</b>			0.94	0.39	0.93	0.97	0.56	0.90		0.62	22
$V_{\text{cmax}}$ at $T_{\text{leaf}}$	<b>0.0048</b>			0.32	0.13	0.37	0.54	0.65	0.25		0.91	17
$J_{\text{max}}$ at $T_{\text{leaf}}$	<b>0.030</b>			0.38	<b>0.017</b>	0.86	0.25	0.94	0.76		0.98	15
$R_{\text{dark}}$ at $T_{\text{leaf}}$	<b>0.0003</b>			0.55	0.16	<b>&lt;0.0001</b>	0.20	0.18	0.76		0.88	23

growth changed (Table 2). In contrast, when trees were grouped by biome (boreal, representing high latitude and altitude species; temperate; and tropical/subtropical species), there were significant differences between these groups in many growth variables (discussed below). While there were some differences in growth response to temperature between conifers and angiosperms, there were far more significant differences in growth between evergreen and deciduous species. Evergreen species showed a more conservative response to changes in temperature than did deciduous species across all indications of growth and biomass accumulation (Table 2, Figure 2), but one of the most pronounced differences was shoot height growth (Figure 2A). An increase in growth temperature of 5 °C did not alter the median height of evergreens, but temperatures above this led to decreased shoot height growth; in contrast, the response of deciduous tree height to increasing growth temperatures was best fitted by an exponential response, with height growth increased by as much as eightfold for a 10 °C warming. The median values for height, stem diameter and all biomass measurements at elevated growth temperatures were always near 1 for evergreens, indicating that for every study that found increased growth with warming, there were a similar number that found a decrease (Figure 2A, B and F).

While growth in height, stem diameter and biomass are all indications of tree growth, they did not show the same degree of response to changes in growth temperature within a functional group (Figure 2). Using the regressions for deciduous

species as an example (from Table 3), a 10 °C increase in growth temperature resulted in an average 3.4-fold increase in shoot height growth, a 1.5-fold increase in stem diameter growth, a 2.3-fold increase in stem volume (as indicated by diameter<sup>2</sup> × height) and a 1.7-fold increase in total biomass (Figure 2A–C and F). Stem mass growth was more responsive than stem diameter to warming, increasing 2.7-fold in deciduous trees for a 10 °C rise in growth temperature (Figure 2E), which correlates well with the increase in stem volume. The response of the ratio of diameter to height (indicating taper) was also significantly lower in evergreen than deciduous trees (Table 2). Root mass growth was not significantly correlated with either day or night temperature changes (Table 2, Figure 2D). Both leaf mass and leaf area were less stimulated by increasing temperatures in evergreen than deciduous trees (Figure 2G and I). Leaf mass and area growth both increased linearly with rising day growth temperatures up to ~13 °C above the control growth temperature. Although there were few data, leaf number also increased as growth temperatures warmed (Figure 2H). There was no evidence for a change in the specific leaf area (SLA) of deciduous species, but evergreen trees showed an increase in SLA with warmer day temperatures (Figure 2J).

The lack of a change in root mass, taken with the increased leaf and stem mass results, corroborate the decline in the root-to-shoot ratio with increasing growth temperature (Figure 3). Unlike the height and biomass responses, the root-to-shoot pattern was better explained by the difference between

Table 3. Regression coefficients for relationships of growth variables versus a change in growth temperature (to a maximum of +13 °C). Equations are in the form: exponential (exp):  $\log(y) = a + bx$ ; polynomial (poly):  $y = a + bx + cx^2$ ; linear:  $y = a + bx$ , where  $x$  = change in temperature (Temp, D = day, N = night); mean indicates there was no significant temperature effect, and gives the mean value and whether that value is different than 1. Line: Dec, deciduous; Ever, evergreen; All, all trees; Broad, broad-leaf; Temp, temperate; Trop, tropical. Means  $\pm$  SE. NS, nonsignificant.

Variable	Figure	Line	Type	Temp	$a$	$b$	$c$	$R^2$	$P$
Shoot height	2A	Dec	Exp	D	$-0.031 \pm 0.061$	$0.12 \pm 0.011$		0.66	<0.0001
	2A	Ever	Poly	D	$0.91 \pm 0.031$	$0.034 \pm 0.0040$	$-0.0016 \pm 0.0004$	0.44	<0.0001
Stem diameter	2B	Dec	Exp	N	$-0.011 \pm 0.033$	$0.040 \pm 0.0096$		0.54	0.0008
	2B	Ever	Exp	N	$-0.35 \pm 0.042$	$0.060 \pm 0.0071$		0.44	<0.0001
$D^2H$	2C	Dec	Exp	N	$-0.034 \pm 0.10$	$0.14 \pm 0.029$		0.61	0.0002
	2C	Ever	Poly	N	$1.11 \pm 0.064$	$0.030 \pm 0.0097$	$-0.012 \pm 0.0018$	0.51	<0.0001
Root mass	2D	All	Mean	N	$1.05 \pm 0.066$				NS
Stem mass	2E	Dec	Exp	D	$-0.0089 \pm 0.071$	$0.099 \pm 0.012$		0.53	<0.0001
	2E	Ever	Exp	D	$-0.48 \pm 0.078$	$0.11 \pm 0.013$		0.40	<0.0001
Total mass	2F	Dec	Exp	N	$-0.089 \pm 0.062$	$0.059 \pm 0.010$		0.28	<0.0001
	2F	Ever	Exp	N	$-0.57 \pm 0.057$	$0.090 \pm 0.0090$		0.34	<0.0001
Leaf mass	2G	Dec	Linear	D	$1.02 \pm 0.12$	$0.097 \pm 0.019$		0.25	<0.0001
	2G	Ever	Linear	D	$0.86 \pm 0.036$	$0.056 \pm 0.0059$		0.45	<0.0001
Leaf #	2H	All	Linear	D	$1.01 \pm 0.033$	$0.047 \pm 0.0057$		0.65	<0.0001
Leaf area	2I	Dec	Linear	D	$1.05 \pm 0.18$	$0.16 \pm 0.036$		0.36	<0.0001
	2I	Ever	Linear	D	$0.90 \pm 0.037$	$0.048 \pm 0.0050$		0.47	<0.0001
SLA	2J	Dec	Mean	D	$1.00 \pm 0.029$				NS
	2J	Ever	Linear	D	$-0.040 \pm 0.020$	$0.020 \pm 0.0026$		0.47	<0.0001
$R:S$	3	Broad	Linear	N	$0.98 \pm 0.021$	$-0.015 \pm 0.0032$		0.13	<0.0001
	3	Conifer	Linear	N	$1.12 \pm 0.031$	$-0.032 \pm 0.0050$		0.30	<0.0001
Total mass	4	Boreal	Linear	N	$0.90 \pm 0.088$	$0.091 \pm 0.014$		0.27	<0.0001
	4	Temp	Linear	N	$0.87 \pm 0.041$	$0.053 \pm 0.0065$		0.33	<0.0001
	4	Trop	Poly	N	$0.98 \pm 0.052$	$-0.0067 \pm 0.0087$	$-0.0064 \pm 0.0013$	0.55	<0.0001
$V_{\text{cmax}}$ at $T_{\text{growth}}$	6B	All	Linear		$0.99 \pm 0.069$	$0.082 \pm 0.011$		0.79	<0.0001
$J_{\text{max}}$ at $T_{\text{growth}}$	6D	All	Linear		$0.92 \pm 0.097$	$0.074 \pm 0.015$		0.66	0.0002
$R_{\text{dark}}$ at $T_{\text{constant}}$	6E	All	Linear		$1.04 \pm 0.079$	$-0.036 \pm 0.0084$		0.48	0.0004
$R_{\text{dark}}$ at $T_{\text{growth}}$	6F	All	Linear		$0.87 \pm 0.11$	$0.033 \pm 0.014$		0.22	0.024

conifers and broad-leaved trees than an evergreen/deciduous contrast (Table 2).

