

Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change

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Abstract

We used 179 tree ring chronologies of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] from the International Tree-Ring Data Bank to study radial growth response to historical climate variability. For the coastal variety of Douglas-fir, we found positive correlations of ring width with summer precipitation and temperature of the preceding winter, indicating that growth of coastal populations was limited by summer dryness and that photosynthesis in winter contributed to growth. For the interior variety, low precipitation and high growing season temperatures limited growth. Based on these relationships, we chose a simple heat moisture index (growing season temperature divided by precipitation of the preceding winter and current growing season) to predict growth response for the interior variety. For 105 tree ring chronologies or 81% of the interior samples, we found significant linear correlations with this heat moisture index, and moving correlation functions showed that the response was stable over time (1901–1980). We proceeded to use those relationships to predict regional growth response under 18 climate change scenarios for the 2020s, 2050s, and 2080s with unexpected results: for comparable changes in heat moisture index, the most southern and outlying populations of Douglas-fir in Mexico showed the least reduction in productivity. Moderate growth reductions were found in the southern United States, and strongly negative response in the central Rocky Mountains. Growth reductions were further more pronounced for high than for low elevation populations. Based on regional differences in the slope of the growth–climate relationship, we propose that southern populations are better adapted to drought conditions and could therefore contain valuable genotypes for reforestation under climate change. The results support the view that climate change may impact species not just at the trailing edges but throughout their range due to genetic adaptation of populations to local environments.

Keywords: climate change impacts, dendroclimatology, dendroecology, plant–climate relationships

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Introduction

Over the last decades, western North America has experienced record temperatures and periods of drought that have been attributed to global climate change (Hoerling & Kumar, 2003; IPCC, 2007). Droughts from 2001 to 2003 caused major forest tree mortality in western Canada (Hogg *et al.*, 2008) and across southwestern North American woodlands (Breshears *et al.*, 2005). Indirectly, climate change has been recognized as a contributing factor to outbreaks of forest pests and diseases that have caused episodic tree mortality throughout western North America (Woods *et al.*, 2005; Raffa *et al.*, 2008). Less visible impacts of climate change have also been detected in seemingly healthy forests at the individual species or population level, affecting tree recruitment and mortality rates (van

Mantgem & Stephenson, 2006, 2007, 2009). When aggregated over time, subtle changes in these rates may also have profound effects on ecosystem composition, structure, and function (Parmesan *et al.*, 2000).

Natural climate cycles and climate variability may play a role in these observations, but they nevertheless raise the question how species will respond to further climate change. Continued temperature increases are expected especially for northern latitudes (IPCC, 2007), and increased drought is expected for the southwestern United States and northern Mexico (Seager *et al.*, 2007). Quantifying plant–climate relationships at landscape scales will be required to predict climate change impacts and to manage and conserve changing forests in a climate-informed way (Millar, 2004; Millar *et al.*, 2007). Historical ecology approaches that investigate biological response to environmental variability and trends of environmental change have become invaluable to inform us about possible biological response to anthropogenic climate change (Millar *et al.*, 2007). A variety of

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empirical and experimental approaches have been used to reveal plant response to climate variability and climate change over large geographic scales, such as long-term provenance test plantations over a wide range of environments (e.g., Matyas, 1994; Rehfeldt *et al.*, 1999), analysis of growth and mortality in forest inventory plots (e.g., van Mantgem & Stephenson, 2007), remote sensing of net primary productivity (e.g., Boisvenue & Running, 2006), and dendro-climatology (e.g., Barber *et al.*, 2000). All of these methods are correlative in nature, inferring biological response from climate (or vice versa).

While historical records of biological response to climate *in situ* are perhaps the most dependable data we have to predict future climate change impacts and develop realistic adaptation strategies, correlative approaches share some common weaknesses with respect to predictions. Correlations observed over one time period may not hold under substantially different climate regimes of the past or future. For example, Briffa *et al.* (1998) reported a significant reduction of correlation between climate and tree rings over the 20th century for the northern hemispheres. This implies possible overestimates of temperature in tree ring based reconstructions of past climate, as well as overestimates of future climate change impacts on tree growth. Similar observations of a change of tree ring sensitivity to limiting climate factors were made in several regional studies (Biondi, 2000; Carrer & Urbinati, 2006; Carrer *et al.*, 2007; Di Filippo *et al.*, 2007). The reason for this change in correlations is subject to speculation, but a plausible explanation would be the adaptation of trees to new environments either through a plastic response over short time periods (e.g., the development of different shoot-to-root ratios) or a fast evolutionary response (e.g., if strong selection pressures act on highly variable phenological or physiological traits).

Most correlative models also do not measure the dependent variable of interest directly (e.g., growth rates or carbon sequestration) but use an easy-to-measure proxy variable, which can be problematic. Lapenis *et al.* (2005) showed that remote sensing data may overestimate primary productivity or carbon sequestration based on an extensive database of forest inventory plots. Remotely sensed 'greenness' may not reflect changes in overall productivity but a changed ratio of wood/leave biomass or aboveground/below-ground biomass. Tree ring width may also be an imperfect proxy of tree growth. Destructive whole-tree analysis showed that expected productivity declines under climate change was more pronounced based on whole stem analysis vs. estimates from breast height, with top diameter growth responding more strongly to climate drivers (Chhin & Wang, 2005; Chhin, 2008).

