

Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers

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Abstract. Does climate determine species' ranges? Rapid rates of anthropogenic warming make this classic ecological question especially relevant. We ask whether climate controls range limits by quantifying relationships between climatic variables (precipitation, temperature) and tree growth across the altitudinal ranges of six Pacific Northwest conifers on Mt. Rainier, Washington, USA. Results for three species (*Abies amabilis*, *Callitropsis nootkatensis*, *Tsuga mertensiana*) whose upper limits occur at treeline (>1600 m) imply climatic controls on upper range limits, with low growth in cold and high snowpack years. Annual growth was synchronized among individuals at upper limits for these high-elevation species, further suggesting that stand-level effects such as climate constrain growth more strongly than local processes. By contrast, at lower limits climatic effects on growth were weak for these high-elevation species. Growth–climate relationships for three low-elevation species (*Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla*) were not consistent with expectations of climatic controls on upper limits, which are located within closed-canopy forest (<1200 m). Annual growth of these species was poorly synchronized among individuals. Our results suggest that climate controls altitudinal range limits at treeline, while local drivers (perhaps biotic interactions) influence growth in closed-canopy forests. Climate-change-induced range shifts in closed-canopy forests will therefore be difficult to predict accurately.

Key words: *Abies* spp.; abiotic; *Callitropsis* spp.; competition; dendroecology; global warming; Pacific Northwest forests; *Pseudotsuga* spp.; range limits; *Thuja* spp.; *Tsuga* spp.

INTRODUCTION

Climate has long been thought to play a dominant role in controlling species' range limits (Darwin 1859, Grinnell 1917, MacArthur 1972). In support of this idea, species distributions often correspond to thermal isoclines (Sorenson et al. 1998, Buckley et al. 2010). Also, species' range shifts during the Holocene, preserved in macrofossil and pollen records, have tracked climatic changes (e.g., Prentice et al. 1991, Davis and Shaw 2001). Finally, many species have moved to higher latitudes and altitudes with warming during the last century (Parmesan 2006).

Despite these compelling links between climate and species' distributions, the role climate plays in determining range limits is still not fully understood. Species' responses to recent warming are inconsistent: although some ranges have moved upward or poleward as expected, others remain static or have shifted in the opposite direction from that expected (e.g., Parmesan 2006, Harsch et al. 2009). This suggests that controls on range limits may not always be climatic. Biotic interactions like competition and facilitation are also known to influence species distributions (e.g., Connell

1961, Brown et al. 1996), and could be more important than climate for some species or locations, perhaps explaining the inconsistent responses to recent warming. Unfortunately, little is known about the influence of biotic interactions on range limits (Sexton et al. 2009). Consequently, forecasts of global-warming-induced changes in species distributions often assume that climate is the sole driver of range limits despite evidence to the contrary (Pearson and Dawson 2003).

Understanding effects of climate change on tree ranges is particularly important, as forests provide important ecosystem services (e.g., carbon sequestration). Trees also offer valuable opportunities for studying climatic controls on range limits because annual rings preserve growth–climate relationships across many years (e.g., Peterson and Peterson 2001, Littell et al. 2008, Chen et al. 2010). The role of biotic factors in limiting tree distributions remains poorly understood, in part because tree rings are generally sampled from extreme environments where competition is low, in order to maximize the climate signal (Stokes and Smiley 1968). While useful for reconstructing past climate, this approach probably will not give an accurate picture of how trees in closed-canopy forests respond to changes in climate.

To address these issues, we examined growth–climate relationships for six conifer species with contrasting altitudinal ranges on Mt. Rainier, Washington, USA

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(Fig. 1). We collected 90+ years of annual tree growth data from over 600 individual trees growing at nine different elevations on Mt. Rainier, where long-term climate records exist. We used this extensive data set to ask (1) whether the relationship between growth and climate suggests climatic controls on upper and lower range limits of focal conifers; and (2) how the relative importance of stand-level drivers (e.g., climate) vs. localized drivers (e.g., biotic interactions) of growth varies across altitudinal ranges. If climate controls altitudinal range limits, we hypothesized that growth would be strongly influenced by climate at range limits, with the sign of these relationships or identity of important climatic drivers differing between upper and lower range limits (Fig. 1A and B). There are strong elevational gradients in climate on Mt. Rainier (Fig. 1C and D), and precipitation consists mainly of winter snowfall, so heavy precipitation reduces the length of the growing season. We therefore expected that temperature would positively influence growth at upper limits and negatively influence growth at lower limits, and that precipitation would negatively influence growth at upper limits and positively influence growth at lower limits, if climate controls range limits. We were also interested in how focal species differ in the identity of the climate variables influencing growth. Finally, we expected growth to be highly synchronized among conspecific individuals at range limits if climate is an important driver; that is, a "good" growth year should be good for all trees in a stand. By contrast, if biotic factors drive altitudinal range limits, we expected annual growth trends to be asynchronous among individuals.

