

Recent, Climate-driven Changes in Demography and Radial Growth of Subalpine
Conifers of the Central Sierra Nevada

By

CHRISTOPHER RYAN DOLANC
B.S. (Missouri State University) 1996
B.S. (Missouri State University) 1999
M.S. (Miami University) 2002

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Approved:

Michael G. Barbour

Mark W. Schwartz

Hugh D. Safford

Committee in Charge

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ABSTRACT

Climate-linked vegetation models predict major areal reduction of subalpine and alpine vegetation over the next 100 years via replacement by lower-elevation vegetation. However, trees native to subalpine zones are typically long-lived and likely to respond to climate change individualistically, instead of as a whole. Empirical data of response to recent climate change may be more useful in understanding how high-elevation trees will continue to respond to climate change into the future. I re-sampled historical US Forest Service vegetation plots from the early 1930s and compared modern versus historical stand conditions to determine how subalpine forests of the central Sierra Nevada, California, have changed over the last 75 to 80 years. I also collected tree cores from most re-sampled locations to examine trends in radial growth increment during the same period. By focusing on high-elevation (2300 – 3500 m) plots relegated to wilderness areas, impacts from human disturbances, including fire suppression should be minimal. My comparison of modern versus historical stand conditions showed that modern subalpine forest structure is considerably different, with 63% more small trees (10.2 – 30.4 cm dbh) and 20% fewer large trees (≥ 61.0 cm). These trends are surprisingly consistent across the landscape and from species to species. These changes are likely due to increasing temperatures over the last few decades, resulting in longer growing seasons. When correlating change in structure with change in climate across the landscape of my study area, plots with greater increases in temperature are more likely to have increased numbers of small trees and decreased numbers of large trees, since the 1930s. This correlation is strongest during the winter (December through February) months. Analyses of radial growth and climate during from 1895 to 2007 showed that, in general, growth of

subalpine species is negatively correlated with maximum temperature and positively correlated with precipitation. Of seven most common subalpine species, lodgepole pine (*Pinus contorta* ssp. *murraynana*) and mountain hemlock (*Tsuga mertensiana*) responded most positively to warmer, drier conditions and may be in the best position to endure predicted change. These species, plus whitebark pine (*Pinus albicaulis*) also showed increased growth in the upper portions of their elevational range, relative to lower portions. For whitebark pine and mountain hemlock, radial growth from the upper portions has actually been higher than that from lower portions for the last few decades. My combined results do not support the prediction that subalpine vegetation will be largely replaced by lower-elevation vegetation over the next 100 years; recruitment and growth of trees in subalpine is good. Temperatures have been increasing and at high elevations and moisture is not yet limiting, allowing for longer, moderated growing-seasons conducive to greater recruitment and growth. However, continued change could eventually tip the scales in the other direction, facilitating factors such as increased fire activity and disease.

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INTRODUCTION

Science has projected a rather dim future for high-elevation ecosystems. With presumed continued global warming, most models are predicting major loss of subalpine and alpine vegetation via displacement by lower-elevation species that are expected to be competitively superior in the warmer climate of the future. In California, subalpine and alpine vegetation is expected to shrink in area by 54 to 78% over the next 100 years (Lenihan *et al.* 2008). However, models such as this involve an enormous array of assumptions and have not been thoroughly tested with empirical data. In addition, though sufficiently alarming, predictions such as these are not particularly useful to people tasked with protecting high-elevation species because they predict the disappearance of entire communities over vast tracts of land making it difficult for conservationists to focus their protection efforts.

This dissertation grew out of my desire to provide a more specific, more accurate understanding of how subalpine tree species may fare under future climatic conditions. Central to this objective is the idea that we can use our knowledge of how species are currently responding to climate change to predict their future response. The advantage of such an approach is the use of empirical data that do not make assumptions about the complex relationships between trees and their environment. My research uses historical data to examine recent trends in demography and growth of subalpine species as well as recent trends in climate. Since temperatures in the Sierra Nevada have been warming steadily for several decades, one may assume that shifts in demography or growth in response to warming may already be occurring. The resulting trends can also be used to extrapolate into the future and test existing models.

In chapter 1, I report that demography of subalpine forests of the Sierra Nevada has changed markedly since the early 1930s. By re-sampling historical vegetation plots, I was able to directly compare modern versus historic (75+ years ago) conditions. Since the early 1930s abundance of small trees has increased by 63% while the abundance of large trees has decreased by 20%. These trends were remarkably consistent across the 5500 km² area of my study region and similar for each of eight conifer species examined. Both recruitment and mortality appear to have increased in subalpine forests, indicative of an overall increasing turnover rate and indicative of warming. Since these stands fall between 2300 and 3500 m elevation and are mostly in wilderness, it is difficult to attribute this change to anthropogenic disturbances such as logging and fire suppression. Instead, it is likely that changing climate, via longer growing seasons is the culprit.

For chapter 2, I correlated the changes observed in chapter 1 – shifts in demography since the early 1930s – with changes in climate during the same period. For this analysis I took advantage of the PRISM climate data set, which interpolates climate data across the landscape. The main question was “Are plots where I observed the greatest change in demographic structure also where we have seen the greatest increase in temperature?” Though the relationship between climate change and demographic change was modest in my analysis, the trends do support the conclusion that longer snow-free periods (growing season) could be affecting small tree recruitment and large tree mortality in opposite fashion as in chapter 1.

In chapter 3 I used the 500+ cores I collected during my re-sampling effort to construct a dendroclimatological analysis of how individual subalpine species responded to climate fluctuations from 1895 to 2007. Though dendrochronological studies on

subalpine species in California are plentiful, no study had yet examined recent growth response to climate over a wide area for several species within one study. This approach makes it easier to determine which species may respond best to different types of future climate scenarios. All seven species examined showed strong negative correlations with maximum temperature during the summer months and most also exhibited strong positive correlations with precipitation throughout the year. These results suggest that growth of subalpine species in the Sierra Nevada will be reduced if the climate warms and/or dries. Interestingly, of all species, mountain hemlock (*Tsuga mertensiana*), which is mostly relegated to the coolest, wettest slopes in the region, responded best to warm and dry conditions. Lodgepole pine (*Pinus contorta* ssp. *murrayana*) also appeared less sensitive to warm, dry conditions. These two species may be positioned to compete best in the subalpine of the future.

Finally, for chapter 4, I examined recent trends in growth by elevation for the three highest-distributed species in my study area, lodgepole pine, mountain hemlock and whitebark pine (*Pinus albicaulis*). All three species show signs of increasing growth at higher elevations of their distributions, relative to lower elevations of their range. In other words, within a given species, individuals growing at higher elevations have seen their growth increase more than individuals at lower elevations. For mountain hemlock and whitebark pine, growth at higher elevations is currently greater than individuals from lower elevations. This result may be related to the well-documented observation that growth of trees growing near treeline is mostly limited by temperature, while those growing further from treeline can be limited by precipitation, competition and potentially a complex suite of factors. This makes sense, knowing that temperatures in the region

have increased while precipitation has changed very little. The limitation on growth by temperature has been relaxed near treeline. Though temperature has also increased in locations further from treeline, other factors, such as increasing drought stress, may still be limiting growth.

Overall, it appears as though models that predict major reduction in subalpine and alpine vegetation over the next 100 years may need to rethink their timing. My observed increases in abundance and growth are not indicative of massive displacement by lower-elevation species, at least not yet. Subalpine trees are very long-lived and famously resilient to climatic fluctuations. Significant displacement by lower-elevation species is likely to take hundreds to thousands of years at the current pace. However, disturbances such as increased fire frequency or disease, which are also affected by climate change, could quickly manifest and tip the scales in favor of more rapid displacement. In addition, the surprising finding that growth of mountain hemlock responds best to warm, dry conditions is an example of why we need more specific, higher-resolution models. Currently, models would probably predict mountain hemlock to be most likely to be displaced due to warmer, drier conditions in the future, but my results suggest otherwise.

Globally, trees that grow at high elevations are more sensitive to temperature than other factors. In the Sierra Nevada, where the growing season is influenced greatly by late-summer drought, precipitation is probably also important to tree recruitment and growth. My results on growth response to climate suggest that all species in the region are dependent on precipitation, but individuals at higher elevations are still mostly limited by temperature. It seems likely that in the Sierra Nevada, precipitation is more important for recruitment and temperature is more important for growth and survival. Regardless,

current and future distributions of subalpine species are likely to be very closely tied to snowpack and future work should focus on high-resolution descriptions of how subalpine trees and snowpack interact.

REFERENCE

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CHAPTER 1

Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007

Christopher R. Dolanc¹, James H. Thorne² and Hugh D. Safford^{2,3}

¹Corresponding author, Department of Plant Sciences and Ecology Graduate Group,
University of California, Davis, CA 95616, USA, crdolanc@ucdavis.edu

²Department of Environmental Science and Policy, University of California, Davis, CA
95616, USA

³USDA Forest Service, Pacific Southwest Region, Vallejo, CA 94592, USA

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ABSTRACT

Aim: Many climate-linked vegetation models predict major contraction of subalpine forests within the next 100 years, which would require a relatively rapid replacement of high-elevation species by lower-elevation species over large portions of subalpine forest. We tested this prediction by comparing empirical data from a historic data set with data collected from resampled sites from 2007-2009.

Location: Central Sierra Nevada, California, USA, 2300 – 3400 m elevation.

Methods: We resampled 139 undisturbed historical vegetation plots across 5500 km² originally sampled from 1929-1934 in the subalpine zone of the Sierra Nevada, and compared historical with current forest structure and composition. We compared historic and modern climatic conditions using two high-elevation climate stations nearby.

Results: Subalpine forests experienced a net increase in tree stem density of 30.4%, including a 63.3% increase in small trees. Six of eight tree species showed statistically significant increases in small tree density, including species with distributions at both the upper and lower boundaries of subalpine. Increases in small tree density were partly offset by a 20% decrease of large trees. These shifts were significant throughout the landscape of our study area. Modern stand composition was indistinguishable from historical composition. Daily minimum temperature (+1.2°C) and precipitation (+15-48%) both increased during the same period.

Main Conclusions: Warming temperatures plus steady to increasing precipitation have led to less stressful conditions for recruitment and survival of small trees, and are probably contributing to increased mortality of large trees. Tree abundance and composition in the subalpine has not changed in the direction predicted by vegetation

models linked to future climate scenarios. Our results underline the fundamental role that moisture balance plays in structuring Mediterranean-zone montane forests. Future shifts in vegetation composition and structure from these regions will likely depend on interactions between water balance and disturbance factors like fire, insects, and disease.

INTRODUCTION

Evidence of recent climate change is widespread (IPCC, 2007) and bioclimatic models based on current and projected trends have predicted significant loss of biodiversity (Sala *et al.*, 2000), range shifts (Loarie *et al.*, 2008) and novel and disappearing climates (Williams *et al.*, 2007). Unfortunately, most bioclimatic models are not able to properly account for factors such as biological interactions, adaptation, dispersal limitation, disturbance, and fine-scale habitat heterogeneity (Heikkinen *et al.*, 2006; Randin *et al.*, 2009; Dobrowski *et al.*, 2010), making them best applied as a first-draft, coarse estimation of climate effects on species ranges and biodiversity (Pearson & Dawson, 2003). There remains a great need for empirical data at regional and local scales as a means to provide a more detailed and practical picture of current (and potentially future) species responses (Parmesan, 2006).

Most vegetation models linked to global warming scenarios predict that shrinking subalpine forests will be replaced by species from lower elevations that move upslope in response to warming (Guisan & Theurillat, 2001; Lenihan *et al.*, 2008), but is it safe to assume that species historically restricted to lower elevations will always outcompete and displace higher-elevation species? Even if this assumption is valid, most high-elevation conifers are extremely long-lived – many subalpine conifer species are known to attain

ages in excess of 750-1000 years – and such species are famously slow to respond to climatic stimuli (Perkins & Swetnam, 1996; Grime, 2001). Adult trees in temperate forest ecosystems are hardly, if ever, at equilibrium with current climate (Svenning & Skov, 2004; Millar *et al.*, 2007b), and mature trees might be expected to survive future change for hundreds of years, depending on the strength of competition, the rate of climate warming, disturbances, and potentially numerous unknown factors (Loehle, 1996).

Studies that resample historical data sets can quantify on-the-ground change and examine its relationship to spatiotemporal variance using a variety of regional or local variables. Results from these types of studies can be used to validate predictions of biotic response to future climates (Parmesan, 2006) and have the potential to reveal much more about how climate-driven responses of different species will manifest at more local scales (Beckage *et al.*, 2008; Moritz *et al.*, 2008). By providing insight into the trajectories of historical to current species demography, resampling studies also allow for more accurate projection of such changes into the future. This should help to identify areas that are more likely to experience climate-driven change, as well as which species or functional types are most or least susceptible to changes in climate (Dobrowski *et al.*, 2010). Such nuanced data should be more valuable to local land managers and conservationists than nebulous predictions of generalized ecosystem responses. Resampling historical field data also permits empirical assessment of temporal changes in ecological variables like phenology, species composition and distribution (Walther *et al.*, 2002; Parmesan, 2006). Recent US resampling studies assessing vegetation change over the last 25-80 years have documented marked increases in hardwood densities at a hardwood-conifer ecotone in Vermont (Beckage *et al.*, 2008); elevation increases for canopy trees in southern

California (Kelly & Goulden, 2008) and shifting slope-aspect preferences for forest understory herbs in southern Oregon (Damschen *et al.*, 2010). In all cases these trends have been at least partly ascribed to climate change.

The area occupied by subalpine and alpine vegetation in California is predicted by dynamic vegetation models to decrease substantially between now and the end of the 21st century (Lenihan *et al.*, 2008). This forecast represents the greatest areal reduction of any major vegetation type in California and mapped projections show alpine and subalpine vegetation almost completely disappearing from the central and northern Sierra Nevada. Although the models behind these projections incorporate mechanistic relationships between climate, fire, and plant physiology, they mostly lack the capacity to predict species-specific responses. Idiosyncratic species-level responses to climate warming and interacting disturbances could compromise the accuracy of projections made at the level of physiognomic types (Peterson, 1998), especially where relatively few species dominate the type. For example, the recruitment of *Pinus albicaulis* (whitebark pine), a dominant subalpine tree throughout western North America, is heavily dependent on seed caching by Clark's nutcracker (*Nucifraga columbiana*), (Hutchins & Lanner, 1982) and the fate of whitebark pine is likely linked to that of the nutcracker. Also, tree species of the Sierra Nevada subalpine zone are differentially fire sensitive, and projected increases in fire activity are not likely to have a single, well-defined effect on the vegetation type as a whole. Dispersal ability also varies substantially among species, and should have a major effect on the ability of models to accurately forecast vegetation impacts of climate (Dobrowski *et al.*, 2010).

Our objective was to determine whether demographic and compositional changes have occurred in the last $\frac{3}{4}$ century in undisturbed subalpine (>2300 m elevation) conifer stands in the Sierra Nevada, California, USA (Figure 1.1). We resampled historical vegetation plots from the central Sierra Nevada to compare modern stand conditions with conditions about 75 years ago (see also Vankat, 2011). The historical data were from the USDA Forest Service's Vegetation Type Mapping (VTM) program, which sampled and mapped vegetation across California from 1929-1934 (Thorne *et al.*, 2008). Other researchers have resampled VTM plots to compare modern and historic conditions (e.g. Minnich *et al.*, 1995), but no study to date has resampled VTM plots with the specific purpose of examining differences that may be attributable to climate change. Our study took advantage of the many high-elevation VTM plots, where human disturbances common at low elevations are minimal, to examine changes in structure and composition of subalpine vegetation over the past 75 years. Given the magnitude of changes in air temperatures and snowpack that have already occurred over the last 50 years (Stewart *et al.*, 2005; Barnett *et al.*, 2008; Coats, 2010), we expected to find that projected future changes in subalpine forest structure and composition were already underway. Specifically, we hypothesized that composition of subalpine forest stands should be shifting to reflect greater proportional representation of tree species centered at lower elevations, and structure should be changing to reflect increasing densities of younger trees.

METHODS

Field Methods and Study Area

VTM crews collected tree data in 2 chains X 1 chain (809 m²; 1/5 acre) plots, by species, in four diameter size classes: 10.2-30.4 cm (4-12 inches), 30.5-60.9 cm (12-24 inches), 61.0-91.3 cm (24-36 inches) and > 91.4 cm (36 inches). These size classes are referred to as (smallest to largest): size class 1 (SC1), size class 2 (SC2), size class 3 (SC3) and size class 4 (SC4). Data were also collected on herb and shrub cover, as well as site physical variables such as slope, aspect, elevation, soil depth and exposure. Plots were oriented perpendicular to the contour of the slope and along a cardinal direction in level areas. Plots were subjectively located, and intended to represent the vegetation of the map polygon in which they were situated. Details of the VTM sampling protocol can be found in the VTM field manual, accessible online (Wieslander *et al.*, 1933; <http://vtm.berkeley.edu/>).

VTM crews did not permanently mark their plots, making it impossible to precisely resample their plot boundaries. However, because the VTM crews placed their plots in areas of continuous, consistent vegetation cover, it is still possible to sample the stand containing each plot, effectively resampling the site. We navigated to the approximate locations of the original plots using GPS points derived from topographic maps on which the VTM project recorded plot location. When on site, we used data recorded by the VTM crews on slope, aspect, elevation, tree species composition and forest structure to refine the final location of our modern plots.

Between 2007 and 2009, we resampled 139 historic VTM plots in the central Sierra Nevada, California between Tioga Pass in Yosemite National Park (37.8° N

Latitude) and the Desolation Wilderness, west of Lake Tahoe (40.0° N; Figure 1.1). Sampling was restricted to elevations above approximately 2300 m within undisturbed stands, to minimize the effect of exogenous factors like logging, grazing and human recreational uses. The plots occur in the subalpine zone of the Sierra Nevada, which is characterized by a short growing season (6-9 weeks) and precipitation ranging from 750-1250 mm, nearly all of which occurs in the winter. Soils are thin and derived mostly from granite (Fites-Kaufman *et al.*, 2007). The eight most-common species in this zone are whitebark pine (*Pinus albicaulis*), lodgepole pine (*Pinus contorta* subs. *murrayana*), mountain hemlock (*Tsuga mertensiana*), western white pine (*Pinus monticola*), red fir (*Abies magnifica*), Sierra juniper (*Juniperus occidentalis* var. *australis*), Jeffrey pine (*Pinus jeffreyi*), and white fir (*Abies concolor*). Of these, *P. albicaulis* and *T. mertensiana* have ranges restricted to the highest elevations of the subalpine zone, while *A. concolor*, *A. magnifica*, *J. occidentalis*, *P. jeffreyi* and are generally restricted to the lower subalpine and *P. contorta* can be found throughout, including at treeline; see Figure 1.2 for typical structure of subalpine forests. For more information on the species and structure of these forests, see Parker (1988), Potter (1998) and Fites-Kauffman *et al.* (2007). Sixty-four plots occur within the boundaries of Yosemite National Park and the remainder occur on US Forest Service land to the east and north: the Inyo, Stanislaus, Eldorado and Humboldt-Toiyabe National Forests (Figure 1.1). Nearly all plots located on Forest Service land were in designated Wilderness areas. Plots were 800 m² rectangular plots (10 X 80 m), with the long axis oriented parallel to the hillslope. Plots were located on slopes that have a consistent slope angle along the length of the plot axis, to match the slope and aspect recorded in VTM plots. Neither VTM nor modern plots

were slope-corrected. UTM coordinates, elevation, aspect, slope and physical and environmental factors were recorded. Diameter at breast height (dbh) was taken, by species, for every live or dead stem >1 cm dbh.

Analyses

To evaluate changes in composition, relative basal area and relative density were determined for each species, then averaged together to get an “importance value” for each species for all sites (Barbour *et al.*, 1999). These calculations were made for both VTM and modern data and compared.

To facilitate direct comparisons of stand structure, stem diameters (dbh) from modern plots were binned into the four diameter categories (SC1 through SC4) used by the VTM program (see Table 1.1). Analyses were carried out on the number of stems per plot in historic versus modern plots using a Generalized Linear Mixed-effects Model (GLMM) with plot as a random factor and a Poisson distribution. Analyses were performed using the lmer procedure in R version 10.1 (R Development Core Team, 2009). Since VTM plots were slightly larger (809 vs. 800 m²), we divided the number of stems in VTM plots by 1.01125 (which is 809/800). Data for both modern and VTM plots are presented as densities in terms of stems per plot.

Three comparisons of modern versus VTM tree data were made: (1) all species combined, all sites; (2) all species combined, grouped by different site types; and (3) each species, all sites. For (1), all 139 plots were considered, with all species combined. For (2), all species were combined but plots were grouped into four pairs of different geographic and topographic variables, to examine whether trends observed for (1) varied by site type. Group pairs were the following: Northern plots (all plots north of Yosemite

region; $n = 57$) versus southern (plots in Yosemite National Park and vicinity; $n = 82$), with the centroid of each cluster separated by approximately 100 km (Figure 1.1); low-elevation plots (2293 – 2638 m; $n = 69$) versus high-elevation (2639 – 3395 m, $n = 70$), divided arbitrarily to place similar plot numbers in each category; warm plots (southeast through west aspects; $n = 61$) versus cool (northwest through east aspects; $n = 78$); and gentle slope ($\leq 30\%$ grade, including level plots; $n = 84$) versus steep slope plots ($> 30\%$ grade; $n = 53$), $> 30\%$ being a typical US federal agency definition of “steep”. For (3), analysis of all plots by each of the eight species was made. The sample size remained the same ($n = 139$) regardless of how many plots the individual species were present in. This approach is supported by a Poisson distribution and enables the design to be balanced.

To determine how the climate of our study area has changed since the early 20th century, we downloaded publicly-available data from the Tahoe City, California (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca8758>) and Huntington Lake, California (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca4176>) weather stations. The Tahoe City station (1899 m elevation) lies about 20 km north of the northern-most plot in our study area; the Huntington Lake station (2140 m elevation) is approximately 45 km south of our southern-most plot. These stations have the two longest weather records of all high elevation stations in the Sierra Nevada. For each station, we calculated means in annual minimum temperature (ATmin), annual maximum temperature (ATmax) and annual precipitation (APrec), for the 30-year period from 1916 to 1945 (Time1) and the 30-year period from 1976 to 2005 (Time2). In addition, we calculated the same variables for the subalpine potential growing season of July through October for each 30-year period, resulting in growing season minimum temperature (GSTmin), growing season maximum

temperature (GSTmax) and growing season precipitation (GSPrec). Change in each variable was calculated by subtracting Time1 from Time2 (Table 1.2).

Keeley (2004) noted that high spatial heterogeneity in vegetation could make plot-by-plot statistical comparisons between historical and resampled modern plots tenuous, where the precise location of the original samples cannot be determined. We went to great efforts to locate VTM plot locations on the ground, using mapped locations and VTM descriptions of elevation, slope, aspect, forest type and forest structure. Although it is likely that many of our plots fell outside of the exact footprint of the original VTM plot, we are confident that the great majority (if not all) of our samples were located in the same forest stand as the VTM plots. Evidence for this comes from the large snag (> 60.9 cm dbh) data we collected in our plots. When large snag density is added to live large tree (> 60.9 cm dbh; SC3 and SC4) density in the resamples, the resulting value is approximately equal to large live tree density in the original VTM plots (4.47 vs. 4.86 trees/plot, modern vs. VTM; means not significantly different). This not only suggests that we were sampling from the same stand (or at least a very similar stand), but that tree mortality accounts for the temporal change in large tree density between the original VTM sample and modern samples. In accordance with Keeley (2004), our study covers a large area (5500 km^2), with a large number of resampled plots ($n = 139$) and we draw conclusions based on aggregated, not individual plots.

Concerns have been raised about the suitability of Wieslander, or Vegetation Type Mapping (VTM) Project data for comparison with modern stand conditions. In particular, it has been suggested that VTM crews chose their plots in a way that favored old-growth, open stands with large trees. In a response to Fellows and Goulden (2008),

Bouldin (2009) suggested that there may be bias within the VTM plots dataset toward older forest conditions. As Fellows and Goulden (2008) point out, this belief is not supported by publications that came out of the Wieslander survey, nor by the VTM field manual or publications by Wieslander himself when describing the purpose and initial results of the study (Wieslander, 1935a; Wieslander, 1935b). On the contrary, Wieslander stated that sample plots should be “representative of the various vegetation types” (Wieslander, 1935a), which is consistent with their objective to use plots to validate the polygons drawn on their maps. Inspection of the spatial locations of VTM plots across the Sierra Nevada shows a surprisingly regular distribution, in contrast to most modern plot arrays, which are often strongly biased toward areas of easy forest access. Even if there is some bias with the VTM dataset toward older forest conditions, it is of little direct statistical significance to our study, as we resampled VTM plot locations and did not carry out a comparison with an independent modern plot array that may have sampled a different statistical population.

RESULTS

Contrary to our first hypothesis, stand composition has changed very little since the original VTM sampling (1929-1934). Of the eight species sampled, *P. albicaulis* exhibited the greatest increase in importance (+1.9%), while *Pinus monticola* (western white pine), showed the greatest decrease (-1.7%). Other species responses fell between these two extremes, but none of the shifts were statistically significant. The relative dominance by different species was unchanged. No tree species absent in the VTM plots

moved up in elevation to be counted in our resample, and no tree species sampled in the VTM plots dropped out.

In agreement with our second hypothesis, the overall density of stems per plot for the smallest size class [SC1; 10.2-30.4 cm diameter breast height (dbh)] was significantly higher in modern plots than historical (VTM) plots, representing a 63.3% increase over historical conditions and an average of 8 more stems per plot (Figure 1.3; Table 1.1). Density in size class 2 (SC2; 30.5-60.9 cm dbh) was not significantly different between modern and historical samples. For the larger trees (SC3; 61.0-91.3 and SC4; ≥ 91.4 cm dbh), tree densities were lower in modern plots (decreases of 21.1% and 19.1% respectively), but only the SC3 decrease was statistically significant while SC4 was marginally significant (Figure 1.3; combining SC3 and SC4 also gave a significant decrease). For all size classes combined, tree density was 30.4% higher in modern plots.

Overall, the trends described above hold for different groups of physical variables: latitude, elevation, aspect and slope (Figure 1.4; Table 1.3). All eight groups had significantly higher tree densities in modern plots for SC1. Seven of eight groups also showed significantly lower densities in SC3 and four of eight exhibited significant decreases for SC4. For SC2, the northern plots showed a significant increase while the southern plots decreased significantly (Figure 1.4; Table 1.3).

All eight species sampled exhibited an increase in stem density over historic levels in SC1, representing increases ranging from 16-147% over historic levels (Figure 1.5; Table 1.1). Densities were significantly higher for six of the eight species sampled: *A. concolor*, *A. magnifica*, *P. jeffreyi*, *P. contorta*, *T. mertensiana* and *P. albicaulis*. Increased densities were statistically significant for higher elevation species (*T.*

mertensiana and *P. albicaulis*), lower elevation species (*A. concolor* and *P. jeffreyi*), and elevation generalists (*P. contorta*). For SC2, two species, *A. concolor* and *P. albicaulis*, showed significantly higher densities in modern plots.

In general, as with the combined species analysis, both SC3 and SC4 showed decreases in stem densities in modern plots, but with fewer statistical differences. *P. monticola* had significantly lower densities in modern plots for SC3 and *P. jeffreyi* showed significantly lower densities for SC4 (Figure 1.5; Table 1.1).

