

AN ABSTRACT OF THE THESIS OF

Kevin C. Knutson for the degree of Master of Science in Forest Science presented on January 5, 2006.

Title: Climate-Growth Relationships of Western Juniper and Ponderosa Pine at the Pine-Woodland Ecotone in Southern Oregon

Abstract Approved: \_\_\_\_\_  
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Pinyon-juniper woodlands throughout the western U.S. have expanded rapidly following European settlement during the late 19th century. In central and eastern Oregon, western juniper (*Juniperus occidentalis* var. *occidentalis* Hook.) encroachment has been previously documented in the sagebrush steppe and upper elevation aspen communities. While these vegetation changes and dynamics have been extensively studied, the ability to accurately predict future effects on vegetation structure in response to climatic effects requires the identification of climatic factors that most directly regulate growth across variations in spatial features, particularly when future climate change is likely. I sought to address this problem at the pine-woodland ecotone using tree-ring data for western juniper and ponderosa pine (*Pinus ponderosa* Dougl. Ex Loud.) from the Fremont National Forest of central Oregon. Site and soil-derived growth chronologies for the period 1950 to 2000 were developed for both species using standard dendrochronological techniques at 17 sites within the Fremont National Forest stratified by elevation (1584 and 1865 meters). Analysis of the climatic relationship with site and

soil-derived chronologies using correlation and linear regression revealed that, similar to previous studies in Oregon, radial growth in both species is highly dependent on winter-spring precipitation events that recharge growing-season soil water. Ordinations of site- and soil-derived chronology principal components (PCA) scores for both species identified distinct gradients in growth patterns related to elevation, slope, and soil infiltration class. Low elevation sites had reduced growth in the nine driest years during 1950-2000 compared to high elevation sites. Slope was also positively associated with the ratio of standardized growth in wet years to dry years (W:D), a measure of climate sensitivity. Tree growth of both species on coarse-textured soils with rapid infiltration rates was more climate-sensitive (higher values of W:D) and was also reduced during drought years when compared to other infiltration classes. These findings suggest potentially significant variation in growth responses to future climate changes across distinct local features at the pine-woodland ecotone. Juniper and pine radial growth at sites that feature poor water-holding capacities (i.e., low elevation, steep slopes, and coarse-textured soils) can be expected to be most sensitive to future drought and climate fluctuations in southern Oregon.

Climate-Growth Relationships of Western Juniper and Ponderosa Pine at the  
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Master of Science thesis of Kevin C. Knutson presented on January 5, 2006

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# **Climate-Growth Relationships of Western Juniper and Ponderosa Pine at the Pine-Woodland Ecotone in Southern Oregon**

## **INTRODUCTION**

Since European settlement in the mid- to late 1800's, western juniper (*Juniperus occidentalis* var. *occidentalis* Hook.) populations have expanded in range and increased in density throughout central and eastern Oregon (Miller and Wigand 1994, Miller and Rose 1995, Soule and Knapp 1999). This expansion has primarily occurred into lower elevation areas dominated by sagebrush steppe (Eddleman 1987). Encroachments into higher elevation areas historically dominated by other species such as aspen (*Populus tremuloides* Michx.) have also been documented (Miller and Rose 1995). The recent western juniper expansions in Oregon as well as pinyon-juniper populations throughout the Intermountain West are unprecedented when compared to previous population expansions during the Holocene (Miller and Wigand 1994, Tausch 1999). Western juniper forests and savannas are now estimated to cover 2.6 million hectares in Oregon (Azuma et al. 2005), composing the single largest species unit by area in eastern Oregon forests.

Current theory suggests that the reduction in mean fire frequency from presettlement conditions has been the primary driver of the current range expansion of juniper and other woody plant species (Burkhardt and Tisdale 1976, Miller and Tausch 2001). Prior to European settlement, juniper populations were generally confined to rocky outcrops (Miller et al. 2005). Periodic fire in the sagebrush steppe restricted the expansion of trees into shrublands, but reductions in fine fuels associated with the

introduction of livestock grazing and twentieth century fire suppression activity resulted in the recent expansion of juniper (Miller and Rose 1999, Miller and Tausch 2001).

While lack of fire has likely been the primary driver of woody plant expansions in the Intermountain West, other factors such as carbon dioxide (CO<sub>2</sub>) fertilization (Johnson et al. 1993, Knapp et al. 2001a, 2001b, Polley 1997) and climate (Miller et al. 2005, Miller and Tausch 2001) have also been implicated. The increase in atmospheric CO<sub>2</sub> concentration associated with burning of fossil fuels during the 19<sup>th</sup> and 20<sup>th</sup> centuries is thought to alter plant water balance through an improvement of plant water use efficiency. At the grassland-woodland transition zone of arid and semiarid environments where water is often a limiting resource, improved water use efficiency can competitively favor woody plants and thus enhance encroachment (Polley 1997). Prehistoric expansions of western juniper during the Holocene generally occurred during periods of increased precipitation and lower temperatures (Miller and Wigand 1994). The latter half of the 19<sup>th</sup> century was a period of increased precipitation in the southern region of the Pacific Northwest (Graumlich 1987), coinciding with the beginning of current juniper expansion in eastern Oregon. The timing of this period of increased precipitation is thought to have enhanced survivorship of western juniper (Miller et al. 2005), acting to prime the expansion into areas previously occupied by sagebrush steppe.

Climate of the Pacific Northwest region is projected to change in the near future, with an average annual temperature increase of 2.5°C (4.5°F) by the year 2050 (Snover et al. 1998, Mote et al. 2003, Snover et al. 2003). Current models suggest that regional climate change will tend towards wetter, warmer winters and drier summers (Snover et

al. 2003). How such a significant climate change will affect western juniper populations is still not completely clear. In the inland region of the Pacific Northwest, ponderosa pine forests and juniper woodlands are generally projected to respond to this climate change with an increased range expansion (Coops et al. 2005, Bachelet et al. 2001, Neilson and Drapek 1998). This projection, however, is based on terrestrial vegetation acting in a negative feedback fashion in relation to the global carbon cycle (e.g., a carbon sink). If global climate were to change more rapidly, leading to greater periods of drought and forest dieback, global vegetation may act in a positive feedback manner (carbon source) with potential for even more rapid global climate change and forest dieback (Bachelet et al. 2001, Neilson and Drapek 1998). In periods of severe climate change and drought, the potential for rapid landscape change in vegetation type is significant, particularly at semiarid forest-woodland ecotones (Allen and Breshears 1998, Neilson 1993).

While some aspects of the relationship of western juniper growth with climate have previously been quantified (Pohl et al. 2002, Knapp et al. 2001a, Graumlich 1991), little research has focused on the ponderosa pine (*Pinus ponderosa* Dougl. Ex Loud.)-juniper woodland ecotone. The future climate of the Pacific Northwest is expected to be much warmer and more variable (Mote et al. 2003). Annual droughts that do occur will therefore likely be more severe, particularly in warm phase periods of the Pacific Decadal Oscillation (PDO). Severe drought could potentially lead to ponderosa pine dieback and replacement by the more drought-tolerant juniper woodland at the transition zone of these two species. Such an effect was documented at the pinyon-juniper woodland to

ponderosa pine ecotone in the southwestern U.S. following severe drought during the 1950's (Allen and Breshears 1998), and led to pinyon-juniper encroachment in upslope areas. Western juniper growth in woodlands generally responds positively to winter-spring precipitation (October to June) in the central and southeastern Oregon region (Knapp et al. 2001a, Graumlich 1991). To better predict how climate will affect juniper populations, a need exists to determine whether juniper at the pine-woodland ecotone responds similarly to climate in southeastern and central Oregon forests.

Tree-rings are frequently used to study relationships between climate and tree growth (e.g., Adams and Kolb 2005, Peterson et al. 2002, Watson and Luckman 2002, Peterson and Peterson 2001, Little et al. 1995, Villalba and Veblen 1994). Tree growth often can vary in relation to local features such as topography (e.g., north versus south aspect), soil texture, and elevation (Fekedulegn et al. 2003, Oberhuber and Kofler 2000, Villalba and Veblen 1994, Fritts 1976), which affect local ecological processes (Swanson et al. 1988). Such features will affect plant community distribution (Barbour et al. 1980), can attenuate or amplify the relationship of growth to climate, and often lead to uncertainties in predictions of vegetation change in models (Bachelet et al. 2001). The extent to which local factors affect relationships between tree growth and regional climate is unclear in western juniper populations.