METHODS

Study site and species

We collected data in Mt. Rainier National Park, located in the western Cascade Mountains of Washington state, USA. Mt. Rainier is a 4392 m high volcano that has remained relatively undisturbed since its creation as a park in 1899. Soils are podzolic, with surface organic horizons that have accumulated over soil horizons buried from multiple volcanic ash deposits (Franklin et al. 1988). The climate is temperate maritime, with dry summers, heavy winter precipitation, and strong elevational gradients in climate (Fig. 1C and D).

We sampled six conifer species that are dominant on Mt. Rainier's south side (Fig. 1B) and abundant in western Washington (Franklin et al. 1988, Burns and Honkala 1990). This included three high-elevation species (*Abies amabilis* Douglas ex J. Forbes [Pacific silver fir], *Callitropsis nootkatensis* (D. Don) Florin ex D. P. Little [formerly *Chamaecyparis nootkatensis*, Alaskan yellow-cedar], and *Tsuga mertensiana* (Bong.) Carrière [mountain hemlock]), whose upper range limits extend to treeline (>1600 m). We also sampled three low-elevation species (*Pseudotsuga menziesii* (Mirb.) Franco [Douglas-fir], *Thuja plicata* (Raf.) Sarg. [western

red-cedar], and *Tsuga heterophylla* (Raf.) Sarg. [western hemlock]), whose upper range limits occur in closed-canopy forests (<1200 m). Sampling locations included upper altitudinal range limits of all focal species and lower limits of the high-elevation species (Fig. 1B; Franklin et al. 1988).

Tree growth data

We collected increment cores from 20 individuals per focal species at nine elevations spanning closed-canopy forests to treeline (704–1603 m in altitude). We cored trees adjacent to nine one-hectare permanent study stands established in the 1970s as part of a Permanent Sample Plot Network (Dyrness and Acker 2000). Cored trees were greater than 40 cm in diameter at breast height and located at least 20 m apart. We collected two cores per individual on opposite sides of the tree, perpendicular to the aspect. Increment cores were sanded, and then scanned with a high-resolution scanner using the program WinDENDRO (Version 2008e; WinDENDRO 2008) to measure annual growth rings to 0.001 mm (Regent Instruments, Quebec City, Quebec, Canada). We used visual cross-dating to identify missing and false rings and to date annual rings to the calendar year (Stokes and Smiley 1968). We verified the accuracy of visual cross-dating with the Dendrochronology Program Library (dplR) package in R, Version 2.10.1 (R Development Core Team 2009, Bunn 2010). The sample size was reduced to 19 individuals for one species–stand combination, *T. mertensiana* at 1197 m, where cores from one tree were discarded due to rot.

We averaged ring widths from the two collected cores for each individual tree, then standardized each tree's ring width series by fitting a spline through the time series to remove size-specific trends (Cook and Peters 1981). We set the spline's rigidity at 100 years and its wavelength cutoff at 50% (e.g., Nakawatase and Peterson 2006, Littell et al. 2008). More- or less-flexible splines did not qualitatively influence our results. After splining, dimensionless ring-width indices (RWI) were used as a measure of annual tree growth.

Climate data

Climate records (1914–2007) came from the Longmire Ranger Station at 842 m, located within our altitudinal transect ([available online](http://www.ncei.noaa.gov/oa/climate/climatedata.html)).² Longmire climate is strongly correlated with climate directly above (Paradise Ranger Station, 1654 m) and below (LaGrande, 293 m) our sampling locations (Appendix B; Fig. B1). We chose nine climate variables as potential explanatory variables in our analyses: mean annual temperature (MAT), mean growing-season temperature (GST, May to September), mean dormant-season temperature (DST, November to March), total annual

² (<http://www.ncei.noaa.gov/oa/climate/climatedata.html>)