Tropical and subtropical species consistently showed reduced biomass accumulation when temperatures were increased or decreased, in contrast to the pattern for temperate and boreal species where warming often enhanced growth (Figure 4). The data set for tropical and subtropical species was small, so while we have sufficient information to see patterns in total biomass, data on other variables (such as stem diameter) were too limited to make definitive statements on.

While there were few data available, there was no consistent evidence for shifts in stomatal traits, leaf anatomy, wood anatomy or hydraulic conductance with warmer growth temperatures (Figure 5).

To evaluate what might constrain growth as growth temperatures change, we analyzed data on three important carbon balance variables: the maximum rate of carboxylation of Rubisco ( $V_{\text{cmax}}$ ), the maximum rate of electron transport ( $J_{\text{max}}$ ) and the rate of dark respiration ( $R_{\text{dark}}$ ). When measured at a common temperature of 25 °C, there was no evidence for acclimation of either  $V_{\text{cmax}}$  or  $J_{\text{max}}$ , while  $R_{\text{dark}}$  measured at a common temperature was much lower in trees grown in warm conditions (Table 2, Figure 6A, C and E). When measured

at the growth leaf temperature, both  $V_{\text{cmax}}$  and  $J_{\text{max}}$  were positively correlated with a change in growth temperature (Figure 6B and D), while  $R_{\text{dark}}$  showed a weak increase with rising growth temperatures (Figure 6F). There were no differences between evergreen and deciduous species in any of the

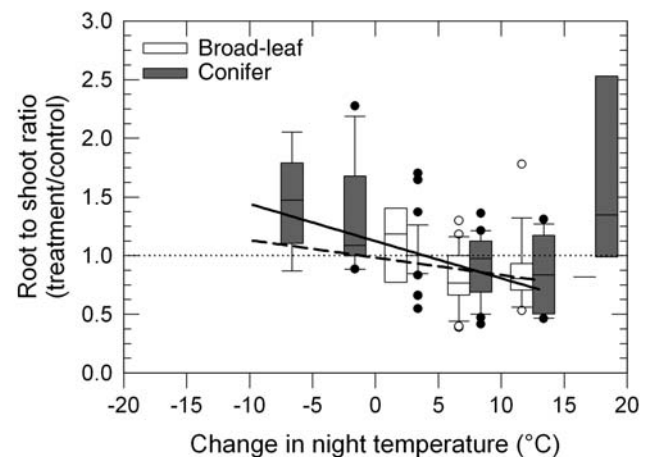


Figure 3. The root-to-shoot ratio declines with increasing night growth temperatures more strongly in conifers (filled symbols, solid line) than broad-leaved trees (open symbols, dashed line).

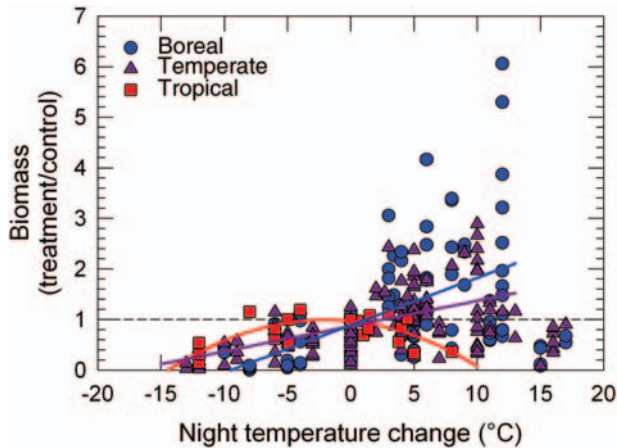


Figure 4. Biomass declines in response to increases in night growth temperature for tropical species (red squares and line) but not for boreal (blue circles and line) or temperate (purple triangles and line) species.

photosynthetic or respiration traits, and although there was a difference in the response of  $J_{\max}$  to temperature between conifers and angiosperms, there were few conifer data points (Table 2, Figure 6).

To summarize our results, we used our regressions from Table 3 and the average global temperature increase of 3.4 °C expected for the year 2100 by the Intergovernmental Panel on Climate Change (IPCC) for the A2 emissions scenario to estimate how tree growth and physiology might be affected by climate warming (Figure 7A and D). While evergreens show little change or suppressed growth, deciduous species are predicted to increase growth under these conditions (Figure 7A). Because not every variable was measured in every study, the data sets for growth variables varied in size. We thus show both the average response using equations from Table 3 (Figure 7A) and biomass responses calculated for a subset of 154 data points where all four variables were measured on the same tree (Figure 7B). While the larger data sets in Figure 7A provide more confidence in the results for a given

