

Response of tree growth to climatic variation

DRAFT Chapter 9 Outline in

Draft: March 11, 2001

Lisa Graumlich, Dean Urban and Andrew Bunn

For inclusion in:

Sierra Nevada Forest Dynamics: Pattern, Pace and Mechanism of Change

1. INTRODUCTION

- 1.1. At some point in their lives, almost everyone has examined the cross-section of a tree, whether it is a fresh cut that removed a hazard tree from a favorite hiking trail or a properly majestic museum specimen complete with labels linking annual rings to key historic events. The ebb and flow of annual growth is often apparent: ‘fat’ years alternate with ‘lean’ years revealing times of feast and famine for the individual tree. Given the growing concern that climate change may seriously affect forest ecosystems, such ring-widths patterns, when methodically analyzed from numbers of trees, have become a key line of evidence for where, when and how climate affects forests.
- 1.2. In this chapter, we present evidence that the impact of climate on forest growth, as reflected in annual tree rings, varies from subtle to substantial in a systematic fashion. The most subtle effects of climate are in the mixed conifer forest (xxxx m to xxxx m, Chapter XX) where the magnificent giant sequoia grows with a host of other merely very large trees including sugar, ponderosa and Jeffrey pines, white fir and Douglas-fir. The most extreme effects of climate are in the uppermost reaches of the subalpine forest (xxxx m to xxxx m, Chapter XX) where whitebark, lodgepole and foxtail pine eke out an existence under cold and dry conditions. The goal of this chapter is interpret the climate-growth relationships of different species in different settings in terms of their relative vulnerabilities to the impacts of climate. Such a comparison has direct implications for technical aspects of how we model the dynamics of the Sierra Nevada forests (Chapter XX) as well as broad implications for the task of predicting when and where we will see unprecedented changes in Sierra Nevada forests during the 21st century.
- 1.3. The chapter begins with a brief discussion of the use of tree-ring analysis (a.k.a., dendrochronology) for ecological research. The results presented in this and other chapters (see Chapter XXX) rely heavily on the analysis of tree-ring patterns but the nature of the tree-ring evidence varies between chapters. This brief discussion alerts the reader to critical issues in the interpretation of tree rings as ecological indicators. The chapter continues by addressing the nature and strength of climate impacts on the growth of dominants of the mixed-conifer forest. The emphasis of this chapter is sorting out species to species differences in climatic sensitivities, as these differences are likely to drive changes in the composition of future forests. The chapter then addresses the same question, that is the nature of climate—growth relationships, for

tree species at the uppermost limit of the subalpine forest. This chapter focuses on the strong evidence for a shift in the late 20th century in the growth rates and interprets this shift as evidence of climate-induced changes in forest dynamics. We conclude by emphasizing that climate-induced changes in growth rate in the forests of the Sierra Nevada are, for the most part, subtle factors as compared to other drivers of change in these forests. However, at certain site, especially the lower elevations of the mixed conifer forest and upper treeline, climate strongly affects growth and will likely be an even more present force in the future.

2. DENDROCHRONOLOGY: A MULTI-FACETED TOOL

- 2.1. Dendrochronology, or the scientific analysis of tree rings to reconstruct past environments and processes, encompasses a wide array of techniques and applications. At the heart of the analysis is the fundamental observation that annual tree rings are the result of changes in the amount and pattern of carbon allocation to the stem of a tree (Waring and Running 1998). As such, the size of a given tree ring is the end product of a web of interacting processes that scale from the cellular (e.g., photosynthesis) to the organismal (e.g., competition between adjacent trees) to the forest stand (e.g., soil mediation of water availability). In using tree-ring data to decipher how climate influences tree growth, we apply three key principles to the design of our sampling strategies and analysis procedures (Fritts and Swetnam 1989).
- 2.2. First, we recognize that factors other than climate influence the width of a given ring in a particular tree for a specific year. More formally, dendrochronologists have defined a “principle of aggregate tree growth” that states that any individual tree-growth series is the product of an aggregate of environmental factors, both human and natural, that affected the patterns of tree growth over time, including:
 - an age related growth trend due to normal physiological ageing processes;
 - the climate that occurred during that year;
 - the occurrence of factors within the forest stand (e.g. death of adjacent trees altering competition for light and soil moisture);
 - the occurrence of factors from outside the forest stand (e.g. an insect outbreak that defoliates the trees, causing growth reduction).
- 2.3. [Figure 1, under construction, multiple tree ring series showing different patterns linked to different processes including](#)
 - 2.3.1. [Ring width series of my most complacent white fir that should have a nice neg exponential growth curve and little variance otherwise](#)
 - 2.3.2. [Ring width series from sequoia showing impacts of big droughts with marker arrows on big drought years](#)
 - 2.3.3. [Ring width series from sequoia showing effects of controlled burn with growth release \(help Nate or Tom for data\)](#)
- 2.4. The principle of aggregate tree growth has the following practical implications. In our studies of the mixed conifer forests, we were particularly interested in determining the relative importance of climate vs. factors within the forest stand and external to the forest stand. As such, we sampled stands where climate and stand factors are both important in governing growth rates. In contrast, in our studies of