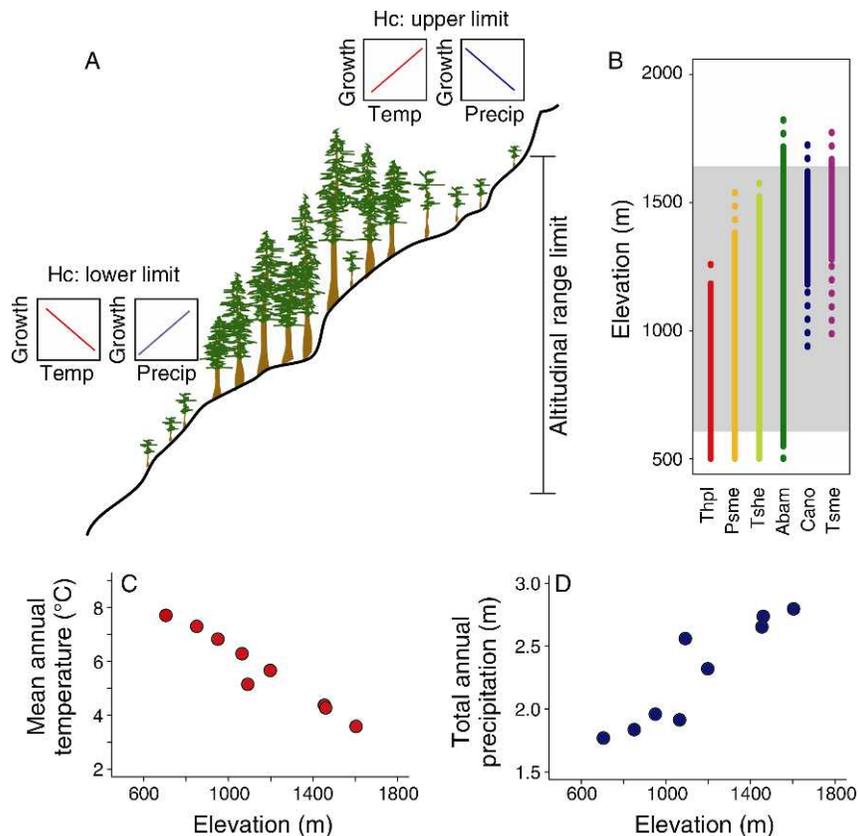


FIG. 1. Climate and species' ranges. (A) If climate controls altitudinal range limits, we hypothesize that growth is strongly influenced by climatic variables at upper and lower range limits, with the direction of these relationships or identity of the climatic driver (temperature [temp] or precipitation [precip]) differing between upper and lower range limits. Hc is the hypothesized (dormant vs. growing). (B) We examined growth–climate relationships in six tree species with different altitudinal ranges: *Thuja plicata* (Thpl), *Pseudotsuga menziesii* (Psme), and *Tsuga heterophylla* (Tshe) at low elevations; and *Abies amabilis* (Abam), *Callitropsis nootkatensis* (Cano), and *Tsuga mertensiana* (Tsme), occurring at high elevations. Solid lines indicate >30% probability of occurrence; dotted lines indicate <5% (data from Franklin et al. [1988]); gray shading is the range of sampling elevations. (C) Mean annual temperature and other temperature-related variables decrease with elevation, while (D) total annual precipitation and precipitation related variables increase with elevation.

precipitation (PPT), total growing-season precipitation (GPT), total dormant-season precipitation (DPT), maximum size of the snowpack in snow water equivalent (SWE), snow duration (SNDR, the number of days the ground was covered by snow in a given year), and growing degree-days (GDD, the annual sum of daily mean temperatures for days with mean temperatures above 5°C). All annual variables were calculated for hydrologic years, from October to September. Tree growth is also influenced by potential evapotranspiration (PET) in the Pacific Northwest (e.g., Littell et al. 2008); however, we did not include PET as an explanatory variable because data are available on much shorter time scales than temperature and precipitation. Moreover, PET is highly correlated with the climatic variables we did include (Appendix B: Fig. B2).

We combined climate data from Longmire with output from a climate-mapping model called PRISM

(Parameter-elevation Regressions on Independent Slopes Model) to estimate a climatic time series at each of our sampling locations. PRISM uses climate station data, digital elevation models, and physiographic climate relationships to estimate temperature and precipitation on a 30-arcsec (~800-m) grid (Daly et al. 2008). We used climate estimates for the grid cells within which sampling locations were located to create a 1914–2007 time series for each climate variable at each sampling location (Appendix A).