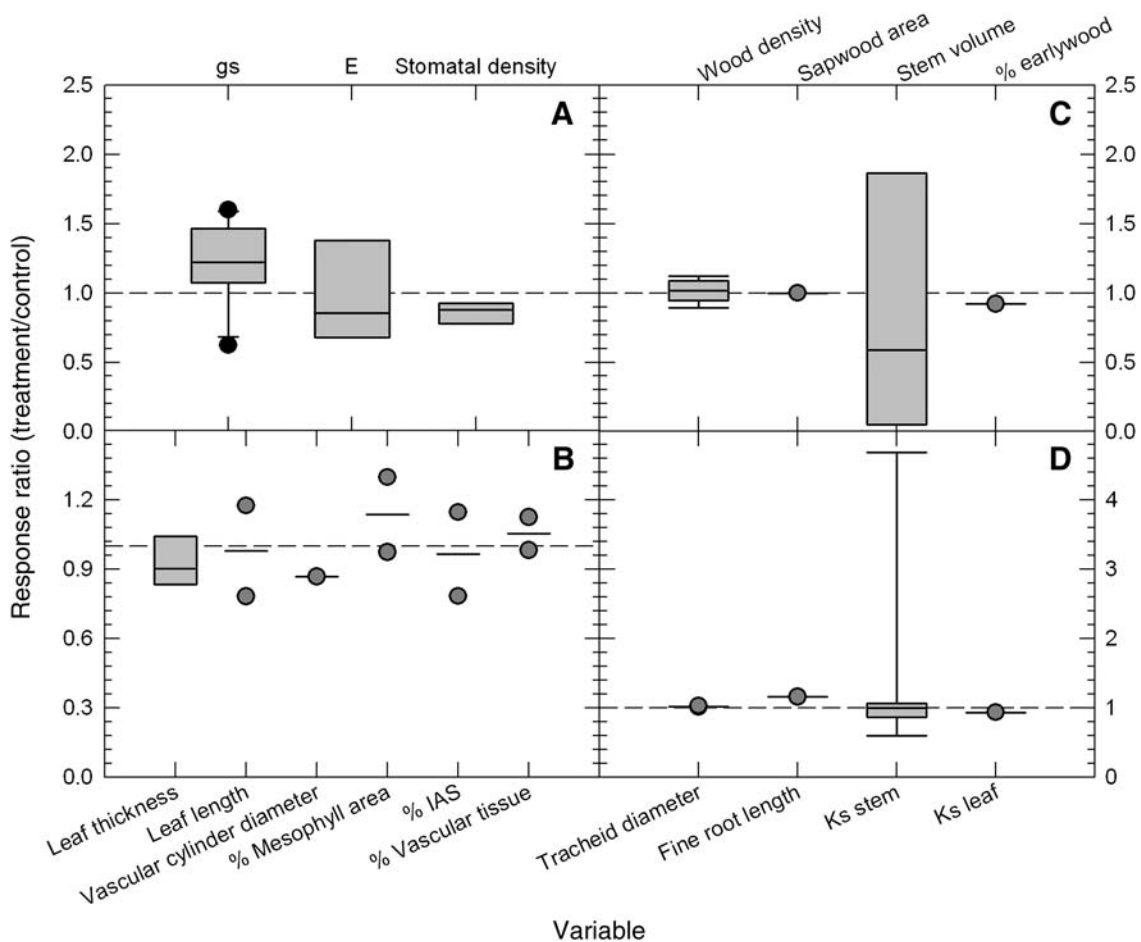


Figure 5. There is little response of (A) stomatal traits; (B) leaf anatomy; (C) wood anatomy; and (D) hydraulic characteristics to an increase in growth temperature. Graphs are box plots showing median values, 10th, 25th, 75th and 90th percentiles; gray points indicate raw values where there were <3 data points. gs, stomatal conductance; E, transpiration rate; % mesophyll area, percent of leaf cross-sectional area filled with mesophyll; % IAS, percent of leaf cross-sectional area filled with intercellular airspace; % vascular tissue, percent of leaf cross-sectional area filled with vascular tissue;  $K_s$  stem, stem specific hydraulic conductivity;  $K_s$  leaf, leaf specific hydraulic conductivity.



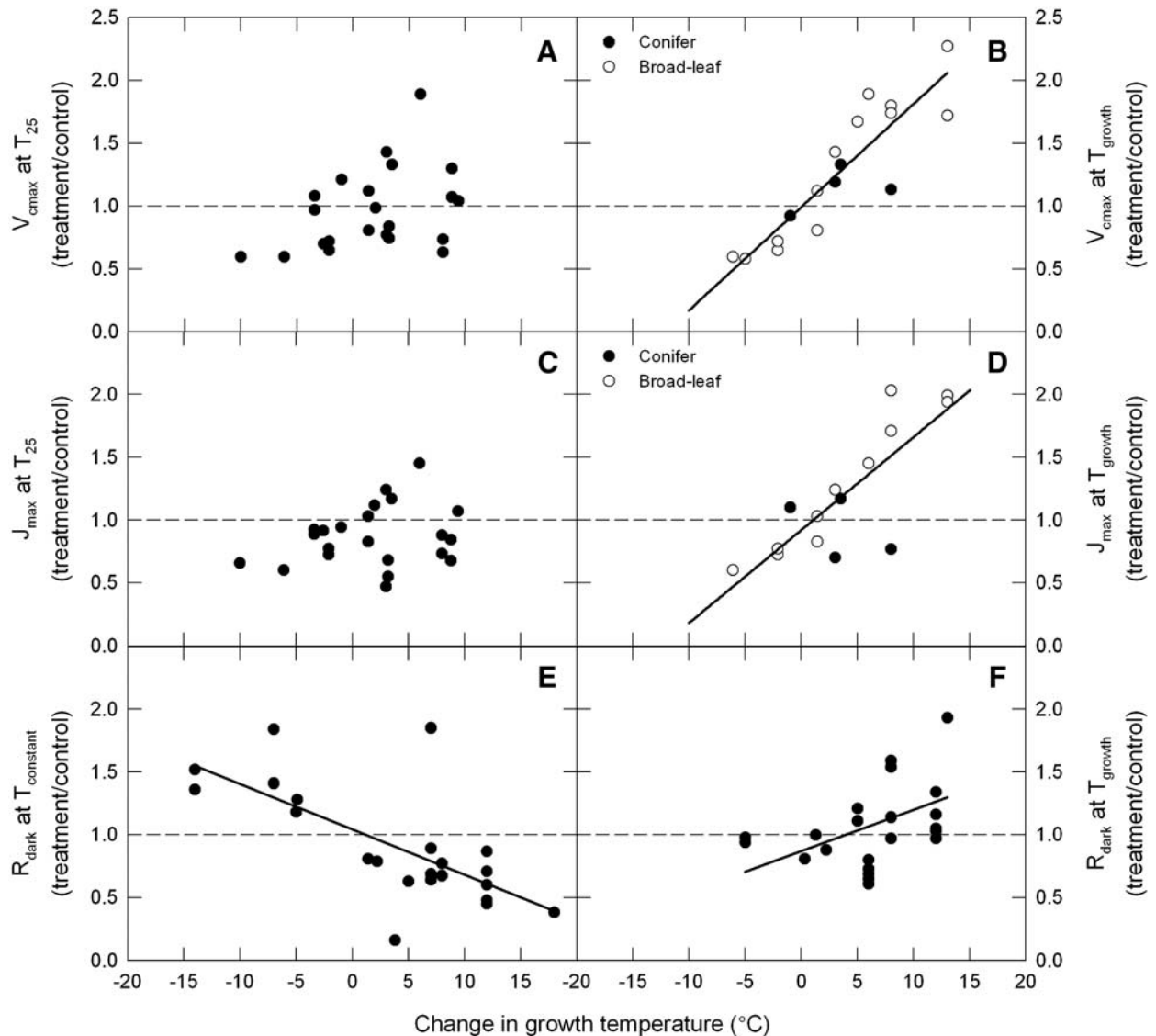


Figure 6. Across all functional types, neither  $V_{cmax}$  nor  $J_{max}$  acclimate to temperature, while  $R_{dark}$  shows strong thermal acclimation. The response of (A)  $V_{cmax}$  measured at 25 °C; (B)  $V_{cmax}$  measured at growth temperature; (C)  $J_{max}$  measured at 25 °C; (D)  $J_{max}$  measured at growth temperature; (E)  $R_{dark}$  measured at a common temperature; (F)  $R_{dark}$  measured at growth temperature to changes in growth temperature. In (B) and (D), broad-leaved species are shown as open symbols, conifer species as filled symbols, lines are fitted to entire data set.

variable, mismatches between responses in total mass and leaf, stem and root masses are due to using different data sets. Where all four variables are measured (Figure 7B), changes in total mass are paralleled by changes in the components of total mass.

Because the suppressed growth at reduced temperatures may have largely driven the exponential relationships seen for many growth variables (Table 3, Figure 2), we also analyzed the subset of data where temperatures were elevated to better estimate the effects of warming, as opposed to general changes in growth temperature, on tree growth (Tables 4 and 5, Figure 7C). Because this data set was smaller than the initial data set (compare the number of data contrasts in Tables 2 and 4), there were insufficient data to analyze some variables (leaf number,  $V_{cmax}$ ,  $J_{max}$  and  $R_{dark}$ ). In agreement with the

growth temperature change analysis, the same trends were generally seen regardless of whether the experiment was performed in a pot or in the field and regardless of the humidity control and length of the experiment. As in the temperature change analysis, evergreen species were less responsive to a change in temperature than deciduous trees (Figure 7C). However, while deciduous trees still showed a much greater growth response than evergreens to a 3.4 °C increase in temperature, evergreen species showed slight stimulations in growth rather than declines. Shoot height growth was still stimulated more strongly than stem diameter, and there was still no response of root mass to warming (Figure 7C). The total biomass of tropical species still declined with increasing growing temperatures, while temperate and boreal species generally grew larger at higher temperatures (Table 5).