Some correlative models make the assumption that the same species (or forest types) in different geographic locations would respond similarly to the same climate drivers. This implies that populations at the southern or low elevation margins would be most affected by climate warming. However, if populations have adapted to local environmental conditions, climate change may cause problems for the species throughout their range. Accounting for population structure makes a major difference: projections by forest growth models that assume a uniform species response have generally positive growth projections under climate change scenarios, whereas models that do not make this assumption and explicitly or implicitly take genetic adaptation of populations to local climate into account are far more pessimistic because of negative effects of maladaptation. For example, compare projections by Monserud *et al.* (2008) vs. Chhin *et al.* (2008) for lodgepole pine in Alberta; O'Neill *et al.* (2008) vs. Nigh *et al.* (2004) for lodgepole pine in British Columbia; or Coops & Waring (2001) vs. St. Clair & Howe (2007) for Douglas-fir in Oregon. Wang *et al.* (2006b) predict lodgepole pine growth with and without the assumption of uniform species response (uniform species response implied by using the best adapted seed source for reforestation) and find a decrease in growth projections by 20%–30% under future climate scenarios if regional population differences are taken into account.

Hence, more regionally explicit information is needed on how species respond to climate variability and projected climate change. In this study, we used 179 tree ring chronologies of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] from the International Tree-Ring Data Bank to study geographic variation in growth response to historical climate variability throughout its natural range from Canada to Mexico, and to make regional growth projections under 18 climate change scenarios. Prior research has established a thorough knowledge of plant–climate relationships in regional studies of Douglas-fir, with study sites concentrated in the Pacific Northwest (Brubaker, 1980; Meko *et al.*, 1993; Little *et al.*, 1995; Watson & Luckman, 2002; Case & Peterson, 2005; Holman & Peterson, 2006; Nakawatase & Peterson, 2006; Pederson *et al.*, 2006; Littell *et al.*, 2008). However, a range-wide analysis that takes advantage of high-quality continental-scale climate databases and consistent analytical methodology that allow regional comparisons is lacking.

The chronologies we analyzed were originally taken for diverse purposes, some of them for reconstructing past climate beyond the weather station record (e.g., Graumlich, 1987; Schweingruber *et al.*, 1991; Schweingruber, 1996; Pederson *et al.*, 2006). Therefore, we have at least a partial sampling bias toward exposed sites at

high elevations for their desired temperature or precipitation sensitivity of tree growth to temperature variability. As a precaution, we quantify this bias and its effects using a GIS-generated topographic convergence index (proxy for soil moisture availability) or slope aspect (proxy for exposure to evapotranspiration), and we further report our results for different elevation bands. However, it is unlikely that prior sampling objectives are confounded with geographic regions (i.e., differences in sampling objectives for different regions) to produce bias relative to our main objective: understanding differences in growth response of Douglas-fir to climate variability and projected climate change at a continental scale.

Materials and methods

Study area

We used tree ring chronologies from 179 sites that were made publicly available by many contributing authors on the International Tree-Ring Data Bank (ITRDB) (NOAA, 2008). The available data cover the natural geographic range of the species but have a limited amount of sites in Canada and on the coast (Fig. 1). Tree-ring data were available for both subspecies (some botanists refer to them as varieties), interior Douglas-fir (*Pseudotsuga menziesii* subsp. *glauca*) and coastal Douglas-fir (*P. menziesii* subsp. *menziesii*). Interior Douglas-fir grows naturally throughout the northern interior plateaus and the extended Rocky Mountain range from British Columbia to Mexico. Coastal Douglas-fir occurs from California to British Columbia along the coast and throughout the Coast Cordilleras. The two subspecies hybridize along mountain valleys in southern British Columbia. For the purpose of summarizing the results of this study, we subdivided the data set into six climate regions aided by a principal component analysis of 15 climate variables for the sample sites (results of this exploratory analysis are not reported). Note that the group 'Pacific Northwest' (Fig. 1) includes samples from both interior and coastal subspecies because climatic conditions (and as subsequent analysis showed: limiting climate factors) are very similar between the coastal and interior samples of this group. The geographic location of the 'Pacific Northwest' interior sample sites is the Columbia Mountain range lying to the west of the Rocky Mountains, a region also referred to as 'Inland Rain Forest.'

Chronology data

To ensure consistent treatment of chronologies for this study, we downloaded and reprocessed raw ring width data for 179 sites with a median number of 24 chronologies per site and a median number of two cores per tree. Multiple increment core samples for each site were cross-dated with the program COFECHA (Holmes, 1983), and cross-dated series were then standardized with the program ARSTAN version 41 (Cook & Krusic, 2005) to remove age-related trends and to produce a

master chronology for each site. Detrending was carried out in one step using a cubic spline with a 50% frequency-response cutoff equal to 67% of the series length according to Cook & Kairiukstis (1990). This is a fairly stiff spline, which we choose to be able to analyze interannual to multidecadal scale patterns. Finally, the chronologies were prewhitened by autoregressive modelling. The residual chronologies were used for all analyses of growth–climate relationships. The resulting dimensionless index, which represents tree growth variability, was normalized with respect to the 1901–1980 average. For later analysis, the index was adjusted to the 1961–1990 climate normal to have a common reference period with climate projections by general circulation models. The index mean for the 1901–1980 period was set to 1 for each chronology series to eliminate negative values. Only the 1901–1980 portion of the data was used for subsequent analysis, because quality climate data was available since 1901 and most chronologies ended around 1980.

Climate data

Our baseline climate data is derived from monthly precipitation and temperature grids that were generated by Daly *et al.* (2008) using the Parameter Regression of Independent Slopes Model (PRISM) to interpolate climate normal data observed at weather stations for the period 1961–1990 for the United States and Canada. We enhance this spatial database for use with sample data by applying lapse-rate based elevation adjustment functions that account for the difference between the recorded elevation of the sample and the elevation that was used to estimate climate variable values with PRISM for a grid cell (Hamann & Wang, 2005; Wang *et al.*, 2006a). Monthly historical data for the sample sites were generated by subtracting or adding historical data expressed as anomalies from the 1961 to 1990 climate normal data according to Mbogga *et al.* (2009). Similarly, climate projections for the sample sites for the 2020s, 2050s, and 2080s were generated by overlaying projections from general circulation models expressed as difference from the 1961 to 1990 normal period.