When dead and live large trees (>60.9 cm dbh) are pooled in the modern plot data, large tree densities in the modern resamples are not significantly different from large (live) tree densities in the VTM plots (4.47 vs. 4.86 trees/plot, modern vs. VTM, $t = 1.164$, $p = 0.246$). The density of large dead trees (“snags”) in the modern resamples shows a weak positive correlation with the density of very small trees (< 10 cm diameter; $r = 0.221$, $p = 0.01$).

Annual and growing season mean temperature and precipitation increased from early to late 20th century (Time1 to Time2; Table 1.2). At Tahoe City, annual minimum temperature (ATmin) increased by 1.27 °C, annual maximum temperature (ATmax) increased by 0.47 °C and annual precipitation (APrec) rose by 112.5 mm, an increase of 15.3%. At this station, growing season minimum temperature (GSTmin) increased by 1.22 °C, growing season maximum temperature (GSTmax) decreased by 0.22 °C and growing season precipitation (GSPrec) increased by 18.03 mm (+27.7%). Of these, ATmin, ATmax and GSTmin were all statistically significant changes (Table 1.2). At the Huntington Lake station, ATmin increased by 1.49 °C, ATmax increased by 0.46 °C and precipitation increased by 360.9 mm, or +47.8%. GSTmin increased by 0.42 °C, GSTmax

increased by 0.28 and GSPrec increased by 30.2 (+41.5%). ATmin and APrec were statistically significant increases (Table 1.2) at the Huntington Lake station.

DISCUSSION

Over the last 80 years, stem density of small trees has significantly increased for most of the conifer species native to the subalpine region of the central Sierra Nevada. Density of small trees increased across the entire landscape of our study area, including both low and high elevation bands, warm and cool aspects, and steep and gentle slopes. Although forest stand structure has become more strongly skewed toward younger size classes during the past $\frac{3}{4}$ century, the relative abundances of the different tree species have not changed appreciably and there is no evidence of lower elevation species replacing higher elevation species. Other sources have documented a general infilling or densification of high-elevation forests (Vankat & Major, 1978; Vale, 1987; Taylor, 1995; Gruell, 2001), but, to our knowledge, our findings represent the first resampling-based empirical evidence of widespread, multiple-species increases in density of young trees.

Our data confirm that densities of larger size-class trees in Sierra Nevada subalpine forests have generally decreased. This pattern has been described for Yosemite National Park (Lutz *et al.*, 2009) and for forests throughout the west (van Mantgem *et al.*, 2009), however our study explicitly accounts for the “lost” trees – they represent mortality and are present in the modern plots as dead snags. The decrease in large tree density we measured was substantial across species, but only statistically significant for two of them: *P. jeffreyi* and *P. monticola*. In a study of old growth forests across the western US, van Mantgem *et al.* (2009) found that over approximately the last two

decades, species of the genus *Pinus* had experienced higher mortality rates than species of any other conifer genus they measured. Similarly, in our study, *Tsuga* experienced relatively low rates of mortality. Lutz et al. (2009), comparing Yosemite National Park VTM plots to an independent modern inventory, found that four of six *Pinus* species had undergone significant decreases in large tree density.

Taken together, our recruitment and mortality results present a picture of how subalpine forest stand structure in the Sierra Nevada is changing. Compared to the early 1930s, subalpine conifer stands are denser overall, with many more small trees and fewer large trees, yet with little difference in relative tree species abundance. These patterns hold across almost all geographic and physiographic clines. This pattern of nearly ubiquitous change is indicative of a factor or factors that are operating with strong influence and at regional, rather than stand-level scale.

Possible causal factors

Structural changes in low- to mid-elevation forests of the Sierra Nevada are often attributed to 20th century fire suppression (McKelvey & Busse, 1996; North *et al.*, 2009). However, higher-elevation subalpine forests (more accurately called woodland) of the Sierra Nevada are sparse and open-canopied, with shallow fuel beds and frequent rock outcrops that restrict the frequency and severity of fire (van Wagtendonk & Fites-Kaufman, 2006; Fites-Kaufman *et al.*, 2007; Figure 1.2). Natural fire return intervals in Sierra Nevada subalpine forests have been estimated at hundreds of years, and landscape fire rotations at thousands to tens of thousands of years (van Wagtendonk & Fites-Kaufman, 2006). Human efforts at fire suppression within the subalpine zone (which are

already relaxed due to wildland fire use policies in many Wilderness areas, as well as the great distances to human population centers) have had little to no effect on forest composition or structure, as these efforts began only 75-100 years ago, a much shorter time period than the natural mean fire free period in Sierra Nevada subalpine forests. As a result, unlike forests where human fire suppression has caused major shifts in fire regime, modern recent fires in high-elevation forests of the Sierra Nevada are burning well within the historical range of variation for fire severity (Miller & Safford, 2008).

Changing concentrations in atmospheric gases potentially affect tree growth and recruitment success and thus stand densities. Carbon dioxide (CO₂) fertilization was originally thought to have sizeable effects on the growth of subalpine conifers (Lamarche *et al.*, 1984) but the equivocal results of studies researching CO₂ effects on high elevation tree growth (Graumlich, 1991; Tang *et al.*, 1999) make it unlikely to account for the widespread shifts reported here. Nitrogen (N) deposition is also a potential factor, but high site to site variability of N pollution based on proximity to downslope fertilization sources (Fenn *et al.*, 2003) makes it unlikely to be responsible for the wide-spread, consistent trends reported here. Also, as with CO₂, so far it has been difficult to demonstrate an effect of N deposition on growth in the field (Saurer *et al.*, 2004).

Historically, the most prevalent anthropogenic disturbance in the high Sierra Nevada was grazing, in particular by sheep in mountain meadows (Kinney, 1996; Menke *et al.*, 1996). Sheep grazing was halted around 1900 in National Parks and slowly abated on Forest Service land throughout the 20th century (Menke *et al.*, 1996). Our study did not include plots from meadows, but rather from sparsely vegetated and rocky sites with little to no cover of palatable forage. Historic grazing and/or subsequent recovery are

unlikely to be major drivers of trends in tree structure from upland locations such as in our study.

Climate Change

Climate data indicate that our study area has warmed and experienced slightly increased precipitation since the first half of the 20th century. As with many other parts of the globe, the nighttime lows (daily minima) in our study area have risen more than daytime highs, with both annual and growing season minima considerably higher in Time2 (1976-2005) than Time1 (1916-1945; Table 1.2). Precipitation is also higher in Time2 at both stations, especially at Huntington Lake, where both annual and growing season precipitation have increased by more than 40%. These trends are corroborated by aggregated climate data from the entire Sierra Nevada region (Figures 1.6, 1.7). Measurement of snow (e.g. snow depth, snow water equivalent, snowfall) is prone to high variability and does not have as complete a record as temperature and precipitation. However, sources indicate that in western North America, snowpack is declining (Mote *et al.*, 2005), the proportion of rain to snow is increasing (Knowles *et al.*, 2006) and snowpack is melting sooner (Stewart *et al.*, 2005). For the Lake Tahoe Basin, the percent of precipitation falling as snow decreased from >50% in 1910 to *c.* 35% in 2010 (Coats, 2010). From 1960 to 2010, the date of snowmelt in the Tahoe Basin moved earlier in the season by 0.4 days/year, resulting in an average snow free date about two weeks earlier now than it was 50 years ago (Coats, 2010).

Changes in climate should be expected to have strong effects on high-elevation ecosystems, where abiotic factors (as apposed to biotic factors such as competition) more

directly shape plant distribution and vegetation structure (Grime, 2001). In addition, climate change should be expected to affect vegetation of a region such as our study area more evenly than other exogenous factors. Temperature and precipitation are known to have both direct and indirect effects on the structure and distribution of subalpine conifers. In California's Mediterranean climate, the principal limiting factors for tree establishment are deep snow cover in the spring and low soil moisture in the summer (Peterson, 1998), both of which are controlled by a temperature-precipitation interaction. Temperature positively impacts growth directly by increasing nutrient uptake and photosynthesis but can negatively affect growth indirectly by driving up evapotranspiration, resulting in more limited available moisture (Korner, 2003). Precipitation can positively affect growth directly by improving moisture availability, especially during the growing season, but it can also limit growth and recruitment of smaller trees via deep, long-lasting snow (Lloyd & Graumlich, 1997). Numerous subalpine tree species demonstrate temperature limitations at their high-elevation range limit and moisture limitations at their low-elevation limit (e.g., Lamarche, 1974; Peterson, 1998; Salzer *et al.*, 2009). Historically, the length of the growing season in the subalpine zone of the Sierra Nevada was 6-9 weeks, with almost all precipitation occurring during the winter (Fites-Kaufman *et al.*, 2007). However, increased temperatures and steady to increased annual and growing-season precipitation have lengthened the growing season and probably ameliorated conditions during the dry season. Such improvement in growing conditions seems a likely explanation for the generalized increase in abundance of small trees that we observed.

Decreased density of large trees in Sierra Nevada subalpine forests over the last $\frac{3}{4}$ century is also consistent with observed climate change. It has been shown that higher temperatures shorten the time to drought-induced mortality of trees (Adams *et al.*, 2009), and warming temperatures can increase tree susceptibility to pathogen and insect attack (Allen *et al.*, 2010). Increasing rates of tree mortality have been attributed to warming-drought interactions for conifer forests in Yosemite National Park (Guarin & Taylor, 2005) and for multiple sites in old-growth forest throughout the western US, including high-elevation (> 2000 m) stands (van Mantgem & Stephenson, 2007; van Mantgem *et al.*, 2009). Van Mantgem *et al.* (2009) found increased mortality rates for both young and old trees, and Smith *et al.* (2005) similarly found high mortality across tree size classes. Our study also found decreasing densities of large trees over time, but small tree densities in our system are increasing, and our seedling and sapling data (not analyzed here) show that tree recruitment is currently outpacing mortality. It seems probable that these opposing trends are interrelated. Studies done in lower elevation forests in the Sierra Nevada have found a strong correlation between small tree density and large tree mortality (Guarin & Taylor, 2005). Our study was done at higher elevations in relatively open stands where competition for resources is presumably less intense. We did find that small tree density was negatively correlated with large snag density, but the relationship was weak. Whatever the case, whether large tree mortality in the subalpine zone is driven primarily by density-independent or density-dependent factors, it seems unavoidable that climate change will play an increasingly fundamental role.

Implications for the Future

Current climate warming trends are thought to pose a significant threat to high-elevation vegetation (Lenihan *et al.*, 2008). However, our data show that warming over the last $\frac{3}{4}$ century has not caused appreciable change in tree species composition in the subalpine forests of the Sierra Nevada. Instead, warming, coupled with steady or increasing precipitation, has enhanced survival and/or recruitment of younger trees of all species. Overall, species appear to be recruiting in proportions more or less commensurate with their canopy abundances. Although young tree densities are increasing for species whose elevational range is mostly below the subalpine zone (e.g., *A. concolor*, *P. jeffreyi*), higher-elevation species are keeping pace.

Is it possible to reconcile our observations with the prediction that subalpine forests will shrink substantially in extent over the next century? We may be witnessing a lag effect, where lower-elevation species may eventually move upslope and displace higher-elevation species, but this process may take many decades to centuries to play out. Currently, mortality rates in older trees (as estimated by temporal changes in density) in the subalpine forests we sampled are not higher for high-elevation vs. low-elevation species, so this sort of process is not yet evident.

Subalpine conifer species are mostly long-lived stress-tolerators, and mature individuals may be able to endure significant environmental change. Such forest ecosystems may require large-scale disturbance (i.e. the death/removal of tree biomass) to provoke major changes in canopy dominance. Fires are currently infrequent in the Sierra Nevada subalpine zone, but linked climate-vegetation models predict increases in fire frequency and intensity as temperatures continue to warm (Lenihan *et al.*, 2008).

Most high-elevation conifers are poorly adapted to fire, and changing fire regimes may benefit fire-adapted lower-elevation species like *P. jeffreyi*.

Other disturbance factors like insect outbreaks and disease could also have important influences on the future composition and geographic extent of subalpine forests. Warming temperatures and increasing drought stress have been implicated in massive outbreaks of pine beetles (*Dendroctonus* spp.) across western North America, with high rates of mortality recorded for *P. contorta* and *P. albicaulis* (Kurz *et al.*, 2008; Logan *et al.*, 2010). Both of these species occur in Sierra Nevada subalpine forests, but pine beetle mortality is not yet a major ecological factor in our study system. Likewise, white pine blister rust (*Cronartium ribicola*) has significantly increased mortality of *P. albicaulis* at many locations throughout the western US mountains (Tomback & Achuff, 2010). This pathogen is present in our study area and infected individuals of both *P. albicaulis* and *P. monticola* have been confirmed; however, to date, impacts in the Sierra Nevada remain minimal (Maloney, 2011). Spread of the disease may be at least partly limited by the cold and dry climate of this region (Maloney, 2011) but increasing growing seasons could facilitate spread. Increased prevalence of either *Dendroctonus* or *Cronartium* could eventually tip the scales in favor of widespread vegetation shifts.

We should expect similar mechanisms of response to climate change in other Mediterranean and semi-arid mountain ranges worldwide, where growing season has historically been severely moisture-limited. In these environments, future trends in forest structure and distribution will likely depend heavily on the degree to which precipitation changes. If precipitation increases, at least during the growing season, rising temperatures should increase tree growth rates, recruitment and/or survival of younger trees. However,

rising temperatures coupled with unchanged or decreased precipitation could lead to widespread mortality (Millar *et al.*, 2007a) and might be expected to differentially affect species (Lutz *et al.*, 2010). The effects of ecological disturbances linked directly or indirectly to these climatological factors may be the ultimate arbiters of the outcome of climate change in the subalpine zone.

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TABLES

Table 1.1. Summary statistics and *p*-values (Generalized Linear Mixed Model) for all species combined and each of the eight species in the study in modern versus historic Vegetation Type Mapping (VTM) Project plots. Each analysis was carried out on all plots (n=139) on stem density per plot for each of four size classes: SC1 (10.2-30.4 cm diameter); SC2 (30.5-60.9 cm); SC3 (61.0-91.3 cm); SC4 (≥ 91.4 cm). Statistically significant results appear in bold.

		SC1 10.2-30.4 cm	SC2 30.5-60.9 cm	SC3 61.0-91.3 cm	SC4 ≥ 91.4 cm
All Species Combined	VTM (Ave. # Stems/Plot)	12.96	8.07	3.30	1.49
	Modern (Ave. # Stems/Plot)	21.18	8.69	2.60	1.20
	Δ Stems/plot	8.22	0.62	-0.70	-0.29
	% Change	+63.3	+7.7	-21.1	-19.1
	<i>p</i> -value (GLM - Mixed Model)	<0.001	0.055	<0.001	0.051
<i>Abies concolor</i>	VTM (Ave. # Stems/Plot)	0.28	0.07	0.09	0.05
	Modern (Ave. # Stems/Plot)	0.51	0.24	0.07	0.04
	Δ Stems/plot	0.23	0.17	-0.02	-0.01
	% Change	+79.5	+233.7	-15.7	-29.9
	<i>p</i> -value (GLM - Mixed Model)	0.003	0.001	0.698	0.591
<i>Abies magnifica</i>	VTM (Ave. # Stems/Plot)	1.66	1.17	0.94	0.59
	Modern (Ave. # Stems/Plot)	3.16	1.41	0.75	0.51
	Δ Stems/plot	1.50	0.24	-0.19	-0.08
	% Change	+90.5	+20.1	-20.3	-13.4
	<i>p</i> -value (GLM - Mixed Model)	<0.001	0.071	0.072	0.131
<i>Pinus jeffreyi</i>	VTM (Ave. # Stems/Plot)	0.12	0.18	0.25	0.18
	Modern (Ave. # Stems/Plot)	0.30	0.17	0.17	0.12
	Δ Stems/plot	0.18	-0.01	-0.08	-0.06
	% Change	+149.8	-2.9	-33.5	-31.9
	<i>p</i> -value (GLM - Mixed Model)	0.003	0.970	0.139	0.045
<i>Pinus monticola</i>	VTM (Ave. # Stems/Plot)	0.63	0.41	0.42	0.26
	Modern (Ave. # Stems/Plot)	0.74	0.35	0.21	0.24
	Δ Stems/plot	0.11	-0.06	-0.21	-0.02
	% Change	+17.0	-16.3	-50.2	-7.4
	<i>p</i> -value (GLM - Mixed Model)	0.295	0.396	0.004	0.618
<i>Juniperus occidentalis</i>	VTM (Ave. # Stems/Plot)	0.40	0.28	0.15	0.13
	Modern (Ave. # Stems/Plot)	0.47	0.25	0.19	0.15
	Δ Stems/plot	0.07	-0.04	-0.04	0.02
	% Change	+17.3	-11.8	-27.8	+17.8
	<i>p</i> -value (GLM - Mixed Model)	0.389	0.690	0.359	0.856
<i>Pinus contorta</i>	VTM (Ave. # Stems/Plot)	5.27	4.12	1.03	0.08
	Modern (Ave. # Stems/Plot)	8.94	3.85	0.86	0.08
	Δ Stems/plot	3.67	-0.27	-0.17	0.00
	% Change	+69.5	-6.6	-16.3	+2.9
	<i>p</i> -value (GLM - Mixed Model)	<0.001	0.289	0.161	0.983
<i>Tsuga mertensiana</i>	VTM (Ave. # Stems/Plot)	2.41	1.33	0.38	0.07
	Modern (Ave. # Stems/Plot)	3.48	1.49	0.37	0.05
	Δ Stems/plot	1.07	0.16	-0.01	-0.02
	% Change	+44.4	+11.9	-4.4	-26.3
	<i>p</i> -value (GLM - Mixed Model)	<0.001	0.271	0.822	0.830
<i>Pinus albicaulis</i>	VTM (Ave. # Stems/Plot)	2.19	0.51	0.04	0.00
	Modern (Ave. # Stems/Plot)	3.58	0.94	0.07	0.01
	Δ Stems/plot	1.39	0.43	0.03	0.01
	% Change	+63.5	+86.5	+68.5	N/A
	<i>p</i> -value (GLM - Mixed Model)	<0.001	<0.001	0.348	N/A

Table 1.2. Change in climate from 1916-1945 (Time1) to 1976-2005 (Time2) for two long-term climate stations at the north and south ends of the study area. The Tahoe City station (north) is located at 39° 10.0 'N, 120° 9.0' W; 1899 m elevation. The Huntington Lake station (south) is located at 37° 13.76' N, 119° 14.63' W; 2140 m elevation. Data presented are the differences (Time2 – Time1) and represent means during their respective periods for Annual Minimum Temperature (ATmin), Annual Maximum Temperature (ATmax), Annual Precipitation (APrec), Growing Season Minimum Temperature (GSTmin), Growing Season Maximum Temperature (GSTmax) and Growing Season Precipitation (GSPrec). Growing season is July through October. Statistical differences were tested using a t-test; significant results are indicated by * = $0.01 < p < 0.05$; ** = $0.001 < p \leq 0.01$; and *** = $p < 0.001$.

<i>Climate Station</i>	<i>ATmin (°C)</i>	<i>ATmax (°C)</i>	<i>APrec (mm)</i>	<i>GSTmin (°C)</i>	<i>GSTmax (°C)</i>	<i>GSPrec (mm)</i>
Tahoe City, California	***+1.27	*+0.47	+112.33	***+1.22	-0.22	+18.03
Huntington Lake, California	***+1.49	+0.46	***+360.93	+0.42	+0.28	+30.17

Table 1.3. Least Squares Means results (Generalized Linear Mixed Model) for the difference in stem abundance for all species combined in four size classes (SC1: 10.2-30.4 cm diameter; SC2: 30.5-60.9 cm; SC3: 61.0-91.3; SC4: ≥ 91.4 cm) for modern versus historic [Vegetation Type Mapping (VTM) Project] plots for four different pairs of site types: latitude (north vs. south), elevation (low = 2293-2638 m vs. high = 2639-3395 m), aspect (warm = SE-W vs cool = NW-E) and slope (gentle $\leq 30\%$ vs. steep $> 30\%$). Statistically significant values appear in bold.

	SC1		SC2		SC3		SC4	
	10.2-30.4 cm		30.5-60.9 cm		61.0-91.3 cm		≥ 91.4 cm	
	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value
Time (all plots)	0.49	<0.001	0.08	0.055	-0.07	<0.001	-0.21	0.051
North	0.84	<0.001	0.51	<0.001	-0.23	0.019	-0.46	<0.001
South	0.33	<0.001	-0.13	0.009	-0.25	0.013	0.23	0.192
Low	0.53	<0.001	0.32	<0.001	-0.22	0.017	-0.27	0.023
High	0.47	<0.001	-0.08	0.121	-0.27	0.014	-0.01	0.960
Warm	0.57	<0.001	0.09	0.179	-0.27	0.010	-0.09	0.556
Cool	0.44	<0.001	0.07	0.169	-0.21	0.025	-0.31	0.034
Gentle	0.53	<0.001	0.09	0.070	-0.26	0.002	-0.06	0.695
Steep	0.36	<0.001	0.06	0.494	-0.21	0.109	-0.40	0.013

FIGURES

Figure 1.1. Map of the central Sierra Nevada, CA showing sites of the historic Vegetation Type Mapping (VTM) Project plots and re-sampled modern plots (n=139; small circles). The entire study area encompasses approximately 5500 km² of subalpine forest (2300 m elevation up to treeline). All re-visited plots occur in minimally-disturbed, wilderness areas within National Parks and Forests. Modern sampling of the sites occurred from 2007-2009, approximately 75 years after original surveys. For analysis, plots were blocked by different groups: northern/southern plots (indicated by the solid black line), low/high elevation, cool/warm aspects and gentle/steep slopes.

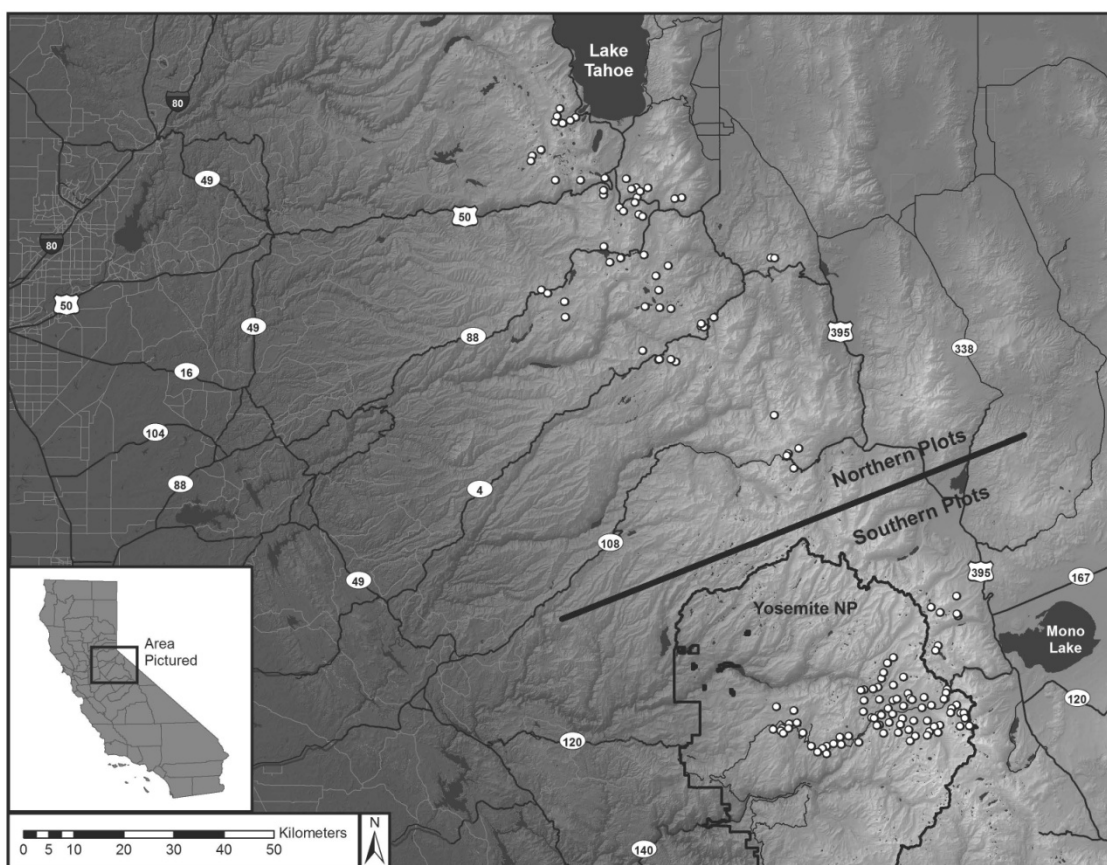


Figure 1.2. Photographs of four typical resampled Vegetation Type Mapping (VTM) Project. Resampling occurred from 2007-2009. All resampled plots were in wilderness areas of the central Sierra Nevada, from approximately 2300 m up to treeline (3400 m), in what is broadly classified as subalpine woodland. All plots in these photos come from Yosemite National Park. Each photo was taken from plot center, looking down the long axis of the 10 X 80 m plots. Note the sparse distribution of trees and lack of live and dead matter (fuel) in three of four plots.



Figure 1.3. Comparison of historic [Vegetation Type Mapping (VTM) Project Plots; clear bars) and “Modern” plots for stem density per plot + SE for all species combined for all 139 plots, aggregated by the four diameter size-classes used by the VTM project (SC1: 10-2-30.4 cm diameter; SC2: 30.5-60.9 cm; SC3: 61.0-91.3; SC4: ≥ 91.4 cm). Statistically significant differences are indicated by * = $0.01 < p < 0.05$; ** = $0.001 < p \leq 0.01$; an *** = $p < 0.001$.