subalpine forests, we were particularly interested in the role of climate at extremely limiting sites. As such, we sampled stands in exposed situations, on shallow soils, where stand density was so low that competition with other trees was negligible, and where climate was by far the most limiting factor to growth. (Trees at extreme sites also form the basis for the reconstruction of past climate as detailed in Chapter XXX.) Finally, in all of the analyses reported here, we statistically removed the age related trend in growth.

- 2.5. Second, we recognize that tree-ring climate relationships have a systematic relationship with the biophysical template (is this word introduced yet?). Specifically, dendrochronologists and ecologists have long recognized that, in general, a tree species is more sensitive to climate variability at the latitudinal and elevational limits of its range. Because this principle is key to the climate—growth parameterization scheme of forest simulation models (see Chapter XXX), we designed our analyses to explore this concept more fully and quantitatively. In our analysis of the mixed conifer forest, we compared trees at their lower elevational range limit, in the middle of their range, and in some cases, at their upper elevational range limit.
- 2.6. Third, we recognize that in seeking to detect the strength and nature of the climate signal in tree growth records, we needed to ensure that our sample sizes were adequately large to capture large-scale, general patterns of growth as opposed to the vicissitude of single trees. The results reported in this chapter are based on analyses of thousands of trees. More specifically, we obtained two increment cores per tree, multiple trees in a given sampling site or stand, multiple stands per species and site. While this resulted in the happy coincidence that we enjoyed some long field seasons in the Sierra Nevada, we seek to emphasize that the large sample sizes and multiple locales are key to our argument that the records from individual trees can in fact be interpreted in terms of forest pattern and process.

3. CLIMATE IMPACTS ON GROWTH IN THE MIXED CONIFER FOREST

- 3.1. John Muir may have been the first to publish speculations on climate-growth relationships in the mixed conifer forest when he wrote:

The coniferous forest of the Sierra are the grandest and most beautiful in the world, and grow in a delightful climate on the most interesting and accessible mountain ranges, yet strange to say, they are not well known (Muir, xxxx as quoted in Arno 1973—track down exact reference).

- 3.1.1. The mid-elevation climate that Muir alludes to is more fully described by Stephenson (Chapter 2, see Figure 8) as one in which *on average* winter rains result in a surplus of water supply over evapotranspiration from November through May. Subsequently, warm, dry summers (the source of Muir's delight) drives potential evapotranspiration to exceed water supply resulting in a several month period of water deficit. The climate where the mixed conifer forests supports a productive forest (cite real NPP figures) with an unusually high number of tree species, and many of which are unusually large (e.g., giant sequoias over 90 m.; sugar pine over 75 m; Figure 1; photo of mixed conifer forest showing big trees). While average conditions clearly promote luxuriant

forest growth, what can we learn about the sensitivity of this ecosystem by examining those years where climate is less favorable?