The IPCC (2007) recommends that climate change projections for different emission scenarios and from different general circulation models should be treated with equal probability, and ideally a full range of climate projections should be used in predictive biological models to quantify uncertainty. We therefore use the four major SRES emission and population growth scenario families (A1FI, A2, B1, B2) and implementations of these scenarios by five modeling groups (CGCM2, Canada; HADCM3, UK; ECAHM4, Europe; CSIRO2, Australia; and PCM, United States). The scenario family A1 represents a trend of globalization, resource-intensive economic growth and rapid population increase; A2 assumes slower population growth and regionally fragmented economic growth. B1 assumes the same global population growth as A1, but a shift towards a service and information economy. B2 represents the lowest population increases and local, environmentally sustainable economies (Nakicenovic *et al.*, 2000).

All grid manipulations of climate data, lapse rate elevation adjustments, data extraction from grids for sample locations,

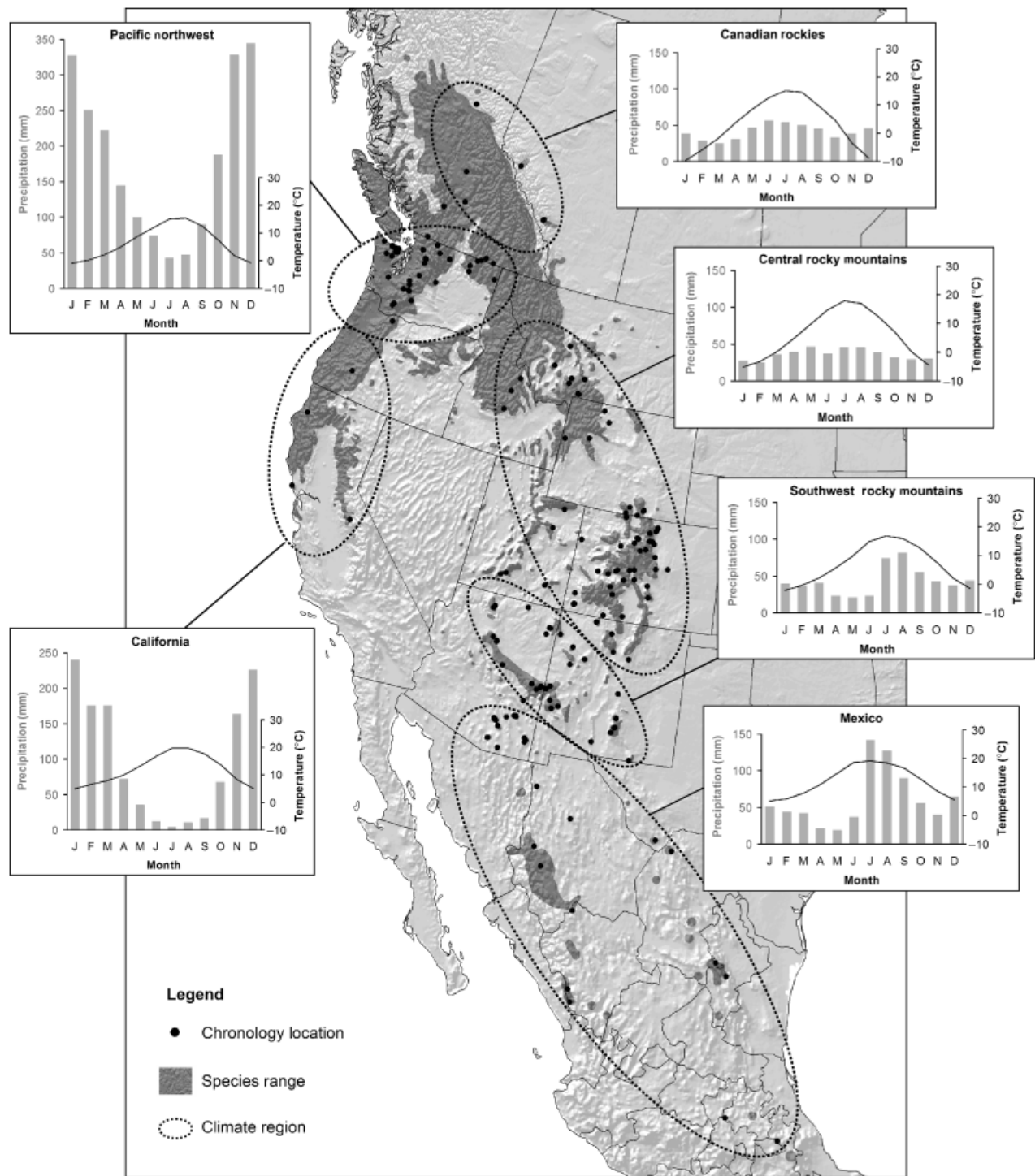


Fig. 1 Douglas-fir species range, sample sites for chronologies, and the average climate of the chronology sites, where groups reflect geography as well as climatic similarity of sample sites.

overlays of historical anomalies and climate projections as described above were carried out with a custom software application that we make freely available (available for download at <http://www.ualberta.ca/~ahamann/climate.html>).

The database and software for western Canada has been released (Mbogga *et al.*, 2009), while an extension of this database to western North America (T. Wang *et al.*, unpublished results) is available upon request.