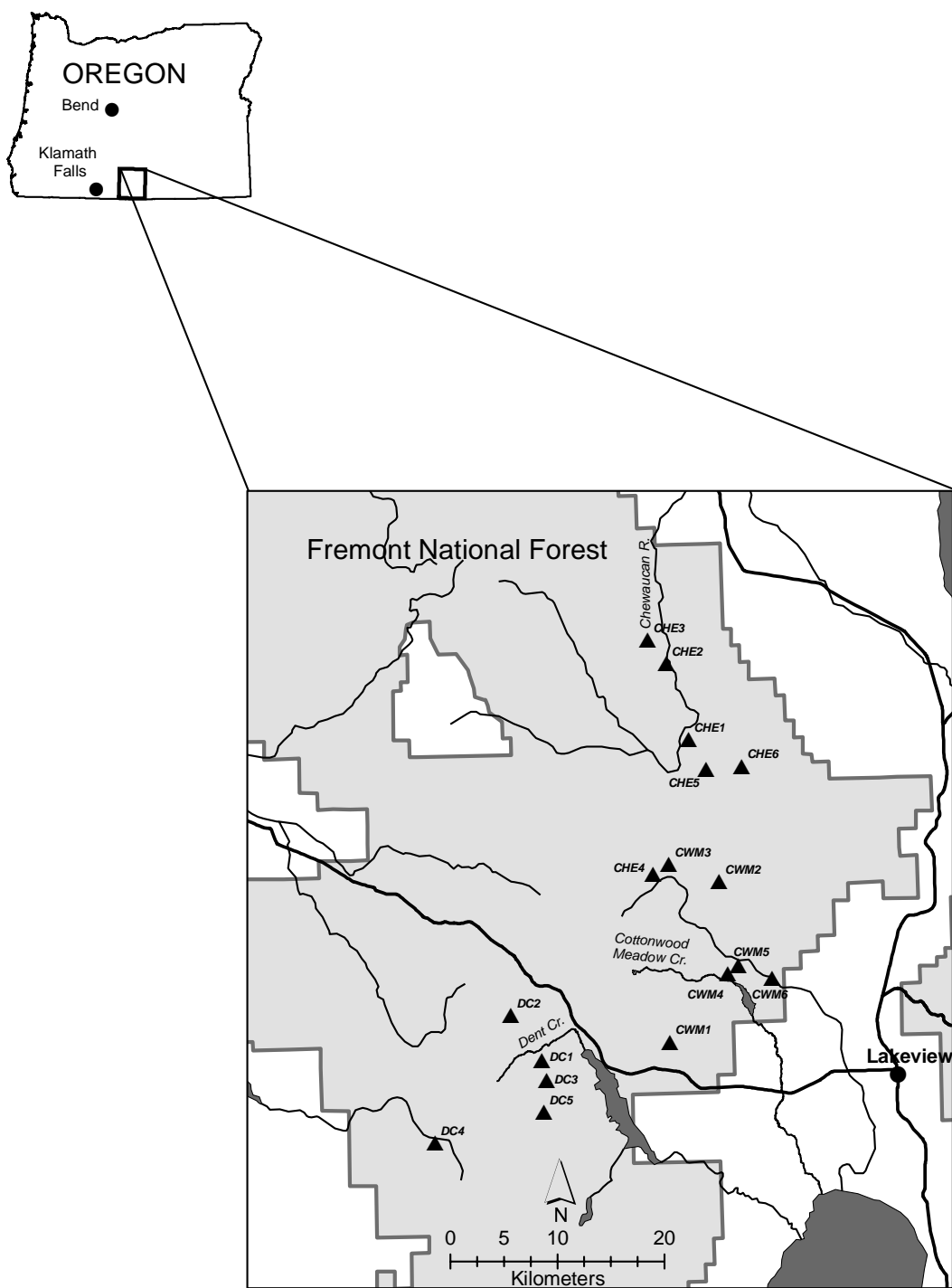
In this study, I sought to determine the relationships of tree growth to climate at the western juniper-ponderosa pine ecotone. I applied a dendroecological approach to determine whether trees (western juniper and ponderosa pine) growing at this ecotone also positively respond to winter-spring precipitation. I also sought to explore how local

factors such as elevation, aspect, and soils (texture, depths, etc.) modify the effect that climate has on tree growth. In particular, I assessed the effect of drought across spatial variability and two physiologically unique species in different pine-woodland ecotones. I hypothesized that while trees at the pine-woodland ecotone would positively respond to winter-spring precipitation, local features such as soil texture and elevation could potentially attenuate or amplify the climate-growth relationship and thus lead to a mixed array of drought sensitivities across the landscape.

## STUDY AREA

The study area was located in the Fremont National Forest of south central Oregon (Figure 1). Most of the forest lies within the northern portion of the Basin and Range physiographic province of the United States (Hunt 1967). Geology is generally volcanic in origin, predominantly basalt and tuff flows or pyroclastic and rhyolite deposits. Soils are primarily derived from residual volcanic parent materials, alluvium and colluvium in areas of dissected topography, or ash deposits from the eruption of Mt. Mazama approximately 7,700 years before present (Wenzel 1979). Elevation ranges from roughly 1220 m to 2577 m at Crane Mountain. Lower elevation areas are primarily dominated by western juniper and grade into ponderosa pine with increasing elevation (Franklin and Dyrness 1988). At elevations roughly above 1677 m, forests of the Fremont are generally mixed conifer characterized by species such as white fir (*Abies concolor* (Gord. & Glend.) Lindl.), incense cedar (*Calocedrus decurrens* (Torr.) Florin), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). The Forest is managed for multiple resource uses including timber production, livestock grazing, and recreation.

The Fremont NF is located east of the Cascade mountain range, and, consequently, the climate is drier and more semiarid than the mountains to the west due to a rain shadow effect (Taylor and Bartlett 1993). Annual precipitation generally ranges from 400 to 800 mm, occurring primarily as snow during winter (December to March) and rain in spring. Summers are typically warm and dry, although isolated thunderstorms often occur at upper elevations. Mean maximum temperatures vary from a low of 4.4°C in January to 27.2°C in July.



**Figure 1.** Location of study sites in the Fremont NF, Oregon where growth chronologies were developed. See Table 1 for location names and characteristics.



## METHODS

### Site selection and topographic features

Seventeen sites were selected in the Lakeview and Paisley districts of the Fremont NF (Figure 1). Three sub-regional areas were chosen to locate sites: Dent Creek (DC), Cottonwood Meadow (CWM), and Chewaucan (CHE). These sub-regional areas spanned a latitudinal gradient with DC the southernmost area, CWM intermediate, and CHE the northernmost area (Figure 1). Within two of the three areas (CWM and CHE), six study sites were located in ponderosa pine-western juniper transition zones of each area, whereas five study sites were located in the DC area. The DC area did not have enough candidate sites in the high elevation class that met the selection criteria to obtain equal numbers of sites in each area. Sites were located near roads or dirt trails for ease of access. Three sites each within the sub-regional areas were identified in low and high elevation classes except in the DC area, which only had two high elevation classes. The final median elevations of the low and high elevation classes were 1584 and 1865 m respectively for all sites after completion of site selection. Sites were also typically north or south aspects, with more sites having southern exposures (Table 1).

At each study site, six plots (0.07 ha) were systematically established at 100-m intervals along a 500-m line transect. Elevation, aspect, slope, and dominant shrub for each plot along the transect were recorded. Of interest in the study was how local features, such as aspect, could potentially alter climate-tree growth relationships in relation to their documented effects on energy budget and water balance (Fritts 1976). Latitude, aspect, and slope of each plot were used to calculate potential annual direct

incident radiation ( $\text{MJ cm}^{-2} \text{ yr}^{-1}$ ) and heat load index (McCune and Keon 2002) at each site (Table 1).