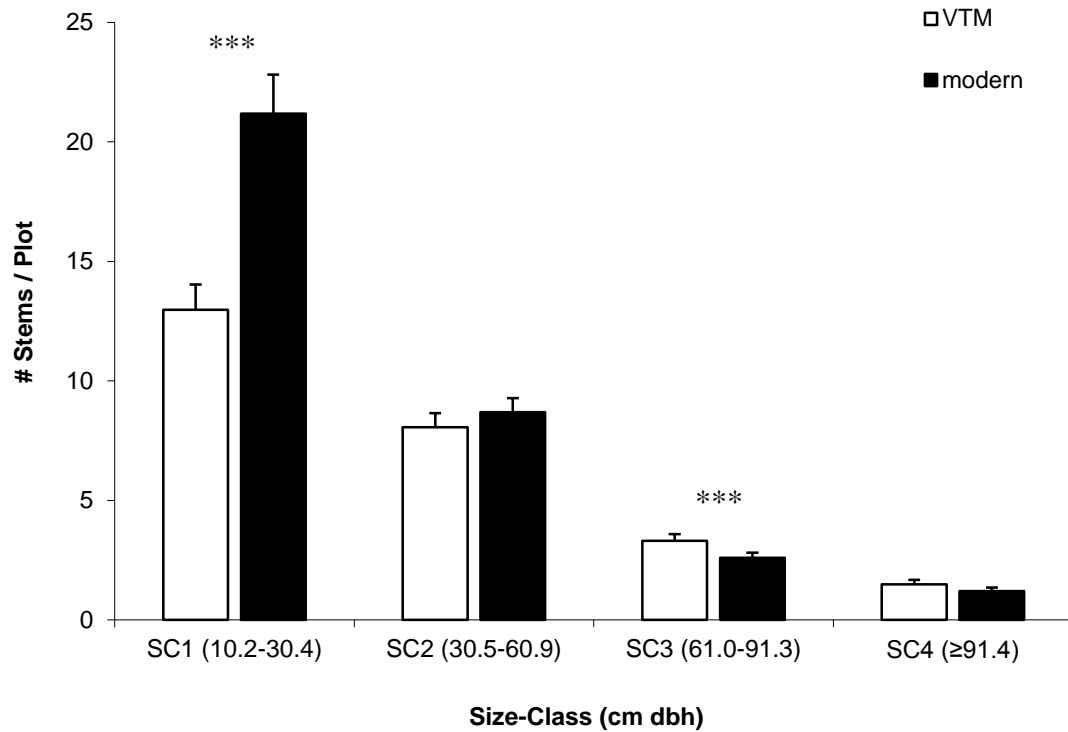
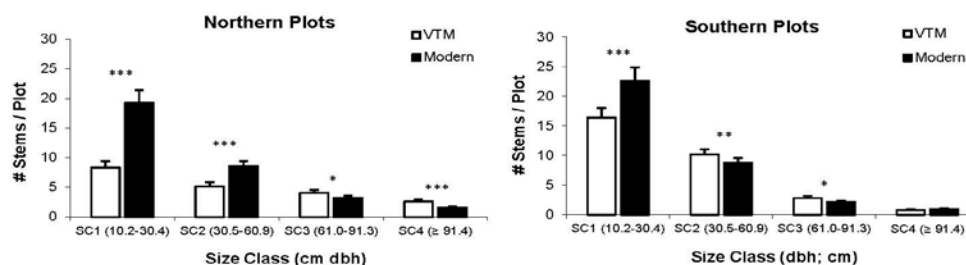
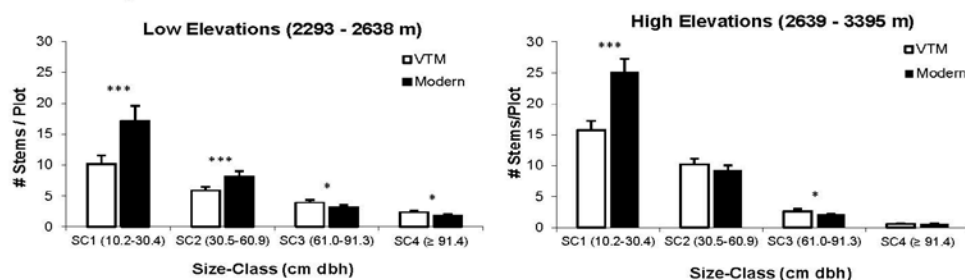


Figure 1.4. Comparison of historic [Vegetation Type Mapping (VTM) Project Plots; clear bars) and “Modern” plots for stem density per plot + SE for 4 different categories of site physical variables: (a) latitude: north vs. south; (b) elevation: low (2293-2638 m) vs. high (2639-3395 m); (c) aspect: warm (SE-W) vs. cool (NW-E); and (d) slope: gentle ($\leq 30\%$) vs. steep ($> 30\%$), aggregated by the four diameter size-classes used by VTM crews (SC1: 10.2-30.4 cm diameter; SC2: 30.5-60.9 cm; SC3: 61.0-91.3; SC4: ≥ 91.4 cm). Statistically significant differences are indicated by * = $0.01 < p < 0.05$; ** = $0.001 < p \leq 0.01$; and *** = $p < 0.001$.

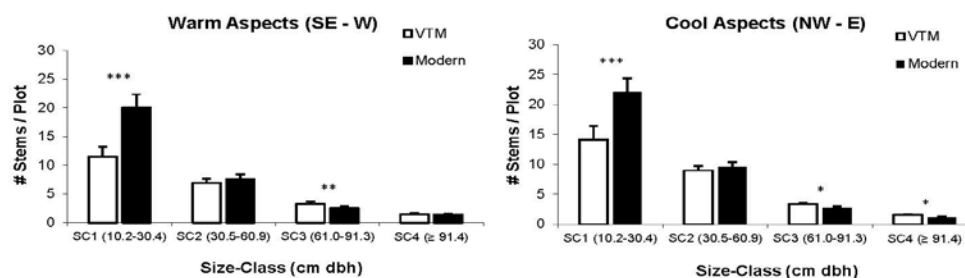
(a) North vs. South



(b) Low vs. High Elevations



(c) Warm vs. Cool Aspects



(d) Gentle vs. Steep Slopes

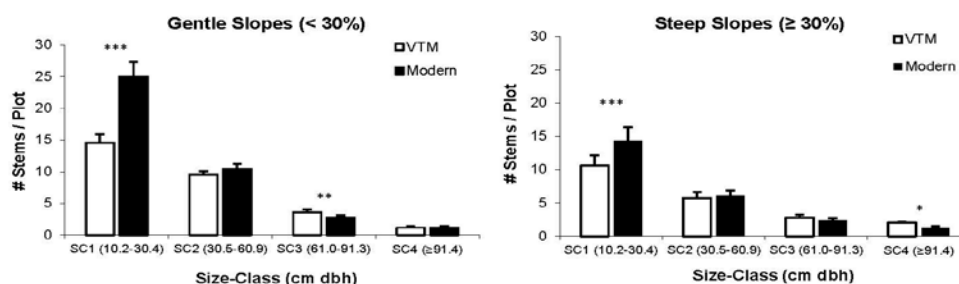


Figure 1.5. Percent change of stem abundance (# stems/plot), from historic [Vegetation Type Mapping (VTM)] plots to modern plots for each of the eight conifer species sampled: ABCO (*Abies concolor*), ABMA (*Abies magnifica*), PIJE (*Pinus jeffreyi*), PIMO (*Pinus monticola*), JUOC (*Juniperus occidentalis* var. *australis*), PICO (*Pinus contorta* subsp. *murrayana*), TSME (*Tsuga mertensiana*), and PIAL (*Pinus albicaulis*). Species are listed approximately in order of elevational distribution, from lower to higher. The four diameter size-classes are indicated by numbers.

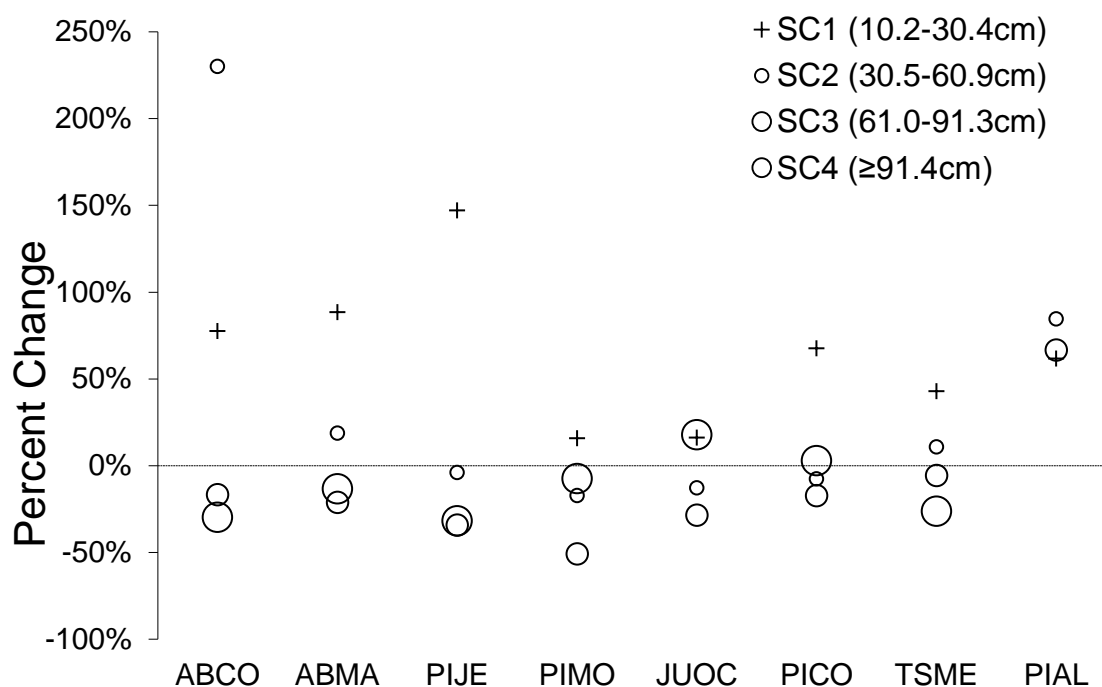


Figure 1.6: Average temperature departure for maximum (red), minimum (blue) and mean (black) temperature, in degrees Celsius from 1895-2010 base period the Sierra Nevada region for every year from 1895-2010. Modified from the Western Regional Climate Center (Abatzoglou *et al.*, 2009).

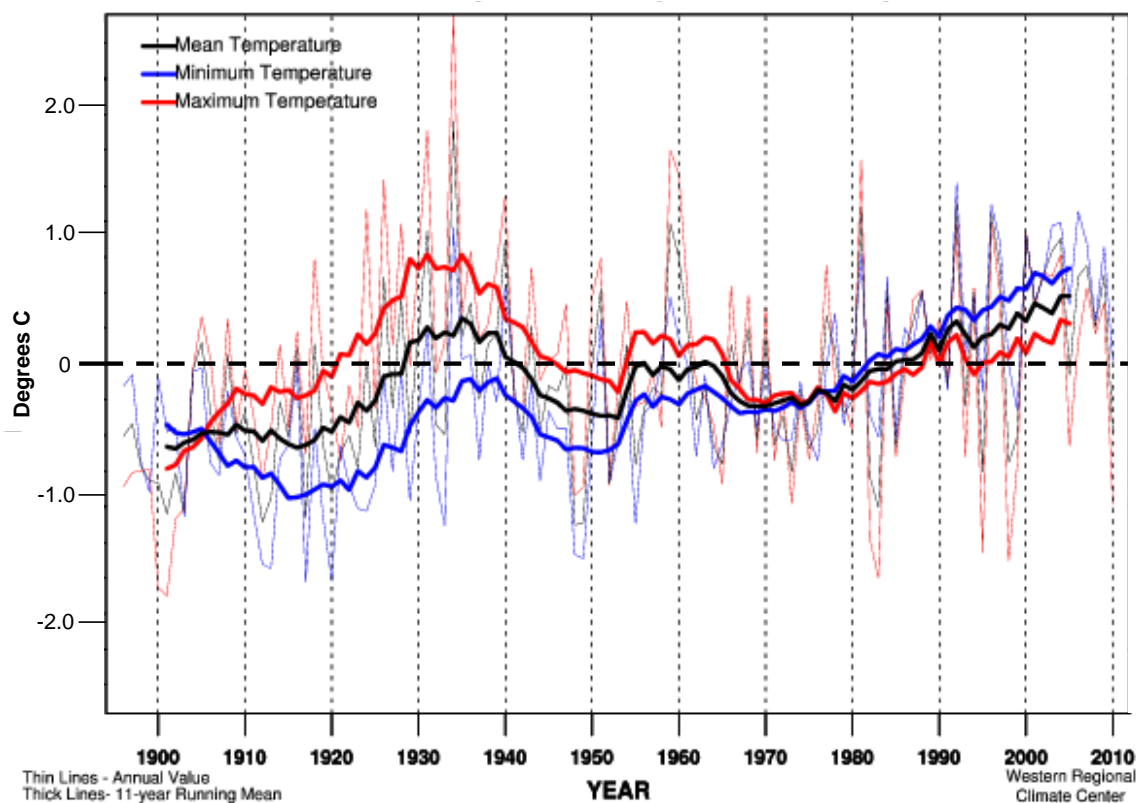
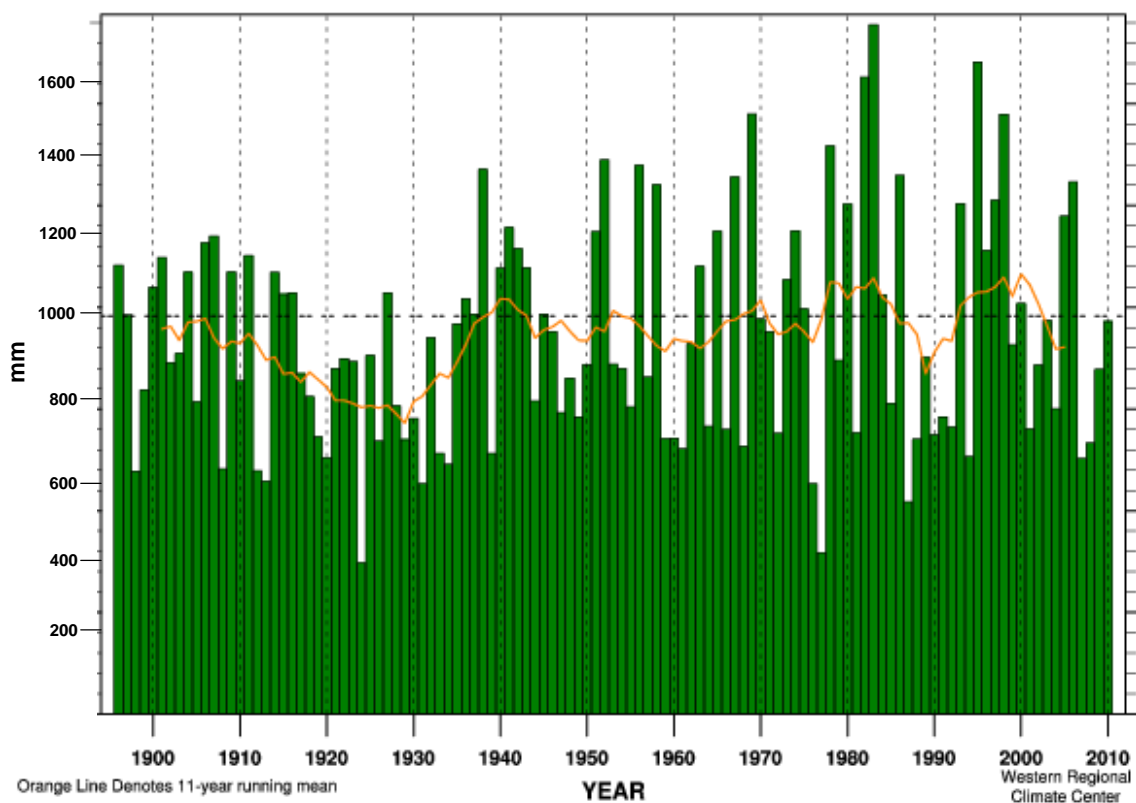


Figure 1.7: Mean annual precipitation for the Sierra Nevada region for every year from 1895-2010. The dotted line represents the mean for the period 1895-2010 and the orange line represents an eleven-year running mean. Modified from the Western Regional Climate Center (Abatzoglou *et al.*, 2009).



Chapter 2

Is climate change driving demographic shifts of subalpine conifers of the Sierra

Nevada, CA, USA?

ABSTRACT

Since the first half of the 20th century, temperatures in the Sierra Nevada have increased and snowpack has declined, leading to longer growing seasons. At the same time, modern subalpine forests are considerably denser overall, with many more small trees but fewer large trees. These generalized changes cannot be accounted for by localized anthropogenic disturbances and fire suppression has had only minor effects on these high-elevation forests. I tested the hypothesis that changes in forest structure are spatially correlated with observed changes in climate. I used climate surface data to calculate change in climate since the early twentieth century for 139 locations in the central Sierra Nevada. These locations were collocated with historical plots that re-sampled historic conditions from 1929-1934. Change in annual and seasonal climate variables were correlated with change in stem density for several plot groupings and all 139 plots combined, to determine if climate change is a major factor driving observed changes in subalpine forest structure. Climate change was found to be a significant factor driving both increases in small trees and decreases in large trees. Further, when analyzed with non-climatic environmental factors and community composition, climate change was as strong or stronger a predictor of demographic change. Trends are similar for both low- and high-elevation plot groupings. The association between increasing temperatures and increasing density of small trees and decreasing density of large trees is strongest during the winter months (Dec-Feb). I believe these results point to a strong influence of snowpack on subalpine forest demography and that future empirical field work and

climate change modeling should focus on the relationship between snowpack and forest demography.

INTRODUCTION

Sources indicate that temperatures in California's Sierra Nevada have risen by one to two degrees C or more since the early 20th century, decreasing the snowpack and increasing the proportion of rain to snow (Mote *et al.*, 2005; Knowles *et al.*, 2006; Coats, 2010). These shifts have likely led to an increased growing season, via earlier snowmelt, effectively ameliorating conditions for recruitment and survival of small trees, while at the same time accelerating drought-induced mortality of large trees (van Mantgem *et al.*, 2009).

The use of historical data for comparison with modern conditions offers a rare opportunity to correlate vegetation change with trends in climate which can then be used to inform and/or test climate-linked vegetation models. Currently, climate-vegetation models are often lacking in the necessary complexity to make accurate predictions of future distributions of vegetation (Pearson & Dawson, 2003) and empirical data of change over time provide real-world departure points indicative of future conditions. For example, Lenihan *et al.* (2008) have predicted reduction of Sierra Nevada subalpine forest over the next 100 years by as much as 78%, presumably via replacement by lower-elevation species moving upslope. Their model assumes that the vegetation change in the region will keep pace with climate change. However, many mature subalpine trees that are standing today have already lived through different climatic shifts (Millar & Woelfenden, 1999), calling into question projections of major shifts over a time frame of

100 years or less and the underlying assumptions of the model. By contrast, correlations between current vegetation trends and current climate trends may be able to elucidate trajectories of real vegetation change even while climate may be changing at a different pace.

The subalpine forests of the Sierra Nevada have undergone major demographic and structural shifts since the first half of the twentieth century. The density of small trees has increased markedly (Vankat & Major, 1978; Vale, 1987; Bouldin, 1999; Gruell, 2001; Dolanc *et al.*, in press), while the density of large trees has decreased (Lutz *et al.*, 2009; Dolanc *et al.*, in press). Both phenomena are likely due to changes in demographic rates such as survival and mortality, but the precise mechanism for these rate changes is still largely unknown.

Tree densification, or infilling, has been reported for multiple elevations in the Sierra Nevada for decades (Vankat & Major, 1978; Vale, 1987; Gruell, 2001). This pattern is usually attributed to fire suppression for low and mid-elevation conifer forests (McKelvey & Busse, 1996; North *et al.*, 2009) and has been linked to grazing cessation for lodgepole pine (*Pinus contorta* ssp. *murrayana*) forests near meadows (Vankat & Major, 1978; Vale, 1987). However, these factors are not sufficient to explain the relatively widespread changes occurring throughout the subalpine zone. At these elevations of the Sierra Nevada, fire suppression policy is not likely to have altered the natural fire cycles (Miller & Urban, 1999; Miller & Safford, 2008), as natural fire-return intervals for subalpine forests have been estimated at hundreds to thousands of years and human fire suppression has a history of <100 years in the Sierra Nevada (van Wagtendonk & Fites-Kaufman, 2006). Grazing cessation cannot fully explain these

patterns either, as grazing impacts at high elevations are focused in or near meadows (Kinney, 1996), and increasing tree densities have been observed even in places like granite domes (Vale, 1987).

Instead, climate change has been suggested as the main driver of structural shifts in higher-elevation subalpine forests, both for increasing densities of small trees (Vankat & Major, 1978; Taylor, 1995; Dolanc *et al.*, in press) and decreasing densities of large trees (Lutz *et al.*, 2009; van Mantgem *et al.*, 2009). I use data from historical and re-sampled forest plots to assess the hypothesis that recent demographic shifts in subalpine forests are due to recent climatic change. To do this I correlate changes in demographic trends over a 75-year period with climatic changes during the same period. I used climate surface data from PRISM (Daly *et al.*, 2008), allowing for fine-scale correlation of climate and structural shifts across the landscape. Both vegetation and climate data come from the subalpine zone of the Sierra Nevada, which has been predicted to decrease markedly in extent over the next 100 years (Lenihan *et al.*, 2008). Specifically, I test **(A)**, whether increases in density of small trees (as a result of enhanced recruitment and/or survival) correlate with locations that have greater rise in minimum or maximum temperature, and **(B)**, whether decreases in density of large trees correlate with plot locations that show decreases in precipitation and/or increases in temperature, effectively exacerbating drought conditions in the summer.

High-elevation ecosystems are considered energy-limited such that treeline vegetation is more driven by temperature than lower elevations in the subalpine zone (Lamarche, 1974; Paulsen *et al.*, 2000; Grace *et al.*, 2002). If this is true then I might expect that vegetation changes in response to temperature are stronger at higher

elevations than lower, even within the relatively high elevations of the subalpine zone. Therefore, I also test (C), whether correlations temperature and change in forest structure are stronger at the higher elevations of subalpine than the lower elevations.

Finally, since changes in forest structure could potentially be driven by a large number of ecological factors, both abiotic and biotic, it is important to determine how strongly changes in demography correlate with changes in climate, relative to other environmental factors. Therefore, I test (D), whether the relationship between demographic change and climate change is stronger than that of demographic change due to other environmental factors (such as elevation and aspect), the composition of the stand or the current climate.

METHODS

Field Data

Data on tree demography for my analyses come from 139 plots that allowed for the re-sampling of the historical Vegetation Type Mapping (VTM; Wieslander, 1935; Thorne *et al.*, 2008) plot locations in the central Sierra Nevada, California from 2007 to 2009. All plots fell between Tioga Pass in Yosemite National Park (37.8° N Latitude) and Desolation Wilderness, west of Lake Tahoe (40.0° N) at elevations ranging from 2300 m up to treeline, totaling 139 plots and covering an area of subalpine forest of approximately 55,000 km² (Figure 2.1). The historical (VTM) plots were originally sampled between 1929 and 1934, so the period between samples ranged from 73 to 80 years. Both historic and modern plots were 800 m², oriented perpendicular to the slope contour. VTM crews collected tree data by four dbh size-classes: Size Class 1 [SC1 (10.2

– 30.4 cm)]; Size Class 2 [SC2 (30.5 – 60.9 cm)]; Size Class 3 [SC3 (61.0 – 91.3 cm)]; Size Class 4 [SC4 (\geq 91.4 cm)]. In modern plots, diameter at breast height (dbh) was determined for every tree in the plot and then subsequently lumped into the four VTM size-classes before analysis (see Dolanc *et al.*, in press).

In modern plots, several additional variables were collected. At the center point of each plot, elevation, slope, and aspect were determined using topographic maps, a compass, inclinometer and global positioning device. Shrub and tree canopy cover was measured along the axis of each 800 m² plot and sapling and seedlings were tallied by height class throughout the plot.

Climate Data

Climate data used in this study were extracted from the Parameter-elevation Relationships on Independent Slopes Model (PRISM) spatial-climate dataset (Daly *et al.*, 2008). The advantage of the PRISM data set is that it offers an examination of climatic variability across the landscape, something that is not currently otherwise possible at the scale of my study. PRISM calculates climate data for a given location by interpolating among existing weather stations, using calculations to account for elevations, slope and other environmental variables. However, this means that there is a fair degree of spatial autocorrelation in the data set, from cell to cell, i.e. for plot locations geographically close to each other, PRISM may calculate variables as more similar than they are in reality. Of course this is a problem common to all models, which have a finite number of input variables. But, this problem may be exacerbated in montane environments, where microclimate heterogeneity can be very high (Leuzinger *et al.*, 2011). Yet, PRISM

remains the best current option if the objective is correlation across a landscape of otherwise sparse weather station data, and its interpolation has been shown to be of higher accuracy than for any other models in montane environments (Daly *et al.*, 2008).

PRISM data are currently available for the coterminous United States at an 800-m grid resolution. For my study, the PRISM data were further downscaled from 800-m to 270-m resulting in a unique raster cell for every re-sampled plot across the landscape. These data were then further modeled using the Basin Characterization Model (BCM) to produce parameters such as snowpack, potential evapotranspiration and climatic water deficit (Flint & Flint, 2007). Climate data were extracted in two, 30-year time periods, 1911 - 1940 (T1) and 1971 - 2000 (T2) resulting in a 60-year period coincident with the 75-year period between tree plot sampling (1934 – 2007). Values for historic and current conditions were extracted for each of the 139 re-sampled plots.

Analyses

Changes in stem abundance (# stems in modern plots - # stems in VTM plots) was calculated for all species combined. Previous work found that the greatest changes in tree abundance were in the smallest size class (10.0-30.3cm) and the two largest size classes (60.9 - 91.2 cm and > 91.2 cm; Dolanc *et al.*, in press). Therefore, analysis was restricted to these two size-classes: SC1, hereafter “Small Trees”, and the sum of SC3 and SC4, hereafter called “Large Trees”. Change in stem number from VTM to modern era plots is denoted as $\Delta\text{SmallTrees}$ and $\Delta\text{LargeTrees}$. For climatic variables, change over the 60-year period was calculated by T2 - T1 for both annual and seasonal variables, for minimum temperature (Tmin), maximum temperature (Tmax), precipitation (Prec), snow

pack depth (Snowpack) and climatic water deficit (CWD). For all variables, seasons were defined as December – February (winter), March – May (spring), June – August (Summer) and September – November (Fall). In addition, because snowpack at subalpine lasts into the summer, I also calculated spring as March – June for Snowpack.

To determine whether demographic shifts are correlated with climatic shifts (Hypotheses A & B), analysis took place in two phases. First, correlation analyses were carried out using both parametric and non-parametric (Spearman rank correlations) approaches of both $\Delta\text{SmallTrees}$ and $\Delta\text{LargeTrees}$ with change in annual and seasonal climate variables. Each variable was then used in Simple Linear Regression (SLR) with $\Delta\text{SmallTrees}$ and $\Delta\text{LargeTrees}$ as the predictor variables. Finally, changes in the three main annual climate variables were used as predictor variables in a Multiple Linear Regression (MLR) model with $\Delta\text{SmallTrees}$ and $\Delta\text{LargeTrees}$ as independent variables:

$$\Delta\text{SmallTrees and } \Delta\text{LargeTrees} = \Delta\text{AnnTmin} + \Delta\text{AnnTmax} + \Delta\text{AnnPrec} \quad [1]$$

Where $\Delta\text{AnnTmin}$ is the change in annual minimum temperature from the T1 to T2; $\Delta\text{AnnTmax}$ is the change in annual maximum temperature and $\Delta\text{AnnPrec}$ is the change in annual precipitation during the same period. These three variables represent the most direct data taken from climate stations and are poorly correlated with each other, lending themselves well to multiple regression (Tables 2.1, 2.2). Though I calculated numerous annual and seasonal climatic variables, the issue of multicollinearity in regression models necessitates a simple model. In addition, these three variables are the most standard measures of climate and can be used to estimate other variables such as climatic water deficit.

To determine if correlation between demographic change and climate change is stronger at higher elevations (Hypothesis C), I divided the 139 plots into two elevation bands of approximately equal sample size: low-elevation plots, 2280 – 2649 m ($n = 72$) and high-elevation plots, 2650 - 3450 m ($n = 67$). Multiple regressions using model 1 above were then carried out for each elevation band. All analyses were performed using JMP version 5.0.1.2 (SAS Institute, 2003).

To determine how much of an influence climate change has had on changes in subalpine forest structure, relative to other factors (Hypothesis D), I performed ordinations on suites of variables in four categories: (1) environment; (2) modern community; (3) modern climate; and (4) change in climate (Table 2.3). The data used for (1) were gathered during plot sampling (described above); I attempted to include as many environmental variables as I had available for this analysis. Data for (2) were simply the abundance scores for each species per plot, as represented by the total number of stems of that species present. Data for (3) and (4) were as described above. Ordinations were performed using PC-ORD, Version 5.0 (McCune & Mefford, 1999).

The first two axis scores from each of the four ordinations were then used in a multiple regression with change in stem number ($\Delta\text{SmallTrees}$ and $\Delta\text{LargeTrees}$) as the response variable and axis scores as predictor variables. Single regressions were performed for each of the eight axis scores, followed by multiple regression on the whole model, with all eight variables in the model, then using stepwise regression to reduce the model down to those variables with the greatest influence. These tests were performed using JMP version 5.0.1.2 (SAS Institute, 2003). Using standard regression techniques, correlated variables tend to reduce each other's effect and any one variable of climate

change may not be significant. However, using ordination to first reduce the variables to pseudo-variables (PC scores) permits the usage of all possible variables, including some that may be perceived as unimportant, without the problem of multicollinearity.