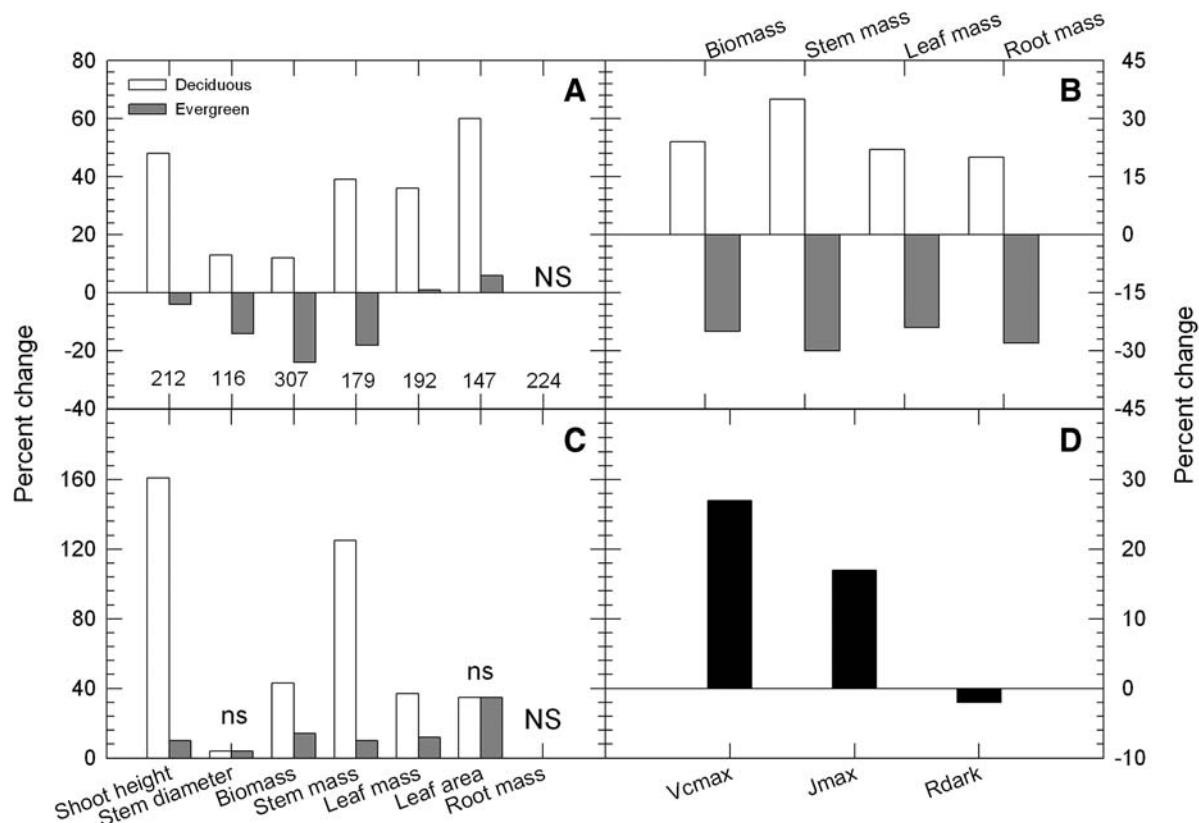


Figure 7. Deciduous tree growth is more responsive to increasing temperatures than evergreen growth. Average response of growth variables to a 3.4 °C increase in growth temperature for deciduous (open bars) and evergreen (filled bars) trees: (A) average response using equations from Table 3, with the sample size shown below the bars; (B) biomass responses calculated for a subset of 154 data points where all four variables were measured on the same tree; (C) average response using equations in Table 5, based on trees grown only at elevated temperatures; (D) photosynthetic variables for all trees. NS, no significant change with temperature; ns, no significant difference between deciduous and evergreen species, value based on regression for all trees.

**Ontogenetic trajectories** Trees grown at warm temperatures showed significantly different relationships between biomass components and total mass, providing evidence that warmer temperatures are not simply accelerating growth

along a constant trajectory (Table 6, Figures 8 and 9). Growth at elevated temperatures increased leaf biomass ( $P = 0.011$ ), did not alter stem mass allocation ( $P = 0.13$ ) and decreased allocation to roots ( $P = 0.0009$ ; Figure 8); for a 425-g seedling

Table 4. Results of a least-squares model of the response of the measured growth variable against increased growth temperatures (between 0.5 and 13 °C), leaf type and experimental type. Bold indicates  $P < 0.05$ . See Table 2 for definitions. Data sets for leaf number and the photosynthetic and respiration variables ( $V_{cmax}$ ,  $J_{max}$  and  $R_{dark}$ ) were insufficient to run the model ( $n = 10-24$ ).

	Tday	Tnight	Tday × Tnight	Evergreen	Conifer	June temp	Biome	Pot	Water	Expt length	$R^2$	$n$
Height	<b>0.02</b>	0.12	0.71	<b>0.0009</b>	0.71	0.13	0.055	<b>0.0081</b>	<b>0.0002</b>	0.23	0.50	134
Stem diameter	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.032</b>	0.19	0.87	0.43	0.33	0.13	0.090	0.28	0.54	71
Leaf area	0.26	0.92	0.18	0.39	<b>0.0019</b>	0.39	<b>0.017</b>	0.080	0.11	0.062	0.45	93
Leaf number												24
SLA	0.31	–	0.88	0.067	0.18	0.57	0.39	0.91	0.31	0.78	0.13	84
Total mass	0.25	<b>0.0002</b>	0.81	<b>0.0003</b>	0.27	<b>0.0022</b>	<b>&lt;0.0001</b>	0.87	0.19	0.69	0.29	182
Leaf mass	<b>0.003</b>	0.16	0.099	<b>0.0035</b>	0.56	<b>0.013</b>	<b>0.001</b>	0.23	0.11	0.99	0.35	132
Stem mass	<b>0.037</b>	0.57	0.51	0.056	<b>0.021</b>	0.39	0.27	0.45	0.47	0.50	0.39	119
Shoot mass	0.92	<b>0.015</b>	0.31	<b>0.0073</b>	0.22	<b>0.021</b>	<b>&lt;0.0001</b>	0.12	0.20	0.35	0.32	151
Root mass	0.79	0.17	0.66	<b>0.0002</b>	0.57	<b>0.0036</b>	<b>0.0033</b>	0.61	<b>0.029</b>	0.40	0.25	141
$R:S$	0.78	0.23	<b>0.019</b>	0.79	<b>0.021</b>	0.42	0.14	0.11	0.25	0.48	0.14	156
$D^2H$	0.14	<b>0.0017</b>	<b>0.043</b>	0.28	0.56	0.52	0.078	0.19	0.13	0.27	0.46	61
$D/H$	0.071	<b>0.0019</b>	0.081	0.37	0.31	0.74	0.18	0.17	0.16	0.23	0.46	61
LA/stem area	0.39	–	0.89	0.40	0.076	0.27	0.075	0.13	0.053	0.11	0.44	27

Table 5. Regression coefficients for relationships of growth variables versus an increase in growth temperature (between 0.5 and 13 °C). See Table 3 for definitions. Means  $\pm$  SE.