- 3.2. Given the dominant role of giant sequoia as well as its value as an important species for the reconstruction of climate and fire history (Chapters XXX and XXX), it is not surprising that it is the most well-studied species of the mixed conifer forest. Giant sequoia, the most moisture sensitive of the mixed conifer forests (ref), are scattered in isolated groves throughout the middle elevations of the central Sierra Nevada (citation). They are restricted to deep soils having sufficient ground water to access during the summer period of water deficit (see some other chapter). At these highly favorable sites, growth is unconstrained by climate, except in times of severe drought.
 - 3.2.1. Add something in consultation with Malcolm and Nate;
 - 3.2.2. Figure 3 from Hughes et al that shows GS chronology with a few bad years.
- 3.3. Compared to giant sequoia, the other dominant species of the mixed conifer forest are less studied and the results presented here are the first comprehensive comparison of the variation within and between five species in the response to 20th century climate variation (Fig. 4). The species studied include ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), Jeffrey pine (*P. jeffreyi*) and red fir (*A. magnifica*). Sampling sites were located at or near the upper and middle range limit for each species and at the upper range limit for the pine species and white fir (Fig. 4). Tree-ring “chronologies” (i.e., mean ring width series for all trees at a site) for each species and site were developed using standard techniques (Cook and Kairiukstis 1990). The relationship between tree growth and climate was analyzed by comparing tree-ring chronologies from Sequoia National Park to a composite climate record from Grant Grove and Giant Forest (ca. 2000m) and the chronologies from Yosemite National Park to the climate record from Yosemite Valley (1200 m, 1928-1990). Three climate variables show important relationships with the tree-ring data: average spring (March through May) temperature, average early summer (June through July) temperature and August Palmer Drought Severity Index (PDSI). PDSI uses meteorological data to categorize soil moisture conditions. The PDSI calculation is affected by both long-term moisture shortages and excesses, and by variability of evapotranspiration (Palmer 1965).
- 3.4. Two broad generalizations can be made regarding species’ response to climate variability in the mixed conifer forest. First, position within a species elevation range alters that species’ sensitivity to climate in a systematic manner. Second, for most species, the response to spring vs. early summer temperature is opposite in direction. White fir and sugar pine climate—growth patterns illustrate these points. At or near its lower range boundary, white fir and sugar pine growth is not affected by spring temperature but is limited by warm early summer temperatures and drought. In contrast, at their upper range boundary, white fir and sugar pine growth is strongly limited by spring temperature but not by summer temperature or drought. Between these two extremes, mid-elevation sites show weakly organized, intermediate patterns. Ponderosa pine and red fir results are similar to those just described but less pronounced. Jeffrey pine climate-growth relationships show almost no pattern with elevation. This is consistent with the more general observation that Jeffrey pine is

found on granite outcrops that differ in soil and microclimate from the surrounding forest (citation?). Taken together, these results support a general model that for white fir, red fir, sugar pine and ponderosa pine:

- Drought stress, including high summer temperatures, limits growth at a species' lower range limit; and
- Low spring temperatures, but not drought, limit growth at upper range limits.

3.4.1. <<need to tie sequoia results into this last bit better>>

3.5. Results such as these allow us to make projects as to how climate change in the future might affect the mixed conifer forest using two different strategies. Qualitatively, these findings point to the vulnerability of the lower elevation stands of the mixed forest under projections of warmer and drier conditions. White fir and sugar pine are the most sensitive to increased summer warmth coupled with drought and thus would be most likely be first to register a response to climate change. <<look for corroborating citations>>. Of the species studied, Jeffrey pine is the least sensitive to warmer and drier conditions. <<citations>>.

3.5.1. Tie to Nate's demography results?

3.6. In a more formal and quantitative fashion, these results have helped us design the simulation model for forest dynamics described in Chapter XX. The results presented here suggest that a relatively simple climate—growth curve robustly describes the impact of year-to-year climatic variability on tree growth across its elevational range. Specifically, models can set the upper range limit for a species by accounting for the impact of early season temperatures or other measures that capture growing season warmth. Models can set the lower range limit set by accounting for mid-summer drought stress on tree growth.

3.6.1. tie more closely to Dean's modeling chapter.

3.7. <<*section summary*>> *Interannual* climate variability, especially drought, is the most important climatic influence for mixed conifer stands. No evidence from tree ring records that long-term trends in growth are evident. Evidence instead for punctuated and short-term low growth anomalies in response to annual to multi-year droughts.