RESULTS

The mean annual minimum temperature (AnnTmin) for my 139 sites was 1.15°C higher for T2 than for T1 (Table 2.4; Figure 2.2). Mean annual maximum temperature (AnnTmax) was 0.18°C lower (-1.7%) and the mean annual precipitation (AnnPrec) was 47.15 mm higher or +4.7% (Table 2.4; Figure 2.2). Spring snowpack (SprPack) during this period increased by 2.9 mm (+0.5 %) and dry season climatic water deficit (DrSeaCWD) increased by 0.28 mm (+0.2 %). Changes in Tmin were relatively consistent from season to season. Tmax has decreased in the fall and winter but increased in spring and summer and precipitation has decreased in winter but increased in all other seasons, especially in fall, where it was 37.7% higher in T2 than T1 (Table 2.4). For my study area, climate of low elevations (2280 – 2649 m) changed more than climate of high-elevation plots. Δ AnnTmin changed by +1.50 °C for low elevations and +0.77 °C for high elevations. Δ AnnPrec was +81.72 mm at low elevations and +10.00 mm at high elevations. Δ AnnTmax was -0.20 °C at low elevations and -0.17 °C at high elevations.

I tested the hypothesis that increased density of small trees is correlated with increased temperatures (Hypothesis A). I found that this is true for Δ AnnTmax; both simple and multiple linear regression models found significant effects of Δ Tmax on Δ SmallTrees (p -values = 0.0087 and 0.018, respectively; Figure 2.3, Table 2.5). There

was very little relationship between ΔT_{min} and $\Delta SmallTrees$ and tests were non-significant.

I tested whether decreased density of large trees is correlated with increased temperatures, decreased precipitation, or both (Hypothesis B). I did not find any statistical relationship between $\Delta LargeTrees$ and $\Delta AnnT_{min}$, $\Delta AnnT_{max}$ or $\Delta AnnPrec$. However, the effect of $\Delta AnnT_{min}$ on $\Delta LargeTrees$ resulted in marginally significant decreases in density in simple regression ($p = 0.068$; Table 2.5).

I tested whether the relationship between changes in temperature and change in forest structure is greater at higher elevations (Hypothesis C). All tests for high-elevation groups were non-significant except for $\Delta AnnT_{min}$ and $\Delta LargeTrees$, which was significant in SLR ($p = 0.0359$) and non-significant in MLR ($p = 0.070$; Table 2.5). At low elevations, $\Delta AnnT_{max}$ did have a significant effect on $\Delta SmallTrees$ at low elevations (SLR: $p = 0.045$; MLR: $p = 0.036$) All other tests in elevation groups were non-significant (Table 2.6).

For hypothesis D, I tested whether trends in stem change were predicted better by climate change than other environmental factors. Of the four categories of change tested, both climate change and modern community were found to be significant, affecting change in stems, with PC1 scores of each category found to affect both $\Delta SmallTrees$ and $\Delta LargeTrees$ (Table 2.5). Climate change and modern community were the only two factors found to have significant effects on both size classes for both models. In the stepped model, PC1 of modern community was the most significant factor ($p = 0.0005$) for $\Delta SmallTrees$, while for $\Delta LargeTrees$, climate change was the most significant factor ($p = 0.0002$). In addition, PC2 of current climate was found to be significant for

Δ LargeTrees in both the whole and stepped model and PC2 of modern community was significant in the stepped model. PC1 scores of the environmental variables had marginally significant effects on Δ SmallTrees (Table 2.5).

DISCUSSION

Climate change appears to have had weak yet measurable impacts on the structure of subalpine forests during the last 75 years. My results indicate that rising temperatures are a significant factor in the increasing density of small trees in my study area, especially at lower subalpine elevations (2280-2649m). In general, the relationship between climate change and structural change of subalpine forests is similar at both higher and lower elevations. Despite subtle trends, climate appears to be as or more important in shaping the change in structure observed over the 20th Century than environmental and community factors.

I am able to accept **hypothesis A**, that rising temperature has led to an increased density of small trees. My statistical tests show that annual maximum temperature (Δ AnnTmax) has had a significant effect on Δ SmallTrees for all plots combined and for low-elevation plots (Figure 2.3; Table 2.5). The trend was also evident at high elevations but not significant (Table 2.5). Further, a positive correlation between temperature change and Δ SmallTrees is especially strong during the fall and winter for Tmax and winter and spring for Tmin, but neutral to negative in the summer (Tables 2.1, 2.2).

These results point toward a positive response by small trees for conditions that reduce snowpack and thus lengthen the growing season. Indeed, snowpack has been shown to be a crucial factor in the distribution of high-elevation conifers in California

(Minnich, 1984; Barbour *et al.*, 1991; Peterson, 1998). Correlation between Δ Snowpack and Δ SmallTrees in my study was negative in all four seasons, meaning increased density of small trees was more likely to occur on sites with decreased snowpack (Tables 2.1, 2.2). This relationship was quite strong for low-elevation plots in spring, summer and winter and a simple regression of change in spring snowpack on change in small trees was statistically significant (Figure 2.4).

Increasing temperature should also increase growth of small trees (Grace *et al.*, 2002), improving their survival and the likelihood of establishing beyond the point where snowpack has negative effects. Tree-ring data from my study area show that radial growth is more sensitive to T_{max} than T_{min} for the seven most common species in the region (C. Dolanc, unpubl. data). This may explain why minimum temperature has not had greater effects on change in structure, despite having increased by 1.15 °C while T_{max} has changed very little (-0.18 °C; Table 2.4).

I am unable to accept the hypothesis that increasing temperature and/or decreasing precipitation (i.e. increased drought stress) has led to decreased density of large trees (**hypothesis B**), based on my statistical results (Table 2.5). However, there is a fair amount of evidence in support of this hypothesis: both T_{min} and T_{max} effects on Δ LargeTrees trend in the direction predicted, i.e. decreased density of trees with increased temperature, and, this trend was marginally significant for Δ Ann T_{min} (Figure 2.3; Table 2.5). Further, this relationship was statistically significant for high-elevation plots.

Mortality of large trees at multiple locations in the west have been attributed to increasing temperatures and thus exacerbated drought (Adams *et al.*, 2009; Lutz *et al.*,

2009; van Mantgem *et al.*, 2009). Again, in my study area, snowpack may be the crucial factor. Negative correlation between density of large trees and $\Delta \text{AnnTmin}$ is especially strong during the fall and winter (Tables 2.1, 2.2). Though non-significant, regression of change in large trees from low-elevation plots against change in spring snowpack shows a positive trend (Figure 2.4), i.e. plots that have declined in snowpack depth are more likely to have lost more large trees. This suggests that mortality is higher when snowpack depth and duration is shorter, or, conversely, when the growing season is longer. Though I have no way of fully attributing stem decreases with mortality, the number of snags present in my modern plots suggests that most of these decreases were indeed due to mortality since 1934 (Dolanc *et al.*, in press).

Despite modest significance in my regression tests for both small and large trees, examination of all possible correlations (Tables 2.1, 2.2) reveals relatively consistent trends. Change in temperature was consistently correlated with increases in small tree density and consistently correlated with decreases in the density of large trees, indicating an overall positive influence of increasing temperature on small trees and a negative influence on large trees. Furthermore, Pearson correlation scores of individual species structural changes with the same climatic variables consistently indicated similar trends, i.e. a positive correlation between density of small trees and temperature and a negative correlation between density of large trees and temperature (Table 2.7). However, sample sizes were generally too low for informative significance testing.

Unfortunately, multiple linear regression does not lend itself well to testing for significance with numerous factors because of the high degree of collinearity among the variables (Neter *et al.*, 1996). While many of the variables represented in Tables 2.1 and

2.2 had significant effects on $\Delta\text{SmallTrees}$ or $\Delta\text{LargeTrees}$ individually, they were non-significant when used in a model with multiple variables. I explored other avenues of analysis but each offered a drawback that negated what I gained by using it

I was unable to accept **hypothesis C**, that the relationship between climate change and changes in forest structure are stronger at higher elevations. Increased T_{\min} was shown to have a negative effect on density of large trees, especially at high elevations (Table 2.5), but in general, there is no support for hypothesis C. My climate data indicate that temperature has actually changed more at lower elevations of the subalpine zone and demographic rates should have higher turnover at lower elevations. This relationship may help compensate for expected greater dependency on climatic influences at higher elevations.

For **hypothesis D**, I tested whether the relationship between demographic change and climate change is stronger than that of demographic change with abiotic environmental factors, community composition or the current climate. I can accept this hypothesis for large trees but reject it for small trees. However, both climate change and community factors appear to have a strong relationship with demographic trend (Table 2.6). I might expect community to have a large effect on change because I should expect species differential rates of structural change due to inherent differences in survival, mortality and recruitment. Therefore, it is interesting that climate change was as strong or stronger a factor in affecting changes in structure.

Despite considerable regional warming (Figure 2.2; Table 2.4), trends in structural changes may be driven more by microsite differences. In my study, overall demographic change was largely driven by a minority (15-20%) of plots that have

changed considerably more than the remainder. It is possible that these plots have physical attributes that interact with climate in a way that creates a response that cannot be easily modeled. PRISM interpolates climate data at a given location based on elevation, aspect and slope but does not account for more local factors such as snowmelt and boulder distribution. Snowpack, for example, has been shown to have large impacts on distributions of subalpine trees (Minnich, 1984). Yet, snowpack and snowmelt patterns are extremely complex (Anderton *et al.*, 2004; Williams *et al.*, 2009) and probably interact with landscape attributes such as canopy cover and water storage at a scale smaller than the 270-m grid system used in this study (Golding & Swanson, 1986; Veatch *et al.*, 2009).

More accurate data on snowmelt and soil water patterns may prove to be much more strongly correlated with stand structure changes than interpolated climate surfaces but unfortunately, it seems there will always be a disconnect in scale between cause and effect that precludes reaching strong conclusions. My study was limited to plots 800 m² in area, which was the size of the historic plots, yet there is likely considerable microsite variation within the plot. These limitations are typical of research that attempts to attribute local biotic shifts to more regional climate change (Stone *et al.*, 2009).

Conclusions

Climate change has driven recent changes in structure of subalpine forests, although the cumulative magnitude of these trends is generally modest. In particular, increasing temperature has led to increases in density of small trees and decreases in

density of large trees. Annual maximum temperature had the greatest effect on densities of small trees while annual minimum temperature led to decreases in density of large trees at high elevations. Differences between low- and high-elevation regions do not indicate that high-elevations have responded more strongly to change overall. Interestingly, climate change is as or more important a factor in affecting demographic shifts in subalpine trees as community or non-climatic environmental factors.

Both snowpack and water balance have been seen as major drivers in tree distributions in semi-arid montane regions (Barbour *et al.*, 1991; Rehfeldt *et al.*, 2008). In California's Sierra Nevada subalpine, where, historically, nearly all precipitation fell as snow (Fites-Kaufman *et al.*, 2007), snow it is likely to be *the* factor. I believe that future work should focus on changes in snowpack depth, distribution and duration, and their variation across the landscape. Data on change in snowpack should come from empirical sources with high spatial resolution over relatively restricted areas, as snowpack and snowmelt patterns are extraordinarily complex (Bales *et al.*, 2006). A long-term, finely sub-divided plot assessing vegetation and snowpack change over time on one slope facet could address snow as well as other, currently poorly-quantified factors that vary at the microsite level.

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TABLES

Table 2.1. Pearson correlation coefficients (R) for several annual and seasonal variables of climate change and change in stem numbers for small trees (SC1; 10.2-30.4 cm dbh) and large trees (SC3&4; ≥ 61.0 cm) for all plots, low-elevation plots and high-elevation plots. Seasons were defined as Dec-Feb (winter), Mar-May (spring), Jun-Aug (summer) and Sep-Nov (fall).

		Δ Ann Tmin	Δ Ann Tmax	Δ Ann Prec	Δ Win Tmin	Δ Spr Tmin	Δ Sum Tmin	Δ Fal Tmin	Δ Win Tmax	Δ Spr Tmax	Δ Sum Tmax	Δ Fal Tmax	Δ Win Prec
All Plots (2280-3450m)	Δ SC1	0.096	0.186	0.119	0.137	0.104	0.062	0.086	0.154	0.017	-0.159	0.193	0.128
	Δ SC3&4	-0.161	-0.086	-0.129	-0.229	-0.132	-0.131	-0.164	-0.234	0.198	0.188	-0.072	-0.143
Low Elevations (2280-2649m)	Δ SC1	0.143	0.249	0.076	0.267	0.208	0.033	0.075	0.219	0.025	-0.120	0.181	0.088
	Δ SC3&4	-0.096	-0.028	-0.081	-0.190	-0.093	-0.057	-0.131	-0.221	0.248	0.300	-0.089	-0.089
High Elevations (2650-3450m)	Δ SC1	0.149	0.132	0.200	0.070	-0.013	0.166	0.181	0.167	-0.010	-0.237	0.200	0.208
	Δ SC3&4	-0.229	-0.185	-0.148	-0.288	-0.184	-0.187	-0.202	-0.240	0.157	-0.009	-0.081	-0.175

		Δ Spr Prec	Δ Sum Prec	Δ Fal Prec	Δ Win CWD	Δ Spr CWD	Δ Sum CWD	Δ Fal CWD	Δ DrSea CWD	Δ Win Pack	Δ Spr Pack	Δ Sum Pack	Δ Fal Pack
All Plots (2280-3450m)	Δ SC1	0.114	0.124	0.108	-0.004	0.103	-0.036	0.011	0.035	-0.035	-0.051	0.012	0.023
	Δ SC3&4	-0.124	-0.175	-0.108	-0.171	-0.065	0.061	0.095	0.177	0.214	0.155	0.010	0.141
Low Elevations (2280-2649m)	Δ SC1	0.048	0.084	0.082	-0.008	0.146	0.053	0.049	0.135	-0.134	-0.269	-0.111	0.181
	Δ SC3&4	-0.108	-0.203	-0.030	-0.187	-0.111	0.168	0.075	0.207	0.386	0.291	-0.022	0.154
High Elevations (2650-3450m)	Δ SC1	0.206	0.189	0.179	0.066	0.090	-0.141	-0.043	-0.065	0.059	0.128	0.156	-0.068
	Δ SC3&4	-0.101	-0.092	-0.159	-0.085	-0.051	-0.133	0.062	0.099	-0.085	-0.046	0.051	0.115

Table 2.2. Spearman-Rank correlation coefficients (r_s) and p -values for several annual and seasonal variables of climate change and change in stem numbers for small trees (SC1; 10.2-30.4 cm dbh) and large trees (SC3&4; ≥ 61.0 cm) for all plots, low-elevation plots and high-elevation plots. Significant values at $p < .05$ are shaded. Seasons were defined as Dec-Feb (winter), Mar-May (spring), Jun-Aug (summer) and Sep-Nov (fall).

			Δ Ann Tmin	Δ Ann Tmax	Δ Ann Prec	Δ Win Tmin	Δ Spr Tmin	Δ Sum Tmin	Δ Fal Tmin	Δ Win Tmax	Δ Spr Tmax	Δ Sum Tmax	Δ Fal Tmax	Δ Win Prec
All Plots (2280- 3450m)	Δ SC1	r_s	0.058	0.247	0.074	0.121	0.169	-0.003	0.045	0.178	0.069	-0.105	0.244	0.096
		p -value	0.496	0.003	0.389	0.156	0.047	0.975	0.600	0.037	0.417	0.219	0.004	0.263
	Δ SC3&4	r_s	-0.154	-0.084	-0.169	-0.206	-0.128	-0.143	-0.155	-0.224	0.179	0.138	-0.093	-0.186
		p -value	0.070	0.325	0.046	0.015	0.133	0.094	0.068	0.008	0.035	0.106	0.275	0.028
Low Elevations (2280- 2649m)	Δ SC1	r_s	0.286	0.339	0.165	0.365	0.331	0.156	0.240	0.354	-0.070	-0.171	0.264	0.196
		p -value	0.015	0.004	0.166	0.002	0.005	0.192	0.042	0.002	0.557	0.151	0.025	0.100
	Δ SC3&4	r_s	-0.030	0.015	-0.121	-0.150	-0.077	-0.051	-0.084	-0.188	0.164	0.254	-0.066	-0.165
		p -value	0.800	0.903	0.313	0.209	0.521	0.668	0.482	0.115	0.168	0.032	0.583	0.166
High Elevations (2650- 3450m)	Δ SC1	r_s	0.155	0.173	0.205	0.001	0.104	0.134	0.135	0.211	0.071	-0.206	0.258	0.199
		p -value	0.210	0.161	0.096	0.994	0.403	0.279	0.275	0.087	0.569	0.094	0.035	0.107
	Δ SC3&4	r_s	-0.249	-0.190	-0.229	-0.345	-0.065	-0.181	-0.231	-0.282	0.241	-0.008	-0.144	-0.209
		p -value	0.042	0.124	0.063	0.004	0.600	0.142	0.060	0.021	0.050	0.951	0.246	0.089

			Δ Spr Prec	Δ Sum Prec	Δ Fal Prec	Δ Win CWD	Δ Spr CWD	Δ Sum CWD	Δ Fal CWD	Δ DrSea CWD	Δ Win Pack	Δ Spr Pack	Δ Sum Pack	Δ Fal Pack
All Plots (2280- 3450m)	Δ SC1	r_s	0.081	0.090	0.049	0.066	0.179	-0.012	0.041	0.098	-0.119	-0.094	-0.138	-0.116
		p -value	0.346	0.295	0.564	0.439	0.035	0.889	0.635	0.250	0.164	0.272	0.104	0.175
	Δ SC3&4	r_s	-0.141	-0.122	-0.155	-0.130	-0.118	0.024	0.132	0.183	-0.224	0.123	0.112	0.004
		p -value	0.097	0.151	0.069	0.127	0.166	0.783	0.122	0.031	0.008	0.150	0.190	0.967
Low Elevation s (2280- 2649m)	Δ SC1	r_s	0.150	0.102	0.195	0.037	0.206	0.141	-0.034	0.101	0.038	-0.210	-0.336	-0.264
		p -value	0.208	0.395	0.101	0.760	0.082	0.238	0.777	0.398	0.751	0.077	0.004	0.025
	Δ SC3&4	r_s	-0.135	-0.182	-0.059	-0.151	-0.151	0.118	0.176	0.216	-0.216	0.304	0.271	0.049
		p -value	0.258	0.127	0.623	0.205	0.207	0.324	0.139	0.069	0.068	0.009	0.021	0.685
High Elevation s (2650- 3450m)	Δ SC1	r_s	0.179	0.188	0.133	0.151	0.126	-0.163	0.000	-0.032	-0.082	0.068	0.077	0.073
		p -value	0.148	0.129	0.284	0.222	0.311	0.189	0.999	0.800	0.512	0.583	0.535	0.556
	Δ SC3&4	r_s	-0.114	0.001	-0.276	-0.103	-0.065	-0.088	0.060	0.051	-0.203	-0.105	-0.047	-0.082
		p -value	0.360	0.995	0.024	0.407	0.602	0.478	0.630	0.680	0.099	0.399	0.703	0.512

Table 2.3. Categories of data involved in analysis. Ordinations were performed on each category and the first two axis scores for each resulting ordination were then used in multiple linear regression, to discern relative influence of each category on changes in stem structure of subalpine forest.

Data Category	Variables Included in Ordination	Type of Ordination
ENVIRONMENTAL	Elevation, Solar Heating Index (incorporates aspect and slope), Shrub Cover, Canopy Cover, Basal Area, Soil Water Storage, Sapling Abundance	Non-metric Multidimensional Scaling (NMS)
COMMUNITY	Stem Abundance for each of the eight species present: <i>Abies concolor</i> (white fir), <i>Abies magnifica</i> (red fir), <i>Juniperus occidentalis</i> var. <i>australis</i> , (Sierra juniper), <i>Pinus albicaulis</i> (whitebark pine), <i>Pinus contorta</i> subs. <i>murrayana</i> (Sierra/Cascade lodgepole pine), <i>Pinus jeffreyi</i> (Jeffrey pine), <i>Pinus monticola</i> (western white pine), <i>Tsuga mertensiana</i> (mountain hemlock)	Non-metric Multidimensional Scaling (NMS)
MODERN CLIMATE [1971-2000 (Time2) Averages]	Annual and seasonal variables (Winter, Spring, Summer, Fall), for Minimum Temperature (Tmin), Maximum Temperature, Precipitation (Prec), Snowpack (Pack) and Climatic Water Deficit (CWD).	Principle Components Analysis (PCA)
CLIMATE CHANGE (Time2 – Time1 Difference)	Same Variables as above plus Dry Season (Aug-Oct) Climatic Water Deficit and Spring (Mar-Jun) Pack	Principle Components Analysis (PCA)

Table 2.4. Summary of climate change for minimum and maximum temperature, and precipitation, for all 139 sites in my study, calculated from the Parameter-elevation Relationships on Independent Slopes Model (PRISM) spatial-climate dataset (Daly et al 2008). Time 1 (T1) corresponds with climatic conditions during the original sampling at each plot. Time 2 (T2) corresponds with climatic conditions close to the time of the re-sampling effort (2007-2009). Means for each time period were calculated first, followed by the mean for all grid points corresponding to each of the 139 plots in the study. For the variables listed, seasons were defined as December – February (winter), March – May (Spring), June – August (Summer) and September – November (fall).

	<i>T1 (1911-1940)</i> <i>Mean</i>	<i>T2 (1971-2000)</i> <i>Mean</i>	<i>T1 – T2</i> <i>Difference</i>	<i>T1 to T2 %</i> <i>Change</i>
Minimum Temperature (°C)				
Annual	-3.40	-2.25	+1.15	
Winter Tmin	-10.00	-8.70	+1.30	
Spring Tmin	-5.71	-4.61	+1.10	
Summer Tmin	4.16	5.10	+0.95	
Fall Tmin	-2.04	-1.00	+1.04	
Maximum Temperature (°C)				
Annual	10.45	10.63	-0.18	
Winter Tmax	3.18	2.43	-0.76	
Spring Tmax	7.90	8.20	+0.30	
Summer Tmax	19.39	19.70	+0.31	
Fall Tmax	12.05	11.47	-0.59	
Precipitation (mm)				
Annual	1103.75	1151.90	+47.15	+4.3
Winter Prec	601.78	567.57	-34.21	-5.7
Spring Prec	285.17	290.78	+5.61	+2.0
Summer Prec	39.13	47.92	+8.79	+22.5
Fall Prec	177.67	244.63	+66.96	+37.7

Table 2.5. Results for (A) Simple Linear Regression tests on stem change ($\Delta\text{SmallTrees}$ and $\Delta\text{LargeTrees}$) as a function of change in annual minimum temperature ($\Delta\text{AnnTmin}$), annual maximum temperature ($\Delta\text{AnnTmax}$) and annual precipitation ($\Delta\text{AnnPrec}$) and (B) multiple linear regression on a model of climate change, with change in $\Delta\text{AnnTmin}$, $\Delta\text{AnnTmax}$ and $\Delta\text{AnnPrec}$ as independent variables and change in stems (ΔSC1 or $\Delta\text{SC3\&4}$) as the dependent variable. Small stems were 10.2 - 30.4 cm diameter while large stems were ≥ 61.0 cm. Significant results at $p < 0.05$ are shaded.

(A) Simple Linear Regression

		Degrees of Freedom	ΔAnnT_{\min}	ΔAnnT_{\max}	$\Delta\text{AnnPrec}$
All Plots (2280-3450m)	$\Delta\text{SmallTrees}$	137	$r^2 = 0.004$ $p = 0.460$	$r^2 = 0.049$ $p = 0.009$	$r^2 = 0.008$ $p = 0.281$
	$\Delta\text{LargeTrees}$	137	$r^2 = 0.024$ $p = 0.068$	$r^2 = 0.010$ $p = 0.247$	$r^2 = 0.015$ $p = 0.150$
Low Elevations (2280-2649m)	$\Delta\text{SmallTrees}$	66	$r^2 = 0.027$ $p = 0.178$	$r^2 = 0.060$ $p = 0.045$	$r^2 = 0.006$ $p = 0.523$
	$\Delta\text{LargeTrees}$	66	$r^2 = 0.001$ $p = 0.824$	$r^2 = 0.003$ $p = 0.638$	$r^2 = 0.001$ $p = 0.824$
High Elevations (2650-3450m)	$\Delta\text{SmallTrees}$	69	$r^2 = 0.012$ $p = 0.358$	$r^2 = 0.037$ $p = 0.106$	$r^2 = 0.035$ $p = 0.118$
	$\Delta\text{LargeTrees}$	69	$r^2 = 0.062$ $p = 0.036$	$r^2 = 0.027$ $p = 0.168$	$r^2 = 0.028$ $p = 0.161$

(B) Multiple Linear Regression

		Mult r^2	p-value	ΔAnnT_{\min}	ΔAnnT_{\max}	$\Delta\text{AnnPrec}$
All Plots (2280-3450m)	$\Delta\text{SmallTrees}$.050	0.075	est. = -0.864 $p = 0.866$	est. = 19.781 $p = 0.018$	est. = 0.010 $p = 0.778$
	$\Delta\text{LargeTrees}$.029	0.268	est. = -1.316 $p = 0.247$	est. = -1.436 $p = 0.434$	est. = 0.002 $p = 0.764$
Low Elevations (2280-2649m)	$\Delta\text{SmallTrees}$.075	0.147	est. = 4.852 $p = 0.498$	est. = 27.226 $p = 0.036$	est. = -0.046 $p = 0.332$
	$\Delta\text{LargeTrees}$.010	0.882	est. = -0.850 $p = 0.633$	est. = -0.141 $p = 0.965$	est. = -0.001 $p = 0.900$
High Elevations (2650-3450m)	$\Delta\text{SmallTrees}$.086	0.127	est. = -16.070 $p = 0.200$	est. = 13.968 $p = 0.224$	est. = 0.123 $p = 0.088$
	$\Delta\text{LargeTrees}$.090	0.113	est. = -4.414 $p = 0.070$	est. = -1.984 $p = 0.370$	est. = 0.018 $p = 0.201$

Table 2.6. Results from whole-model and stepwise-type multiple linear regressions on categories of potential factors affecting changes in stem structure. Italicized headers represent independent variables in the model with *p*-values listed below. Independent variables were represent the first and second axis scores of ordinations on suites of variables for each category, carried out prior to regression tests. Δ SmallTrees (10.2 - 30.4 cm diameter) and Δ LargeTrees (≥ 61.0 cm) were dependent variables. Significant results at $p < .05$ are shaded.

		<i>Mult</i> <i>Sq</i>	<i>R-</i> <i>Sq</i>	<i>Adj</i> <i>Sq</i>	<i>R-</i> <i>Sq</i>	<i>Env</i> <i>PC1</i>	<i>Env</i> <i>PC2</i>	<i>Curr</i> <i>Clim</i> <i>PC1</i>	<i>Curr</i> <i>Clim</i> <i>PC2</i>	<i>Mod</i> <i>Comm</i> <i>PC1</i>	<i>Mod</i> <i>Comm</i> <i>PC2</i>	<i>AClim</i> <i>PC1</i>	<i>AClim</i> <i>PC2</i>
Whole Model	Δ SmallTrees	0.137	0.084	0.054	0.199	0.528	0.503	0.001	0.092	0.049	0.743		
	Δ LargeTrees	0.115	0.060	0.941	0.741	0.963	0.020	0.039	0.927	0.015	0.989		
Stepped Model	Δ SmallTrees	0.133	0.113	0.065	0.170	--	--	0.001	0.030	0.038	--		
	Δ LargeTrees	0.100	0.093	--	--	--	0.001	0.036	--	0.000	--		

Table 2.7. Pearson correlation coefficients (R) for several annual and seasonal variables of climate change and change in stem numbers for small trees (SC1; 10.2-30.4 cm dbh) and large trees (SC3&4; ≥61.0 cm) for individual species occurring in the central Sierra Nevada. Seasons were defined as Dec-Feb (winter), Mar-May (spring), Jun-Aug (summer) and Sep-Nov (fall).