Statistical analyses

Growth–climate relationships.—We used linear mixed-effects models to evaluate the relationship between growth and climate for each species at each sampling location. Unlike most standard dendroecological analyses (where analyses are based on average RWIs of all individual trees at a site), mixed-effects models allowed us to accommodate differences among individual tree

TABLE 1. Climate sensitivity across focal tree species' ranges.

Species and elevation	Location in range	Best-fit model	Temperature variables		Precipitation variables	
			Growing season†	Dormant season‡	Growing season§	Dormant season¶
Low-elevation species						
<i>Pseudotsuga menziesii</i>						
704 m	mid	DST		0.0306*		
851 m	mid	GDD	-0.0137			
950 m	mid	DST		0.0123		
1064 m	mid	SNDR				0.0067
1091 m	upper	GDD + SWE	-0.0002			0.0251
<i>Thuja plicata</i>						
704 m	mid	SNDR				-0.0628*
851 m	mid	SWE				-0.0068
950 m	mid	Null				
1064 m	mid	GDD + GPT + DPT	0.0312*		0.0402*	-0.0440*
1091 m	upper	GDD + GPT	0.0158		0.0301*	
<i>Tsuga heterophylla</i>						
704 m	mid	SWE				-0.0032
851 m	mid	GST + DST	-0.0304*	0.0290*		
950 m	mid	GST	-0.0229*			
1064 m	mid	SNDR				-0.0024
1091 m	mid	GST + SNDR	-0.0441*			-0.0526*
1197 m	upper	SWE				0.0091
High-elevation species						
<i>Abies amabilis</i>						
704 m	lower	SWE				-0.0058
950 m	mid	Null				
1064 m	mid	Null				
1197 m	mid	GDD + DST + GPT + DPT	0.0298	-0.0206	0.0372*	-0.0309
1454 m	mid	SWE				-0.0534*
1460 m	mid	GDD + SWE	0.0058			-0.0851*
1603 m	upper	SWE				-0.1338*
<i>Callitropsis nootkatensis</i>						
1197 m	lower	GDD	0.0506*			
1454 m	mid	GST + SWE	0.0106			-0.0530*
1460 m	mid	GST + GPT + SWE	0.0455*		0.0483*	-0.0480*
1603 m	upper	GDD + SWE	0.0342*			-0.1107*
<i>Tsuga mertensiana</i>						
1197 m	lower	GDD	0.0363*			
1454 m	mid	GDD + SWE	0.0443*			0.0247
1460 m	mid	GDD	0.0557*			
1603 m	upper	GDD + SWE	0.0405*			-0.0734*

Notes: Climate determines some, but not all, range limits in focal species, based on best-fit models, climate coefficients, comparison of coefficients with Hc (hypothesized sign of climate coefficients if climate drives range limits; Fig. 1), the strength of climatic influence on growth ($AIC_{Null} - AIC_{Best}$), the proportion of trees sensitive to climate, and synchrony (the degree to which individual tree growth was correlated within a stand; Pearson's r). Model abbreviations are: mean growing-season temperature, GST; growing degree-days, GDD; mean dormant-season temperature, DST; total growing-season precipitation, GPT; total dormant-season precipitation, DPT; snow water equivalent, SWE; and snow duration, SNDR. Text is boldface if results match Hc at range limits. Climate variables are standardized, so coefficients are directly comparable. Empty cells indicate that data are not applicable.

† Mean growing-season temperature (GST) and growing degree-days (GDD).

‡ Mean dormant-season temperature (DST) and mean annual temperature (MAT).

§ Total growing-season precipitation (GPT).

¶ Total dormant-season precipitation (DPT), snow water equivalent (SWE), and snow duration (SNDR).

* Indicates significant effects of coefficients ($P < 0.05$), based on MCMC sampling (see *Methods: Statistical analyses*).

responses to climate. We designated both individual tree and year as random effects to account for nonindependence of data from the same individual or within years (Crawley 2007); all climate variables were fixed effects. We used the lme4 package in R for fitting mixed-effects models (R Development Core Team 2009, Bates and Maechler 2010).