Topographic indices

In order to better understand possible sampling bias of chronology sites for exposed locations (assuming that many of the original investigators were aiming to find trees that are sensitive to local temperature variability), we supplemented the ITRDB-provided geographic data (latitude, longitude, and elevation) with additional site characteristics: a radiation index as a proxy for exposure due to slope and aspect, and a topographic convergence index as a proxy of water availability. We found empirically that elevation data extracted from a 250 m resolution digital elevation model (DEM) result in the smallest discrepancy with the recorded elevations of sample sites when they are referenced to the nearest minute, resulting in a random location error of a few 100 m. Therefore, the indices were generated at 250 m resolution and values were subsequently extracted for the chronology sites with standard geographical information system software. Index values were also extracted for recorded occurrences of Douglas-fir in the Forest Inventory and Analysis database (FIA) for comparison of chronology sites with general occurrences of Douglas-fir throughout the climatic regions of the study area (Bechtold & Patterson, 2005).

In order to obtain a 250 m DEM, we mosaiced, reprojected, and resampled the 90 m resolution product of the Shuttle Radar Topography Mission (Farr *et al.*, 2007). Before further processing into indices, the 250 m DEM was geo-referenced aided by orthographically corrected remote sensing data (Landsat 5) to improve spatial accuracy of the DEM. A potential relative radiation index (PRR) was then calculated according to Pierce *et al.* (2005). PRR is an estimate of the amount of solar radiation received as a function of sun angle, slope, aspect, and shadowing by adjacent topography. A compound topographic index (CTI) to describe the effect of soil water accumulation resulting from topography was calculated according to Gessler *et al.* (1995). CTI accounts for slope and the upstream contributing area per unit width of the of the perpendicularly oriented down-slope water flow.

Analysis

The relationship between annual tree ring width and climate variables was examined using the 'response function' algorithm of the program PRECON v5.1 (Fritts & Shashkin, 1994). The program calculates principal components of climate data and relates the resultant components with the chronology data using multiple regression. The significance of the resulting regression coefficients were tested using a bootstrap routine included in the software package. Several studies suggested that radial growth was normally affected by the climatic conditions of the current and previous year (Fritts, 1976; González-Elizondo *et al.*, 2005; Dang *et al.*, 2007). Therefore, we evaluated 14 months of precipitation and temperature data, starting with July of the previous year to August of the current year as predictor variables for tree ring width.

Based on the results of the chronology response function analysis we constructed a simple heat moisture index, described by Tuhkanen (1980). We divided temperature (in units of °C) by precipitation (in units of meters) to arrive at an index

for dryness. Therefore, the index value increases as temperature increases and precipitation decreases. While more sophisticated dryness indices exist that estimate evapotranspiration and soil water balances (e.g., Alley, 1984; Hogg, 1997), this index has the advantage that it can be composed of different months for precipitation and temperature (Rehfeldt *et al.*, 1999). In this study, the average April–June temperature of the current growing season was divided by the total precipitation from September of the previous year to June of the current year, which covers the monthly climate variables that influence growth for interior Douglas-fir according to the response function analysis. For the climate data of this study, the heat moisture index represents precipitation more closely than temperature. The index is linearly correlated with temperature ($r = 0.46$) and approximately linearly with the logarithm of precipitation ($r = -0.86$). Moving correlation functions (7–15 years) were used to investigate the stability of the correlations between this index and ring width over the 1901–1980 period.

Growth predictions under climate change scenarios for the 2020s, 2050s, and 2080s were carried out individually for each chronology site using simple linear regression equations that were developed with the composite heat moisture index as independent variable and ring width as dependent variable for the 1901–1980 period. The predicted chronology value for the 1961–1990 climate normal period was set to 1 in order to have a common reference period with climate projections by general circulation models. Therefore, projected tree ring indices >1 imply increased growth and projected indices smaller than 1 indicate decreases in growth under climate change scenarios relative to the 1961–1990 normal period. The projections for individual chronology sites were summarized in various ways using boxplots and averages for regions and elevation bands within regions.

Results and discussion

Climatic groups and species representation by samples

The two coastal groups 'Pacific Northwest' and 'California' are characterized by high winter precipitation and summer droughts that are more severe in the southern coastal group (Fig. 1). The climate of sample sites for the four interior groups 'Canadian Rockies' to 'Mexico' is remarkably homogeneous. Although there is a large difference in winter temperature among the regions, growing season temperatures peak at around 18 °C for all groups and total precipitation for the April–September period is around 380 mm. There is a slight increase in growing season temperature and precipitation from the north to the south. The two southern interior groups 'Southwest Rocky Mountains' and 'Mexico' further show an increasingly pronounced dry season between April and June, followed by a period of higher precipitation (Fig. 1).

Chronology samples appear to be representative of the general Douglas-fir populations recorded in forest

Table 1 Representation of Douglas-fir populations in climate regions by chronology sample sites used in this study

Region	Forest Inventory Databases			Chronology sites		
	<i>N</i>	Mean	Range	<i>N</i>	Mean	Range
<i>Central Rocky Mountains</i>						
Topographic convergence index	2728	8.5	6.8–11.1	67	8.8	6.8–12.1
Potential relative radiation (%)		45	27–62		45	27–60
Elevation (m)		2322	1699–2896		2251	1700–2835
<i>Southwest Rocky Mountains</i>						
Topographic convergence index	498	8.7	7.2–10.9	32	9.0	7.6–10.5
Potential relative radiation (%)		46	31–57		44	36–56
Elevation (m)		2493	2225–2764		2492	2012–2940
<i>Mexico</i>						
Topographic convergence index	(no data)			30	8.2	6.8–10.1
Potential relative radiation (%)					42	22–60
Elevation (m)					2515	2044–3073
<i>Canadian Rockies</i>						
Topographic convergence index	3809	9.0	7.0–11.7	8	8.1	6.4–9.9
Potential relative radiation (%)		47	33–62		50	22–65
Elevation (m)		991	655–1404		944	200–1432
<i>California</i>						
Topographic convergence index	2574	8.4	6.8–10.7	4	9.1	7.4–12.7
Potential relative radiation (%)		45	25–63		45	9–65
Elevation (m)		889	267–1510		1110	120–1560
<i>Pacific Northwest</i>						
Topographic convergence index	1955	8.5	6.8–10.9	38	8.0	6.7–9.9
Potential relative radiation (%)		46	27–61		43	22–63
Elevation (m)		837	168–1432		1046	710–1550