Small Trees (10.2-30.4 cm)	ΔAnn Tmin	ΔAnn Tmax	ΔAnn Prec	ΔWin Tmin	ΔSpr Tmin	ΔSum Tmin	ΔFal Tmin	ΔWin Tmax	ΔSpr Tmax	ΔSum Tmax	ΔFal Tmax	ΔWin Prec	ΔSpr Prec	ΔSum Prec	ΔFal Prec	ΔSpr Pack	ΔFal Pack	ΔDrSea CWD
white fir (<i>Abies concolor</i>)	0.144	0.306	0.285	0.185	0.185	-0.031	0.035	0.234	0.026	-0.189	0.228	0.344	0.213	0.121	0.344	-0.122	0.061	-0.231
red fir (<i>Abies magnifica</i>)	0.210	0.311	0.122	0.316	0.259	0.104	0.132	0.289	-0.052	-0.166	0.241	0.108	0.099	0.110	0.142	-0.362	0.189	0.169
Sierra juniper (<i>Juniperus occidentalis</i> var. <i>australis</i>)	0.379	0.253	0.306	0.387	0.226	0.358	0.474	0.436	-0.308	-0.382	0.239	0.374	0.286	0.351	0.242	-0.130	-0.287	-0.373
whitebark pine (<i>Pinus albicaulis</i>)	0.040	0.029	0.012	-0.137	0.007	0.090	0.078	0.038	0.041	-0.140	0.078	0.050	0.010	0.058	-0.024	0.074	-0.014	0.149
lodgepole pine (<i>Pinus contorta</i> ssp. <i>murrayana</i>)	-0.073	0.160	-0.079	0.006	-0.017	-0.099	-0.081	-0.010	0.177	0.037	0.137	-0.052	-0.086	-0.076	-0.088	-0.106	-0.010	0.133
jeffrey pine (<i>Pinus jeffreyi</i>)	0.169	-0.049	0.122	0.221	0.107	0.152	0.211	0.183	-0.273	-0.249	0.010	0.106	0.134	0.173	0.103	-0.184	-0.126	-0.214
western white pine (<i>Pinus monticola</i>)	0.198	-0.051	0.315	0.219	0.053	0.172	0.229	0.169	-0.256	-0.071	-0.084	0.256	0.323	0.259	0.344	0.343	0.404	-0.243
mountain hemlock (<i>Tsuga mertensiana</i>)	0.043	-0.058	0.152	0.100	-0.138	0.038	0.109	0.066	-0.111	-0.129	0.100	0.151	0.138	0.092	0.167	0.203	-0.068	-0.176
Large Trees (≥61.0 cm)																		
white fir (<i>Abies concolor</i>)	0.211	0.135	0.009	-0.191	0.239	0.315	-0.007	-0.138	0.275	0.351	-0.023	0.094	-0.084	-0.119	0.066	0.258	0.390	0.466
red fir (<i>Abies magnifica</i>)	-0.106	-0.123	-0.164	-0.186	-0.142	-0.038	-0.081	-0.222	-0.176	0.261	-0.174	-0.173	-0.175	-0.236	-0.129	0.243	0.076	0.163
Sierra juniper (<i>Juniperus occidentalis</i> var. <i>australis</i>)	0.194	-0.404	0.063	0.075	0.125	0.225	0.183	-0.065	-0.169	0.069	-0.474	0.008	0.024	-0.017	0.137	0.014	-0.175	-0.004
whitebark pine (<i>Pinus albicaulis</i>)	-0.134	-0.158	-0.143	-0.088	-0.041	-0.128	-0.159	-0.186	0.073	0.095	-0.146	-0.158	-0.141	-0.128	-0.127	-0.094	0.089	-0.027
lodgepole pine (<i>Pinus contorta</i> ssp. <i>murrayana</i>)	0.113	0.023	0.147	0.029	0.114	0.118	0.101	0.110	-0.074	-0.227	0.113	0.130	0.174	0.208	0.123	0.046	0.044	0.028
jeffrey pine (<i>Pinus jeffreyi</i>)	-0.217	0.007	0.033	-0.222	-0.190	-0.236	-0.217	-0.171	0.365	0.185	-0.077	0.058	0.002	-0.167	0.084	0.215	0.079	-0.109
western white pine (<i>Pinus monticola</i>)	-0.148	-0.117	-0.137	-0.169	-0.171	-0.102	-0.124	-0.209	0.122	0.159	-0.107	-0.174	-0.126	-0.185	-0.108	0.088	0.015	0.081
mountain hemlock (<i>Tsuga mertensiana</i>)	-0.189	-0.113	-0.098	-0.114	-0.224	-0.200	-0.165	-0.167	0.094	0.099	-0.032	-0.109	-0.101	-0.125	-0.083	-0.001	-0.009	0.030

FIGURES

Figure 2.1. Map of study area in the central Sierra Nevada, CA showing locations of plots re-sampled modern plots (n=139; small circles) collocated on sites of historic Vegetation Type Mapping (VTM) plots. The entire study area encompasses approximately 5500 km² of subalpine forest (2300 m elevation up to treeline) and occurs entirely in minimally-disturbed, wilderness areas within National Parks and Forests. Modern sampling of the sites occurred from 2007-2009, approximately 75 years after original surveys.

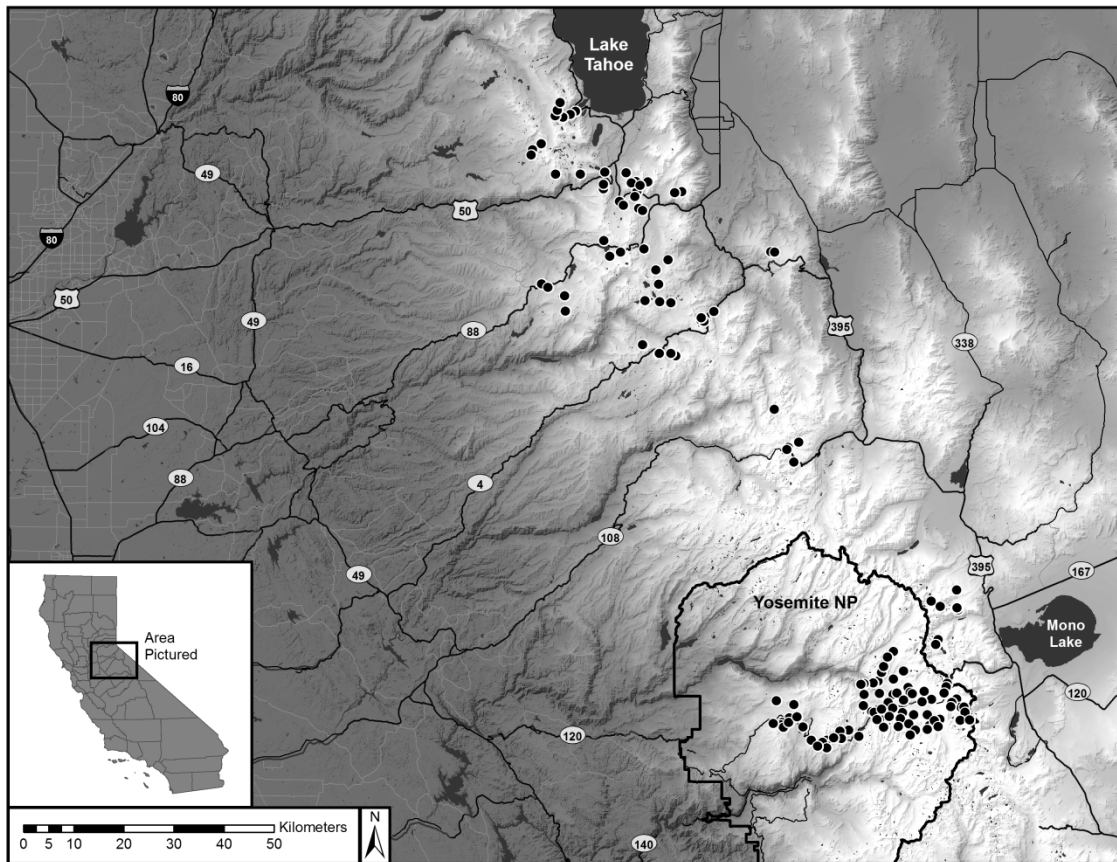


Figure 2.2. Change in annual minimum temperature, annual maximum temperature and annual precipitation versus change in small trees (SC1; 10.2 - 30.4 cm dbh) and large trees (SC3&4; ≥ 61.0 cm), across the landscape of my study area. Note that the greatest increases in minimum temperature and precipitation have been in the northern region of my study area. Climate data are from raster cells from PRISM collocated with 139 re-sampled plots throughout the central Sierra Nevada (see Methods).

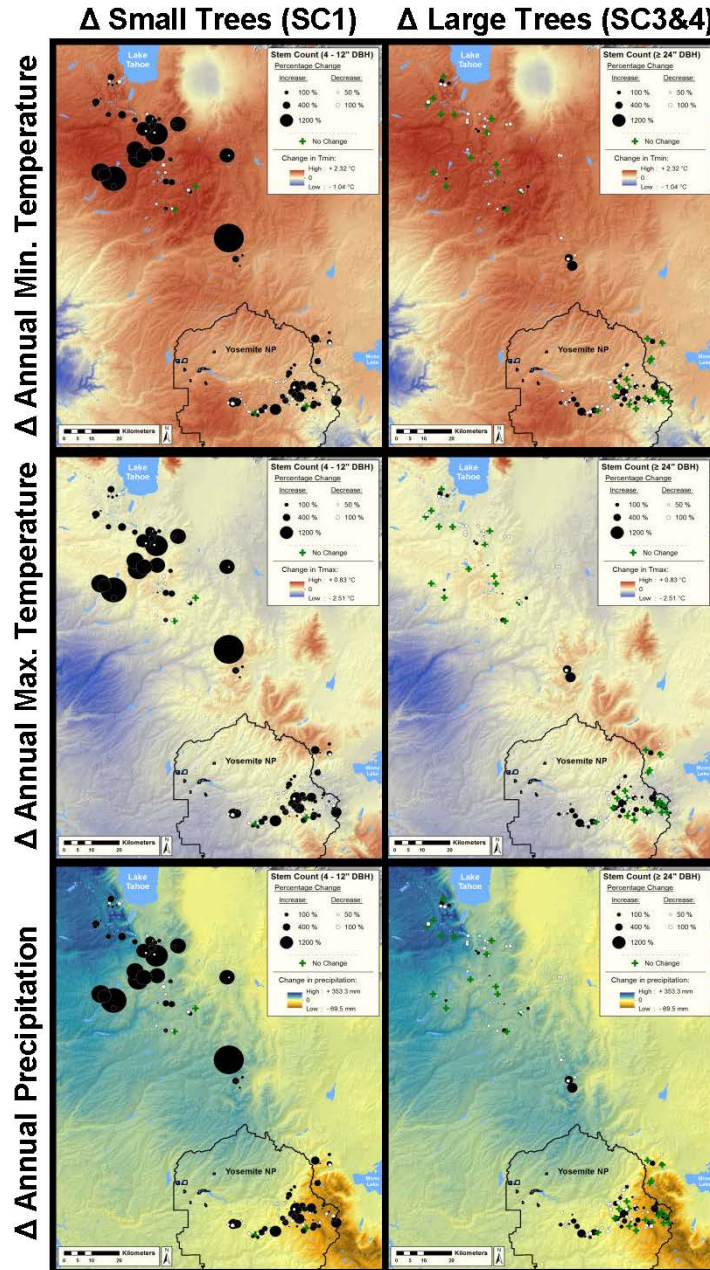


Figure 2.3. Simple linear regressions of change in stem number for small trees (10.2 – 30.4 cm diameter) and large trees (≥ 61.0 cm) against change in annual minimum temperature ($\Delta\text{AnnTmin}$), change in annual maximum temperature ($\Delta\text{AnnTmax}$) and change in annual precipitation ($\Delta\text{AnnPrec}$). Significant effects at $p = 0.05$ are indicated by “*”.

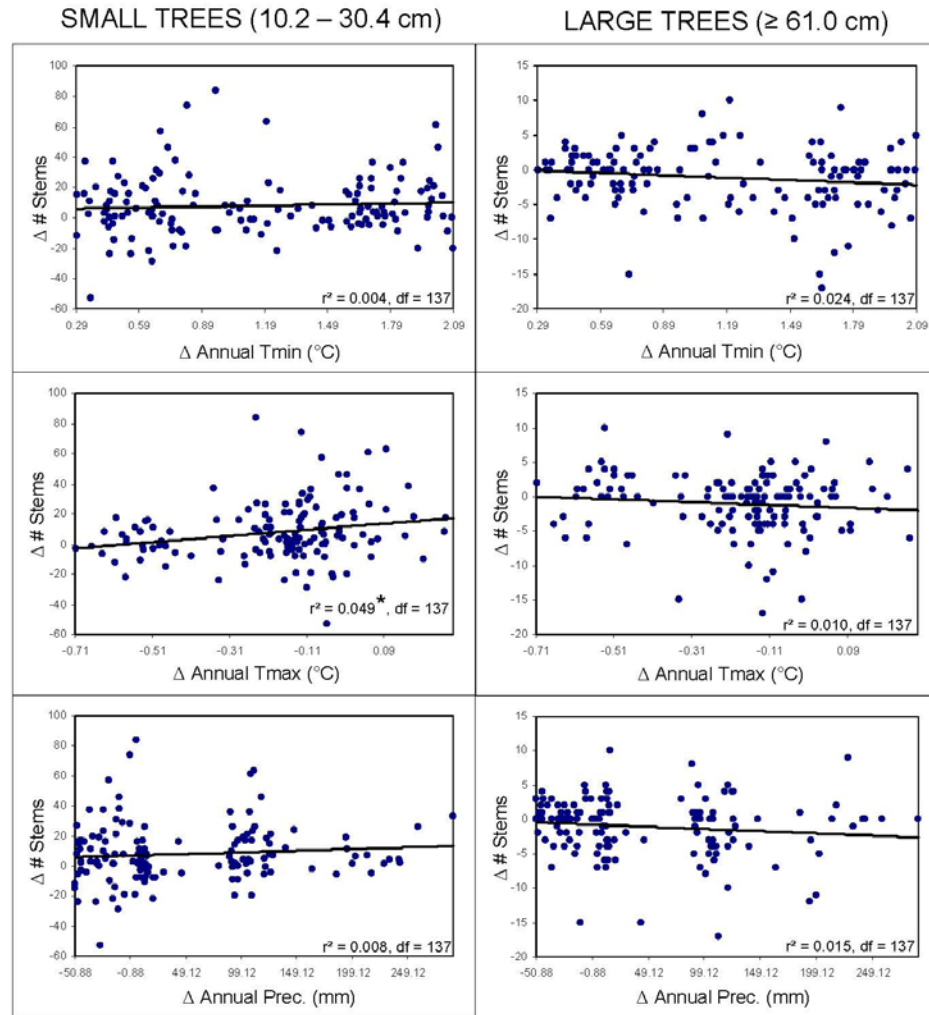
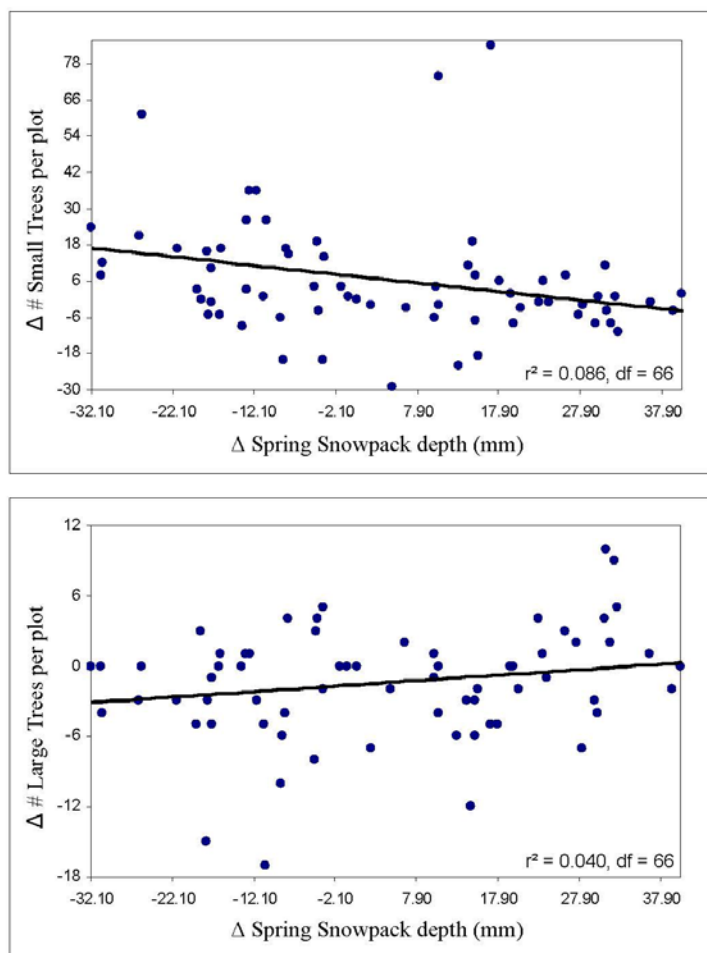


Figure 2.4. Simple linear regression of change in stem number for small trees (10.2 – 30.4 cm diameter) and large trees (≥ 61.0 cm) against change in spring (March – June) snow pack depth (mm) for low-elevation plots. Significant effects at $p = 0.05$ are indicated by “*”.



Chapter 3

Climatic drivers of 20th century radial growth for seven subalpine conifers from the Sierra Nevada and implications for their future

ABSTRACT

Biogeographic climate (or “climate-envelope”) models assume that species are highly adapted to their current climate and will shift their geographic range in synch with future climates. However, long-lived trees, dependent on numerous interactions, are likely to respond in a much more complex manner. I examined the response of radial growth of seven subalpine conifers to climate of the twentieth century (1895-2007) across a wide variety of sites throughout the central Sierra Nevada. By analyzing concurrently, all common species native to the region, over the same time-period, I provide greater resolution of how subalpine conifers of the region have responded to recent climate and how I may expect them to fare under future climate scenarios. My results highlight a general negative growth response to warm temperatures and low moisture availability. Response to maximum temperatures was much stronger than response to minimum temperatures for all species. All seven species were significantly negatively correlated with maximum temperature for much of the previous year’s growth and were significantly positively correlated with precipitation from the previous January through the current February. Lodgepole pine (*Pinus contorta* ssp. *murrayana*) was the least responsive to changes in precipitation and most responsive to warmer minimum temperatures. Mountain hemlock (*Tsuga mertensiana*) responded most positively to warm, dry conditions. This was contrary to my expectations, as mountain hemlock is primarily relegated to cool, wet slopes and is at the southern end of its distribution in the Sierra Nevada. Future climates that are warmer and/or drier may favor lodgepole pine and mountain hemlock over other species native to the region.

INTRODUCTION

Despite broad consensus among scientists that the earth's climate will continue to warm over the next 100 years (IPCC, 2007), our understanding of how individual species will respond to that change remains poor. Models that predict biological response to future climates are often very broad, focusing on future distributions of entire habitats or communities (Rehfeldt *et al.*, 2006; Randin *et al.*, 2009); however, response to changing climate is likely to be highly individualistic.

Forest tree species may be especially difficult to model. They are long-lived and often not in equilibrium with current climatic conditions (Svenning & Skov, 2004). Trees also generally have high rates of pollen flow and genetic diversity within populations (Hamrick, 2004), making them more robust to environmental change. Certainly, trees have undergone extinctions and migrations as a response to major climatic shifts in the past (Davis, 1989; Coats *et al.*, 2008), but it is unclear how the current trajectory of climate change compares with historical changes and whether current change will produce similar biological responses. Climate envelope models use predict future distributions of species by projecting the "bioclimate envelope" for that species onto future climatic conditions (Pearson & Dawson, 2003). These models assume that species are perfectly adapted to current climate and that alterations of this climate, in any direction, will necessarily lead to a reduction in adaptive ability and ultimately local extinction. Of course, to really understand the degree to which this is true, it is necessary to elucidate how species respond to current/recent climatic fluctuations and how these responses vary from species to species within a given community.

Dendrochronological studies that focus on the response of tree growth to environmental fluctuations (dendroecology) are valuable for understanding the historical range of species responses to climatic variability. Response to certain historic climatic conditions can be used to predict near-term response to those same conditions (Fritts, 1976). Historically, dendrochronology studies focused on one or two tree species from highly stressful sites, where response to climate is likely to be accentuated (Speer, 2010). The response to climate of trees occurring on these sites is easier to parse out from other environmental signals, but is less applicable to the entire distribution of the species. Recently, however, there has been an effort to sample across wider environmental gradients, within the broader range of a given species (Villalba *et al.*, 1994; Peterson *et al.*, 2002; Bunn *et al.*, 2005a; Littell *et al.*, 2008).

I analyzed the growth response to climate over the last century of seven conifer species from subalpine forests of the central Sierra Nevada. Tree cores were collected from 83 sites over an area covering about 5500 km², including a wide range of topographic, elevational and latitudinal positions for each species. By collecting from a wide range of environmental gradients, I not only develop a more complete picture of growth response for each species but I can also examine how those responses vary across environmental gradients. I benefit from the considerable amount of previous dendrochronological work from subalpine regions of California (Lamarche, 1974; Peterson *et al.*, 1990; Graumlich, 1993; Scuderi, 1993; Millar *et al.*, 2004; Bunn *et al.*, 2005b; Millar *et al.*, 2007; Salzer *et al.*, 2009). However, since most of these studies were from different locations, took place at different times, and each used different analytical

techniques, comparison of the ecological response among the species analyzed is difficult.

By analyzing all seven of the most common species occurring in the subalpine zone of the central Sierra Nevada together, collected from sites throughout the region, I hope to provide a more accurate representation of how individual subalpine species have responded to recent climate change. This approach can provide more specific predictions of how each species may respond individually to continued change into the future. For example, it is important to understand which of these seven species respond most positively to warm temperatures, since the climate will almost certainly continue to warm well into the coming century if not beyond. Although future precipitation trends in California are much less certain, it is similarly important to determine which species respond most positively or most negatively to drier or wetter conditions.

METHODS

Study Area and Field Sampling

Climate of the subalpine zone of the Sierra Nevada is characterized by a short, dry growing season and cool temperatures throughout the year. The annual snow-free period has historically been 6-9 weeks with frost possible any month of the year. Annual precipitation ranges from 750-1250 mm/yr and nearly all precipitation falls as snow between October and May. Soils are commonly thin and winds often severe, contributing to a generally stressful environment for tree growth (Fites-Kaufman *et al.*, 2007). Vegetation is extremely heterogeneous and tree diversity is high, especially compared with subalpine forests from other mountain ranges. Tree species found in the subalpine

zone of the central Sierra Nevada (generally from Yosemite National Park north to Lake Tahoe) include whitebark pine (*Pinus albicaulis*), Sierra/Cascade lodgepole pine (*Pinus contorta* subs. *murrayana*), mountain hemlock (*Tsuga mertensiana*), western white pine (*Pinus monticola*), red fir (*Abies magnifica*), Sierra juniper (*Juniperus occidentalis* var. *australis*), Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), and quaking aspen (*Populus tremuloides*). Stands can be made up of single species or various combinations of multiple species and are typically sparse, with low-lying or absent shrub cover (Sawyer *et al.*, 2009). This structure, together with the short growing season, extensive exposed rock, and thin soils, make fire rare (van Wagtendonk & Fites-Kaufman, 2006). For more information on Sierra Nevada subalpine vegetation see Parker (1988), Potter (1998) and Fites-Kaufman (2007).

Tree cores were collected between 2007 and 2009 from 83 sites in the central Sierra Nevada, from Mono Pass in the south (37.812° N latitude) to the northeast edge of the Lake Tahoe basin in the north (39.312° N latitude), and ranging from 2300 m elevation up to treeline at about 3500 m (Figure 3.1). Coring sites were collocated with vegetation plots that re-sampled historical US Forest Service plots that supported vegetation mapping in the early 1930s (Dolanc *et al.*, in press), and thus each core has considerable stand structure and site physical data associated with it. Nearly all (> 95%) sites occur west of the Sierra Nevada crest and all sites were in relatively undisturbed public land.

One to ten cores were collected per site, resulting in 429 cores used for analysis. Cores were taken from all eight species listed above with sample sizes more or less commensurate with the frequency of the species (Table 3.1). Cores were collected from

all species listed above. However, for analysis, both white fir and quaking aspen were removed due to extremely low sample sizes (< 10 cores per species). The 83 sites cover a wide gradient of elevation, slope, aspect and latitude within the study area; a strong effort was made to sample from as many different habitats and site physical conditions as possible for each species. Core extraction was done on the midslope side of the tree at breast height for large trees (≥ 25 cm dbh) and 30 cm above ground for small trees (< 25 cm dbh). Since I was only interested in growth response during the previous 110 years, I was not concerned about hitting the center on large trees. However, mean core length was over well over 100 years for most species (Table 3.1). As part of my effort to sample as wide a variety of site conditions and tree growth responses as possible, one core was taken per tree and all diameters were sampled from very large trees down to 6 cm dbh. Shading conditions of cored trees ranged from partial shade to full sun.

Core Preparation and Chronology Development

Tree cores were prepared in the laboratory using standard techniques (Stokes & Smiley, 1968). Cores were cross-dated visually using the list method (Yamaguchi, 1991). Rings were measured to the nearest 0.001 mm width using a Velmex stage measuring system and associated MeasureJ2X software. After measurement, cross-dating accuracy was verified with COFECHA (Holmes, 1983; Grissino-Mayer, 2001). Problematic cores flagged by COFECHA were checked and if changed, re-measured and re-analyzed with COFECHA.

Standardization and chronology development was carried out with the aid of ARSTAN for Windows (Cook, 1985). One chronology per species was created for the

entire study area. The development of chronologies that cover such a large area has the effect of reducing interseries correlation and mean sensitivity for each chronology (Table 3.1); however, this approach is tailored to my objective of determining species-level responses across multiple gradients. ARSTAN produces three types of standardized chronologies, called the standard, residual and arstan chronology, via different methods of standardization. For more information on their differences and the underlying analyses see Speer (2010).

Climate Data

I downloaded data from the PRISM (Parameter-elevation Regressions on Independent Slopes Model) 800-m grid spatial data set (Daly *et al.*, 2008) for a grid cell located at 119.60 °W; 38.33 °N from the PRISM Climate Group website (<http://www.prism.oregonstate.edu/>). This location is just west of Sonora Pass at approximately 2805 m elevation and represents a central point for my study area (Figure 3.1), as well as a mid-range elevation, latitude and topographic position. for comparison with growth response over the same period. Climate stations at high elevations have historically been sparse and PRISM data have been shown to account reasonably well for the variable topography and elevation of montane environments (Daly *et al.*, 2008). I used data for maximum temperature (Tmax), minimum temperature (Tmin) and precipitation from 1895 to 2007, for both annual and monthly means.