**Table 1.** Summary characteristics of the 17 study sites sampled. Sites with more than one aspect contained varying topography along the 500 m transect used for sampling. Dominant shrub codes are: ARTR = *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle, PUTR = *Purshia tridentata* (Pursh) DC, ARPA = *Arctostaphylos patula* Greene, BERE = *Berberis repens* Lindl. CHE = Chewaucan, CWM = Cottonwood Meadow, DC = Dent Creek

Site Code	Elevation (m)	Slope (deg)	Aspect(s)	Potential Radiation ( $\text{MJ cm}^{-2} \text{ yr}^{-1}$ )	Dominant Shrub
CHE1	1593	5.5	N, NE	0.88	ARTR
CHE2	1549	7.0	SE, NW	0.94	ARTR/PUTR
CHE3	1565	8.2	N, SW	0.92	ARTR/PUTR
CHE4	1824	5.3	S	0.96	ARTR
CHE5	1810	10.3	N, SW	0.86	ARTR
CHE6	1857	12.8	NW	0.80	ARTR
CWM1	1874	2.8	S	0.95	ARPA
CWM2	1909	12.0	SW	0.95	ARTR/PUTR
CWM3	1776	7.7	W, NW, SW	0.92	ARTR/PUTR
CWM4	1643	8.3	S	0.98	ARTR/PUTR
CWM5	1584	3.0	S	0.95	ARTR/PUTR
CWM6	1583	4.2	S	0.96	ARTR/PUTR
DC1	1599	5.3	SW	0.96	ARTR/PUTR
DC2	1916	7.0	NE, SE	0.94	BERE
DC3	1619	8.0	SE, NE	0.94	ARTR
DC4	1891	2.0	SW	0.94	ARTR
DC5	1542	9.0	NE	0.86	ARTR/PUTR

## **Site-derived growth chronology development**

A total of 24 trees of each species (western juniper and ponderosa pine) were sampled at each site during 2001 and 2002. At each plot, 4 trees of each species were sampled using a point-quarter sampling scheme (Cottam and Curtis 1956, Brower et al. 1998). Individuals of each species nearest to the plot center within each of four plot quadrants were selected. Trees were considered for sampling only if they were dominant or co-dominant, or occupied a position that had an open canopy position. Trees with major defects (i.e., multiple stems, heavy insect damage, or severe scarring) were not sampled. Tree-ring samples were collected from individual trees using a different method for each species (Stokes and Smiley 1968). For ponderosa pine, two increment cores were extracted from opposite cross-slope sides of each tree at breast height (1.4 m). Cores were stored in paper straws for transport. We used destructive sampling methods for western juniper, and therefore large individuals that displayed old-growth juniper characteristics (Waichler et al. 2001) were excluded from sampling in accordance with Fremont NF resource management objectives. Individual junipers were felled using a chain saw roughly 30 centimeters above ground level, and a cross-section was removed from the stem at this height for laboratory analysis.

Tree-ring samples (cores and cross-sections) were allowed to dry at room temperature for a minimum of four days. Ponderosa pine cores were mounted to grooved white poplar mounts; pine increment cores and juniper cross-sections were then sanded with progressively finer grades of sand paper (60- to 320-grit) using a belt sander to reveal the tree-ring growth structure (Stokes and Smiley 1968, Phipps 1985). Ring

widths of each sample were measured to the nearest 0.01 mm using a sliding stage Velmex measuring system and Measure J2X computer software (Voortech Consulting, Holderness, NH, USA). Cores and cross-sections were crossdated using skeleton plots and marker years (Stokes and Smiley 1968). Crossdating was validated using COFECHA (Holmes 1983) computer software to ensure that accurate dates were assigned to individual tree-rings. Only trees in which two ring-width measurement series could be accurately dated were used in growth chronologies. Site chronologies were based on 12 to 22 trees per site for western juniper and 5 to 22 trees per site for ponderosa pine (Appendix A) after crossdating.

Tree-ring width and variation often decreases as tree diameter increases, and therefore all ring-width measurements typically need to be standardized to remove age-related growth trends and to meet assumptions of most statistical analyses (Fritts 1976). Residual site chronologies (“site chronologies”) were developed for the years 1950-2000 for each species using program ARSTAN (Cook and Holmes 1996). The 1950-2000 period was chosen because this period maximized sample depth. Low frequency variations resulting from age were removed by fitting a negative exponential curve or a linear regression of negative slope to each growth series. Growth index series were then created for each tree by dividing the measurement value of each year by the fitted value for the same year. The site chronology for each species was then determined by averaging the residuals from autoregressive modeling for all individual growth series at the site. Tree-ring chronologies often exhibit persistence (serial correlation) resulting from stored polysaccharides of previous growth or other low frequency processes such as

disturbance that alter tree allocation patterns (Fritts 1976). Autoregressive modeling is a procedure used in time series analysis in which residuals from the autocorrelation function are estimated (Chatfield 2004). This procedure results in stationary and independent residuals required for some statistical analyses and can improve the estimate of the climatic signal in tree-ring chronologies (Fritts 1976, Villalba and Veblen 1994). A total of 17 site chronologies for each species were developed using this technique. As a result of detrending, site chronologies are unitless indicators of average site growth patterns through time, with mean growth equal to a value of one. Mean sensitivity, a unitless measure of the relative change in the growth index from year-to-year, was calculated as the absolute difference between two adjacent indices divided by the mean of the two indices. The individual yearly mean sensitivity values were then averaged across all years from 1950 to 2000 to obtain the mean of the entire series for each site chronology.

### **Soil-derived growth chronology development**

To address whether soil texture or other fine-scale landscape features such as aspect attenuate or amplify climate signals in tree growth, GPS coordinates of each sampled western juniper and ponderosa pine tree were overlaid on Fremont NF soil resource inventory (Wenzel 1979) map units. In summer 2003, soil map units were field-confirmed using soil pits, field texture tests, and observation of map unit characteristics such as surface litter or fragment composition. Plots and trees were then assigned to a specific soil map unit classification (Table 2).

**Table 2.** Soil map unit, subgroup, surface texture, and infiltration class of the research sites. Soil data are from Wenzel (1979). CHE = Chewaucan, CWM = Cottonwood Meadow, and DC = Dent Creek.

site code	soil map unit	# of plots	Soil Subgroup Classification	Surface Texture	Infiltration Class
<b>CHE1</b>	50	2	Lithic Argixeroll	silty clay loam	moderate-slow
	53	2	Lithic Xerorthent	loam	moderate
	62A	2	Typic Argixeroll	silt loam	moderate
<b>CHE2</b>	53	2	Lithic Xerorthent	loam	moderate
	57	2	Typic Xerorthent	sandy loam	rapid
	76B	2	Typic Xerorthent	sandy loam	rapid
<b>CHE3</b>	40B	6	Typic Xerorthent	sandy loam	rapid
<b>CHE4</b>	62B	4	Typic Argixeroll	silt loam	moderate
	67B	2	Mollic Haploxeralf	silty clay loam	moderate-slow
<b>CHE5</b>	57	3	Typic Xerorthent	sandy loam	rapid
	67B	1	Mollic Haploxeralf	silty clay loam	moderate-slow
	76B	2	Typic Xerorthent	sandy loam	rapid
<b>CHE6</b>	62A	2	Typic Argixeroll	silt loam	moderate
	63A	2	Entic Haploxeroll	sandy loam	rapid
	63B	2	Entic Haploxeroll	sandy loam	rapid
<b>CWM1</b>	67B	6	Mollic Haploxeralf	silty clay loam	moderate-slow
<b>CWM2</b>	30B	6	Typic Argixeroll	clay loam	moderate-slow
<b>CWM3</b>	62B	6	Typic Argixeroll	silt loam	moderate
<b>CWM4</b>	60	6	Typic Argixeroll	loam	moderate
<b>CWM5</b>	60	6	Typic Argixeroll	loam	moderate
<b>CWM6</b>	67A	6	Mollic Haploxeralf	silty clay loam	moderate-slow
<b>DC1</b>	50	2	Lithic Argixeroll	silty clay loam	moderate-slow
	34B	4	Typic Argixeroll	loam	moderate
<b>DC2</b>	68B	2	Entic Haploxeroll	loamy sand	rapid
	62B	2	Typic Argixeroll	silt loam	moderate
	37B	2	Typic Argixeroll	sandy loam	moderate-rapid
<b>DC3</b>	56B	6	Pachic Haploxeroll	loam	moderate
<b>DC4</b>	37A	6	Typic Argixeroll	sandy loam	moderate-rapid
<b>DC5</b>	56B	6	Pachic Haploxeroll	loam	moderate