Listed are the number of samples (*N*), the sample means for elevation and indices of sample site exposure, and the range of values from the 10th to the 90th percentile.

inventory databases with respect to elevation and exposure (Table 1). For the interior groups 'Canadian Rockies,' 'Central Rocky Mountains,' and 'Southwest Rocky Mountains,' means and ranges of elevation and exposure indices of the chronology samples are very similar to those of the larger inventory databases. Nevertheless, we should point out that the low spatial accuracy of chronology sites (nearest arcminute) and the corresponding resolution of our topographic databases (250 m) do not allow us to reconstruct microsite conditions. Although there is no bias in elevation, it remains possible that there is sampling bias toward exposed sites that we cannot detect. However, unless there is an unlikely systematic geographic variation in this bias, it should not compromise our analysis. We do find bias in chronology samples toward higher elevation in the 'Pacific Northwest' group, which is mainly caused by lack of chronology sample sites at low elevations (between 200 and 700 m). A very small sample size for the 'California' group does not allow us to draw inferences on the general population, and we cannot investigate sample representation for the 'Mexico' group for lack of inventory data.

Climate factors limiting growth

A dendro-climatic response function analysis was used to identify climatic factors that may limit growth (Fig. 2). To summarize significant coefficients for the monthly climate variables with individual chronologies, we indicate with an asterisk if more than 25% of samples within a group have significant coefficients. Particularly for interior Douglas-fir, instances of significant monthly precipitation variables are more common than in temperature variables. Standard errors of the average regression coefficients, including nonsignificant coefficients, are indicated by thin lines. The coefficients are expected to approach zero at the end of the growing season, and this is the case for July or August for both temperature and precipitation for all regions.

The standard error for the estimate of regression coefficients suggests that the four sample sites available from California were not sufficient to obtain interpretable results. However, the region 'Pacific Northwest' reveals some interesting patterns. As has been previously shown (Brubaker, 1980; Meko *et al.*, 1993; Little *et al.*, 1995; Holman & Peterson, 2006; Nakawatase &