I also downloaded data from the National Climatic Data Center (NCDC) website for U.S. Climatological Division CA-5, San Joaquin Drainage. Divisional data such as these are frequently used in dendrochronological studies because they provide long-term

averages for the region. I downloaded monthly data for mean temperature (Tmean), Prec and Palmer Drought Severity Index (PDSI) for the period 1895 to 2007. The PDSI integrates both temperature and precipitation effects (Palmer, 1965) and can be particularly revealing in Mediterranean climates, where the growing season corresponds with prolonged drought. PDSI is scaled so that “drought” covers a wide range of conditions.

Climate-Growth Analyses

The association between radial growth and climate was analyzed as correlation and response functions using DENDROCLIM2002 (Biondi & Waikul, 2004). The standard chronology, residual chronology and arstan chronology from ARSTAN were analyzed for each species along with mean monthly data for Tmax, Tmin and Prec from PRISM and Tmean, Prec and PDSI from the Divisional data. A 24-month window, from January of the previous year, through December of the current year (the year represented by ring width of interest) was analyzed for every pair of variables, for the entire 1895-2007 window of time. The best relationships, consistently for all seven species, were the correlation response between the standard chronology and PRISM data, and between the standard chronology and PDSI; therefore, these are the only results presented in this paper.

Growth Response by Elevation Bands

To determine whether growth response is different at low vs. high elevation bands, I divided the series for each species into low and high elevations bands and re-ran

analyses. For this analysis, I only included species for which my cores cover a majority of their natural elevational range at the latitude of the central Sierra Nevada. Species included were whitebark pine, lodgepole pine, western white pine and mountain hemlock, the four highest-elevation species in my study area. The remaining three species (red fir, Sierra juniper and jeffrey pine) have the center of their elevational distribution near or below 2300 m, which is the lower limit of my study.

Elevation bands were made for each species by dividing the total elevational range of cores for that species into “low” and “high” elevations, resulting in mostly equal groups for each species. For example, I collected cores for mountain hemlock ranging from 2431 m up to 3014 m. All cores collected at elevations from 2431 to 2722 were lumped into the “low elevation” band; all cores collected at elevations from 2723 to 3014 were placed in the “high elevation” band. I developed separate chronologies for each elevational band, for each species, for a total of eight chronologies. These were standardized with ARSTAN and analyzed for correlation and response with climate with DENDROCLIM2002 as with the other chronologies, using the same climate data from PRISM for 1895-2007 from Sonora Pass.

RESULTS

Chronologies (1895-2007)

Several periods of synchronous growth response are apparent in the chronologies for the seven focal species, as well as a few periods of clear anti-synchronous response (Figures 2, 3). All seven species experienced an extended period of generally slowing growth between the 1890s and the early 1930s. Four of the seven species experienced

their absolutely lowest measured growth rates during the warm and dry early 1930s, but growth recovered to at least average values for all species by the early 1940s. The early 1980s, which were unusually wet, were a particularly poor period of growth for lodgepole pine and a particularly good period for Sierra juniper and Jeffrey pine. A lagged positive growth response to the very wet years of 1982 and 1983 is visible in all of species, and three of them (red fir, Jeffrey pine, and mountain hemlock) show their absolute highest measured growth rates between 1984 and 1986. Since that time, tree growth has tended to slow (Figure 3.3).

Interseries correlation and mean sensitivity among species and within species (among tree cores for a given species) are given in Table 3.1. Interseries correlation is a measure of the relationship (Pearson correlation) among chronologies and represents their similarity to each other. Mean sensitivity is a measure of variability in growth within a chronology (Grissino-Mayer, 2001; Speer, 2010). The interseries correlation (R) among all seven species chronologies ranged from 0.285 to 0.788 with a mean of 0.626. Interseries correlation was considerably lower for Sierra juniper than all other species ($r = 0.285$; Table 3.1) than the other six species, suggesting that its growth response to climate is unique among all subalpine species native to the region (Table 1; Figure 3.3).

Growth Response to Climate

With some notable exceptions, correlations of growth with temperature were generally negative, while correlations with precipitation and PDSI were positive (Figure 3.4). Though both correlation and response functions were carried out for each analysis, the correlation values were generally stronger yet consistently in the same direction as

response function values; thus I report only correlations here. Results are focused only on statistically significant correlations. Correlation between growth and Tmax was much stronger than growth with Tmin, especially during the previous growing season. Negative correlations with Tmax occurred in more months for all seven species and were more strongly negative on average (Figure 3.4).

Most species showed significant negative correlations between growth and Tmax from the previous March through the previous November and a few had significant negative correlations well into the current growing season. Negative correlations were strongest in July and August of the previous year (ranging from -0.25 to -0.47), with all seven species showing significant negative correlations in the previous July. Three species - mountain hemlock, Jeffrey pine and western white pine - exhibited positive correlations with Tmax in May of the current year. Mountain hemlock also had positive correlations in April and June of the current year (Figure 3.4).

Correlation with Tmin was most negative during the previous April, with red fir, whitebark pine, jeffrey pine, western white pine and mountain hemlock all showing significant correlations ranging from -0.20 to -0.32 (Figure 3.4). Similar to Tmax, three species - mountain hemlock, lodgepole pine and western white pine - correlated positively with Tmin in the current May. Lodgepole pine was the only species showing significant positive correlations with Tmin from the previous year.

Correlation between growth and precipitation was generally positive for most species from January of the previous year through the current March. All but mountain hemlock correlated positively with precipitation during the current February (ranging from +0.21 to +0.33) with the previous August, previous September and previous March

also showing numerous significant positive correlations. Mountain hemlock exhibited positive correlations with precipitation during the previous year and negative correlations during the current year and it had the most consistent negative correlation with precipitation of all species. Negative correlations for mountain hemlock were especially strong in March through June of the current year, with correlations ranging from -0.19 to -0.29). Western white pine also showed three months of negative correlation with precipitation, the previous December, current May and current June (Figure 3.4).

Correlations between growth and PDSI showed similar trends as with precipitation. In general, most species correlated positively with PDSI from the previous January through the current May. Mountain hemlock correlated positively during the previous year and negative during the current year. Overall, correlation with PDSI was stronger than all other variables, ranging from -0.33 to +0.52 during the 24- month analysis window.

Correlation between temperature and growth by low and high elevation bands demonstrate a general trend of a more negative response to temperature at low elevations (Figure 3.5). Conversely, positive correlations with temperature were more likely for trees from high elevations. In addition, growth was generally more sensitive to Tmax and to Tmin at both low and high elevations (Figure 3.5). Whitebark pine and lodgepole pine were both considerably more sensitive to Tmax at low elevations than high. There were no obvious trends between low and high elevations for correlation of growth and precipitation (data not shown).

DISCUSSION

Climate-Growth Trends 1895-2007

The species in this study tended to grow more rapidly during cool and wet climatic conditions between 1895 and 2007. This preference is illustrated by the chronologies for each species and correlations between growth and climate. All seven species exhibited poor growth years during the early 1930s (Figure 3.3). This period corresponds with a particularly warm (especially for maximum temperatures) and dry period in the climate record (Figure 3.2). The decreasing trend in growth from the late 1890s to the early 1930s also corresponds with a rising trend in maximum temperatures. All species (with the possible exception of Sierra juniper) show a marked positive growth response in 1984, following extremely wet and cool years in 1982 and 1983 (Figures 2, 3). However, notable differences in species responses exist from 1980 to 1982, a warm and wet period. During these years, lodgepole pine exhibited suppressed growth, while Sierra juniper and Jeffrey pine were well above average for the entire period.

All seven species exhibited negative correlations between radial growth and maximum and minimum temperatures, particularly during the previous year. Likewise, all seven species exhibited positive correlations with precipitation and Palmer Drought Severity Index (PDSI) during the previous year and many showed positive correlations continuing in the current year (a more positive PDSI indicates greater water availability.) This pattern corresponds with that of other dendrochronology work from subalpine of the Sierra Nevada and White Mountains (Lamarche, 1974; Peterson *et al.*, 1990; Graumlich, 1993), but is in contrast with typical responses from the west side of the Cascades, where growth of subalpine conifers is especially negatively correlated with precipitation, but

also often positively correlated with temperature (Peterson & Peterson, 1994, 2001; Peterson *et al.*, 2002).

Moisture Availability and Maximum Temperature

Studies have shown that moisture availability (via snowpack) is crucial for good growth years in the Sierra Nevada (Peterson *et al.*, 1990; Graumlich, 1991; Millar *et al.*, 2007). My results suggest that snowpack during the previous growing season continuing through to spring of the current growing season may be the most important factor for good growth. Both precipitation and PDSI generally elicited significant, positive growth responses starting during the previous winter and lasting through the current spring (Figure 3.4). Maximum temperature is negatively correlated with growth during this same period, for most species (Figures 3.4, 3.5). Minimum temperature, though generally eliciting weak correlations with growth, was a particularly important factor for five of seven species during April of the previous year. Growth was negatively correlated with minimum temperature during this period, when snowpack has reached its peak and has begun to decline. All of these results support long-lasting snowpack as possibly the most important factor for good radial growth.

In the dry Sierra Nevada growing season, temperature may play its greatest role as a regulator of snowpack (Peterson, 1998). Further evidence for this comes from my comparison of low versus high elevation bands for each species (Figure 3.5). The negative sensitivity of growth to temperature is generally weaker at higher elevations for all species. Temperatures at higher elevations are generally lower, with longer lasting

snowpack, despite lower annual precipitation at these elevations compared to my low-elevation band.

Correlation with maximum temperature was particularly strong and generally negative, especially compared with minimum temperature. To my knowledge, no other studies have reported on subalpine species in the region responding so consistently and strongly to maximum temperature, especially compared with minimum temperature. Millar et al. (2007) found a negative correlation between radial growth of limber pine (*Pinus flexilis*) from the eastern Sierra Nevada and maximum temperature, but found even stronger responses to minimum temperature and precipitation. My results suggest that maximum temperature is more limiting to growth than minimum temperature, for all seven species examined. This is supported not only by the stronger and more consistent negative correlations of growth with maximum temperature (Figures 3.4, 3.5), but the correspondence between a decline in growth in the early 1930s and a rapid, sustained period of high maximum temperatures; minimum temperatures rose appreciably 2-3 years after this period (Figures 3.2, 3.3)

That subalpine tree species should be more sensitive to maximum temperature than minimum is surprising, considering the subalpine zone is characterized by short, cool growing seasons during which frost can occur at any time (Fites-Kaufman *et al.*, 2007). Maximum temperature may play a greater role in the control of snowpack depth and duration during the first half of the growing season, especially at lower elevations. Although both minimum and maximum temperatures should contribute to snowmelt, maximum temperatures may be more important to trees during the early part of the growing season, when night-time minima still dip well below freezing but daytime high

temperatures range from near freezing to well-above. Studies in Norway found that the upper limit of timberline best correlated with maximum temperatures of the warmest month (Odland 1996; Mook & Vorren 1996, as cited in Holtmeier, 2003). In cold environments, growing season warmth may be more dependent on daytime highs than nighttime lows.

Implications for Climate Change

Models predict with high certainty that temperatures in California will rise significantly over the next 100 years (Cayan *et al.*, 2008; Moser *et al.*, 2009). Though there is more uncertainty about annual precipitation, earlier snowmelt (Stewart *et al.*, 2004; Maurer, 2007) and increasing proportions of rain to snow (Knowles *et al.*, 2006) mean that, regardless, trees will likely be more drought-stressed during the growing season. Evidence of increased impacts from drought is seen in increasing rates of tree mortality (van Mantgem *et al.*, 2009) and rising activity of large wildfires (Westerling *et al.*, 2006) in the western US.

Warmer temperatures and greater drought-stress would likely lead to a reduction in radial growth for the species in my study, which show a general preference for cooler, wetter conditions. Reduced radial growth does not necessarily translate to range contraction or displacement from lower-elevation species. Evidence indicates that subalpine species of the Sierra Nevada have generally increased their abundance since the early 20th century, including species from lower and higher elevations (Dolanc *et al.*, in press). However, it is assumed that sustained reduction in growth of subalpine species would eventually lead to replacement by lower-elevation species adapted to warmer

conditions as predicted by models (Hayhoe *et al.*, 2004; Lenihan *et al.*, 2008), but it is unknown how long this process may take.

Species-level differences may provide clues as to which species may best handle predicted increased competition from species moving upslope. Perhaps the most surprising response to recent climate comes from mountain hemlock, which appears to prefer cool and wet conditions during the previous year, but warm and dry conditions the following year. This 2-phased response may be reflected in the up-and-down nature of its chronology (Figure 3.3). Perhaps more important though is that, of all species in the study, mountain hemlock responds most positively to warm and dry conditions (Figures 3.4, 3.5), yet, of all the species I measured, mountain hemlock would on the surface seem to be the most at-risk under projected future climates. In the central Sierra Nevada, mountain hemlock is relegated to the coolest and wettest (snowiest) slopes in the region (Fites-Kaufman *et al.*, 2007; Sawyer *et al.*, 2009) and is close to the southern end of its distribution in the Sierra Nevada (Griffin & Critchfield, 1972). Climate-envelope models (see Pearson & Dawson, 2003) should predict mountain hemlock to be the biggest “loser”, in a climate that is warming and/or drying. This discrepancy exemplifies one reason why these models may be inaccurate for many species, i.e. many factors other than climate combine to shape the current distribution of a species (Heikkinen *et al.*, 2006). Mountain hemlock, though relegated to cool, wet slopes may actually prefer warmer, drier sites but has historically been out-competed in these habitats. Data from the Pacific northwest suggest that though regeneration of mountain hemlock is poor on warmer sites, their growth is better there than on cooler sites where they are more abundant (Franklin & Dyrness, 1973). If a warming climate reduces the growth of all

other subalpine conifers in the central Sierra Nevada, this may impart a surprising advantage to mountain hemlock.

Another big “winner” in a future that is warmer and/or drier may be lodgepole pine. Lodgepole pine only responded negatively to maximum temperature in three months of the 24-month period I analyzed; this was the fewest of all species in my study (Figure 3.4). For minimum temperature, lodgepole pine growth was actually significantly positively correlated in three months, more than any other species, and showed no negative correlations. Since minimum temperatures have risen over the past century much more than maximum temperatures (Coats, 2010), and can probably be expected to continue increasing, lodgepole pine may show enhanced average growth relative to most other species over the next 100 years.

In addition, lodgepole pine is fairly non-responsive to moisture availability (Figure 3.4). Correlation of lodgepole pine growth with both precipitation and PDSI resulted in the fewest significant relationships of any of the seven species examined, and those that were significant were relatively modest. Lodgepole pine can tolerate a wide range of soil moisture in my study area, occurring commonly in meadow complexes as well as dry ridge tops (Fites-Kaufman *et al.*, 2007; Sawyer *et al.*, 2009). These characteristics place lodgepole pine in a good position to handle a warmer future, regardless of precipitation. Lodgepole pine has increased in abundance since the 1930s, probably in response to warmer temperatures, though at levels commensurate with other subalpine species (Dolanc *et al.*, in press).

Conclusions

Growth response of subalpine conifers of the central Sierra Nevada to twentieth century (1895-2007) climate suggests that most species will suffer reduced radial growth if the climate warms and/or gets drier. Reduced growth should eventually lead to reduced competitive ability or reduced survival and thus a contraction of distributional limits for many species. These changes will likely be differential across species though, which could lead to alterations in community structure. Mountain hemlock and lodgepole pine may be in an improved competitive position, relative to the other subalpine species, if the climate warms and dries.

Interestingly, all seven subalpine species are more sensitive to maximum temperature than to minimum temperature. It is unclear how this may affect continued response to a changing climate. So far, minimum temperatures have risen much more in the Sierra Nevada (Coats, 2010). This suggests that projecting future conditions with models that use simple climatic variables (e.g. means) may miscast future response by failing to attribute change to differences in response to maximum versus minimum temperatures. Nevertheless, it is difficult to imagine that maximum temperature would not eventually rise as well, given that global mean temperatures are projected to rise at least 2.0 °C over the next 100 years (IPCC, 2007). Significant increases in maximum temperatures, as shown by response of tree growth to existing climatic variability, may drive a population-level response that is at odds with recent shifts in forest demography (Dolanc *et al.*, in press).

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TABLES

Table 3.1. Species sampled plus sample size (number of cores) and statistics produced during chronology development. The number of cores is approximately commensurate with the abundance of each species for the 83 sites where coring took place across the landscape of the central Sierra Nevada. Two other species, white fir (*Abies concolor*) and quaking aspen (*Populus tremuloides*), which occur intermittently in my study area were also cored but their samples sizes were too low for inclusion in this study. “Interseries Correlation Among Species” represents the correlation between chronologies of species while “Interseries Correlation Within Species” represents correlation between cores, or series, of a species. Mean correlation among species was 0.626. Mean sensitivity is an index of the variability from ring to ring. See Fritts (1976) or Speer (2010) for more information on these measures.

Species	# Cores (Series)	Mean Series Length (yrs)	Interseries Correlation Among Species (r)	Interseries Correlation Within Species (r)	Mean Sensitivity Within Species
<i>Abies magnifica</i> (red fir)	50	103.1	0.788	0.489	0.203
<i>Juniperus occidentalis</i> var. <i>australis</i> (Sierra juniper)	12	255.8	0.285	0.192	0.267
<i>Pinus albicaulis</i> (whitebark pine)	64	171.4	0.584	0.354	0.209
<i>Pinus contorta</i> ssp. <i>murrayana</i> (Sierra/Cascade lodgepole pine)	135	111.8	0.674	0.308	0.234
<i>Pinus jeffreyi</i> (jeffrey pine)	24	163.1	0.681	0.292	0.247
<i>Pinus monticola</i> (western white pine)	55	143.5	0.741	0.398	0.236
<i>Tsuga mertensiana</i> (mountain hemlock)	58	108.4	0.620	0.592	0.249

FIGURES

Figure 3.1. Map of study area, Sierra Nevada, CA, USA. Coring sites are indicated by dark triangles. All sites were in undisturbed locations between 2430 and 3397 m elevation and 37.812 and 39.312° north latitude. One core per tree was taken from the midslope side of each individual and most trees were in open or partly open shading conditions. Sampling intentionally covered a wide range of topographic positions within the study area.

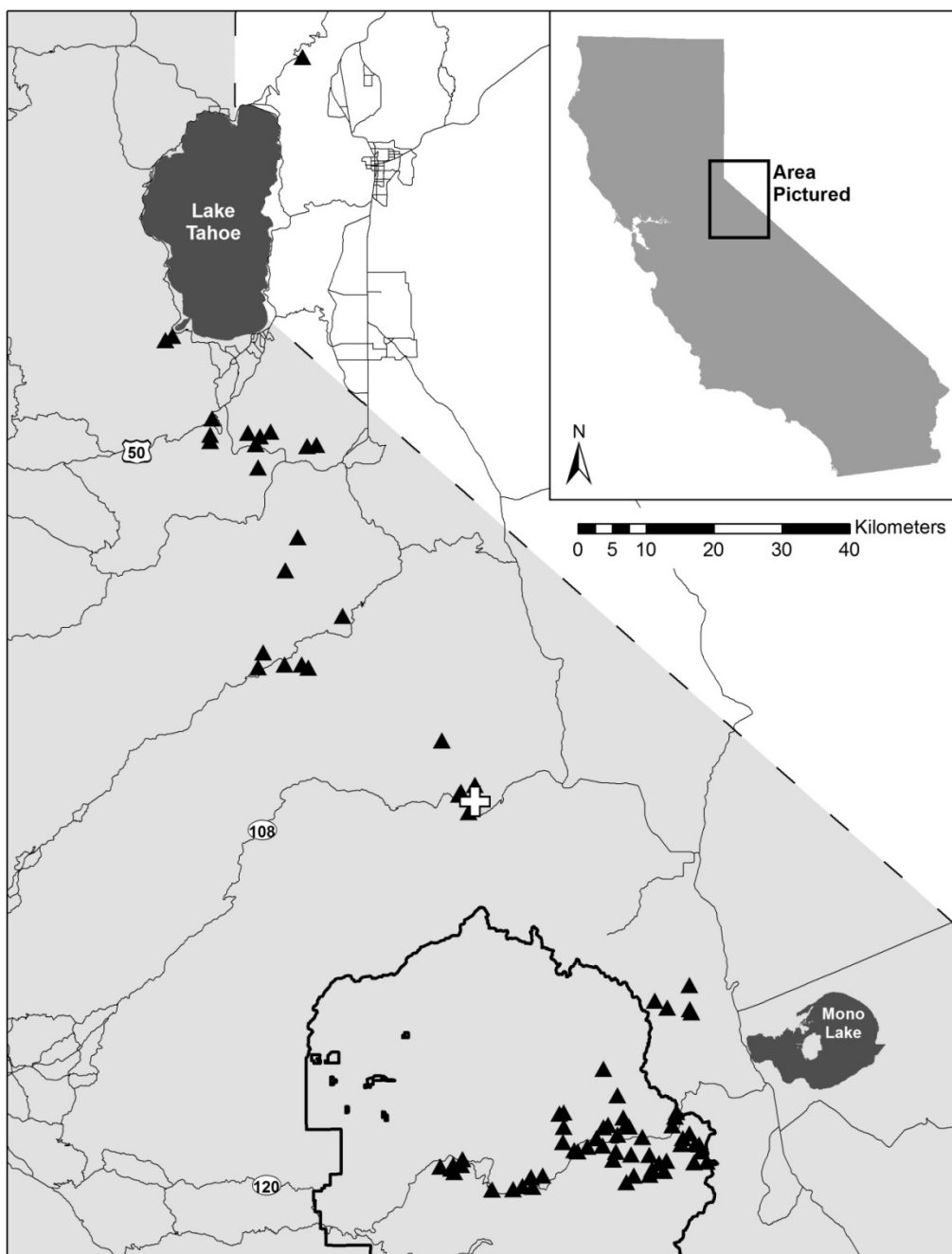


Figure 3.2. Climate, 1895-2007 near Sonora Pass (-119.60 W; 38.33 N; 2805 m elevation), a central point for my study area. Data were taken from PRISM (Parameter-elevation Regressions on Independent Slopes Model) downloaded from the PRISM climate group website (<http://www.prism.oregonstate.edu/>) for the grid cell at the coordinates listed above. Data are mean maximum temperature, mean minimum temperature and total precipitation for each year listed (January 1 – December 31). Mean annual maximum temperature for the 1895-2007 period was 10.4 °C; mean annual minimum temperature was -3.5 °C and mean precipitation was 908.5 mm/year.

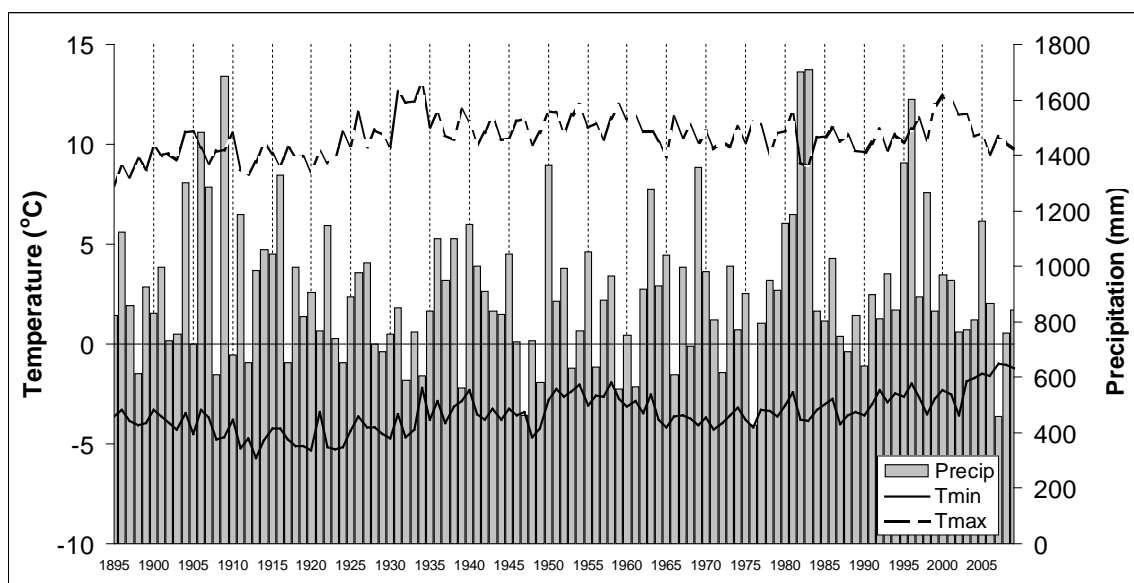


Figure 3.3. Standardized chronologies from ARSTAN (Cook 1985) for the seven subalpine species in this study: red fir (*Abies magnifica*), Sierra juniper (*Juniperus occidentalis* var. *australis*), whitebark pine (*Pinus albicaulis*), Sierra/Cascade lodgepole pine (*Pinus contorta* ssp. *murrayana*), jeffrey pine (*Pinus jeffreyi*), western white pine (*Pinus monticola*), and mountain hemlock (*Tsuga mertensiana*), for the 1895 to 2007 period. Y axes represent growth indices with the solid center line representing mean growth over the entire period.

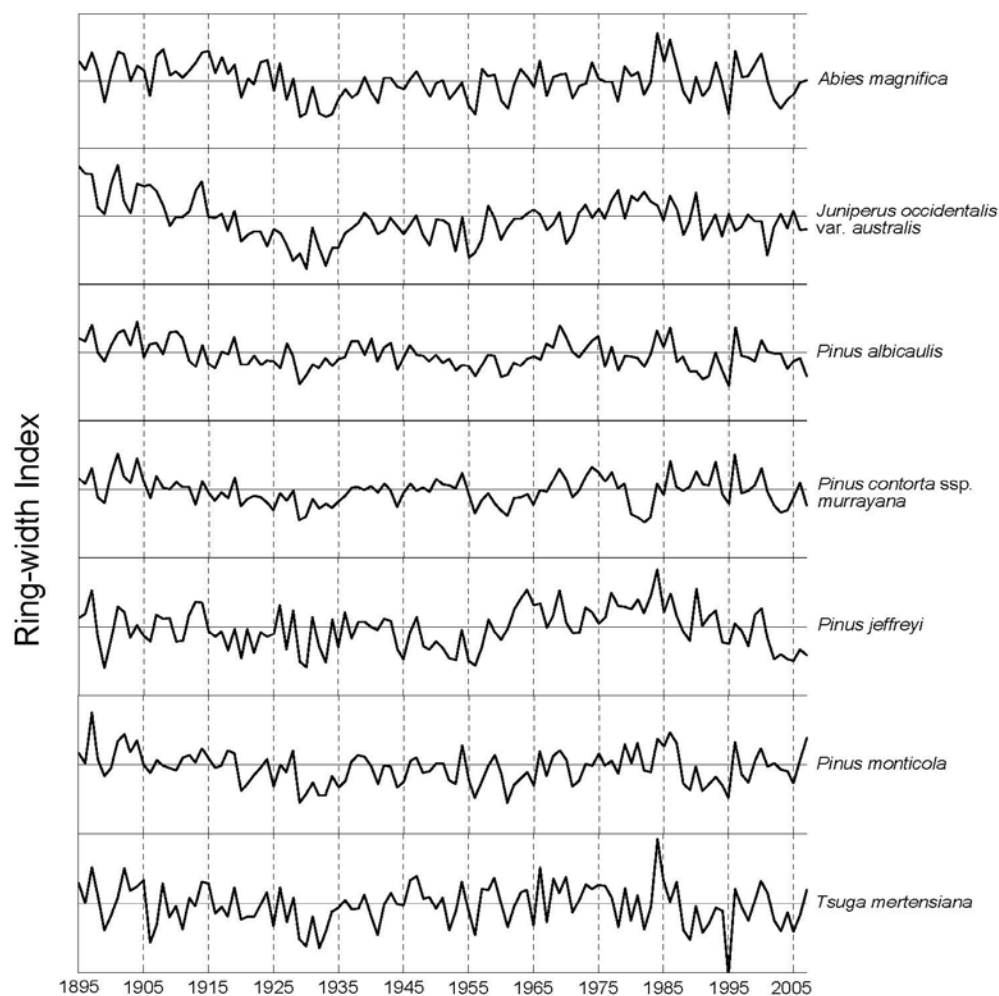


Figure 3.4. Correlation coefficients (Pearson's R) for correlations between annual growth and monthly climate variables: (a) maximum temperature, (b) minimum temperature, (c) precipitation, and (d) Palmer Drought Severity Index (PDSI), for the 24-month period starting with January of the previous year's growth through December of the current year's growth, for the period 1895-2007. Analysis was carried out using DENDROCLIM2002 (Biondi and Waikul 2004). Only statistically significant correlations at $P < 0.01$ are shown. Species shown are red fir (*Abies concolor*; **ABMA**), Sierra juniper (*Juniperus occidentalis* var. *australis*; **JUOC**), whitebark pine (*Pinus albicaulis*; **PIAL**), Sierra/Cascade lodgepole pine (*Pinus contorta* ssp. *murrayana*; **PICO**), jeffrey pine (*Pinus jeffreyi*; **PIJE**), western white pine (*Pinus monticola*; **PIMO**), and mountain hemlock (*Tsuga mertensiana*; **TSME**).