To evaluate which combination of climate variables (if any) best explained annual growth patterns, we fit 32 linear mixed-effects models for each species at each sampling elevation using maximum-likelihood estimation. Our models ranged from a null (only an intercept) and all single climate variable models (models with only mean annual temperature, only growing-season precipi-

TABLE 1. Extended.

Do coefficients match Hc at range limits?	AIC _{Null} – AIC _{Best}	Proportion of trees sensitive	Synchrony (mean <i>r</i>)
	4	0.32	0.25
	9	0.10	0.31
	9	0.15	0.34
	16	0.20	0.30
no	15	0.24	0.41
	43	0.21	0.26
	8	0.25	0.19
	0	NA	0.31
	17	0.50	0.34
no	7	0.27	0.30
	7	0.10	0.19
	10	0.20	0.13
	3	0.10	0.14
	9	0.15	0.18
	23	0.60	0.38
no	4	0.15	0.24
	18	0.25	0.07
no	0	NA	0.23
	0	NA	0.33
	18	0.35	0.34
	20	0.45	0.41
	69	0.74	0.38
yes	70	1.00	0.59
	15	0.35	0.36
no	39	0.45	0.40
	32	0.65	0.41
yes	67	0.95	0.47
	27	0.53	0.12
no	26	0.55	0.21
	21	0.50	0.25
yes	69	0.90	0.31

tation, and so forth) to more complicated models with two-way interactions between climate variables (see Appendix A for a list of models). The 32 models we fit constitute only a subset of all possible models; we excluded models with highly correlated explanatory variables ($r > 0.6$, e.g., mean annual temperature and dormant-season temperature; Appendix B: Figs. B2 and B3) and what we viewed as biologically implausible combinations of explanatory variables (e.g., three-way interactions). We standardized climate variables by subtracting the mean and dividing by the standard deviation to facilitate direct comparison of climate coefficients from different explanatory variables. We used Akaike's Information Criterion (AIC) to identify the "best-fitting" model for each species at each sampling elevation, choosing the model with the fewest parameters when AIC values of the best-fitting and next best-fitting

model(s) differed by less than 2.0 units (Burnham and Anderson 2002). We also used the difference in AIC values between the null model and the best-fit model to indicate the extent to which climate explains variation in observed tree growth (AIC_{Null} – AIC_{Best}). We calculated significance of coefficients using the LanguageR package in R, which estimates *P* values using Markov chain Monte Carlo (MCMC) sampling (Baayen et al. 2008). We also applied linear regression to the growth–climate relationship of each individual tree to determine the proportion of trees sensitive to climate at each elevation. These linear models included climate variables identified in the best-fit mixed-effects model. We considered an individual tree sensitive to climate if climate explanatory variables were significant ($P < 0.05$) in the linear regressions.

Synchronized growth.—We assessed the importance of stand-level effects vs. localized factors by calculating all pair-wise correlations (Pearson's *r*) between the RWIs of all individual conspecific trees within each sampling location, and then averaging correlation coefficients per species and sampling location. This single measure of growth synchrony allowed us to contrast the importance of stand-level processes for annual growth at different elevations. We assumed that a high degree of growth synchrony, as indicated by high tree-to-tree correlations, implies that stand-level processes like climate influence growth, while low synchrony, indicated by low correlations, suggests local drivers like biotic interactions.

RESULTS

The strength of growth–climate relationships and the identity of climatic variables in best-fit models differed by elevation and by tree species (Table 1, Figs. 2 and 3). For example, snowpack was inversely related to *C. nootkatensis* growth at the three highest elevations, influencing between 45% and 95% of individual trees. However, growing degree-days alone best explained growth at the lowest elevation where this species occurred, but only 35% of individuals were influenced by this climate variable (Table 1). In contrast, growing degree-days had minimal influence on the growth of *T. heterophylla*; instead, growing-season temperature was important at three of the seven locations for this species, and it was negatively related to growth in all cases. *T. heterophylla* was less sensitive to climate than the other five species, with fewer than 20% of individuals sensitive to climate at all but one location (Table 1, Fig. 2).