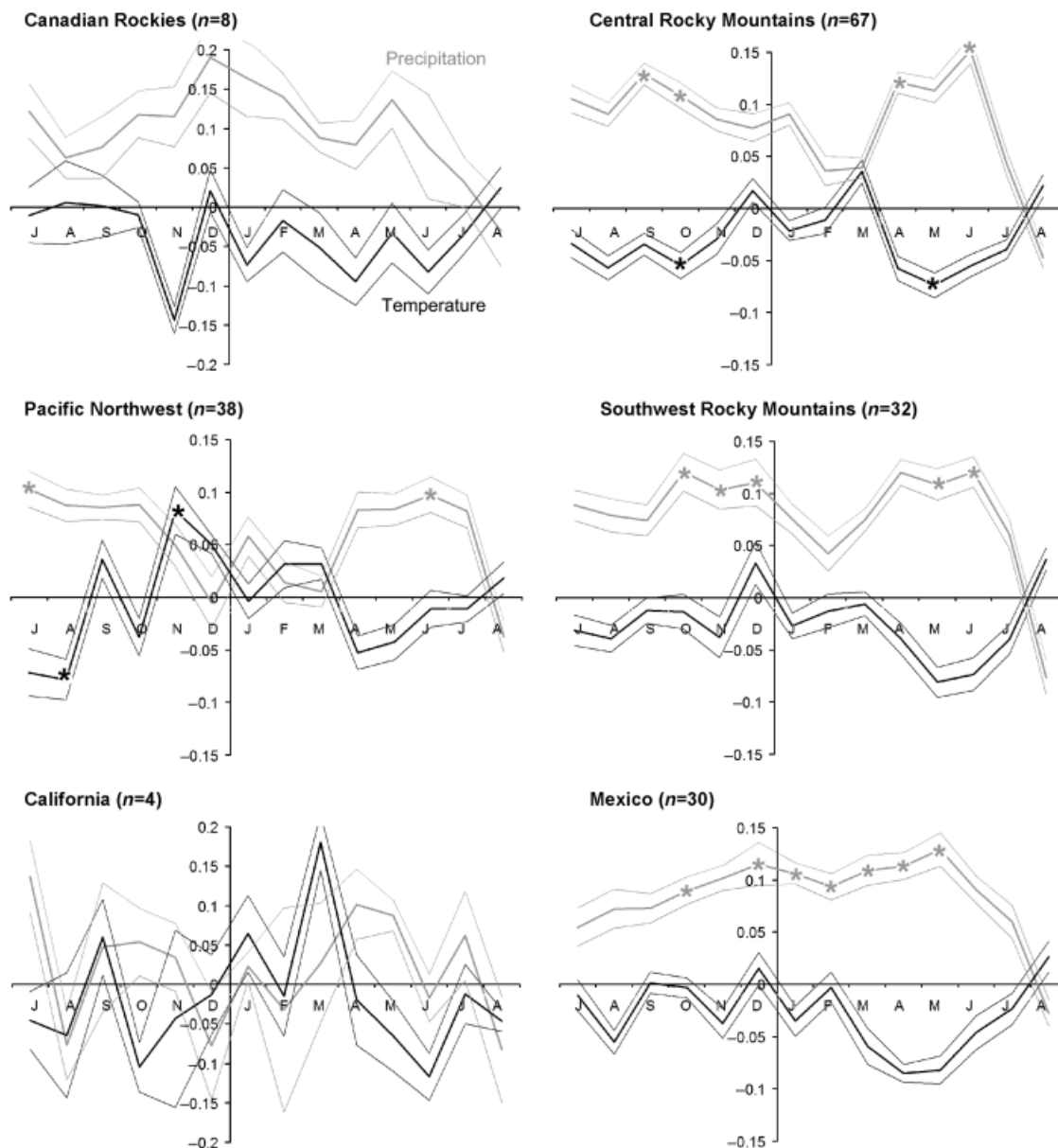


Fig. 2 Regional averages of regression coefficients between ring width and monthly precipitation (gray) and temperature (black). The standard error of the estimates is indicated by thin lines. Asterisks indicate that more than 25% of the correlations of individual chronologies are significant after adjustment for multiple inference.

Peterson, 2006; Littell *et al.*, 2008), growing season dryness (low precipitation and to some degree high temperature between April and July) limits growth of Douglas-fir on the coast. We also found a pronounced positive influence of November temperature of the previous year on growth in many samples, which suggests that photosynthesis in winter is an overall important contributor to conifer growth in the Pacific Northwest. This result supports Waring & Franklin's (1979) original hypothesis that winter photosynthesis is a key advantage that conifers have over broadleaves,

partially explaining their prevalence in the Pacific Northwest (Waring & Franklin, 1979; Brubaker, 1980).

For the interior variety, we found growth–climate relationships somewhat similar to those observed in a number of regional studies (Watson & Luckman, 2002; Case & Peterson, 2005; Pederson *et al.*, 2006; Littell *et al.*, 2008). Consistently across all interior regions, ring width is correlated to precipitation in fall of the previous year and the current growing season. Temperature of the current growing season has a negative influence, indicating an overall growth limitation

through water stress, where water availability is a stronger limiting factor than heat. Except for the region 'Mexico,' the strength of the positive influence of winter precipitation drops in February or March, which we interpret as two conflicting effects of precipitation: fall and early winter precipitation replenish soil moisture reserves, but late winter precipitation and the resulting spring snow pack shorten the growing season. Spring temperatures in Mexico are too high to result in a significant snow pack that has this effect (Fig. 1).

In addition to these regional summaries, we also investigated the influence of elevation and topographic indices (CTI, PRR) by grouping samples above and below the median elevation or index value within regions. Generally, we found that the strength of the relationships increases with altitude but topographic indices had no effect (data not shown). For different elevation bands we did not find qualitatively different plant–climate relationships as, for example, Case & Peterson (2005) in a regional study that thoroughly investigates small-scale changes in plant–climate interactions along an elevation gradient. In this broad geographic sample, plant–climate relationships did not change qualitatively along elevation or exposure gradients within geographic groups as they did between groups. For conciseness, we chose not to report high and low elevation plant–climate relationships separately in this section, but we used elevation bands above and below the approximate median elevation within regions in the next section to account for differences in the strength of the relationship.

Growth predictions under climate change

After exploring several options to predict growth under climate change scenarios, we decided to use a simple composite heat moisture index and limit our projections to three interior regions where we had the largest sample sizes and the strongest correlations between climate factors and ring width. Given the caveats outlined in the introduction, we think it is prudent to use a parsimonious predictive model and even then interpret the results with caution. The heat moisture index we choose reflects the results shown in Fig. 2 for the regions 'Central Rocky Mountains,' 'Southwest Rocky Mountains,' and 'Mexico': we divided the average of monthly mean temperatures of April, May, and June by the sum of monthly precipitation from September of the previous year to June of the current growing season (in units of meters). For 105 tree ring chronologies (or 81% of the interior samples), we found significant linear correlations with this heat moisture index (without adjustment for multiple inference), and visual inspection showed that all relationships with individual

chronologies were linear. We could not find a comparable population-level climate index that would show consistent positive or negative impacts of climate variability on growth of coastal Douglas-fir.

Given the results by Briffa *et al.* (1998) that plant–climate relationships may change over time, we used 7- to 15-year moving correlation functions to investigate the stability of the growth response to the heat moisture index. We found largely constant relationships for most individual chronologies and virtually perfectly constant correlations for regional means of chronologies for any moving correlation window (data not shown). The result is not unexpected because we did not evaluate chronology data for recent decades, where the climate regime generally shifted to warmer and drier conditions. We also could not find any evidence in this data set that short-term cyclical climate phenomena, such as the El Niño Southern Oscillation or the Pacific Decadal Oscillation lead to temporal adaptations through plasticity (e.g., different needle biomass) that detectably alter plant–climate relationships.

The second important check when using correlative approaches to predict climate change impacts is to understand the degree of extrapolations beyond historical data coverage. We found that regional climate projections from all 18 general circulation models for the 2020s, 2050s, and 2080s are within the range of observed climate variability for the 1901–1980 period (Fig. 3). However, it is important to keep in mind that general circulation models generate projections for 30-year normal periods, i.e., what is referred to as a projection for the 2020s is a prediction for the 2011–2040 normal period. Thus, individual years within that period are likely to exceed the observed range of climate variability from 1901 to 1980. Nevertheless, for predicting an average growth response corresponding to a 30-year climate change projection up to the 2080s, the available data appears to be suitable.