To develop soil-derived chronologies, first the minimum number of trees for the chronology was determined. Trees from three sites that spanned the latitudinal extent of the study area (DC2, CWM6, and CHE3) were used. A random sample of 4, 6, 8, 10 and 12 trees was selected from each of the 3 sites and a chronology (“random chronology”) was developed using the same method as the site chronologies. Pearson’s correlation coefficient ( $r$ ) associated with each of the random chronologies and the site chronology was then determined. A correlation coefficient of 0.9 was set as a minimum threshold to retain relevant climate information. Using the randomization process, six trees were deemed sufficient for the purpose of soil-based chronologies. For each site, soil chronologies were then created based on soil map units for each site, provided that six or more trees were found on the map unit at the site. Growth chronologies were not developed from soil map units having less than six trees, and these units were excluded from analyses of soil chronologies. If a site had a single soil type but changed aspect or slope, then trees were grouped according to aspect or slope. An effort was made to stratify the trees such that soil-derived chronologies had a relatively similar number of trees and similar landscape-level characteristics. All final soil-derived chronologies that were developed had from 6 to 13 trees. A total of 28 ponderosa pine and 36 western juniper soil-derived chronologies were developed.

### **Climatic data**

Monthly mean temperature and monthly total precipitation records for the region that encompassed the study area (Oregon climate division 7, Oregon Climate Service, Oregon State University, Corvallis, OR) were obtained. Although data can be obtained

from local stations in Lakeview or Paisley, divisional records were chosen because they better represent fluctuations in the regional climate. Local station data also often have missing data that must be estimated, and neither of the aforementioned stations is in an elevation or vegetation zone adequately similar to the study sites.

### **Climate-growth relationships**

Correlation functions between precipitation, temperature, and tree growth were determined for site and soil chronologies using program Dendroclim (Biondi and Waikul 2004). A bootstrapped Pearson's correlation coefficient ( $r$ ) was calculated between each growth chronology and monthly climate variables spanning from August before the growth year to September of the current year's growth. Significant correlations ( $n = 51$ ,  $p < 0.05$ ) were determined at a significance level of  $|r| \geq 0.28$ . Patterns of correlation were assessed to determine whether tree growth responded to specific seasonal climate variables (e.g., October to June precipitation). Qualitative comparisons were also made between sites and soils to assess whether patterns of correlation differed with landscape-scale changes.

Tree growth often responds more closely to seasonal climate variations (Fritts 1976). Therefore, composite climate variables were created based on the climate-growth correlations. A total of 9 variables (5 precipitation, 4 temperature) were created. Stepwise regression in S-Plus 6.1 for Windows statistical software (Insightful Corporation, Seattle, WA) was used to determine which seasonal composite climate variable was the single best predictor of growth for all developed chronologies. The single best predictor model with the largest extra sum of squares F-test statistic and with



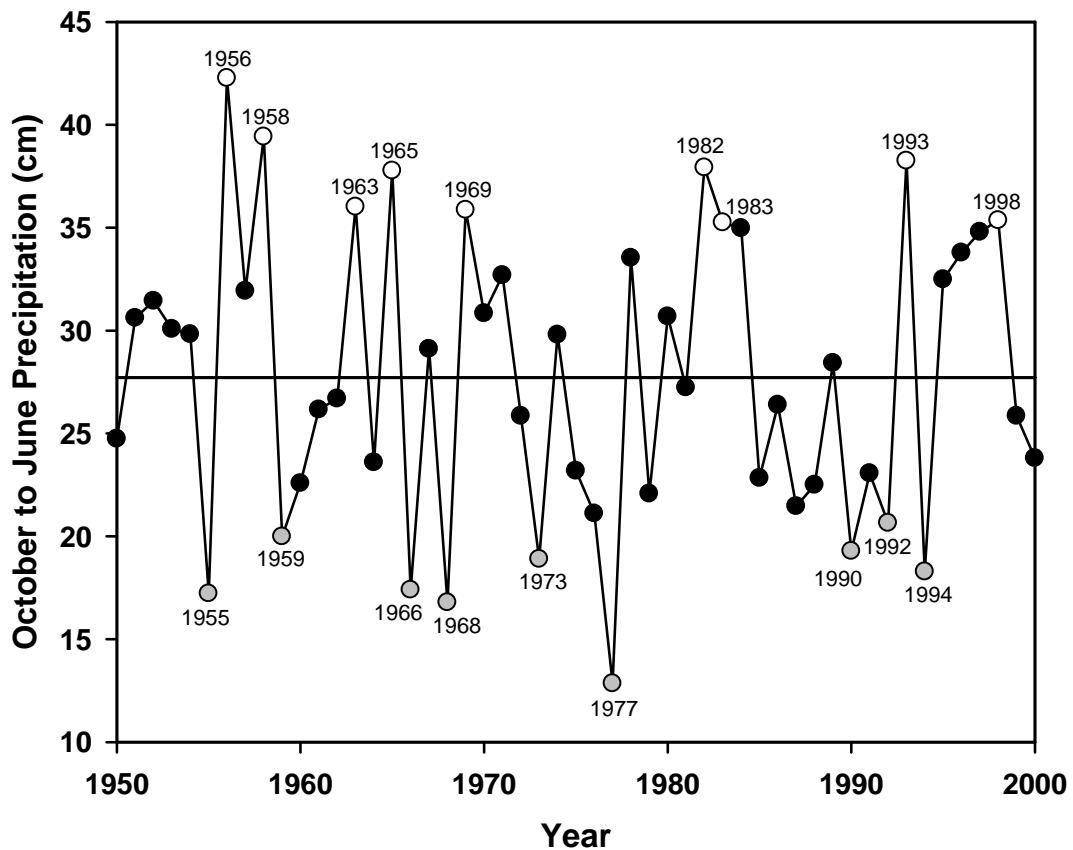
the minimum Bayesian Information Criterion (BIC) value was used to identify the climate composite variable most strongly associated with growth. Plots of residuals were evaluated to determine the adequacy of model fits.

### **Spatial variations in growth and drought effects**

Principal components analysis (PCA) using the PC-ORD software package version 4.33 (McCune and Mefford 1999) was used to assess environmental gradients in the correlation structure of both site and soil-derived chronologies. The analysis was performed on the residual growth index matrix for each species at both the site and soil levels. Thus, four PCAs were performed: juniper site by growth index (17x51), pine site by growth index (17x51), juniper soils by growth index (36x51), and pine soils by growth index (28x51). Relationships between environmental features (elevation, soil surface/subsurface texture, heat load, etc.), coefficients of determination ( $R^2$ ) from climate models, and the correlation structure of growth were explored through an indirect gradient analysis (McCune and Grace 2002). Biplot ordinations of the first two PCA axes were examined to determine if specific site- or soil-derived chronologies clustered in distinct regions of the ordination space and also to test whether tree growth similarities or differences were related to potential environmental gradients.

When an environmental gradient such as elevation was correlated with PCA scores of growth chronologies, relationships of growth sensitivity to climate were then explored based on the environmental gradient of interest. To assess whether chronologies were more sensitive to climate or drought, the ratio of wet to dry years (W:D) and the drought mean (DRHT) were calculated for all site and soil-derived

chronologies. To calculate W:D, the ratio of the average ring-width index for the nine wettest years was divided by the average ring-width index of the nine driest years (DRHT) during the period 1950-2000 (Figure 2). Total monthly precipitation during October to June was used to determine the nine wettest and driest years during the period of interest. The use of nine years assured adequate replication and temporal dispersion of wet and dry years. Both W:D and DRHT have previously been used to assess drought and climate sensitivity (Adams and Kolb 2005, Fekedulegn et al. 2003).