In the three high-elevation species, growth–climate relationships were consistent with expected relationships for climatic drivers on upper range limits (Table 1, Fig. 3). For example, our data suggests that *A. amabilis* growth was negatively affected by snowpack, which increases with elevation, at its upper range limit (Table 1). Climate sensitivity was greatest at higher elevations (i.e., upper limits), as indicated by the large size of climate coefficients and large AIC_{Null} – AIC_{Best} values (ranging from 67 to 70) for these species. Additionally, populations of high-elevation species were consistently

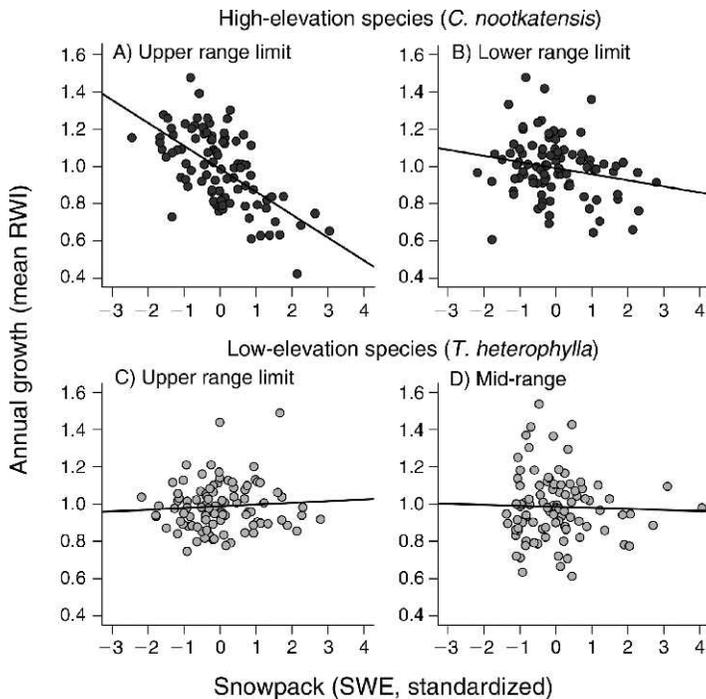


FIG. 2. Climate determines some, but not all, range limits in focal species. (A) Annual growth (measured by mean ring width index, RWI) of high-elevation conifers, such as *Callitropsis nootkatensis* (shown), was inversely related to snow water equivalent (SWE, standardized) at upper range limits. (B) The effect of SWE on growth of a high-elevation species was weaker at the lower range limit, and the sign of the effect of SWE on growth was not consistent with climatic controls on the lower range limit (see Fig. 1A). Growth in low-elevation conifers, including *Tsuga heterophylla* (shown), was poorly explained by climate variables, such as SWE, at its (C) upper range limit and (D) mid-range. (The lower limit does not occur for this species in Mt. Rainier National Park.) See Table 1 for results from all species.

sensitive to climate (90–100% of trees) at upper range limits, where growth was synchronized across individual trees, suggesting stand-level drivers (like climate) of performance.

In contrast, at the lower range limits of high-elevation species, climate coefficients and $AIC_{Null} - AIC_{Best}$ values (ranging from 15 to 27) were lower relative to upper range limits. Additionally, the sign of climate variable coefficients was not consistent with expectations of climatic controls on lower range limits (Fig. 1). Growth of *C. nootkatensis*, for example, was positively related to growing degree-days at its lower limit, even though values of growing degree-days decrease with elevation (Table 1). Furthermore, fewer individual trees were sensitive to climate at lower than upper range limits (25%, 35%, and 53% for *A. amabilis*, *C. nootkatensis*, and *T. mertensiana*, respectively). Finally, growth was much less synchronized among individual trees at lower range limits, suggesting localized drivers of growth at lower limits (Table 1).

Growth–climate associations for the three low-elevation species (*P. menziesii*, *T. plicata*, and *T. heterophylla*) were not consistent with expectations of climatic drivers on their upper altitudinal range limits. Climatic effects on these species' growth were weaker than for the high-elevation species, as indicated by lower values of $AIC_{Null} - AIC_{Best}$ and lower coefficients (Table 1, Fig. 3). Second, even when $AIC_{Null} - AIC_{Best}$ values increased with elevation (e.g., *P. menziesii*; Table 1), as expected if climate determines upper range limits, the proportion of individuals sensitive to climate and growth synchrony was low compared to high-elevation

species (Fig. 3). Furthermore, the sign of climate coefficients was generally inconsistent with expectations for climatic controls on range limits for low-elevation species. For example, our results suggest that at the upper range limit of *T. heterophylla*, snow had a nonsignificant positive effect on growth; however, if snowpack limits growth, it should negatively affect growth at upper range limits.