4. CLIMATE IMPACTS ON GROWTH AT UPPER TREELINE

4.1. The Sierra Nevada and adjacent White Mountains are characterized by an unusually high concentration of long-lived tree species in conjunction with preservation of subfossil wood in a cold, dry setting (refs). As a result, tree-ring chronologies from this region have been pivotal in shaping our concepts regarding the nature of climate change since the 1960s (See Hughes et al. Chapter). Tree-ring chronologies from this region have also been key evidence in a lively dispute over the degree to which late 20th century trends in growth are caused by increasing atmospheric CO₂ levels (Graybill and Idso; Graumlich; Mann et al. 1999, others). Here we make use of these tree-ring questions to address the issue of climatic impacts of growth in the subalpine forests, especially for those stands at and near upper treeline.

4.2. In this section we make use of tree-ring data collected by Graumlich or others in the

tree-ring community, representing nine sites and five species, spanning the years from AD 1000 to 1996 (Fig. 6). In order to extract general patterns from this data set, we used a data reduction technique with minimal assumptions regarding whether growth responses to climate are linear and uniform over time (see end note which is actually right below at present). The procedure reduced the nine chronologies into two new synthetic factors that captured 86% of the variation in the original data set. **This indicates that species to species differences are relatively minor compared to the overall synchronization of growth by climate.**

- 4.2.1. <<put this stuff into an end note>> We compressed the dataset from 9 dimensions into 2 using non-metric multidimensional scaling (MDS). MDS is an ordination technique whereby data are simultaneously arranged into space based on their Euclidean distance from all other samples (ref). We used the software package PC-ORD to perform the MDS (ref). The basis of the ecological dissimilarity matrix used was a 9x9 Euclidean distance matrix, measured as the 9-dimensional version of the Pythagorean theorem. The index is metric and triangular so there can be a direct mapping of ecological distance into ordination space (ref). To determine the best number of axes in which to project the data swarm, we conducted MDS in a step-down fashion where solutions of varying dimensionality (from 6 to 1) were compared for their ability to minimize a goodness of fit metric (stress) in the ordination space and accurately compress the data. A scree plot suggests that a 2-dimensional solution (stress=17.2%) is appropriate. We performed a varimax rotation in order to align the axes in a more intuitive way. This 2-d solution captures 86.4% of the variation in the 9-d space with 71.6% of that loading on axis 1.
- 4.3. We compared the year to year variation in the two factors to the 20th century instrumental records from Yosemite National Park (1907 to present; 1209 m; Fig. 1). The trees at upper treeline sensitive to precipitation and temperature (Graumlich 1993; Hughes and Graumlich 1996, Graybill and Idso 1993; LaMarche 1974). The Yosemite climate data was used to interpret the ordination axes. Previous winter (December, January, February) temperature and previous November through March precipitation are significantly correlated to axis 1 ($p < 0.001$). Previous winter temperature is correlated with axis 1 ($r = 0.41$) and only slightly with axis 2 ($r = 0.09$). Previous winter precipitation correlates positively for axis 1 ($r = 0.42$) and slightly negatively with axis 2 ($r = -0.08$). As the correlations are based on a subset of ordination scores that were obtained from the entire chronology, the interpretation applies to the entire ordination space. Unlike other recent studies of tree growth-climate relationships at treeline (Briffa and Osborne 1999; Barber et al. 2000), we see no evidence for a reduced or altered sensitivity to climate in the most recent decades.
- 4.4. <<*this and subsequent paragraphs will be rewritten in simpler terms*>> We used cluster analysis to assess the degree to which multivariate patterns in tree growth define climate episodes. Four clusters were chosen that have not only distinctive patterns within the ordination space (Fig. 7) but also distinctive mean growth index values (Table 1).
 - 4.4.1. <<stick into end note>>The samples were organized into discrete clusters using hierarchical agglomerative classification (ref). This was accomplished

by establishing a joining algorithm that unites individual samples into similar groups based on pairwise dissimilarity in ecological distance. Again, we used Euclidean distance to form the dissimilarity matrix. We used Ward's (ref) minimum variance method as a joining rule. This linkage method produced tight clusters with low chaining (16%). As the same dissimilarity matrix was used for clustering and ordination, the results can be viewed in the same space. We used multi-response permutation procedures (MRPP; ref) to determine the best number of clusters to represent this data set by comparing the within-group homogeneity to a random expectation (ref). The relationship of chance-correlated within-group agreement as a function of number of groups was non-linear with a threshold indicating that 4 clusters offers the best trade-off between group fidelity and interpretability. Ellipsoids were drawn around clusters 1, 3 and 4 and superimposed on the ordination space. Cluster 2 is omitted for clarity.