**Figure 2.** Total precipitation for Oregon climate division 7 from previous October to June of the growing season, 1950-2000. Open and shaded circles represent the nine wettest and driest years, respectively, that were used in tree growth comparisons and calculations (e.g., W:D).

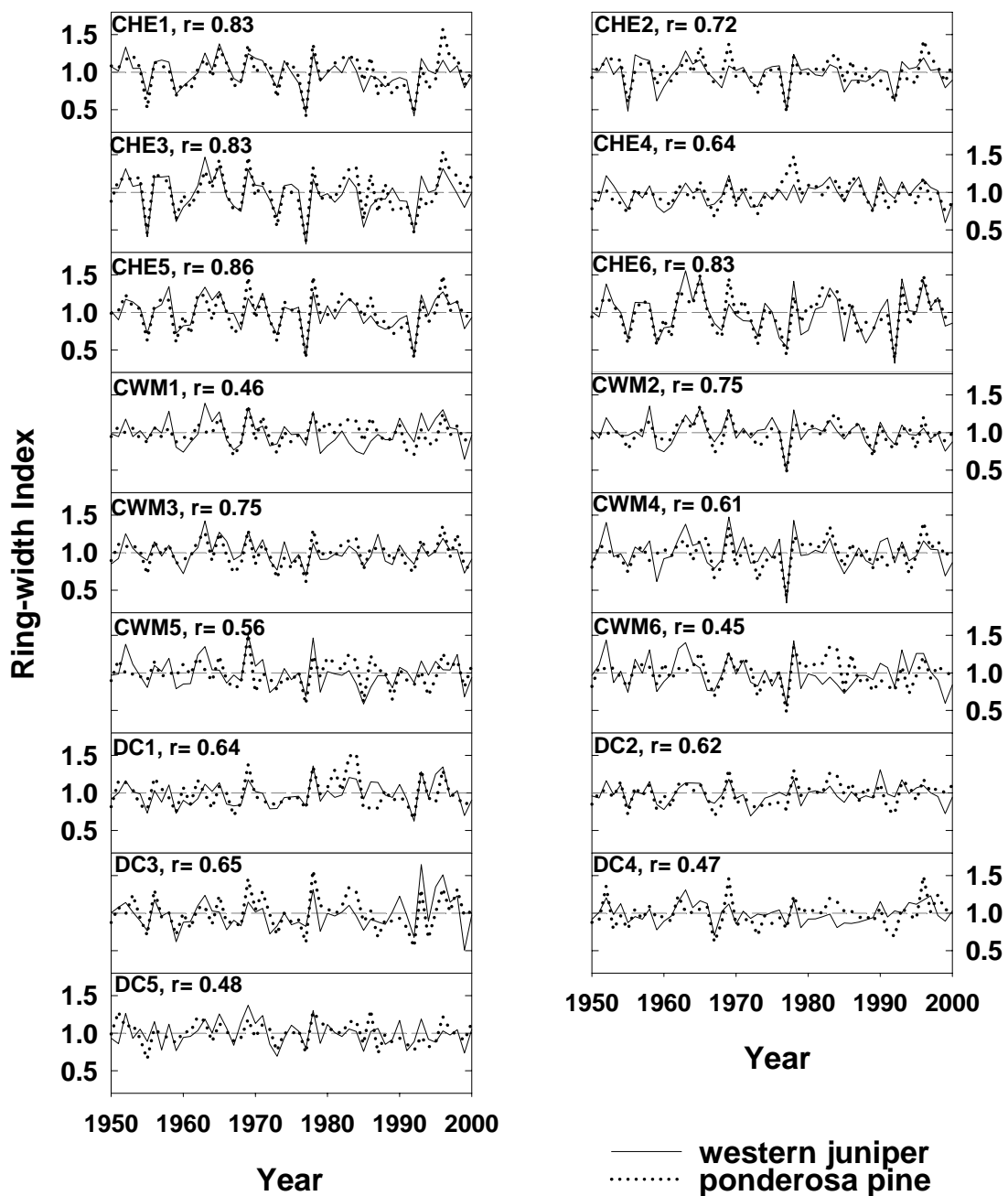
## RESULTS

### Site chronology growth patterns

Mean age at core height ranged from 58 to 105 years for western juniper site chronologies and 65 to 109 years for ponderosa pine site chronologies (Appendix A). Significant autocorrelation coefficients at lags greater than 1 were present in 32 of the 34 site chronologies prior to autoregressive modeling. The remaining two chronologies also had significant first-order autocorrelation coefficients. Residuals from autoregressive modeling were therefore required for all site chronologies.

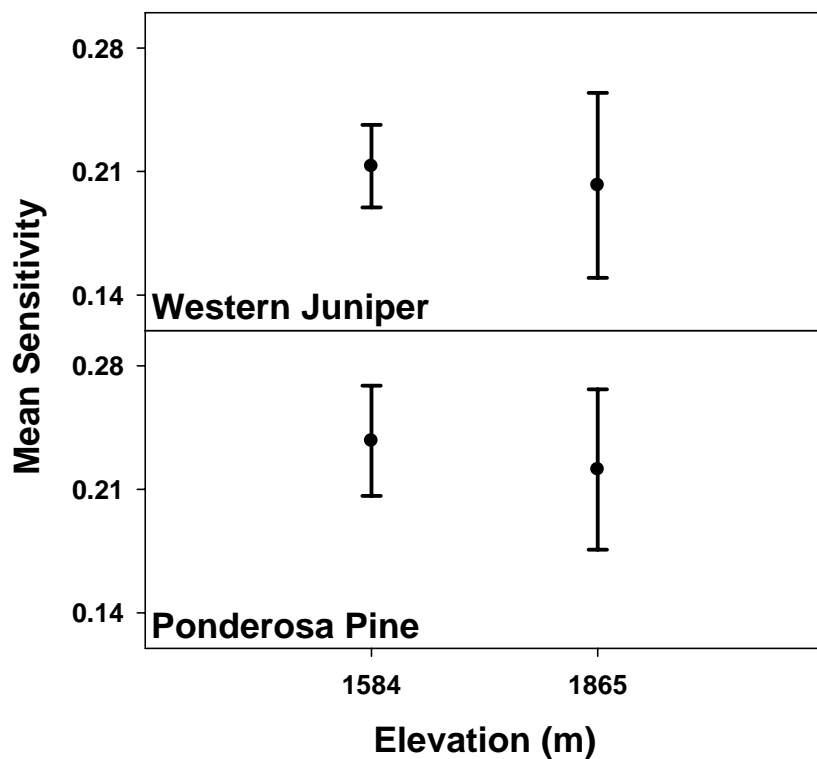
Site chronologies of each species displayed similar patterns of variation from 1950 to 2000 (Figure 3). With the exception of five sites (CWM1, CWM5, CWM6, DC4, and DC5), correlation coefficients between ponderosa pine and western juniper growth at each site (Figure 3) exceeded 0.60, and in four cases (CHE1, CHE3, CHE5, and CHE6) exceeded 0.80. The within-species mean correlation coefficients between all site chronologies were 0.67 and 0.72 for western juniper and ponderosa pine, respectively. Low growth-index values were commonly found for the years 1955, 1968, 1973, and 1977 as well as the early 1990's; periods of above average growth included 1963 to 1965, 1978, the early 1980's, and the mid to late 1990's.

Visually, all site chronologies exhibited considerable interannual variability (Figure 3); however, northern sites (CHE) typically tended to deviate greatest from mean growth (ring-width index equal to 1.0) and this was apparent in site chronology mean



**Figure 3.** Time-series plots of residual ponderosa pine and western juniper site chronologies for the period 1950-2000. Site codes and correlation coefficients between each pair of site chronologies are presented in the upper left-hand corner.

sensitivities (Appendix A). CHE site chronologies of both species had significantly greater mean sensitivity than chronologies from other sites ( $t_{32} = -3.26$ ,  $p = 0.001$  from a one-sided t-test). Mean sensitivity averaged 0.23 and 0.27 for western juniper and ponderosa pine, respectively, at the CHE sites versus 0.19 and 0.21 for all other sites. No statistically significant trend was found between mean sensitivity and elevation; the means did, however, decrease and variance increased in the higher elevation class (Figure 4). Overall, the tendency of interannual variability and the relatively large interseries correlations of the growth chronologies imply potential climate-growth associations.