DISCUSSION

Our results suggest that climate drives some, but not all, range limits. Annual growth of high-elevation conifers declines with high levels of snow, low growing-season temperatures, or low growing degree-days at upper range limits (Table 1, Fig. 2). This likely reflects constraints on the tree life-form or species-specific physiological tolerances. Other studies have found that snowpack limits growth and prevents tree expansion into Pacific Northwestern subalpine meadows (Taylor 1995, Nakawatase and Peterson 2006), and temperature is thought to strongly control treeline across the globe (Körner and Paulsen 2004). Growth–climate relationships of high-elevation species did not support climatic controls on lower range limits, however. Annual growth was less sensitive to climate in lower- vs. upper-elevation populations, and the identities and signs of climatic drivers were similar across lower and upper range limits for individual species, contrary to expectations if climate determines lower range limits (Fig. 1A). Additionally, growth of the low-elevation species was not strongly limited by climatic variables at upper altitudinal range limits, nor was the sign

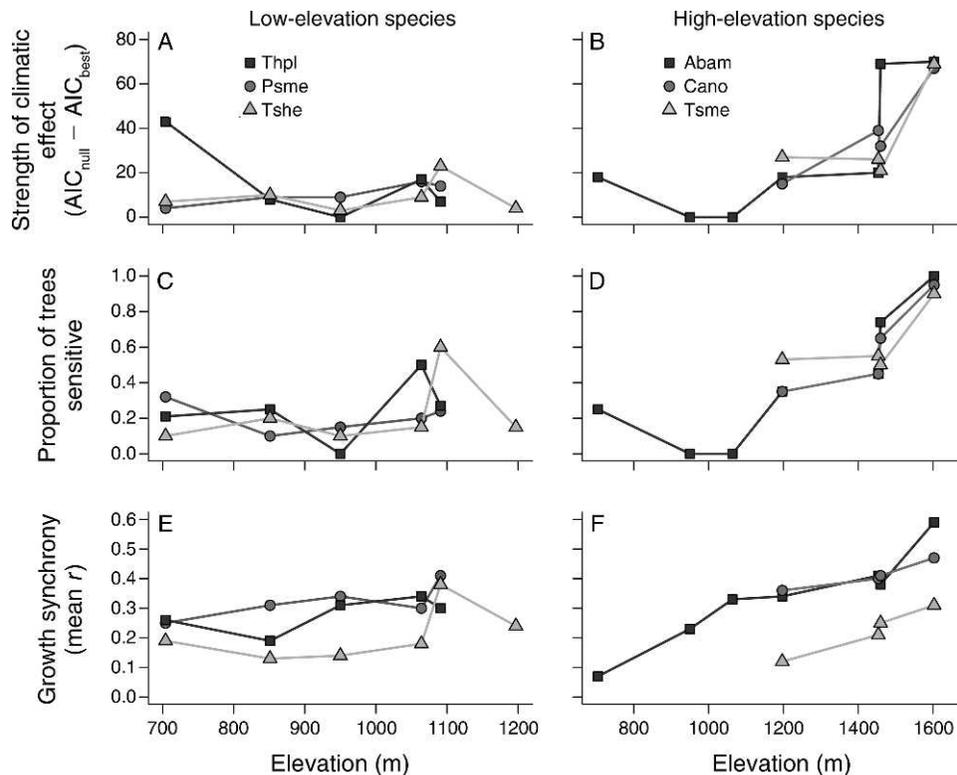


FIG. 3. Climatic effects on growth are stronger in high-elevation species than in low-elevation species. (A, B) The strength of climatic effects on model fit ($AIC_{Null} - AIC_{Best}$), (C, D) the proportion of individual trees sensitive to climate, and (E, F) growth synchrony are shown for the six focal species across their altitudinal ranges. Low-elevation species, whose upper limits occur in closed-canopy forests, do not show consistent altitudinal trends for changes in (A) model fit with the addition of climate, (C) proportion of sensitive trees, or (E) growth synchrony. In contrast, for high-elevation species, (B) climate increases model fit at upper range limits, with (D) the proportion of individual trees sensitive to climate, and (F) synchrony increasing with elevation. See Fig. 1 for clarification of the abbreviations.

of climate coefficients consistent with climatic drivers on range limits (Table 1). Climate may play a more important role in determining range limits of these species elsewhere. For example, Littell et al. (2008) found that *P. menziesii* is negatively influenced by summer water deficit in populations east of our study area that experience much drier conditions. Alternatively, populations in different regions may have adapted to local environments and respond differently to climate (Chen et al. 2010).