Regional differences growth response

While projected changes in dryness as described by the heat moisture index is comparable among the three interior sample regions 'Central Rocky Mountains,' 'Southwest Rocky Mountains,' and 'Mexico,' the predicted growth response is markedly different (Fig. 3). The average projected growth response to the range of climate change scenarios is far more pronounced in the north and center of the interior Douglas-fir range than at the southern fringe and for outlying populations in Mexico. A breakdown of the projected growth response for each chronology site and climate change scenario by region and elevation class is shown in Fig. 4. Douglas-fir in Mexico showed the least reduction in productivity.

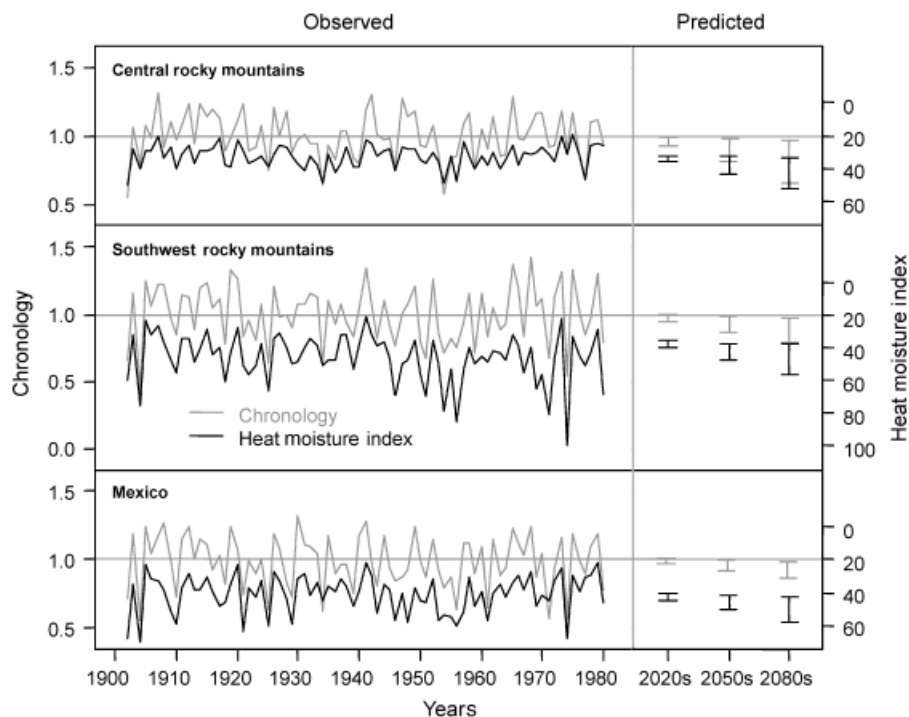


Fig. 3 Observed relationship between ring width and heat moisture index averaged by region (left panels) and projected changes in climate and growth for the 2020s, 2050s, and 2080s (right panel). The bars represent the range of climate change projections from 18 general circulation models and corresponding growth predictions.

Moderate growth reductions were found in the southern United States, and strongly negative response in the central Rocky Mountains. Variability of the growth response among populations decreased from northern to southern latitudes, and growth reductions were more pronounced for high than for low elevation populations.

These regional differences do not reflect differences in the strength of the plant–climate relationships. There are no noteworthy latitudinal or elevational trends in the R^2 values for chronologies and the heat moisture index (Fig. 5). Instead, regional differences in growth projections are driven by a latitudinal trend in the slope value of climate–chronology relationships. For a given change in the heat moisture index, northern sources showed on average a higher decrease in ring width than southern sources. The latitudinal trend is more pronounced for the high-elevation subset, but statistically significant for both subsets as well as for high and low elevation chronologies combined ($P < 0.0001$ after log-transformation of the ‘Slope’ value to meet the assumption of homogeneity of variances).

We can think of two possible explanations for these results. Douglas-fir populations in northern latitudes may occupy an ecological niche space that is more strongly determined by climate factors, while southern and outlying populations tend to occur at sites where

topographic factors contribute to soil moisture availability and therefore buffer the impact of climate on growth. However, we could not find significant differences of Douglas-fir occurrences among regions with respect to a topographic convergence index as proxy for soil moisture availability or PRR as a proxy for exposure to evapotranspiration (Table 1). It is difficult to demonstrate the absence of a relationship, but the indices are suitable to detect regional differences in site characteristics: Bunn *et al.* (2005) using a very similar topographic convergence index and PRR index found a clear influence on ring width in foxtail pine. However, it should be noted that the resolution of their data was much higher (10 m) so that micro-site conditions could be modeled. The accuracy of location information of this chronology database (approximately 250 m) did not allow matching micro-site information for analysis. The second and more convincing argument against this explanation is that microsite conditions were buffering the impact of climate on growth in southern and outlying populations, we would expect R^2 values to decrease accordingly, which is not the case.

The alternative explanation could be that southern and outlying populations are genetically better adapted to drought conditions, and are therefore relatively less affected by drier conditions. Interpreted in this way, our

data would support the case made by Hampe & Petit (2005) that populations from the rear edge of the species range may be more stable and resilient to climate change than expected from metapopulation theory (e.g., Lawton, 1993; Vucetich & Waite, 2003) or projected by bioclimate envelope models (e.g., Thomas *et al.*, 2004). Our results suggest that climate change impacts will not be primarily restricted to populations in the

southern or trailing edge of the species distribution. Instead the data support the view that climate change may impact species throughout their range due to genetic adaptation of populations to local environments (e.g., Hampe, 2004). Here we even found that northern and high-elevation populations may be the most vulnerable, a generally opposite conclusion to results from bioclimate envelope models, which assume genetic homogeneity of species populations throughout their range.