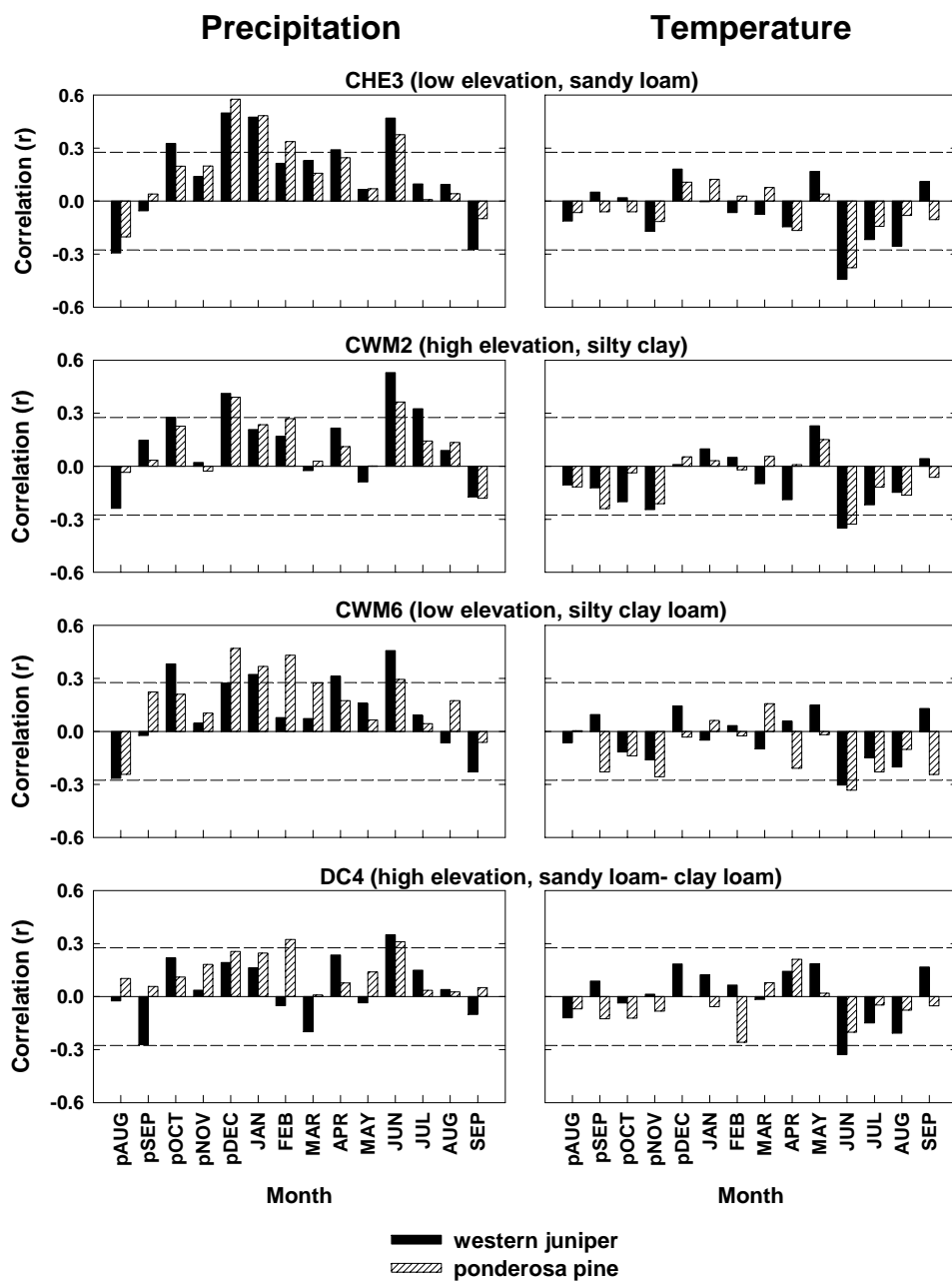


**Figure 4.** Plot of mean sensitivity ( $\pm 95\%$  CI) of western juniper and ponderosa pine site chronologies at 1584 ( $n=9$ ) and 1865 ( $n=8$ ) m.

## **Climate-growth relationships of site chronologies**

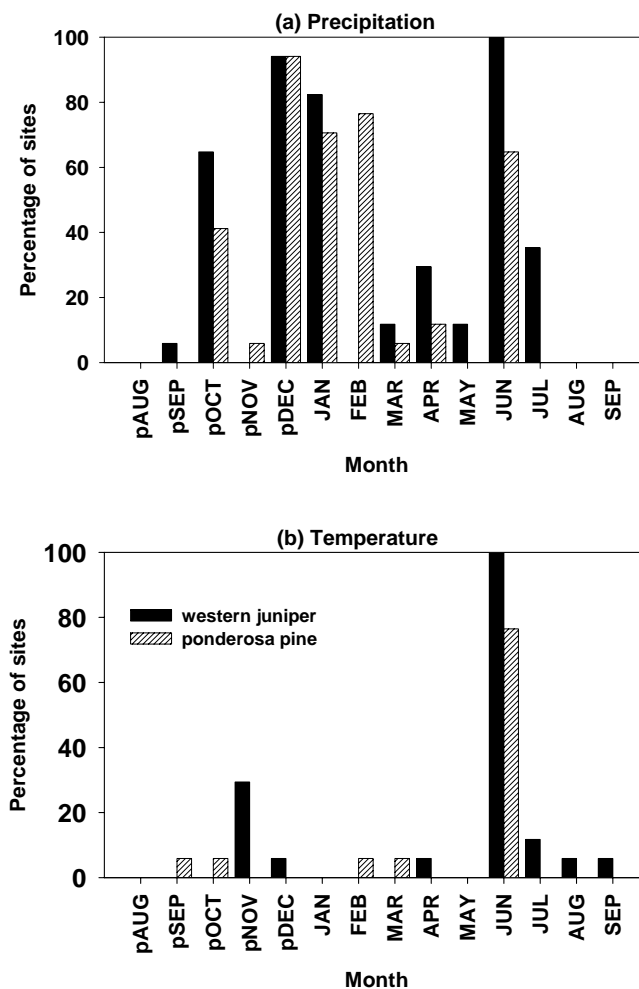
Western juniper and ponderosa pine growth displayed similar patterns of correlation with precipitation and temperature (Figure 5) at each study site. Monthly precipitation totals were often positively correlated with growth of both species, with most significant correlations occurring in the months from October prior to the growing season to June of the growing season (Figure 5, Figure 6). A majority of the site chronologies of both species were significantly correlated with prior October, prior December, January, and June precipitation, whereas February precipitation was correlated to ponderosa pine but not western juniper. Mean temperature typically exhibited negative correlations with growth, particularly in the summer months. Although few monthly mean temperatures were significantly correlated with growth (Figure 6), June was consistently a significant and negative correlation in both species (Figure 5, Figure 6). At the site level, correlation functions between monthly climate variables and growth had similar patterns across different soil textures. Low elevation sites with predominantly coarse-textured soils such as sandy loams (e.g., CHE3 in Figure 5) did, however, typically have larger absolute correlation coefficients than high elevation sites and sites with fine-textured soils ( e.g., CWM2 in Figure 5).

Stepwise regression models of site chronologies with climate composite variables also implicated precipitation in winter to spring months as the strongest climatic predictor of tree growth (33 of 34 cases, Table 3). Winter-spring precipitation (October to June) was the best composite climate predictor for 68% of all site chronologies (23 of 34 cases,



**Figure 5.** Pearson correlations ( $r$ ) between selected ponderosa pine and western juniper site chronologies and monthly climate variables for the period 1950-2000. Climate variables include total monthly precipitation and mean monthly temperature from prior August (pAUG) to September of the year of ring formation. Bars indicate correlation coefficients and horizontal lines at  $r = \pm 0.28$  represent 95% confidence intervals.