Variable	Figure	Line	Type	Temp	<i>a</i>	<i>b</i>	<i>c</i>	<i>R</i> <sup>2</sup>	<i>P</i>
Shoot height	2A	Dec	Exp	D	0.028 $\pm$ 0.078	0.11 $\pm$ 0.014		0.54	<0.0001
	2A	Ever	Poly	D	1.08 $\pm$ 0.046	0.014 $\pm$ 0.012	-0.0067 $\pm$ 0.0027	0.08	0.041
Stem diameter	2B	All	Linear	N	0.97 $\pm$ 0.027	0.019 $\pm$ 0.0056		0.14	0.0012
	2C	All	Poly	N	1.07 $\pm$ 0.096	0.11 $\pm$ 0.030	-0.020 $\pm$ 0.0060	0.21	0.0012
Root mass	2D	All	Mean	N	1.18 $\pm$ 0.061				NS
Stem mass	2E	Dec	Exp	D	0.047 $\pm$ 0.091	0.090 $\pm$ 0.016		0.39	<0.0001
	2E	Ever	Mean	D	1.10 $\pm$ 0.068				NS
Total mass	2F	Dec	Poly	N	1.18 $\pm$ 0.14	0.083 $\pm$ 0.023	-0.0081 $\pm$ 0.0065	0.14	0.0025
	2F	Ever	Poly	N	0.98 $\pm$ 0.070	0.052 $\pm$ 0.016	-0.0047 $\pm$ 0.0035	0.11	0.0048
Leaf mass	2G	Dec	Linear	D	1.06 $\pm$ 0.15	0.091 $\pm$ 0.025		0.16	0.0006
	2G	Ever	Linear	D	1.01 $\pm$ 0.072	0.033 $\pm$ 0.015		0.08	0.029
Leaf #	2H	All	Linear	D	0.97 $\pm$ 0.055	0.058 $\pm$ 0.015		0.39	0.0012
Leaf area	2I	All	Mean	D	1.35 $\pm$ 0.079				0.041
SLA	2J	All	Mean	D	1.03 $\pm$ 0.020				NS
<i>R</i> : <i>S</i>	3	All	Mean	N	0.93 $\pm$ 0.017				NS
Total mass	4	Boreal	Linear	N	1.01 $\pm$ 0.13	0.077 $\pm$ 0.022		0.14	0.0008
	4	Temp	Linear	N	1.07 $\pm$ 0.079	0.038 $\pm$ 0.014		0.09	0.0064
	4	Trop	Linear	N	1.01 $\pm$ 0.0052	-0.072 $\pm$ 0.018		0.51	0.0014
<i>V</i> <sub>max</sub> at <i>T</i> <sub>growth</sub>	6B	All	Linear		1.04 $\pm$ 0.16	0.077 $\pm$ 0.022		0.56	0.0052
<i>J</i> <sub>max</sub> at <i>T</i> <sub>growth</sub>	6D	All	Linear		0.78 $\pm$ 0.19	0.092 $\pm$ 0.026		0.58	0.0063
<i>R</i> <sub>dark</sub> at <i>T</i> <sub>constant</sub>	6E	All	Mean		0.71 $\pm$ 0.090				NS
<i>R</i> <sub>dark</sub> at <i>T</i> <sub>growth</sub>	6F	All	Linear		0.69 $\pm$ 0.16	0.054 $\pm$ 0.019		0.30	0.0097

Table 6. Regression coefficients for ontogenetic relationships of growth variables (Figures 8 and 9). Equations are in the form: log–log: log(*y*) = *a* + *b*\*log(*x*); linear: *y* = *a* + *b**x*. Means  $\pm$  SE. NS, not significant.

Variable	Figure	Line	Type	<i>a</i>	<i>b</i>	<i>R</i> <sup>2</sup>	<i>P</i>
Leaf mass	8A	Control	Log–log	-0.29 $\pm$ 0.022	0.96 $\pm$ 0.019	0.99	<0.0001
	8A	Warmed	Log–log	-0.30 $\pm$ 0.012	1.02 $\pm$ 0.011	0.99	<0.0001
Stem mass	8B	All trees	Log–log	-0.85 $\pm$ 0.028	1.10 $\pm$ 0.023	0.98	<0.0001
	Root mass	8C	Control	Log–log	-0.52 $\pm$ 0.024	0.98 $\pm$ 0.020	0.99
8C		Warmed	Log–log	-0.61 $\pm$ 0.021	0.96 $\pm$ 0.021	0.98	<0.0001
Shoot height	9A	Control	Linear	8.71 $\pm$ 4.72	4.16 $\pm$ 0.77	0.81	0.001
	9A	Warmed	Linear	-0.033 $\pm$ 2.48	6.52 $\pm$ 0.46	0.90	<0.0001
Stem mass	9B	All trees	Linear	-11.31 $\pm$ 4.37	4.48 $\pm$ 0.50	0.90	<0.0001

(the mean mass of the largest control and warmed data points), growth at elevated temperatures would increase leaf mass by 40% and decrease root mass by 30% compared with a control seedling (Table 6). Trees from higher temperatures also grew taller for a given stem diameter than control trees ( $P = 0.016$ ; Figure 9A), although both control and warmed trees added a similar amount of stem mass for a given increase in stem height ( $P = 0.57$ ; Figure 9B), indicating that wood density was not greatly affected (also see Figure 5C). The relationship between shoot height and biomass accumulation was not significantly different between warmed and control trees ( $P = 0.37$ ).

#### Scope of inference: inter- versus intraspecific responses

As in meta-analyses of growth responses to elevated CO<sub>2</sub> and ozone (Curtis and Wang 1998, Ainsworth and Long 2005, Ainsworth and Rogers 2007, Leakey et al. 2009, Wittig et

al. 2009), our goal was to evaluate broad trends in tree growth that hold across species and sites while acknowledging the large variability between studies. However, where there are no existing data for a species, the equations we generated could be used to estimate growth responses for a particular temperature change scenario. To determine how valid our regressions are for specific cases requires knowing whether a given species: (i) has a predictable response to a change in temperature; and (ii) has a similar shape of temperature response to that predicted by our general equations. There were only six species with multiple, independent studies examining temperature–growth relationships: all of these were evergreen conifers and only one species (Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco)) had more than three studies, severely limiting our ability to answer these questions. To address the first question, we looked at biomass and shoot height patterns in three studies of black spruce (*Picea mariana* (Mill.) B.S.P.) grown from seed at similar

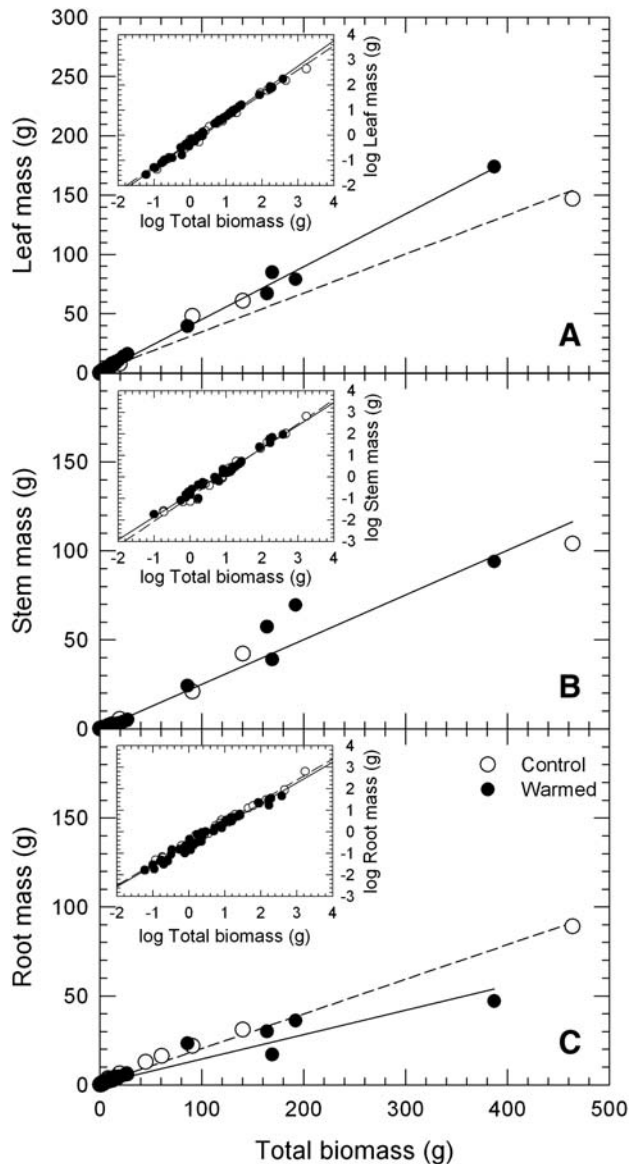


Figure 8. Trees grown at elevated growth temperatures follow different developmental trajectories than control trees. Changes in (A) leaf mass, (B) stem mass and (C) root mass in relation to total biomass between trees grown at control temperatures (open symbols) or elevated temperatures (warmed; filled symbols). (A) and (C) Dashed line, control trees; solid line, warmed trees; (B) solid line, all trees.