What do projections of decreased ring width due to climate change mean at the forest stand, or ecosystem level? Van Mantgem *et al.* (2009) has shown that subtle changes to mortality rates may have profound effects on ecosystem composition, structure, and function over time. Reduced growth projections could certainly lead to changes in stand productivity or increased mortality rates. Nevertheless, we should be careful in drawing conclusions in absolute terms, rather than comparing effects among different regions. For example, possible sampling bias for dominant or co-dominant trees may not capture more severe climate change impacts on small trees. Further, in a mixed forest community, the overall climate change impact on Douglas-fir growth and population dynamics will depend on how competing tree species respond to changing climate as well.

Our results also suggest that dendrochronology approaches may have potential to detect genetic differences among populations that can normally only be revealed in long-term provenance trials, where sources from various locations are grown together in a common garden environment. Such information is invaluable to identify suitable genotypes for reforestation under climate change. We propose that a purposeful sampling design (e.g., controlling for site index, soil moisture availability, and exposure) may disentangle the confounding effects of genotypes and environmental factors at smaller scales and allow the identification of populations suitable for reforestation under climate change without expensive and decade-long plantation

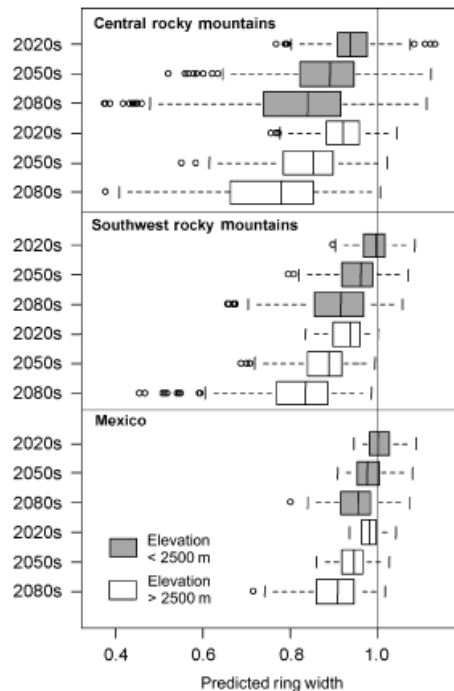


Fig. 4 Regional projections for of climate change impacts on Douglas-fir growth based on 18 climate change scenarios. Boxplots are based on 18 predictions for each of 179 individual chronology sites (removing sites with nonsignificant correlations does not alter the boxplot in a perceptible way). For each regional subset, 50% of predictions fall within the box, and outliers according to Tukey's inner fence criteria are indicated by circles.

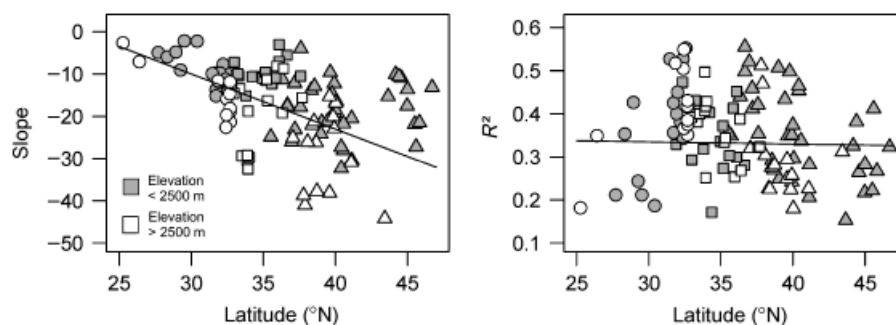


Fig. 5 Slope and R^2 values of regression equations between ring width and heat moisture index for 129 chronologies from the regions Mexico (○), Southwest Rocky Mountains (□), and Central Rocky Mountains (△). The slope value for individual chronologies (left) are significantly correlated to latitude ($P < 0.0001$, for testing slope values were multiplied by -1 and log-transformed).

experiments. This potential of dendro-climatology for research in ecological genetics could be tested by sampling trees in provenance trials to confirm genetic control of plant–climate relationships, and by sampling *in situ* populations that were previously tested in provenance trials to verify that similar patterns of genetic variation in adaptive traits can be found.

Conclusions

We conducted a continental scale analysis of existing Douglas-fir chronologies to complement detailed regional scale studies. While the distribution of the available samples did not allow the detection of small-scale differences in plant–climate relationships (as for example in Case & Peterson, 2005; Littell *et al.*, 2008), the analysis did reveal broad geographic structure. Plant–climate interactions and genetic adaptations at both scales need to be considered to predict potential climate change impacts (Littell & Peterson, 2005).

For the interior variety, we found that low precipitation and high growing season temperatures limit growth, with the more southern and outlying populations responding less negatively to drought conditions. The results indicate genetic adaptations to local climate and support the view that climate change may impact species throughout their range due to genetic adaptation of populations to local environments (e.g., Hampe, 2004). Projection of growth under 18 climate change scenarios suggest minor growth impacts for outlying populations in Mexico, and the greatest vulnerability of Douglas-fir populations at higher latitudes and higher elevations, confirming concerns that have previously been raised for example by Pederson *et al.* (2006) for a Montana study site.

For the coastal variety of Douglas-fir, we found positive correlations of ring width with summer precipitation and temperature of the preceding winter, indicating that growth of coastal populations was limited by summer dryness and that photosynthesis in winter contributed to growth. However, we could not find a regional-level climate index that shows consistent positive or negative impacts of climate change on the observed chronology samples. We propose that while there may be local variations, climate change impacts are likely to be overall neutral for the coastal Douglas-fir variety and interior populations of the 'inland rain forest' ecosystems.

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