Table 3). Eight other site chronologies were best predicted by smaller components of winter- spring precipitation (December to February precipitation, 3 chronologies, and April to June precipitation, 5 chronologies). Summer mean temperature (June to August) was the best climate predictor for the DC4 western juniper site chronology. There was considerable spread, ranging from 0.08 to 0.60, in the coefficient of determination ( $R^2$ ) of climate-growth models, with most explaining between 20 and 50% of the variation.



**Figure 6.** The percentage of western juniper ( $n = 17$ ) and ponderosa pine ( $n = 17$ ) site chronologies showing significant correlations ( $p < 0.05$ ) during 1950-2000 with (a) monthly total precipitation and (b) monthly mean temperature from Oregon division 7 climate data. The significant correlation level was  $|r| \geq 0.28$ .



**Table 3.** Regression models of site growth chronologies using the single best climate predictor determined from stepwise analysis of nine composite climate variables. Oct-Junppt = summed monthly precipitation from October to June, Dec-Febppt = summed monthly precipitation from December to February, Apr-Junppt = summed monthly precipitation from April to June, Jun-Augppt = summed monthly precipitation from June to August, and Jun-Augtemp = mean monthly temperature of June to August. All climate variable regression coefficients were statistically significant ( $p < 0.05$ :  $F_{1,49} \geq 4.04$ ;  $p < 0.01$ :  $F_{1,49} \geq 7.19$ ).

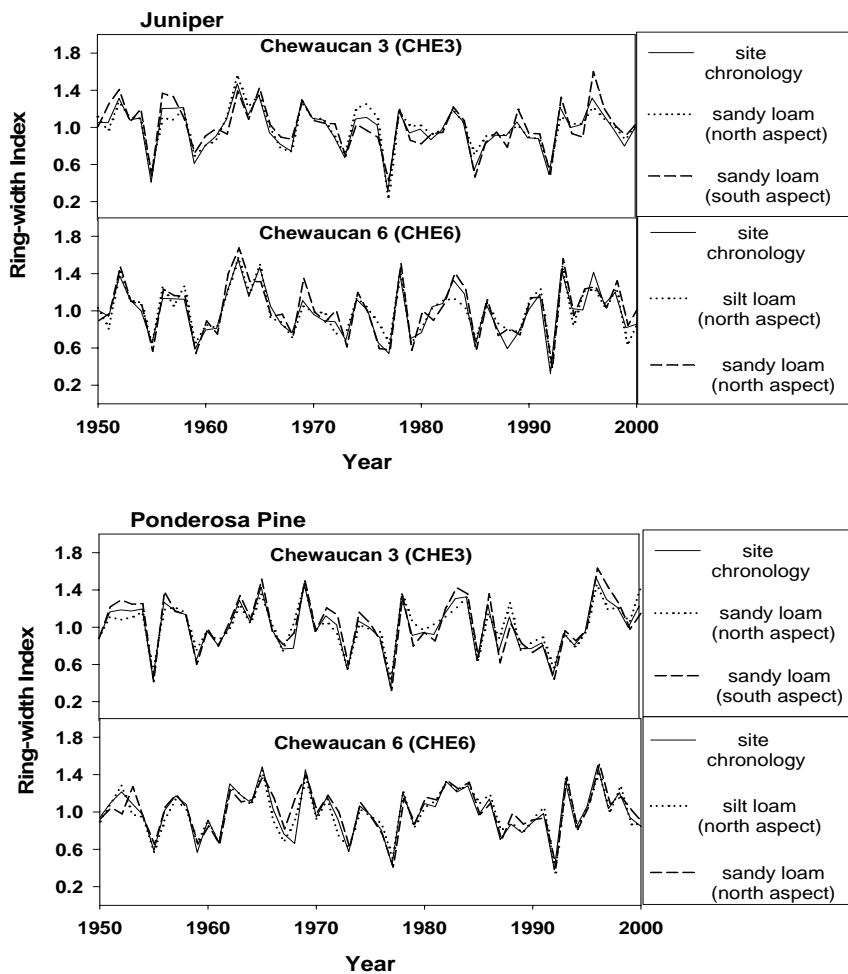
Site Code	Species	Growth-Climate Regression Model	$F_{1,49}$	$R^2$
<b>CHE1</b>	juniper	width = 0.438 + 0.051(Oct-Junppt)	51.48	0.51
	ponderosa	width = 0.340 + 0.060(Oct-Junppt)	48.56	0.50
<b>CHE2</b>	juniper	width = 0.492 + 0.045(Oct-Junppt)	45.23	0.48
	ponderosa	width = 0.678 + 0.076(Dec-Febppt)	42.77	0.47
<b>CHE3</b>	juniper	width = 0.277 + 0.065(Oct-Junppt)	60.76	0.55
	ponderosa	width = 0.203 + 0.073(Oct-Junppt)	64.11	0.57
<b>CHE4</b>	juniper	width = 0.726 + 0.080(Apr-Junppt)	24.98	0.34
	ponderosa	width = 0.793 + 0.016(Oct-Junppt)	4.30	0.08
<b>CHE5</b>	juniper	width = 0.365 + 0.058(Oct-Junppt)	67.12	0.58
	ponderosa	width = 0.311 + 0.063(Oct-Junppt)	51.45	0.51
<b>CHE6</b>	juniper	width = 0.259 + 0.067(Oct-Junppt)	42.61	0.47
	ponderosa	width = 0.224 + 0.071(Oct-Junppt)	65.59	0.57
<b>CWM1</b>	juniper	width = 0.664 + 0.104(Apr-Junppt)	28.49	0.37
	ponderosa	width = 0.658 + 0.031(Oct-Junppt)	23.59	0.33
<b>CWM2</b>	juniper	width = 0.838 + 0.083(Jun-Augppt)	18.12	0.27
	ponderosa	width = 0.800 + 0.045(Dec-Febppt)	14.01	0.22
<b>CWM3</b>	juniper	width = 0.659 + 0.031(Oct-Junppt)	21.62	0.31
	ponderosa	width = 0.488 + 0.046(Oct-Junppt)	51.36	0.51
<b>CWM4</b>	juniper	width = 0.534 + 0.043(Oct-Junppt)	23.34	0.32
	ponderosa	width = 0.600 + 0.036(Oct-Junppt)	19.55	0.29
<b>CMW5</b>	juniper	width = 0.605 + 0.126(Apr-Junppt)	41.02	0.46
	ponderosa	width = 0.598 + 0.036(Oct-Junppt)	20.54	0.30
<b>CWM6</b>	juniper	width = 0.533 + 0.042(Oct-Junppt)	22.13	0.31
	ponderosa	width = 0.517 + 0.044(Oct-Junppt)	37.14	0.43
<b>DC1</b>	juniper	width = 0.589 + 0.036(Oct-Junppt)	29.37	0.37
	ponderosa	width = 0.539 + 0.041(Oct-Junppt)	22.58	0.32
<b>DC2</b>	juniper	width = 0.779 + 0.067(Apr-Junppt)	21.98	0.31
	ponderosa	width = 0.636 + 0.032(Oct-Junppt)	23.70	0.33
<b>DC3</b>	juniper	width = 0.570 + 0.134(Apr-Junppt)	38.29	0.44
	ponderosa	width = 0.314 + 0.063(Oct-Junppt)	74.73	0.60
<b>DC4</b>	juniper	width = 2.479 - 0.024(Jun-Augtemp)	6.00	0.11
	ponderosa	width = 0.6685 + 0.030(Oct-Junppt)	13.17	0.21
<b>DC5</b>	juniper	width = 0.8448 + 0.078(Jun-Augppt)	16.11	0.25
	ponderosa	width = 0.795 + 0.048(Dec-Febppt)	20.28	0.29