- 4.5. The complex inter-annual and decadal variability in tree-ring data over the last 1000 years makes visualizing simultaneous temporal trends difficult. However, by computing a running, 50-year average of ordination scores the temporal trends in ordination space can be readily interpreted (Fig. 7). The temporal variability is highly structured with distinct multi-decadal deviations from the centroid that have no analog in the twentieth century (Fig. 7). In previous work we have interpreted these periods as distinct climate episodes with conditions quite different from those of the 20th century <<or something like that—link to Hughes et al. chapter>>.
- 4.6. **Our most important finding is that the late twentieth century is characterized by growth rates far exceeding average conditions of the past millennium. long-term average. This is the most easily interpretable period, mapping directly onto the temperature vector. Our results support the emerging paradigm that the climate of the last millennium was highly variable as compared to the twentieth century. Further, our results indicate that these high elevation conifers coherently demonstrate that modern growth trends have no analog in the last millennium and show a correlation with increasing temperatures. This is a distinctive biological signature of unprecedented warming in the last millennium.**
- 4.6.1. <<add something on CO2 fertilization issue?>>

5. CONCLUSIONS

- 5.1. Multiple lines of evidence point to the great potential for climate change to affect forest ecosystems, with impacts ranging from subtle shifts in the range of species to large-scale forest decline or dieback (refs). One of the key tools in projecting forest response are climate—growth relationships, both as stand-alone analyses, such as the results presented here, and more formally incorporated into numerical models (see Chapter xxx).
- 5.2. Our results indicate that climate variability, for the most part, affects the growth of forest trees in the Sierra Nevada forests in subtle ways, especially as compared to the impacts of fire exclusion (Chapter xxx). Climate variability is most important for certain species at specific sites. Clearly, white fir and sugar pine have registered

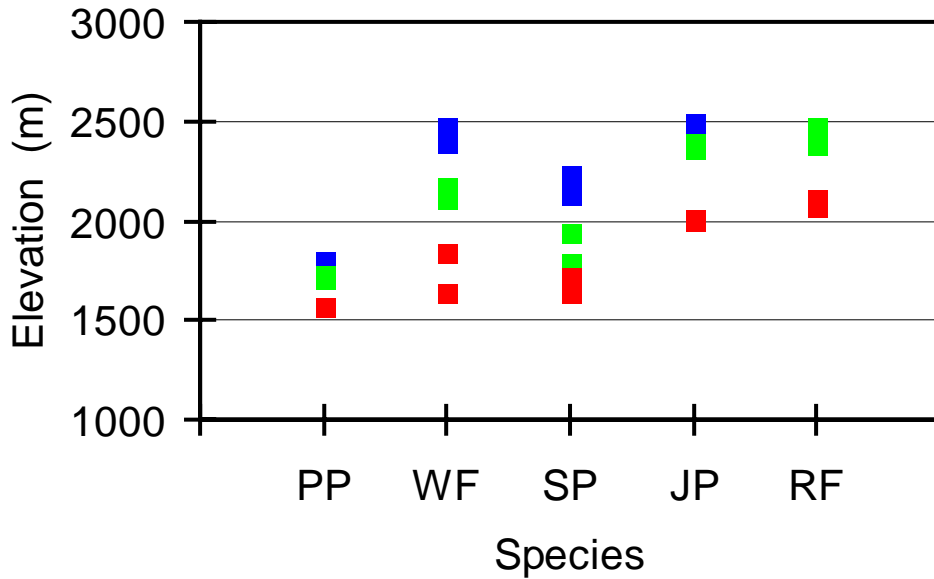
growth impacts of summer drought during the 20th century, especially at their lower range limits. Similarly, trees growing at upper treeline are responding to late 20th century temperature trends by increasing their growth to rates that are unprecedented during the past 1000 years.