day and night temperature combinations (Tjoelker et al. 1998, Way and Sage 2008a, 2008b) and predicted changes in these variables using both the general temperature and the warming-only regressions (Tables 3 and 5). The measured response ratio of biomass to a 6–8 °C warming ranged from 0.32 to 0.47 (mean = 0.38), while the predicted biomass response ratio was between 0.95 and 1.43 (mean = 1.17); for shoot height, the measured response ratio ranged from 0.32 to 0.90 (mean = 0.70), while the predicted response was between 0.76 and 1.07 (mean = 0.95). Thus, we found considerable variation in the growth response of a single species to a similar change in growth temperature, albeit always in the same direction. While our predictions for biomass consistently

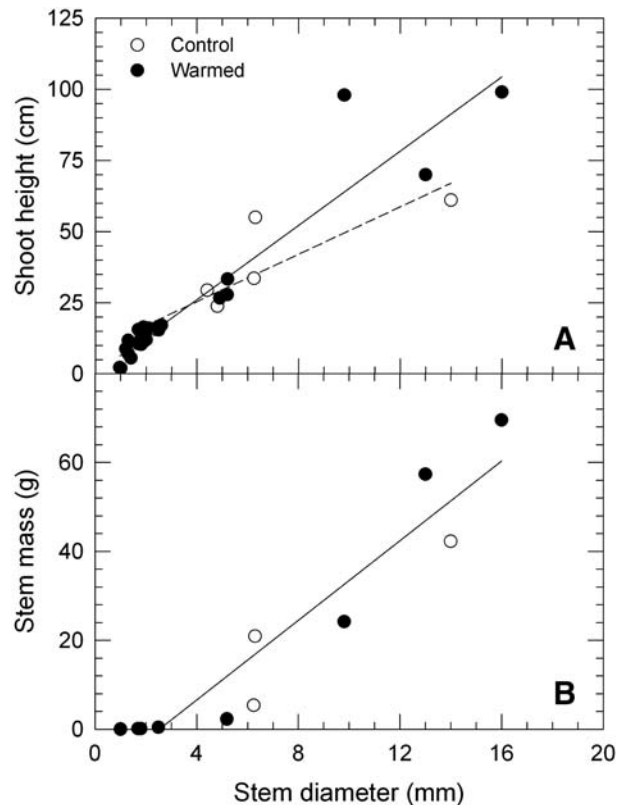


Figure 9. Trees grown at elevated growth temperatures follow different developmental trajectories than control trees. Changes in (A) shoot height and (B) stem mass in relation to stem diameter between trees grown at control temperatures (open symbols) or elevated temperatures (warmed; filled symbols). (A) Dashed line, control trees; solid line, warmed trees; (B) solid line, all trees.

overestimated the measured response, the predicted shoot height response using the warming-only regression (0.76) was similar to the measured responses (0.70). To address the second question, we compiled the biomass response ratios for *P. menziesii* from the four studies where both day and night temperatures were altered by the same degree to determine the shape of the growth response to temperature within a species and how well this was captured by the two regressions (all temperature changes and warming only). Figure 10 shows the data points, a regression fit to the data, as well as our two regression equations. While the regression for a general change in temperature (Table 3) does a poor job of fitting the data, the warming-only regression (Table 5) does a reasonable job of fitting the data within its restrictions: it has a similar shape to the *P. menziesii*-only regression, and while it underestimates the low temperature data (where it was not optimized to fit), it performs well with the high temperature studies.

## Discussion

By examining the effects of a change in growth temperature instead of simply warming, we were able to derive temperature–growth relationships for measurements such as biomass and height across a wide range of growth temperature



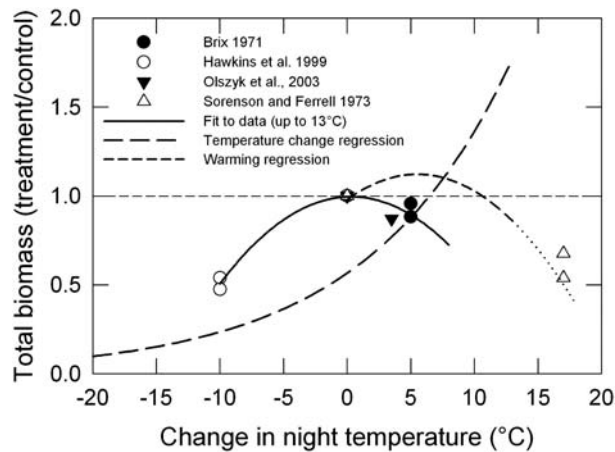


Figure 10. Comparison of predicted to measured biomass responses to changes in growth temperature in *P. menziesii*. Symbols are data from studies listed, solid line indicates polynomial regression for data points (excluding points above 13 °C), long-dashed line indicates predicted response from temperature change regression equation for evergreen species (Table 3), short-dashed line shows predicted response using warming-only regression for evergreen trees (0–13 °C but continued by dotted line to 18 °C) (Table 5).

changes. However, by focusing on temperature effects in general, we also had sufficient data to investigate the role of functional group and thermal niche in factors such as  $V_{\text{cmax}}$ ,  $J_{\text{max}}$ ,  $R_{\text{dark}}$  and leaf number, where there were too few warming studies from which to draw conclusions. Analyzing the response of growth to a general change in temperature and to warming alone, we found that rising temperatures increase tree growth in many species, up to a point (Figures 2 and 7). While the two analyses differed in whether evergreen growth would be increased or decreased in a warmer climate, both concurred that deciduous species would be much more responsive than evergreens to warming. This trend was seen in both field and pot studies and was not related to the length of the experiment. The similarity between field and pot studies of temperature acclimation is consistent with Kattge and Knorr (2007), who found that thermal acclimation of photosynthetic variables was not different between controlled and natural growth settings. The results from this analysis are consistent with provenance studies that show enhanced growth in trees planted in warmer locales (e.g., Rehfeldt et al. 1999) and with tree ring studies that often show faster growth in trees during warmer growing seasons (e.g., McKenzie et al. 2001, Bunn et al. 2005). It is important to note, however, that many of the studies in our analysis provided well-watered, fertilized conditions that are optimal for growth, in contrast to the natural environment. Our results are thus likely to be an estimate of the best-case scenario for tree growth at warmer temperatures, bearing in mind that, while rising  $\text{CO}_2$  may increase growth further, nutrient limitations may constrain the  $\text{CO}_2$  response (Oren et al. 2001, Finzi et al. 2002, McCarthy et al. 2009).

We also found that trees from tropical and subtropical regions were more susceptible to growth declines in a warmer

climate than trees from higher latitudes (Figure 4, Tables 3 and 5). Consistent with Figure 1, the warm-adapted species showed both less variation and more negative growth responses to increasing growth temperatures than species from cooler environments: for a temperature increase of 3–6 °C, the biomass response ratio was  $1.38 \pm 0.91$ ,  $1.27 \pm 0.49$  and  $0.77 \pm 0.32$  for boreal, temperate and tropical species, respectively (means  $\pm$  SD). Since many of the tropical trees were evergreen, their reduced growth correlates well with the deciduous/evergreen division seen in our other analyses, although excluding the tropical data set did not change the results of the deciduous/evergreen contrast (data not shown). Interestingly, the trend for greater sensitivity in warm-adapted species was not found when we used the long-term average June temperature for the tree seed source as an indication of thermal niche. Growing season temperatures all fall within favorable conditions for growth and photosynthesis, and because these temperatures form a gradient from high to low latitudes, they may not supply sufficient power for differentiating these trends. The set of data on low latitude trees was also much smaller than the data available for temperate and high latitude species, so while we found support for our hypothesis that warm-adapted species may suffer greater declines than cool-adapted species as the climate warms, more data are clearly needed from tropical and other warm-adapted tree species.