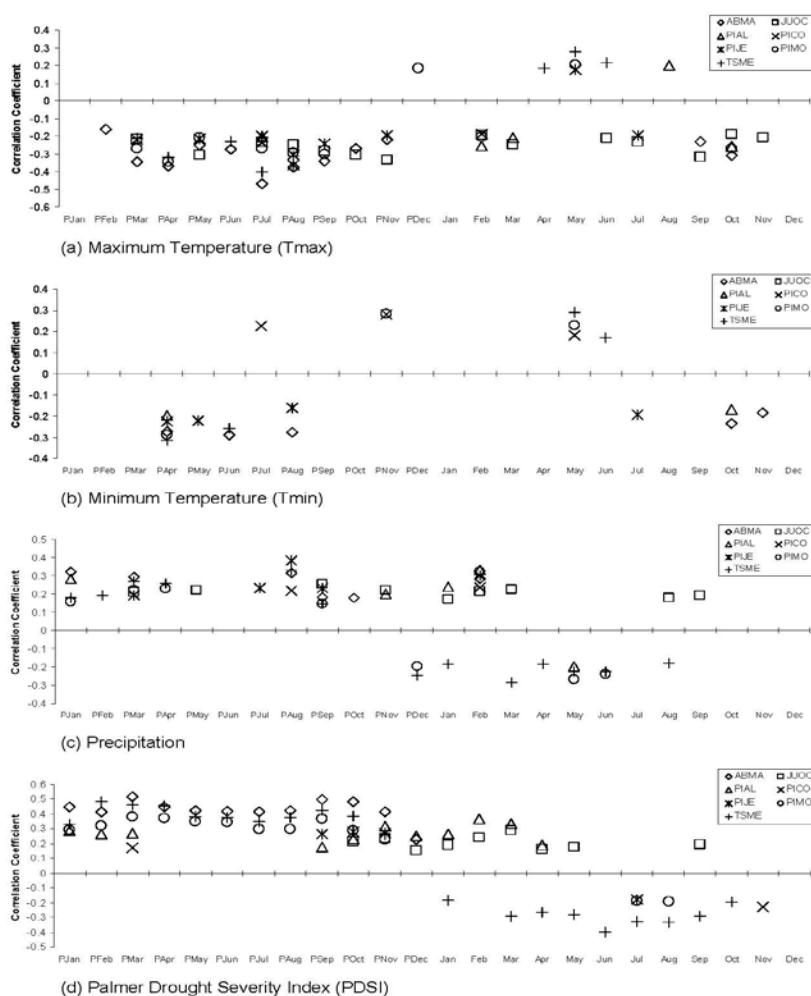
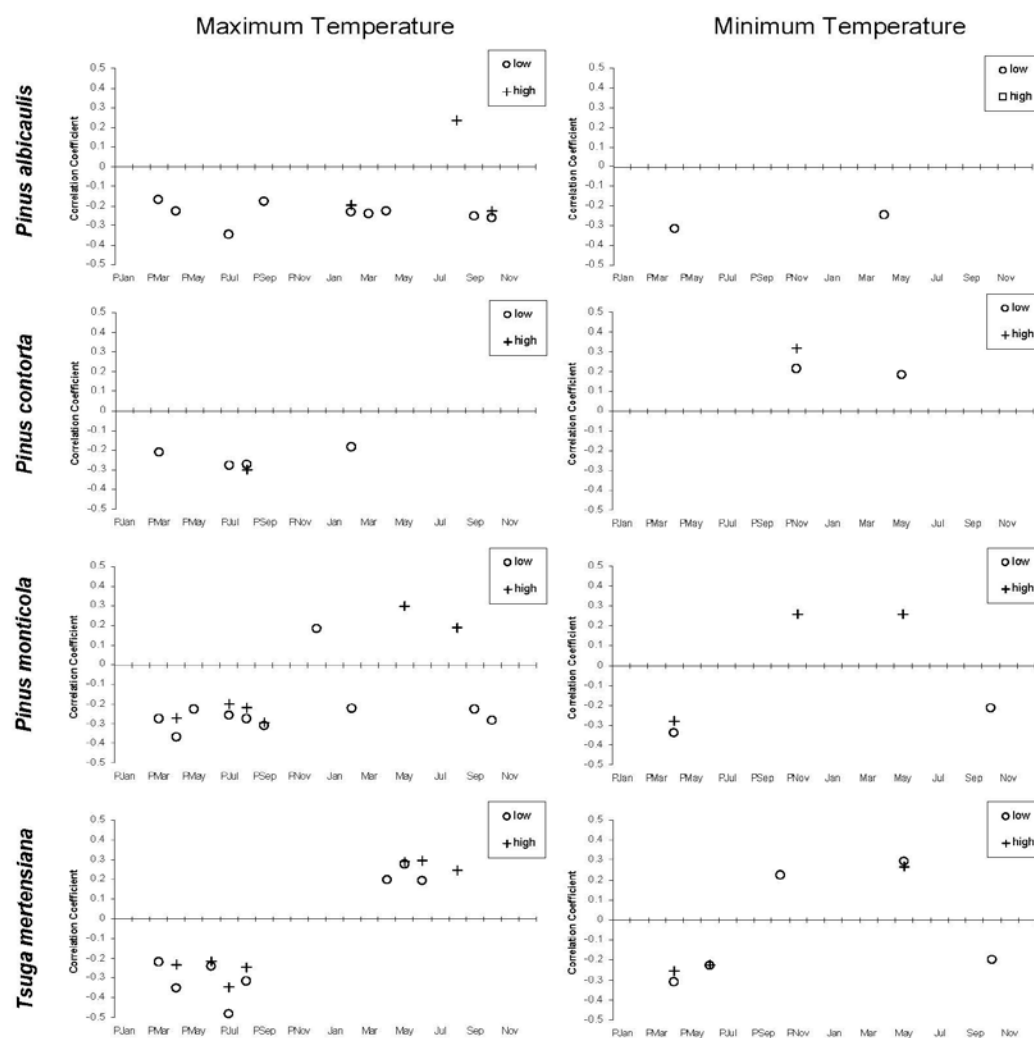


Figure 3.5. Correlation coefficients (Pearson's R) for correlations between annual growth and monthly maximum temperature and minimum temperature, for the 24-month period starting with January of the previous year's growth through December of the current year's growth, for the period 1895-2007. Analysis was carried out using DENDROCLIM2002 (Biondi and Waikul 2004). Only statistically significant correlations at $P < 0.01$ are shown. Series were divided into "low" and "high" elevation bands for each species and thus represent the lower half and upper half of the elevational distribution for that species for my study. Analysis was restricted to the four species with the most complete elevational distribution in my study area: whitebark pine (*Pinus albicaulis*), Sierra/Cascade lodgepole pine (*Pinus contorta* ssp. *murrayana*), western white pine (*Pinus monticola*), and mountain hemlock (*Tsuga mertensiana*).



Chapter 4

**Increasing growth with elevation for three subalpine conifers of the Sierra Nevada,
CA, USA**

ABSTRACT

Growth near upper treeline is closely tied to temperature, thus changes in temperature via global warming may have early and profound effects on tree growth near treeline, relative to lower elevations. I tested whether radial growth is increasing at high elevations more than growth from low elevations within the same elevational range for three subalpine tree species, mountain hemlock (*Tsuga mertensiana*), Sierra/Cascade lodgepole pine (*Pinus contorta* ssp. *murrayana*) and whitebark pine (*Pinus albicaulis*). I extracted 58-102 cores per species, sampled from 68 sites covering a wide range of topographic variability in the central Sierra Nevada, CA, USA. I examined trends over time in decadal growth, from 1801 to 2009, by elevation for each species. I found evidence for increasing growth at higher locations relative to lower locations in all three species, especially whitebark pine. For whitebark pine, mean growth of individuals from upper locations has been approximately 0.2 mm/year higher (+26 to 41%) than individuals from lower locations over the last eight decades (since 1931). Since the early 1800s, the relationship between growth and elevation has switched from negative to positive (increasing growth with increasing elevation) for both mountain hemlock and whitebark pine. Climate data indicate that temperature of the region has increased while precipitation has changed very little. Growth of trees at upper elevations is likely due to longer growing seasons that still retain moisture while individuals from lower elevations may be limited by other factors, including increased drought stress and increased competition.

INTRODUCTION

High-elevation regions are predicted to endure greater warming over the next century than lower-elevation areas (Kotlarski *et al.*; Bradley *et al.*, 2004). Evidence from several international locations indicates that warming during the twentieth century was already greater at high-elevations (Beniston *et al.*, 1997; Diaz & Bradley, 1997). In response, biological communities at high-elevations are predicted to undergo major changes over the next 100 years, including shifting or contracting ranges, species extinction and re-organized community structure (Theurillat & Guisan, 2001; Walther *et al.*, 2002; Nogues-Bravo *et al.*, 2007). Species that live at high-elevations are more limited by climate than those from most lower-elevation climates (Körner, 2003), and may therefore be expected to exhibit a stronger response to climate change. Recent shifts in distribution, composition, demography and growth of high-elevation species in response to changing climate have been reported from multiple mountainous regions (Grabherr *et al.*, 1994; Klanderud & Birks, 2003; Hemp, 2009; Salzer *et al.*, 2009; Dolanc *et al.*, in press).

The response of high-elevation tree species to changing climate is valuable for understanding the magnitude of change of both climate and the biological response. High-elevation trees are usually quite long-lived, with life spans of hundreds to thousands of years. Such long-lived organisms experience multiple profound climatic shifts during their lifetime (Millar & Woolfenden, 1999). Growth of high-elevation trees, reflected in the annual ring for a given year, is very closely tied to climatic conditions during the current and antecedent years (Fritts, 1976). Examination of tree rings from such trees can

help set biological response to recent climatic change within the context of the longer-term record of climate shifts.

Some tree-ring studies from high elevations have concluded that high rates of recent radial growth are unprecedented (Nicolussi *et al.*, 1995; Bunn *et al.*, 2005; Salzer *et al.*, 2009). Salzer *et al.* (2009) determined that this was true only for the trees from the highest locations in their study (near treeline). Growing-season temperature greatly limits growth of trees at upper treeline and is the best single predictor of treeline location (Tranquillini, 1979; Ellenberg, 1988; Holtmeier, 2003; Körner, 2003; Wieser & Tausz, 2007). The relationship between growth and temperature at treeline is so tight that global locations of treeline occur within a belt of elevations that correspond to a narrow range of 5 to 8 °C mean growing-season temperatures (Körner & Paulsen, 2004). Taken together, these observations suggest that tree growth near treeline should be expected to increase in response to warming, with the sensitivity of this response weakening with declining elevation from the upper treeline. Perhaps we should expect response of trees growing at the highest locations of montane environments to be stronger and happen sooner. Could these trees be harbingers of future change at lower elevations?

I examined mean radial growth, by decade, from 1800 to 2009, for three high-elevation tree species across an elevational gradient to test the hypothesis that: **radial growth is increasing more at higher elevations than lower elevations** for a given species. Tree cores from mountain hemlock (*Tsuga mertensiana*), Sierra/Cascade lodgepole pine (*Pinus contorta* ssp. *murrayana*) and whitebark pine (*Pinus albicaulis*) were sampled from 68 sites in the central Sierra Nevada, spanning the elevational distribution of each species, ranging from 2430 m up to 3397 m (near treeline). Increased

growth at high elevations, relative to low elevations within a given species range, may indicate greater warming at higher elevations. This result would seem to be consistent with predictions that higher elevations will endure greater changes and/or that individuals from high elevations should exhibit a stronger response to change.

METHODS

Study Area and Field Sampling

Tree cores were extracted for three subalpine conifer species native to the Sierra Nevada: mountain hemlock [*Tsuga mertensiana* (Bong.) Carrière], Sierra/Cascade lodgepole pine [*Pinus contorta* subsp. *murrayana* (Grev. & Balf.) Critchf.] and whitebark pine [*Pinus albicaulis* (Engelm.)]. Sampling occurred at 68 sites ranging from 37.812° to 39.312° north latitude and 2430 m to 3397 m elevation, in designated US federal wilderness areas of the central Sierra Nevada, CA (Figure 4.1). Sampling sites cover the full range of elevational distribution of all three species at these latitudes, with the exception of lodgepole pine, which occurs intermittently below my lower limit, down to approximately 1800 m elevation. One to ten cores were taken per site, resulting in 226 total cores used in analysis. I extracted one core per tree from the midslope side of the trunk at breast height (approximately 1.3 m above ground). Sampled trees were generally open-grown and larger than 30 cm diameter at breast height (dbh). Coring was done in conjunction with detailed sampling of 800 m² vegetation plots at each site. Data on stand structure, canopy, shrub and herb cover, as well as physical variables such as slope, aspect, elevation, soil depth and parent material were recorded for each site.

All three species grow in the subalpine zone of the Sierra Nevada, which is characterized by a short (6-9 weeks), dry growing season and 750 to 1250 mm/year precipitation, 90% of which falls during the winter as snow (Fites-Kaufman *et al.*, 2007). Physiognomy of this vegetation type is heterogeneous, but stands are generally sparse and soils thin and rocky. Tree species can occur as single-species dominants or in various combinations in mixed stands (Fites-Kaufman *et al.*, 2007; Sawyer *et al.*, 2009). All three species sampled can occur at treeline at these latitudes, but whitebark pine occurs in much greater abundance at treeline than lodgepole pine or mountain hemlock. Lodgepole pine and whitebark pine can be found on all slope facets but are generally in greater abundance on exposed (warm) slopes while mountain hemlock is found in much greater abundance on protected (cool) slope facets.

Sample Preparation and Analysis

Cores were dried and prepared in the laboratory using standard techniques (Stokes & Smiley, 1968; Speer, 2010). Ring width was measured using a Velmex stage measuring system and accompanying MeasureJ2X software; rings were measured to the nearest 0.001 mm. Tree rings were cross-dated visually using the list method (Yamaguchi, 1991) and verified with COFECHA (Holmes, 1983; Grissino-Mayer, 2001). Cores flagged by COFECHA as problematic were checked, re-measured and re-analyzed with COFECHA.

Standardization, as it is typically carried out, sets the average ring width of each core equal to one, removing differences in growth rates between sites and between trees. Standardization also removes long-term growth trends from each series, such as the

gradual reduction in growth (age-related growth trend) seen in most cores (Speer, 2010). Since I was interested both in changes in long-term growth trends and differences from site to site (particularly different elevations), I chose to use non-standardized ring widths for my analyses. Most trees in my study area exhibit a negative exponential growth trend, where the first few decades of growth decline exponentially to a relatively flat position that is maintained throughout the rest of the tree's life. Often, this latter, more flat portion of the growth trend can also decline slowly over time, but at a much lower rate. To remove the potentially confounding effect of rapid reduction in growth rate near the beginning of the tree's life, I pruned that portion of the record from my analyses. This was done by visually examining the growth curve of each tree and deleting the portion exhibiting early negative growth trend.

Running my analyses on non-standardized ring widths also leaves open the possibility for local, low-frequency factors such as long-term competition or gap creation to confound results. However, these factors should be minimal in the open-canopied, undisturbed subalpine woodland I sampled. In addition, my large sample size (58-102 cores per species) should sufficiently minimize the impact of such factors on overall trends.

For each core, the mean for each decade was calculated back to the oldest complete decade. Decades were defined as 1801 to 1810, 1811 to 1820, and so on. For analysis, I excluded decades with sample sizes less than 15 cores for each species, resulting in slightly different periods per species (Table 4.1). I tested my hypothesis that growth has increased more at higher elevations, with two approaches: (1) I divided the elevational range, based on the elevations of collected cores, into "low" and "high"

halves for each species and examined the trends over time for each group; (2) To examine trends in growth by elevation in a more continuous manner, I carried out simple linear regressions for each decade, for each species, with mean decadal growth and the dependent variable and elevation as the independent variable. For (1), I also ran simple t-tests on “low” vs. “high” groups to determine whether growth for that decade was greater at higher elevations. All analyses were performed using JMP 5.0.1 (SAS Institute SAS Institute, 2003). I also calculated the coefficient of variation for mean decadal growth, to determine if the range of growth rate, independent of sample size, has increased or decreased over time.

To determine how much climate has changed during the same period, I downloaded publically-available data from two weather stations on either end of my study area: Tahoe City, California (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca8758>), and Huntington Lake, California (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca4176>). These stations have the longest records from the highest elevations in my study region. I calculated means for mean annual temperature and annual precipitation for the two stations combined, for the period 1916 to 2008. I determined the regression line of mean temperature over this period to provide a visual aid in understanding the long-term trend.

RESULTS

For the three species tested in this study, I accept the hypothesis that growth is increasing more at high elevations. In addition, for both whitebark pine and mountain hemlock, radial growth of individuals from the upper half of the species distribution is

currently higher than the lower half and has been higher for several decades (Figure 4.2). Mean growth for the upper group of whitebark pine increased sharply from the 1920s to 1940s and has been significantly higher than the lower group for six of eight decades since the 1930s. Mean growth of the upper group was 26 to 41% (approximately 0.2 mm/year) greater than the lower group during this period (Figure 4.2).

Mean growth of the upper group of mountain hemlock was not significantly higher than lower elevation growth for any single decade, but it increased sharply from the 1950s to 1970s and has been higher than the lower group since, ranging from 15 to 26% higher since the 1970s (Figure 4.2). Mean growth of the lower group for mountain hemlock remained mostly unchanged during this period. Mean growth for lower and upper groups of lodgepole pine was similar during the 20th century, but trends show that growth of the lower group was higher during the last part of the 19th century (significantly so for the 1861 to 1890) but has been similar to growth of the higher group since that time (Figure 4.2). The difference in mean growth between upper and lower groups has become significantly more positive over time for all three species (Figure 4.3).

Radial growth of whitebark pine has increased at higher elevations relative to lower elevations, such that mean growth per decade has been significantly positively correlated with elevation for the past three decades (1980 to 2009; Figures 4.3, 4.4; Table 4.1). This is a reversal of the trend from the first part of my record, when growth was negatively correlated with elevation (i.e. growth decreased with elevation). In general, the relationship between mean growth and elevation for whitebark pine has gradually transitioned from negative to positive over time (Figures 4.3, 4.4).

The relationship between growth and elevation for mountain hemlock over time exhibits a similar trend; the four most-recent decades exhibited the strongest positive correlation between mean growth and elevation [and 3 of 4 of these were marginally significant ($0.05 < p < 0.1$); Table 4.1]. The relationship between growth of lodgepole pine and elevation shows very little trend over time and is weak for nearly every decade tested (Figure 4.4; Table 4.1). Variability in growth increment also appears to be increasing over time for all three species, as evidenced by gradually increasing standard deviation and coefficient of variation, over time, for all three species (Table 4.1).

Mean temperature from the two weather stations I examined exhibited a positive trend over time, with a slope of $+0.0153$ °C/Year and a correlation coefficient (R) of $+0.5071$. This increase amounts to a rise of approximately 1.4 °C from 1916 to 2008.

DISCUSSION

Radial growth of the three subalpine tree species in my study is increasing at high-elevations relative to lower elevations. For whitebark pine and mountain hemlock, growth during the last few decades has actually been higher for trees from the upper portion of their elevational ranges, than trees from the lower half (Figure 4.2). The third species in my study, lodgepole pine, shows increased growth at high elevations relative to low elevations, but growth at low elevations is still currently higher (Figure 4.3). For mountain hemlock and whitebark pine, the relationship between growth increment and elevation has switched from negative (decreasing with elevation) to positive (increasing with elevation) over the course of the 20th century (Figures 4.3, 4.4; Table 4.1). These trends are particularly strong for whitebark pine, the highest-ranging species in my study

area. To my knowledge, this is the first reported evidence of radial growth being greater at higher than lower elevations within the elevational range of a given species.

Dendrochronological studies have demonstrated that incremental growth of subalpine trees is closely tied to temperature (Peterson & Peterson, 1994; Carrer & Urbinati, 2004). For subalpine trees, growth initiation at the beginning of the growing season is probably controlled by soil temperatures (Tranquillini, 1979; Oberhuber, 2007). This suggests that warmer temperatures during the late spring and early summer could extend the growing season by causing growth initiation to happen earlier, leading to greater growth for that year (assuming sufficient precipitation). Studies from multiple subalpine regions have reported a recent uptick in radial growth of conifers when compared with previous centuries (Rolland *et al.*, 1998; Bunn *et al.*, 2005; Salzer *et al.*, 2009). All of these studies attributed their observed shifts to warming during the 20th century and this is likely the cause of my observations as well.

Multiple sources suggest that mean annual temperature of my study region has increased by at least 1.0 °C since the beginning of the 20th century, while precipitation has changed relatively very little (Coats, 2010; Figure 4.5; Figures 4.7, 4.8). My observed shifts in growth response by elevation actually appear to track shifts in temperature. Regional temperatures were high during the late 1920s and early 1930s (Figure 4.5; Figures 4.7), which corresponds with a period of marked increased growth of whitebark pine at high elevations (Figures 4.2, 4.3). Despite a return to lower temperatures for several decades in the middle of the century, growth of high-elevation whitebark pine remained high and currently appears to be deviating further from growth of the same

species at lower elevations (Figure 4.2). The shifts in growth for mountain hemlock appear coincident with the more recent warming trend that began in the late 1970s.

In a similar study on Swiss stone pine (*Pinus cembra*) and Norway spruce (*Picea abies*) from the European Alps, Paulsen et al. (2000) reported a gradual reduction in the negative relationship between growth and elevation over time, resulting in no relationship during the most recent decades (i.e. growth was similar at all elevations in their study). A shift in this relationship seems to have occurred starting between 1920 and 1940 (Paulsen et al., 2000; Grace et al., 2002). Interestingly, the rate of increase of 0.015 °C/year since 1916 from the two weather station data for my study area, is very similar to the increase rate reported by Paulsen et al. (2000) for the Swiss Alps, since the early 19th century. Perhaps it is no surprise that both studies show comparable shifts in growth by elevation. Unlike Paulsen et al (2000), my study demonstrates that growth at upper locations has increased relative to lower locations, but is currently higher for two of three species examined.

Fertilization from increased concentration of carbon dioxide (CO₂) and nitrogen deposition has been suggested as potential factors in increasing growth at high elevations. Results from studies examining the effects of these compounds on growth of high-elevation trees have been mixed and indicate that response is highly variable (Graumlich, 1991; Tang et al., 1999; Fenn et al., 2003; Saurer et al., 2004). Increasing concentration of CO₂ is unlikely to explain increases in growth of subalpine trees because growth in these areas is limited by temperature, not carbon assimilation (Körner, 1998), and this seems likely to be the case for nitrogen as well. Though more research is needed on the

effects of both of these factors, they seem unlikely to explain the increased growth observed in ours and other studies.

Under static conditions, growth increment should be expected to decline with elevation gain for a given subalpine tree species, as temperature declines and growing seasons shorten. Indeed, there is plenty of evidence of decreasing growth of both tree height and diameter as treeline is approached (Tranquillini, 1979; Körner, 2003). Therefore, it is particularly surprising that radial growth of both whitebark pine and mountain hemlock in my study area is higher in trees from upper locations than trees growing at lower locations. Since my samples came from dozens of locations that include a full range of topographic variability, these differences are not likely due to some sort of site-specific microclimatic anomaly, such as cold-air drainage.

I suggest that these results reflect the greater sensitivity of growth to temperature as treeline is approached and the greater complexity of factors at lower elevations. This greater sensitivity to temperature may manifest in a greater biological response to moderating conditions, while individuals from lower elevations are still limited by factors such as low precipitation (or moisture availability). This explanation may be particularly applicable in Mediterranean mountains, where tree growth is often doubly-limited by low temperatures in spring and drought in late summer (Lloyd & Graumlich, 1997; Peterson, 1998). Near treeline though, temperatures are cool enough and the growing season is short enough that impacts from late-summer drought should be minimal (Fites-Kaufman *et al.*, 2007). Thus, warming conditions could lead to diverging growth responses for species that range from treeline to well below. Individuals from upper locations are responding positively to a lengthened growing season with sufficient moisture

throughout. However, those from lower locations are now limited by more severe drought at the end of the growing season; though growth initiation happens earlier in the spring, drought also occurs earlier in summer or fall, which may result in a net reduction of the period favorable for growth.

There is also evidence that subalpine stands are increasing in density throughout the entire subalpine zone of the Sierra Nevada (Dolanc *et al.*, in press). Densification appears consistent in low and high portions of subalpine. However, stands at the lower end of the subalpine tend to have greater canopy cover (C. Dolanc, personal observation) and are generally taller in stature. Trees growing in lower portions of subalpine may be experiencing greater competition for light while those at higher locations may still have abundant light even with densification.

The trends on growth by elevation reported here support predictions of upslope shifts of species and vegetation types (Thuiller *et al.*, 2005; Lenihan *et al.*, 2008). The lower portions of elevational distributions (at least for mountain hemlock and whitebark pine) are showing signs of decreased vigor at the trailing edge – where increased competition from species moving upslope should be felt first. These results may be taken as a sign that more profound changes, such as shifts in distribution and eventually species extirpation may follow. Upslope shifts have been reported from multiple mountain ranges (Kullman, 2002; Beckage *et al.*, 2008; Kelly & Goulden, 2008), and upward shifts of treeline have occurred in 52% of sites while only 1% have reported downward shifts (Harsch *et al.*, 2009).

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TABLES

Table 4.1. Summary statistics and p-values for mean radial growth per decade for mountain hemlock (*Tsuga mertensiana*), lodgepole pine (*Pinus contorta* ssp. *murrayana*) and whitebark pine (*Pinus albicaulis*) growing in the central Sierra Nevada, CA. Sample size (n) refers to the number of cores represented for each group. Only decades with a minimum of n = 15 cores/decade for each species were considered in analyses. Results from simple linear regression of mean growth by elevation for a given decade with significant results at $p < 0.10$ in bold and significant results at $p < 0.05$ underlined.