6. FIGURES

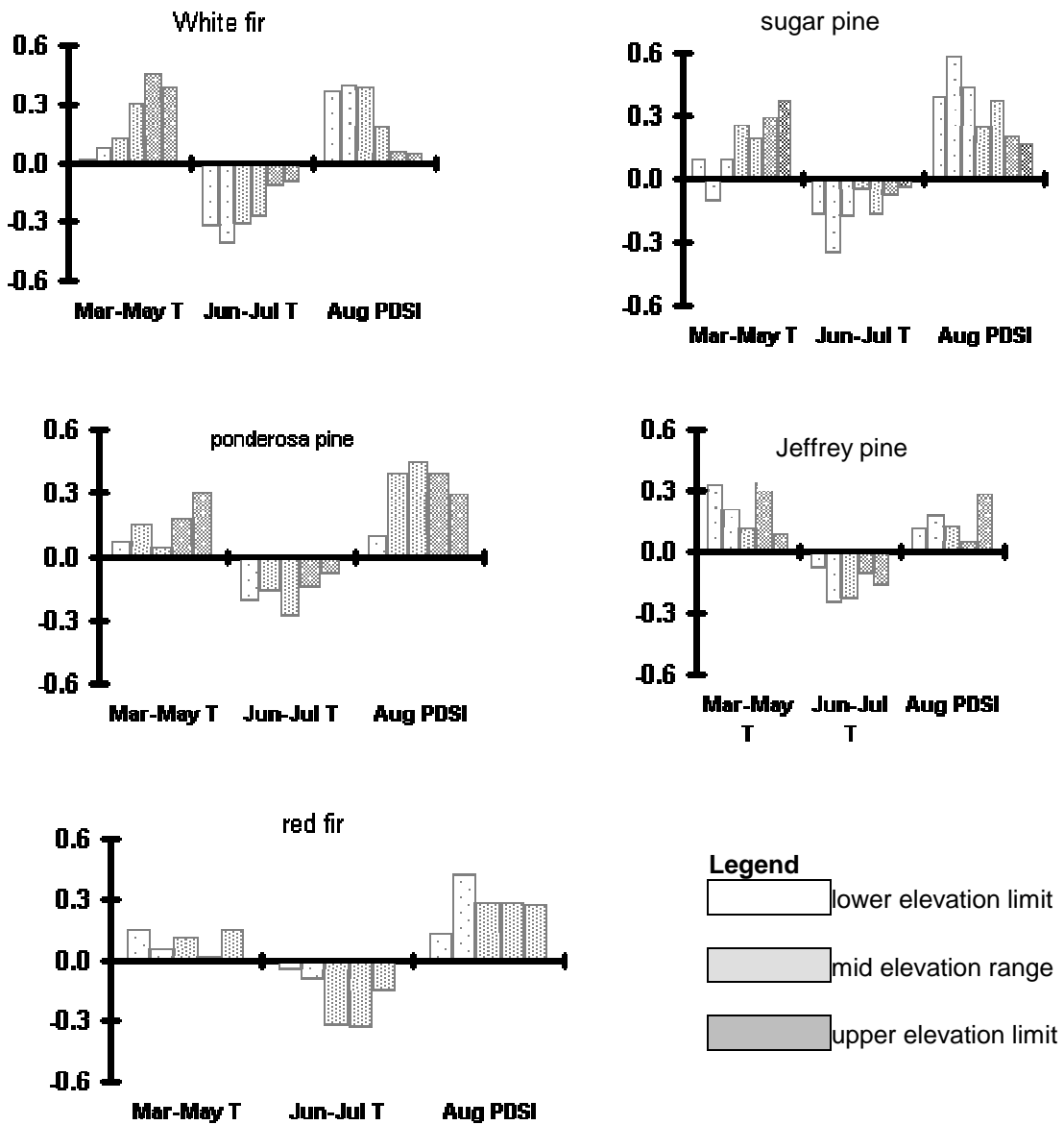
- 6.1. Fig. 1. Tree-ring width series from a variety of species and settings reveal different aspects of environmental history. See notes for 2.3
- 6.2. Fig. 2. Photo of mixed conifer forest with giant sequoia and person for scale.
- 6.3. Fig. 3. Figure from Hughes, M.K., Brown, P.M. 1992 Drought frequency in central California since 101 B.C. recorded in giant sequoia tree rings., *Climate Dynamics* 6: 161-167