Could the results seen here be explained by factors other than temperature itself? There are at least two other possibilities to be discarded. First, the temperatures selected as representative of the growing season (the control temperatures) may be lower than the actual growing season temperature. If maximum growth actually occurs in the warmest months of the summer (July and August in the Northern Hemisphere), our choice of control temperatures could be underestimates. While this could explain a mismatch between maximum growth and current growth temperatures in pot studies, field studies use in situ growing season temperatures as controls but still see the same growth response, indicating that an error in control temperatures does not explain the growth increase. Second, higher growing temperatures could extend the growing season length, allowing warm-grown trees more time to grow (i.e., altered phenology). This could explain the field data, where growing season length increases, but growth chamber and greenhouse studies grow seedlings for the same duration regardless of the temperature treatment, so longer growing seasons cannot explain the trends found here.

Instead, the most likely explanation for why trees grow bigger at temperatures warmer than where they are currently found is that tree growth is not necessarily optimal in the native environment, particularly for temperate and boreal species. This is commonly reported in provenance trials: growth of *Acer rubrum* L. was optimized at sites 5 °C warmer than their seed source origin, while *Abies balsamea* (L.) Mill. and *Pinus taeda* L. growth was maximal at sites 3–4 °C cooler than their origin (Schmidting 1994, Carter 1996). In the most extreme cases, height growth can be maximized at

mean annual temperatures of up to 9 °C warmer than where the trees originated (Rehfeldt et al. 1999). So why are trees not found in their optimal growth habitat? In many cases, trees from warmer populations have inherently faster growth rates and can outcompete cooler genotypes, thus displacing cool-adapted trees from where their growth is optimal. This appears to be due to a common trade-off between cold tolerance and growth potential in different populations (*P. taeda*, Schmidting 1994; *Pinus contorta* Douglas ex Louden, Rehfeldt et al. 1999; *Pinus banksiana* Lamb., Savva et al. 2007; and even *Drosophila* spp., Kellermann et al. 2009): when shifted to warmer climates, individuals from northern populations cannot keep pace with the faster growth of the more southern populations (Rehfeldt et al. 1999). Importantly, while height growth is often suboptimal at the native site in provenance studies, survival and fitness are usually optimized near the site of origin, demonstrating that local adaptation is not driven only by growth (Rehfeldt et al. 1999, Savolainen et al. 2007). While our data thus provide insight into how established trees may respond to climate warming, it is important to remember that future forest communities will be determined not only through growth but also through survival, seed production, germination success and the ability to establish in a warmer site.

Our data provide support for the idea that temperature thresholds may play a role in the divergence problem in tree ring studies. Warmer conditions generally increase growth, but beyond a certain temperature, growth will decrease. This problem was more prevalent in evergreen trees (Figure 2A and C), the same group where the divergence problem has been most studied. Because pot and field studies showed the same response, our results also indicate that decreased growth in response to warming can occur even when trees have sufficient water and nutrients and is not necessarily related to drought stress. While warming-related drought can reduce tree growth and survival (van Mantgem and Stephenson 2007), declines in forest productivity have also been attributed to increasing temperatures when associated changes in water stress have been ruled out (Piao et al. 2008).

#### *Why is growth enhanced at higher temperatures?*

We sought a plausible mechanism for the observed growth changes by assessing how temperature changes affected carbon assimilation and loss. Biochemical processes, such as photosynthesis and respiration, are generally enhanced at higher temperatures because of quicker enzyme function. While rates may increase solely because of increased temperatures, acclimation can also enhance performance. In a synthesis of 36 species, Kattge and Knorr (2007) found that warm-grown plants acclimate to increase the thermal optimum of both  $V_{\text{cmax}}$  and  $J_{\text{max}}$ , thus enhancing photosynthetic rates at high temperatures. While  $R_{\text{dark}}$  also increases with temperature, thermal acclimation of  $R_{\text{dark}}$  can happen rapidly, often due to substrate limitations, offsetting the increase in temperature (Atkin and Tjoelker 2003).

Our results show how both increased temperatures and acclimation affect photosynthesis and respiration in trees. Comparing the temperature response of  $V_{\text{cmax}}$  measured at 25 °C (Figure 6A) and  $V_{\text{cmax}}$  measured at leaf growth temperature (Figure 6B) shows the effect of both acclimation and an increase in temperature on  $V_{\text{cmax}}$ , where the rate of carboxylation is faster at higher measurement temperatures. Similarly, both  $J_{\text{max}}$  and  $R_{\text{dark}}$  are greater when measured at warmer temperatures than when assessed at a common temperature. In contrast, when measured at a single common temperature, we see no evidence for thermal acclimation of either  $V_{\text{cmax}}$  or  $J_{\text{max}}$  but strong respiratory acclimation (Figure 6A, C and E). Thus, across our studies, we find that  $V_{\text{cmax}}$  and  $J_{\text{max}}$  respond more strongly to an increase in leaf temperature, mainly through direct temperature effects, than does  $R_{\text{dark}}$ , which, through acclimation, offsets the direct temperature effect. In other words, photosynthesis shows less acclimation potential to a change in temperature than respiration, consistent with a number of recent studies (Campbell et al. 2007, Way and Sage 2008a, 2008b, Ow et al. 2009). The greater  $V_{\text{cmax}}$  and  $J_{\text{max}}$  seen at higher growth temperatures should lead to increased carbon assimilation rates, while the weaker response of  $R_{\text{dark}}$  to increased growth temperatures means that increases in carbon losses should be minimized at warmer conditions. Taken together, the greater carbon gain implied by these results could explain the increased growth that we found in trees grown at warmer temperatures.

#### *Evergreens versus deciduous species*

If the combination of greater  $V_{\text{cmax}}$  and  $J_{\text{max}}$  with acclimated  $R_{\text{dark}}$  at warmer temperatures leads to increased growth, why do evergreen trees show decreased (Figure 7A and B) or much smaller growth responses than deciduous species (Figure 7C)? While we cannot definitively explain this difference, there are a number of reasons why evergreen trees may be less responsive to growth temperature. The evergreen strategy most commonly occurs in sites with low nutrient or water availability (Chabot and Hicks 1982, Givnish 2002). Because species from resource-poor environments are generally more conservative in their response to changing environmental conditions, evergreen species may be expected to be less responsive than deciduous species. Aerts (1995) argued that evergreen species were less responsive to environmental changes because they possess traits that limit nutrient loss; since there is a trade-off between nutrient retention and the ability to maximize productivity, evergreen species are constrained in their ability to increase growth when conditions (such as temperature or nutrient availability) become favorable (Chapin et al. 1995, Valladeres et al. 2000).