If climate does not control tree growth at all range limits of our focal species, what does? Localized drivers, not climate, appear to be responsible. The extent to which growth is synchronized among individuals across altitudinal ranges mirrors growth–climate relationships for the three high-elevation species, with greatest synchrony and strongest growth–climate relationships at upper range limits (Table 1, Fig. 3). This suggests that when climate limits growth, it does so consistently for all individuals. For low-elevation species, growth synchrony between individuals did not vary consistently across altitude and growth–climate relationships were weak (Table 1, Fig. 3). Thus, where climate effects are weak, factors in the local neighborhood of individual trees

appear to drive growth. Other studies have also found that tree growth is buffered from regional climate by local conditions (e.g., Holman and Peterson 2006).

Local drivers of tree growth at range limits where climate does not play a strong role may reflect biotic interactions such as competition and facilitation. Studies suggest that the importance of biotic interactions increases as abiotic conditions become less stressful (Menge and Sutherland 1987, Brown et al. 1996), i.e., with decreasing elevation (Fig. 1). Indeed, tree range limits may be influenced by biotic interactions, such as interspecific competition (Armand 1992, Loehle 1998, Price and Kitckpatrick 2009). Facilitation is also known to affect plant distributions (e.g., Choler et al. 2001), and may play a role at Mt. Rainier. We did not explicitly examine biotic factors, and believe that the exact biotic drivers of focal species range limits (if any) deserve further study.

It is also possible that climatic constraints on range limits occur at other life history stages, as species differ in sensitivity to climate across life stages (Garcia et al. 2000, Bansal and Germino 2010). For example, focal species may be more climatically sensitive as juveniles, as

the well-developed root systems of adults can better withstand severe conditions, such as freezing or low moisture, than seedlings (Mote et al. 2003). However, increased annual growth for adult trees corresponds to increased fitness in conifers (e.g., Despland and Houle 1997), and mortality of most trees follows years of low growth (Wyckoff and Clark 2002). Thus, we believe that the strength and direction of growth–climate relationships for adults (as in Fig. 1A) are a good indication of how and whether climate determines population persistence at range limits.

Our results imply that climate change impacts on Pacific Northwestern forests will be difficult to accurately predict using climate envelope models (e.g., Hannah et al. 2007), which assume that all range limits are determined by climate (Pearson and Dawson 2003). Average temperatures are expected to increase 3°C by the 2080s, with strongly declining snowpack (Mote and Salathé 2009). Although high-elevation species will likely show increased growth at treeline in response to these changes (Table 1, Salzer et al. 2009), responses at lower altitudinal range limits will be more idiosyncratic. For example, if summer precipitation decreases, as forecasted (Mote and Salathé 2009), *T. plicata* growth rates may decline at their upper range limit (where growing-season precipitation positively influenced growth; Table 1). Contrary to expectations under climate warming, this could lead to upper range limit contractions in this species at Mt. Rainier. Additionally, where climate does not determine range limits at all (e.g., upper limit of *T. heterophylla*; Table 1), species' ranges should remain static or shift for reasons not related to climate change (as has been seen in some recent studies, e.g., Harsch et al. 2009).

CONCLUSIONS

Despite decades of ecological research, the role of climate in determining species' ranges remains poorly understood. We applied sophisticated analyses to extensive data and show that, contrary to common assumptions, climate does not determine all range limits. Climate strongly constrains performance at upper limits of conifer species reaching treeline, but more localized processes drive growth at upper range limits within closed-canopy forests. We suggest that biotic interactions are likely to be strong in closed-canopy forests, and may constrain performance more than climate (Menge and Sutherland 1987). The distribution of Pacific Northwestern conifers may therefore conform to the hypothesis that physiological tolerance limits species distributions where climate is harsh, but biotic interactions affect distributions where climate is not stressful (e.g., Brown et al. 1996). The lack of climatic constraints on all range limits suggests that range shifts in a time of climate change will be difficult to accurately predict, particularly in closed-canopy forests where biotic interactions may be important range determinants.

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APPENDIX A

Supplemental methods: a detailed description of climate data and statistical models compared for model fit (*Ecological Archives* E092-111-A1).

APPENDIX B

Supplemental figures showing relationships between climate variables (*Ecological Archives* E092-111-A2).