6.4. Fig 4. The climate-growth relationship for the dominants of the mixed conifer forest was analyzed by sampling trees at sites at the lower and upper range limit as well as near the middle of the species range. Species include ponderosa pine (*Pinus ponderosa*, PP), white fir (*Abies concolor*, WF), sugar pine (*P. lambertiana*, SP), Jeffrey pine (*P. jeffreyi*, JP) and red fir (*A. magnifica*, RF). Sites for each species were located in both Sequoia and Yosemite National Parks.

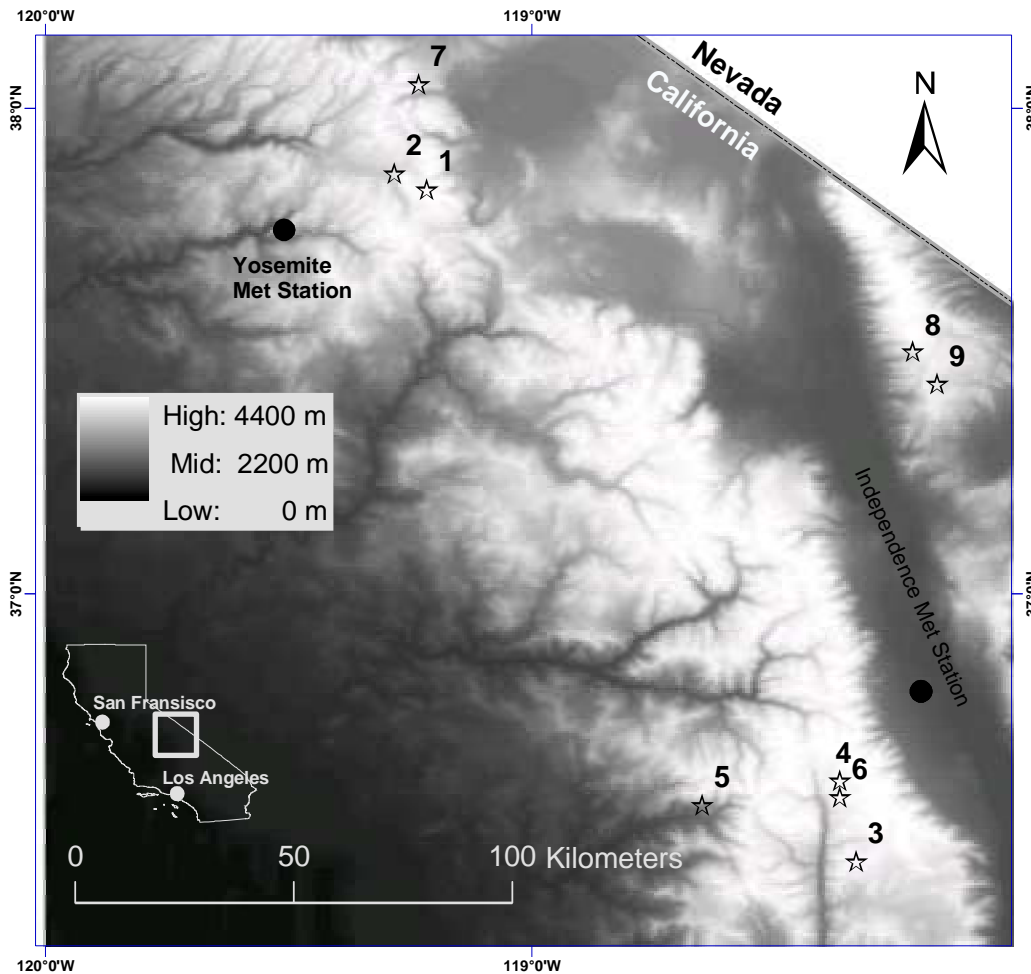
■ upper range limit ■ mid-range ■ lower range limit