It may thus be too simplistic to assume that an increase in both  $V_{\text{cmax}}$  and  $J_{\text{max}}$  at high temperatures will lead to increased growth or that acclimation will completely offset the direct temperature effect on  $R_{\text{dark}}$  (Way and Sage 2008b). While the greater biomass of deciduous species re-

quires an increase in carbon supply and our photosynthesis and respiration data thus support our deciduous growth results, a greater ability to fix carbon biochemically does not necessarily mean more growth. For example, an inability to acclimate stomatal conductance to optimize carbon gain could lead to lower intercellular CO<sub>2</sub> concentrations, thus leading to little increase in carbon fixation despite a higher  $V_{\text{cmax}}$ . Differences between functional groups in the ability of stomata to respond to other environmental conditions have been noted: stomatal conductance is more responsive to elevated CO<sub>2</sub> in broad-leaved trees than in evergreen conifers (Medlyn et al. 2001), and the same may be true for temperature, although there were not enough studies to determine if this was true. There could also be differences between how available carbon stores are used between evergreen and deciduous species (or tropical, temperate and boreal species). If evergreens increase root exudation rates, volatile organic compound production or other carbon-demanding processes at higher temperatures preferentially over growth, there could be little coupling between photosynthesis and growth. In temperate and tropical forests, but not boreal forests, the fraction of gross primary productivity invested in belowground carbon flux is positively correlated with mean annual temperature (Litton and Giardina 2008), demonstrating that carbon allocation patterns can change with growing temperature and that trees from different biomes (or different functional groups) may have different carbon allocation strategies.

#### *Implications for shifting allometry*

For deciduous species, increases in shoot height growth were greater than increases in stem mass, implying that stem elongation, rather than general stem growth, is most affected at higher temperatures. This conclusion is supported by the much weaker response of stem diameter to temperature: stem diameter growth could be doubled at high growth temperatures, while stem height growth increased up to eightfold in the most extreme case, leading to less tapered stems. A similar response to warmer days is seen in horticultural species: increases in day temperatures increase cell elongation but not cell width in the stem of many flowering plants (reviewed in Myster and Moe 1995). For evergreen trees, height was only increased until about 5 °C above normal growing temperatures, while biomass continued to increase above this temperature. Rather than increasing height, evergreens may be investing in girth and leaves at temperatures more than 5 °C above normal, as evidenced by increasing stem diameter and leaf mass with increasing temperatures. Reduced stem taper could decrease the mechanical stability of tree stems, making them more vulnerable to ice storm and wind damage. Because these environmental factors can limit the northern range of some tree species (e.g., *P. taeda*, Wahlenberg 1960, Fowells 1965), altered stem allometry could impact community structure in a warmer climate.

Root mass responses were not significantly predicted by changes in growth temperature, but warmed trees as a group had lower root mass than control trees of the same size. Buffering of temperature by soils means roots do not experience the same degree of temperature change as aboveground components. A study of root biomass across ecosystems found no relationship between root mass and mean annual temperature, but direct soil warming of boreal soils reduced black spruce root biomass (Bronson et al. 2008, Burton et al. 2008). Even if warming results in no change in root mass, allocation between above- and belowground components would shift with growth temperature (i.e., a lower root-to-shoot ratio). Leaf mass increased with increasing growth temperature, such that above current growing temperatures, there was more leaf material demanding water from a similar root mass. Because the specific leaf area also increased with higher growth temperatures (at least for evergreen species), this greater leaf mass could result in a large increase in leaf surface area in warmer climates. Since a decrease in the ratio of root area to leaf area increases the likelihood of drought stress (Sperry et al. 1998, Ewers et al. 2000, Hacke et al. 2000, Addington et al. 2006), trees that develop at warm temperatures may be more susceptible to episodic drought.

When combined with the trend for longer, thinner stems in deciduous species at high temperatures, the increased allocation to leaves over roots could mean that these trees will have more difficulty accessing and transporting water to supply canopy transpiration demands. These changes could be offset by changes in the structure of xylem and/or by increasing the amount of sapwood for a given tree diameter. We have little information on how hydraulic conductivity changes with growth temperature, but the existing data do not point to large changes in wood anatomy or allocation nor to offsetting trends in hydraulic conductivity or leaf anatomy. In addition, where we had both stem diameter and leaf area data for the same tree, we found no change in the ratio of basal area to leaf area, used as a proxy for the sapwood-to-leaf-area ratio (data not shown). Without these types of changes, trees that develop in a warmer climate may be more vulnerable to periodic water stress. While there are not many studies investigating this link, pinyon pines (*Pinus edulis* Engelm.) grown at 4.3 °C warmer temperatures died 28% faster than control trees when exposed to a severe drought (Adams et al. 2008), lending support to this hypothesis.

#### *Day versus night temperature changes*

For some traits, day temperatures were a better predictor than night temperatures. In general, leaf traits (leaf area, number, mass) were linked to changes in daytime temperature, which is consistent with studies showing that leaf elongation rates are greater during the day than at night in trees and many crop species (McDonald et al. 1992, Munns et al. 2000). Shoot height was also significantly correlated with day temperatures, again consistent with previous findings that stem



elongation is maximized during the day (Berman and DeJong 1997). High daytime temperatures increase shoot elongation rates in crops (Carvalho et al. 2002) and in trees: Cremer (1976) found that stem elongation rates were doubled in *Pinus radiata* D. Don and *Eucalyptus regnans* F. Muell. when day temperatures were increased from 12 °C to 25 °C. In contrast, stem diameter and non-leaf biomass traits were more significantly correlated with night than day temperatures. If night temperatures increase more rapidly than day temperatures, as predicted (Christensen et al. 2007), leaf mass and area may increase at a lower rate than other tree growth variables, which could help reduce the increased transpirative demand implied by the allometric changes outlined above.

#### Where do we go from here?

While we found support for our hypotheses that the growth response to changing temperatures varies between different functional groups and thermal niches in a broadly predictable way (Figure 1), our analysis also highlights areas where information is currently lacking.

- (1) At larger scales where responses among individual species may average out and for species where there are no existing data, the regressions we produced, particularly those summarizing warming-only experiments, provide our current best estimates for tree growth responses. However, given the variability both within a single species (such as *P. mariana*) and the variability across studies for a given temperature change (see Figure 2), it is not surprising that these generalized regressions may not accurately predict the growth response for a given species (Figure 10). Where predictions are necessary at the species level, studies are required to generate specific response functions.
- (2) Our results indicate that tropical species are more vulnerable to rising temperatures than temperate or boreal species, possibly related to the prevalence of the evergreen strategy in these forests. While temperatures are not predicted to increase to the same extent at low latitudes as they will in higher latitudes, there is already evidence that small degrees of warming can reduce tropical tree growth (Clark et al. 2003, 2010, Feeley et al. 2007). More data are needed on how trees from different biomes and thermal niches respond to changes in growth temperature.
- (3) Differences in the ability of various functional groups (especially conifers and broad-leaf trees) to acclimate both photosynthesis and respiration to changes in temperature need to be specifically addressed. Understanding these potential differences will significantly improve our ability to predict how tree species will respond to a changing climate by providing generalizations that can be broadly applied.
- (4) We also need more information on how hydraulic characteristics change in response to shifts in growing temperature. There are very few studies measuring hydraulic conductivity or wood anatomy in trees grown at different temperatures despite the fact that a warmer climate will increase transpiration demand. Our results indicate that water transport may also become more difficult in a warmer climate due to changes in allometry, which should be given more attention in future studies.
- (5) Lastly, increases in temperature will occur concurrently with rising CO<sub>2</sub>, but there are few studies that examine the interaction of this response on tree growth. Because photorespiration rates increase with increasing temperature and elevated CO<sub>2</sub> suppresses photorespiration (see Sage and Kubien (2007) for a review of temperature–CO<sub>2</sub> interactions on photosynthesis), increased CO<sub>2</sub> may moderate the growth decline seen here in evergreen trees and could also enhance the growth of deciduous species further. However, in an analysis of crop species, the relative increase in biomass caused by elevated CO<sub>2</sub> did not depend on growth temperature (Morison and Lawlor 1999). While CO<sub>2</sub>–temperature experiments require substantial space and funding to provide long-term data and sufficient replication, understanding how these two factors will interact to alter tree growth is critical for making realistic predictions about future forest growth and should be a key priority in future research.

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(\* indicates reference used in data analysis)

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