Decade	<i>Tsuga mertensiana</i>						<i>Pinus contorta</i>						<i>Pinus albicaulis</i>					
	n	Mean growth	st dev	coeff var	r ²	p-value	n	mean growth	st dev	coeff var	r ²	p-value	n	mean growth	st dev	coeff var	r ²	p-value
1801 - 1810													17	0.55	0.20	36.2	0.22	0.060
1811 - 1820													19	0.51	0.29	57.2	0.06	0.295
1821 - 1820													22	0.57	0.26	46.1	0.05	0.321
1831 - 1840							18	0.81	0.31	37.9	0.06	0.341	24	0.64	0.28	43.0	0.00	0.618
1841 - 1850							20	0.80	0.36	44.9	0.01	0.699	27	0.62	0.24	38.3	0.00	0.747
1851 - 1860							25	0.88	0.30	34.1	0.02	0.480	29	0.62	0.28	45.1	0.00	0.984
1861 - 1870							30	0.74	0.27	36.3	0.18	0.021	34	0.54	0.26	47.7	0.04	0.284
1871 - 1880	17	0.90	0.42	46.4	0.00	0.934	33	0.82	0.28	34.0	0.02	0.402	37	0.59	0.30	50.8	0.00	0.808
1881 - 1890	24	0.90	0.38	41.6	0.01	0.588	36	0.79	0.30	38.0	0.09	0.075	40	0.61	0.31	51.0	0.00	0.692
1891 - 1900	24	1.01	0.42	42.1	0.00	0.807	42	0.80	0.31	38.1	0.08	0.065	44	0.66	0.32	48.1	0.02	0.339
1901 - 1910	30	1.06	0.39	36.7	0.00	0.920	49	0.83	0.32	37.9	0.00	0.632	44	0.67	0.32	48.5	0.02	0.427
1911 - 1920	34	0.99	0.39	39.9	0.00	0.987	58	0.84	0.42	49.9	0.01	0.396	49	0.60	0.32	53.4	0.01	0.612
1921 - 1930	37	0.94	0.41	43.1	0.03	0.338	71	0.86	0.47	55.4	0.00	0.791	54	0.61	0.34	55.2	0.00	0.915
1931 - 1940	44	0.96	0.50	51.6	0.00	0.650	77	0.91	0.46	51.0	0.00	0.772	60	0.67	0.35	52.7	0.04	0.113
1941 - 1950	47	1.02	0.47	46.0	0.00	0.646	83	1.02	0.56	55.1	0.06	0.024	61	0.69	0.37	53.9	0.06	0.068
1951 - 1960	49	0.97	0.42	43.6	0.00	0.936	94	0.95	0.53	56.2	0.02	0.151	63	0.62	0.34	54.0	0.01	0.431
1961 - 1970	54	1.05	0.45	42.7	0.01	0.498	97	0.98	0.61	61.9	0.03	0.073	63	0.68	0.35	51.1	0.04	0.115
1971 - 1980	57	1.12	0.56	49.9	0.07	0.051	102	1.07	0.63	58.8	0.02	0.117	64	0.65	0.32	49.1	0.06	0.058
1981 - 1990	57	1.12	0.62	55.3	0.06	0.060	102	0.98	0.60	61.4	0.02	0.121	64	0.66	0.37	56.0	0.06	0.049
1991 - 2000	58	1.02	0.56	55.2	0.06	0.072	102	1.01	0.60	59.6	0.00	0.499	64	0.61	0.37	59.8	0.08	0.026
2001 - 2009	58	1.05	0.58	55.2	0.03	0.182	102	0.85	0.49	58.0	0.01	0.363	64	0.61	0.37	61.6	0.12	0.006

FIGURES

Figure 4.1. Map of study area, Sierra Nevada, CA, USA. Coring sites are indicated by dark triangles. All sites were in undisturbed locations between 2430 and 3397 m elevation and 37.812 and 39.312 ° north latitude. Sampling intentionally covered a wide range of topographic positions within the study area and spanned the elevational distribution for each species sampled.

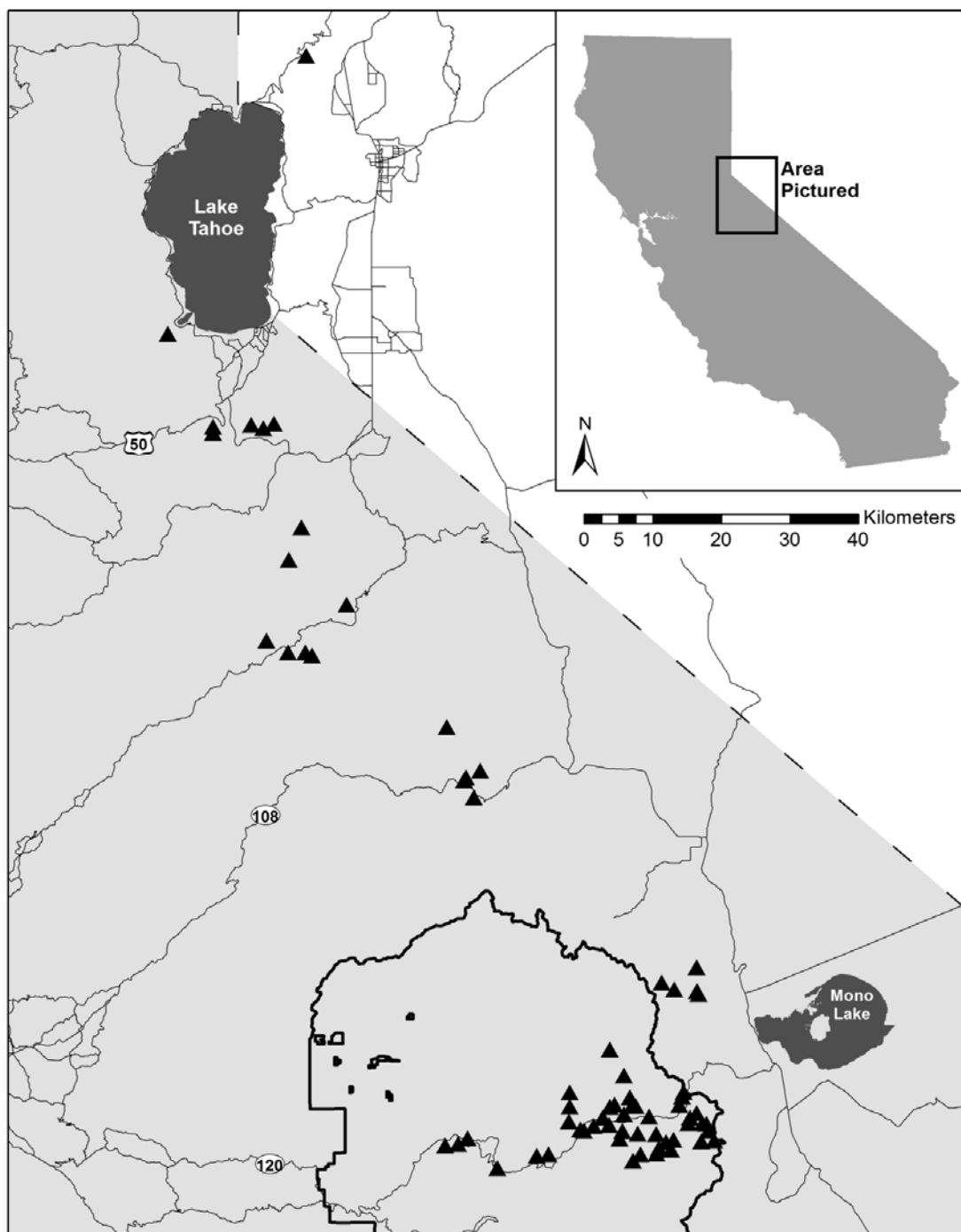


Figure 4.2. Mean radial growth and standard error by decade for “low” and “high” elevational portions for mountain hemlock (*Tsuga mertensiana*), lodgepole pine (*Pinus contorta* ssp. *murrayana*) and whitebark pine (*Pinus albicaulis*) growing in the central Sierra Nevada, CA. “Low” and “high” portions were created by dividing the total number of cores for each species into upper and lower halves based on their elevational distribution in my study. Asterisks indicated significant results at $p < 0.05$ for t-tests of differences between “low” and “high” portions for each species.

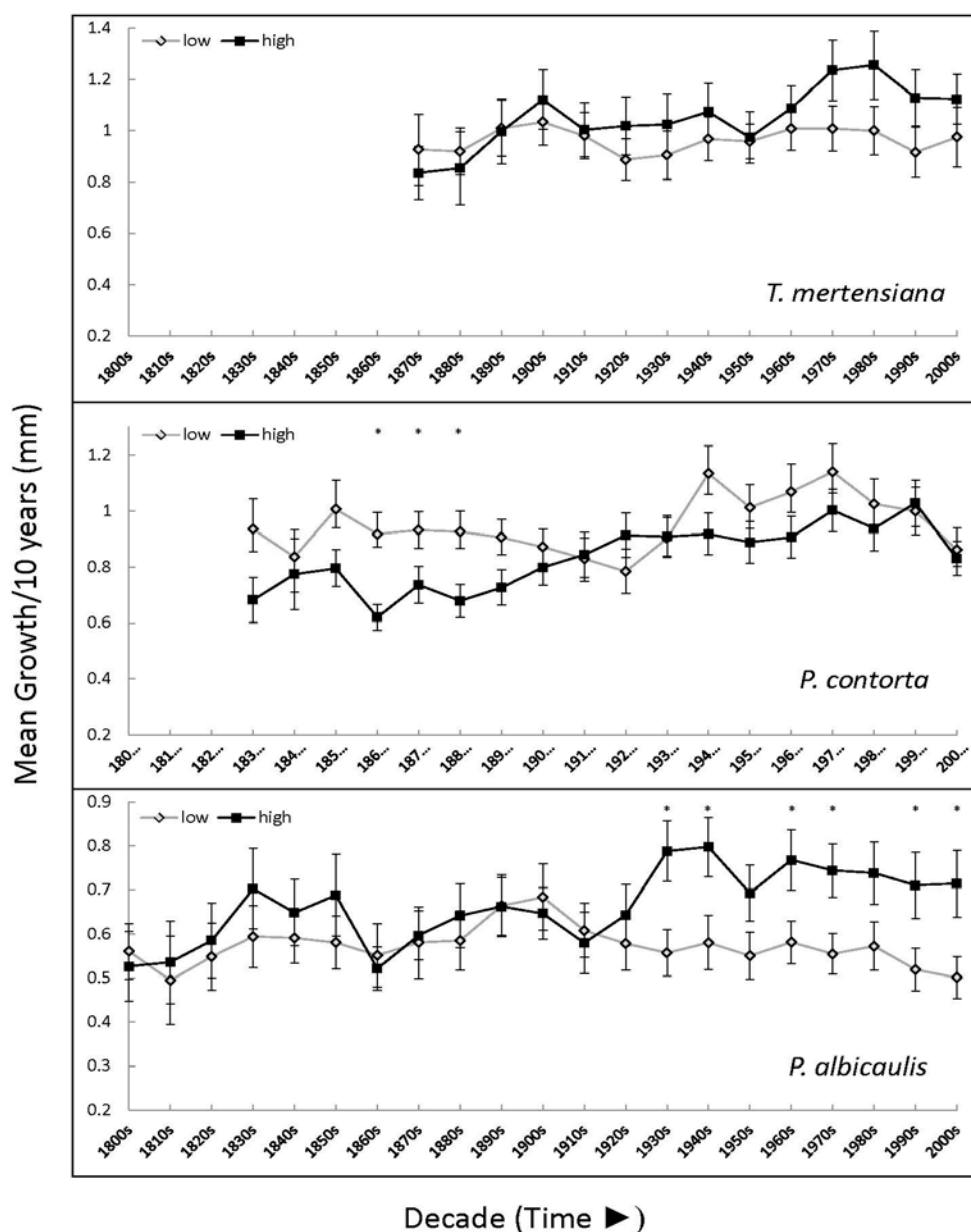


Figure 4.3. Difference in mean growth per decade from high-elevation locations to low-elevation locations plus regression trendlines for mountain hemlock (*Tsuga mertensiana*; TSME; $r^2 = 0.59$; slope = 0.025; $p = 0.006$), lodgepole pine (*Pinus contorta* ssp. *murrayana*; PICO; $r^2 = 0.39$; slope = 0.012; $p = 0.009$) and whitebark pine (*Pinus albicaulis*; PIAL; $r^2 = 0.31$; slope = 0.008; $p = 0.009$) growing in the central Sierra Nevada, CA. Points above the line mean that growth was higher at higher elevations for that species during that decade.

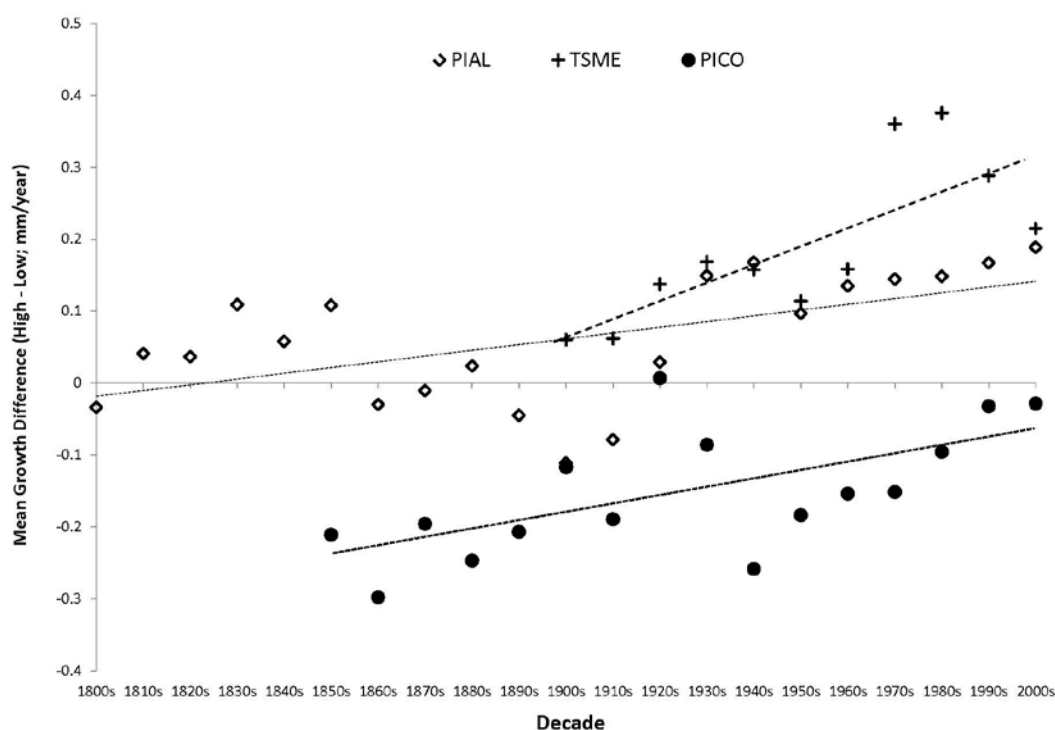


Figure 4.4. Decade by decade trend of mean radial growth (growth increment) by elevation for whitebark pine (*Pinus albicaulis*) growing in the central Sierra Nevada, CA, from 1801 to 2009. Note the shift from a negative relationship (decreased growth with increasing elevation) at the beginning of the period, to a positive relationship (increased growth with increasing elevation) over the last few decades.

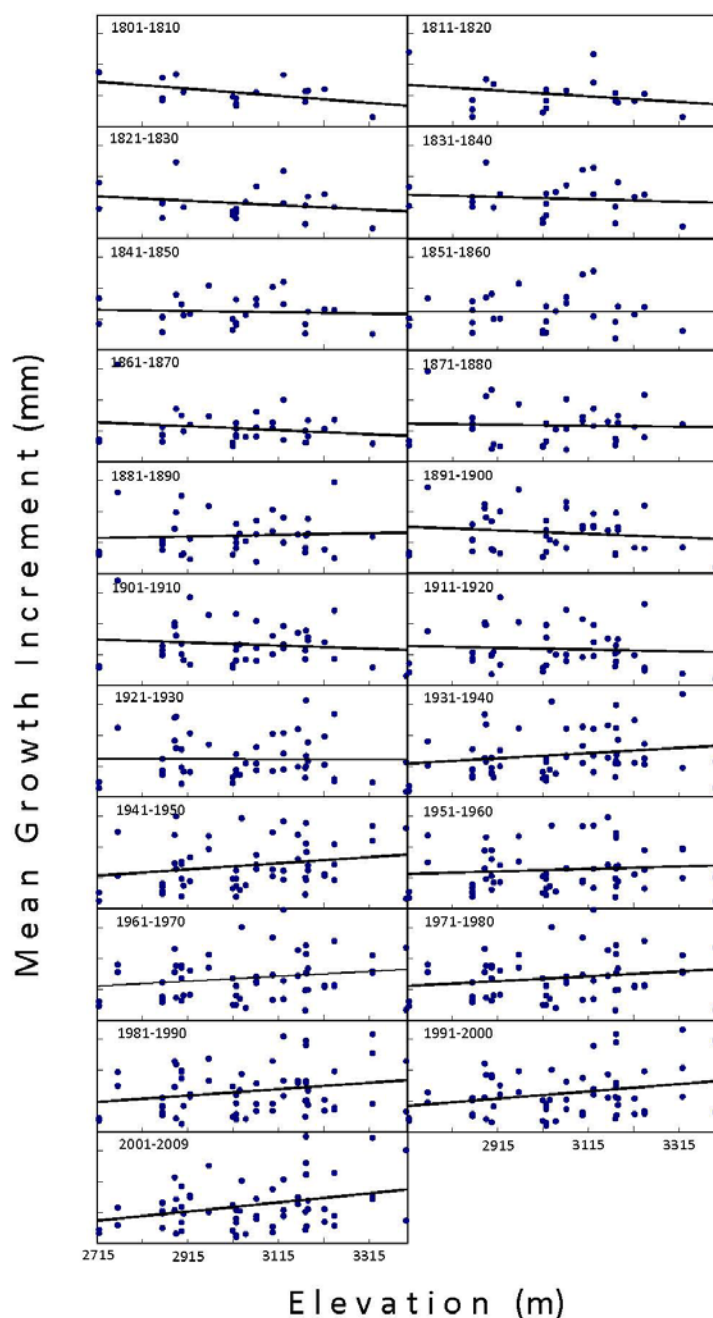


Figure 4.5. Slope and correlation coefficient (R) for mean radial growth by elevation by decade for mountain hemlock (*Tsuga mertensiana*), lodgepole pine (*Pinus contorta* ssp. *murrayana*) and whitebark pine (*Pinus albicaulis*) growing in the central Sierra Nevada, CA. Only decades with a minimum of $n = 15$ cores/decade for each species were considered in analyses. Note the general increasing trend for mountain hemlock and whitebark pine, indicating a shift over time from a negative relationship (decreased growth with increasing elevation) at the beginning of the period, to a positive relationship (increased growth with increasing elevation) over the last few decades.

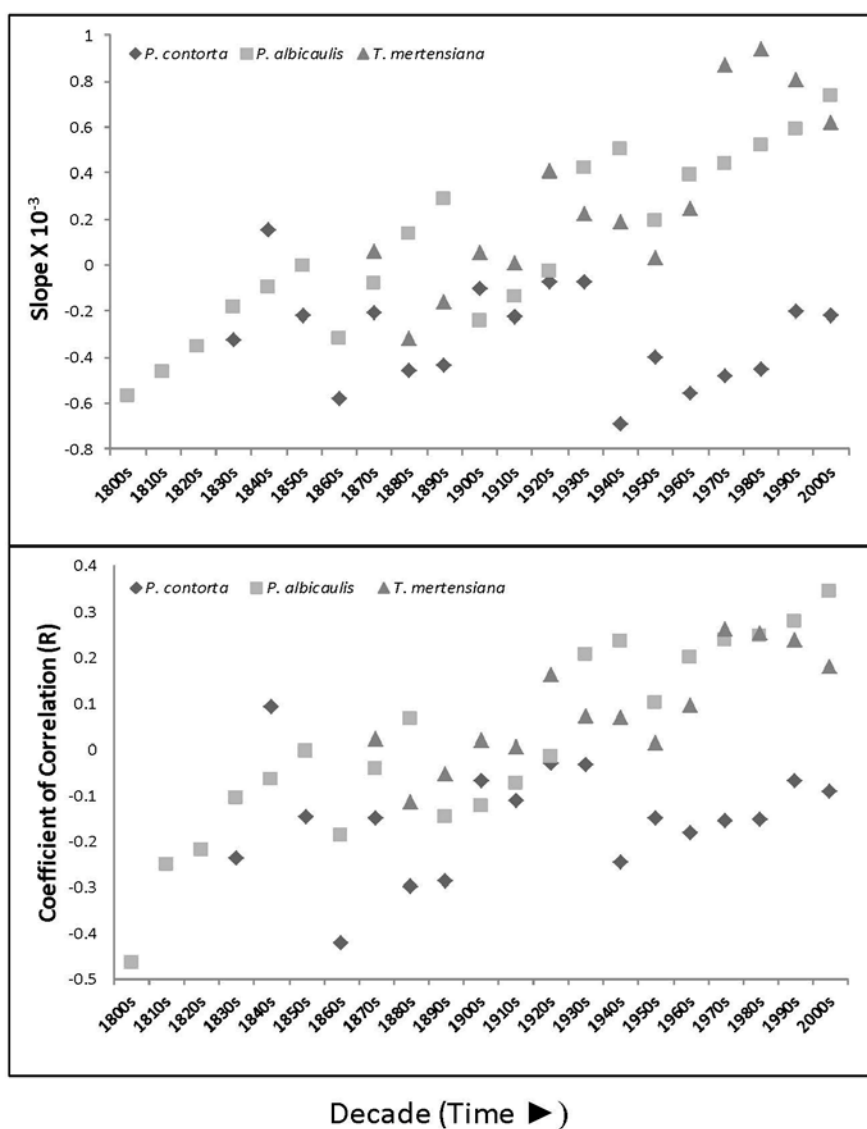


Figure 4.6. Average of mean annual temperature from 1916 to 2008 for the Tahoe City, CA (39°10' N; 120°09'W; 1899 m elevation) and Huntington Lake, CA (37°14' N; 119°13'W; 2140 m elevation) weather stations. The Huntington Lake station only goes back to 1920, so the values for 1916-1919 represent data from Tahoe City only. The dotted line represents the regression line for mean annual temperature by year: $R = 0.5071$; slope = $+0.0153$ °C/year.

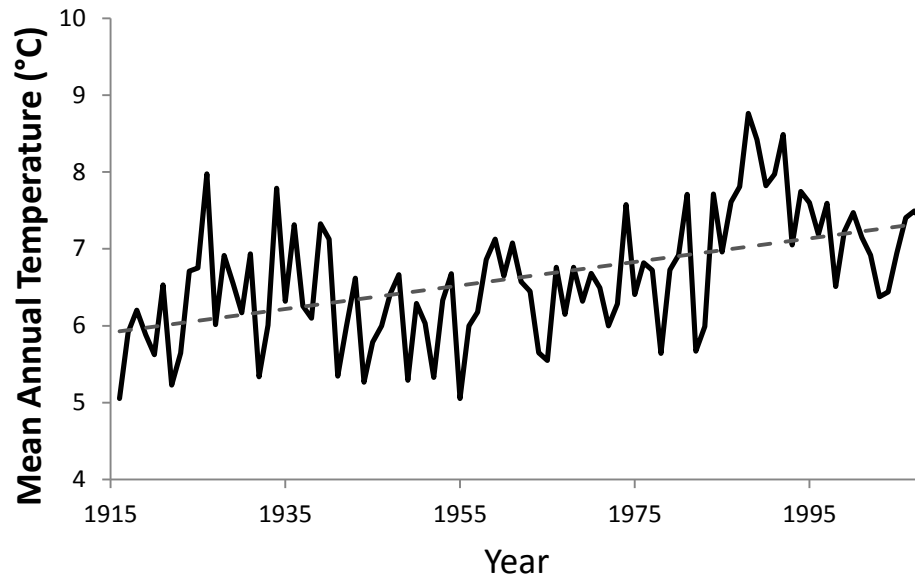


Figure 4.7. Average temperature departure for mean maximum (red), mean minimum (blue) and mean (black) temperature, in degrees Celsius from 1895-2010 base period the Sierra Nevada region for every year from 1895-2010. Modified from the Western Regional Climate Center (Abatzoglou *et al.*, 2009). Note that minimum temperature has risen considerably more than maximum temperature during this time period.

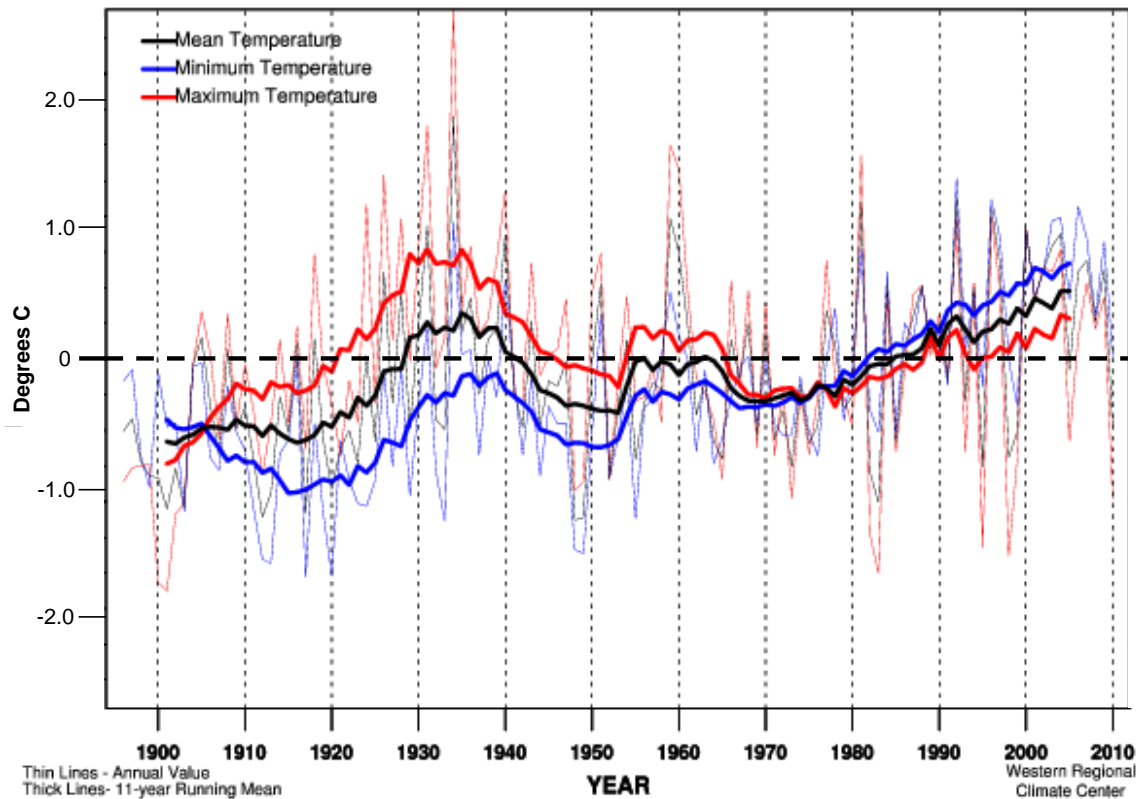


Figure 4.8. Mean annual precipitation for the Sierra Nevada region for every year from 1895-2010. The dotted line represents the mean for the period 1895-2010 and the orange line represents the eleven-year running mean. Modified from the Western Regional Climate Center (Abatzoglou *et al.*, 2009). Note that year to year variation in precipitation has increased, since the beginning of the 20th century, while average annual precipitation has changed very little.