6.5. Fig 5. climate—growth relationships for mixed conifer species.



6.6. Fig 6. map of upper treeline sites



Id	Site Name	Species	Elevation (m)	Source/Contributor
1	Spillway Lake	<i>P. albicaulis</i>	3300	ITRDB/King
2	Mammoth Peak	<i>P. albicaulis</i>	3350	ITRDB/King
3	Boreal Plateau	<i>P. balfouriana</i>	3420	Graumlich
4	Upper Wright Lakes	<i>P. balfouriana</i>	3510	Graumlich and Lloyd
5	Hamilton	<i>J. occidentalis</i>	2630	Graumlich
6	Crabtree	<i>P. balfouriana</i>	3380	Graumlich
7	Lundy Lake	<i>P. flexilis</i>	2925	Graumlich and King
8	Campito Mountain	<i>P. aristata</i>	3400	ITRDB/Graybill & LaMarche
9	Methuselah Walk	<i>P. aristata</i>	2805	ITRDB/Graybill

Figure 1. Location of tree-ring sites (numbered stars) and meteorological stations (circles).

Sources for tree-ring data include the authors' data archives and the International Tree Ring Data bank (ITRDB).

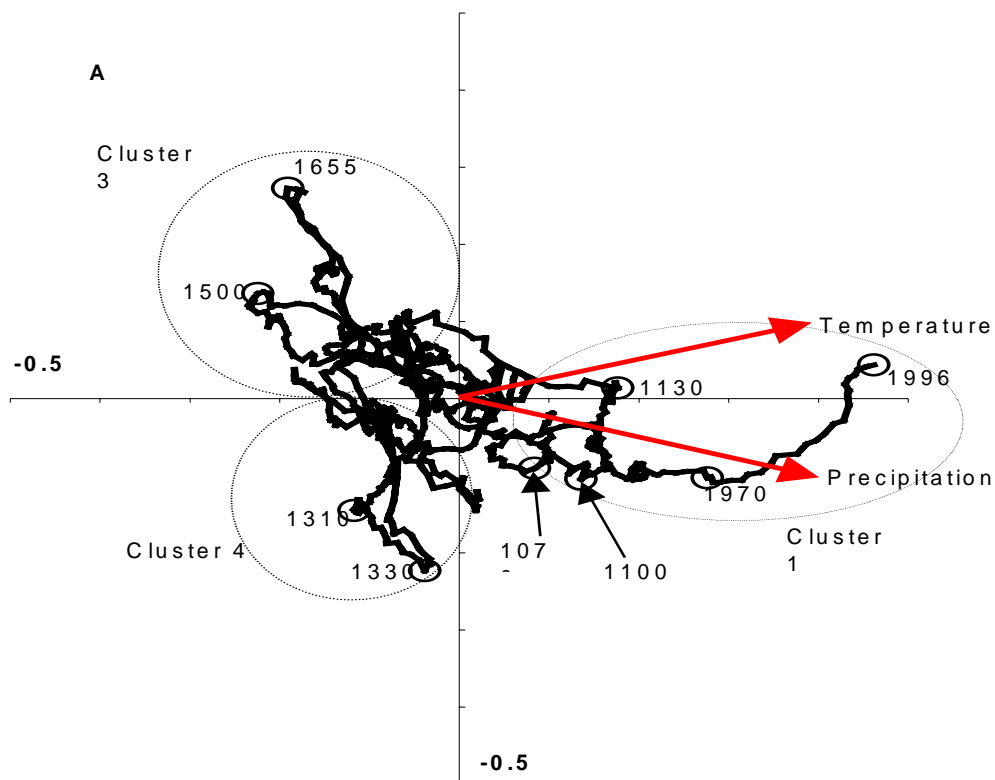


Figure 7. Temporal vector of smoothed ordination scores (50-year running average) mapped onto ordination space. Axis 1 reflects the dominant pattern of variability shared among all five species. Axis 2 reflects contrasting growth anomalies between the more or less water stressed sites. Multi-decadal anomalies in tree growth are mapped using the clusters identified above onto the ordination space. Labels have been inserted at several points and clusters 1, 3, and 4 are superimposed as ovals. Cluster 2 occupies the middle of the ordination space (centroid $\sim 0,0$) and has been omitted for clarity. Temperature vectors are previous winter's temperature and precipitation derived from instrumental data.