## **Growth patterns and climatic sensitivity of soil-derived chronologies**

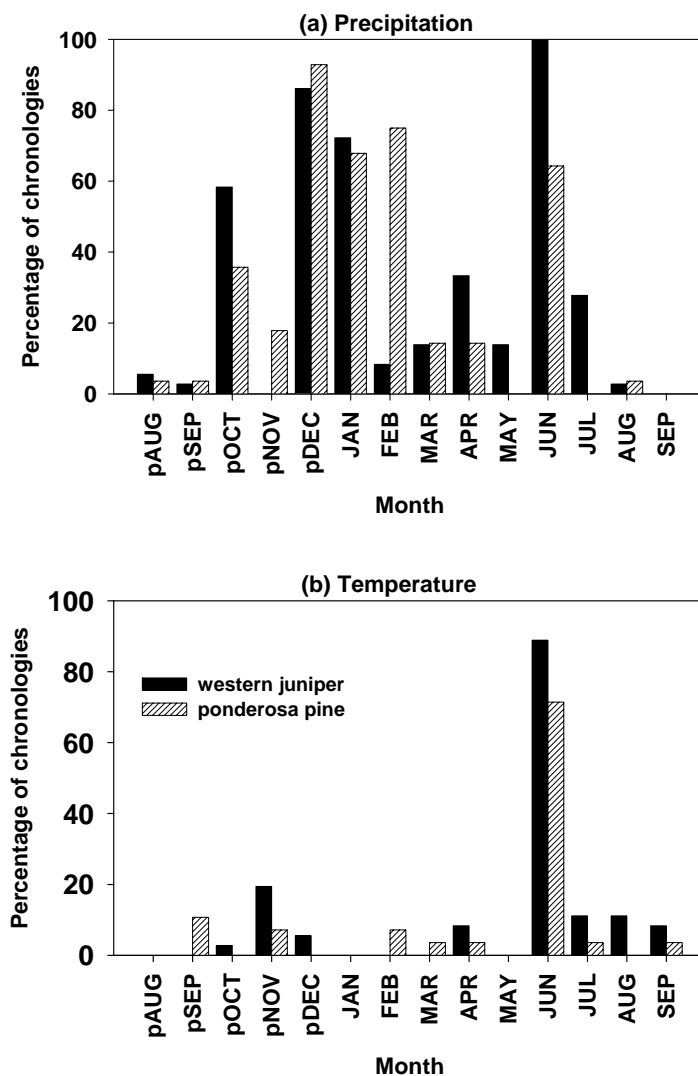
Western juniper and ponderosa pine soil-derived chronologies (hereafter referred to as soil chronologies) exhibited similar patterns in growth index statistics when compared to site chronologies (Appendices A, B, and C). Mean sensitivities were similar to those found in site chronologies, but had slightly wider ranges (0.14 to 0.37 for western juniper and from 0.18 to 0.36 for ponderosa pine). Temporal growth patterns of soil chronologies were in strong agreement with overall site chronologies (Figure 7); deviations reflected changes in magnitudes of index values rather than shifts in temporal patterns.

Climate-growth associations based on soil chronologies were similar to those based on site chronologies. Correlation with monthly precipitation was most often significant in the winter to spring months for a majority of soil chronologies of both species (Figure 8), particularly in October, December to January, and June. Ponderosa pine was also correlated to February whereas western juniper was not. Correlations between precipitation and growth were positive in October to June. Significant correlations between mean monthly temperature and soil indices were also uncommon, with the single exception of a large number of negative correlations in June in both species (Figure 8). Climate-growth regression models for soil chronologies had little difference with site chronology climate-growth models. Precipitation, particularly in the winter and spring months, again exerted the greatest influence on ponderosa pine and western juniper radial growth (Appendices D and E). October to June total precipitation was found to be the best composite climate predictor of growth for 61% of western

juniper and 71% of ponderosa pine soil chronologies. Most climate models for soil chronologies were very similar to site chronology models. Soil chronology climate-growth models only tended to display differences from site chronology models when climate was a poor predictor of growth (e.g., site CHE4 ponderosa pine chronologies).



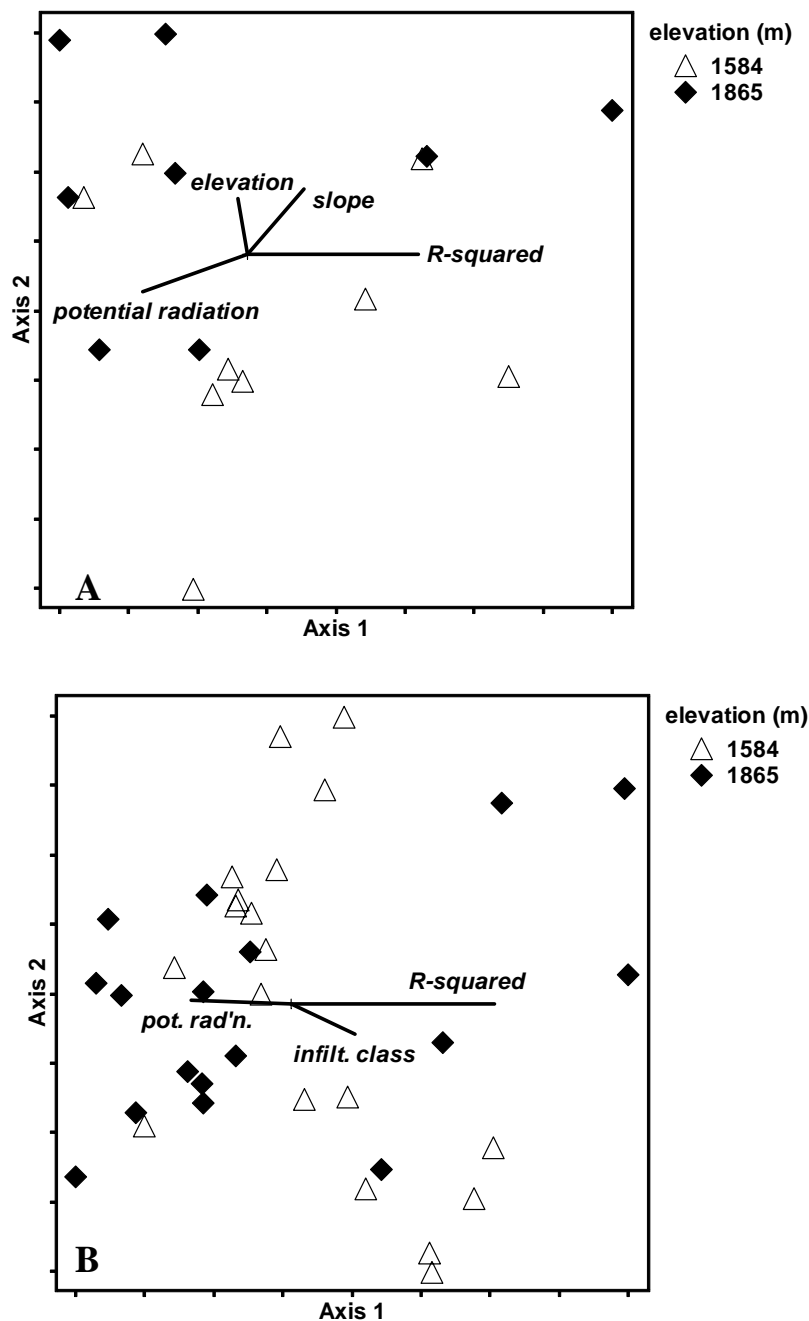
**Figure 7.** Time series plots of site growth chronologies and their corresponding soil chronologies for two of the 17 sites (CHE3 and CHE6). Western juniper (upper) and ponderosa pine (lower) chronologies are plotted separately. CHE3 soil chronologies were developed based on within-site aspect variation.



**Figure 8.** The percentage of western juniper ( $n = 36$ ) and ponderosa pine ( $n = 28$ ) soil chronologies showing significant correlations ( $p < 0.05$ ) during 1950-2000 with (a) monthly total precipitation and (b) monthly mean temperature from Oregon division 7 climate data. Significant correlations were determined using program Dendroclim and a significance level of  $|r| \geq 0.28$ .

## **Spatial variations of growth and climatic sensitivity**

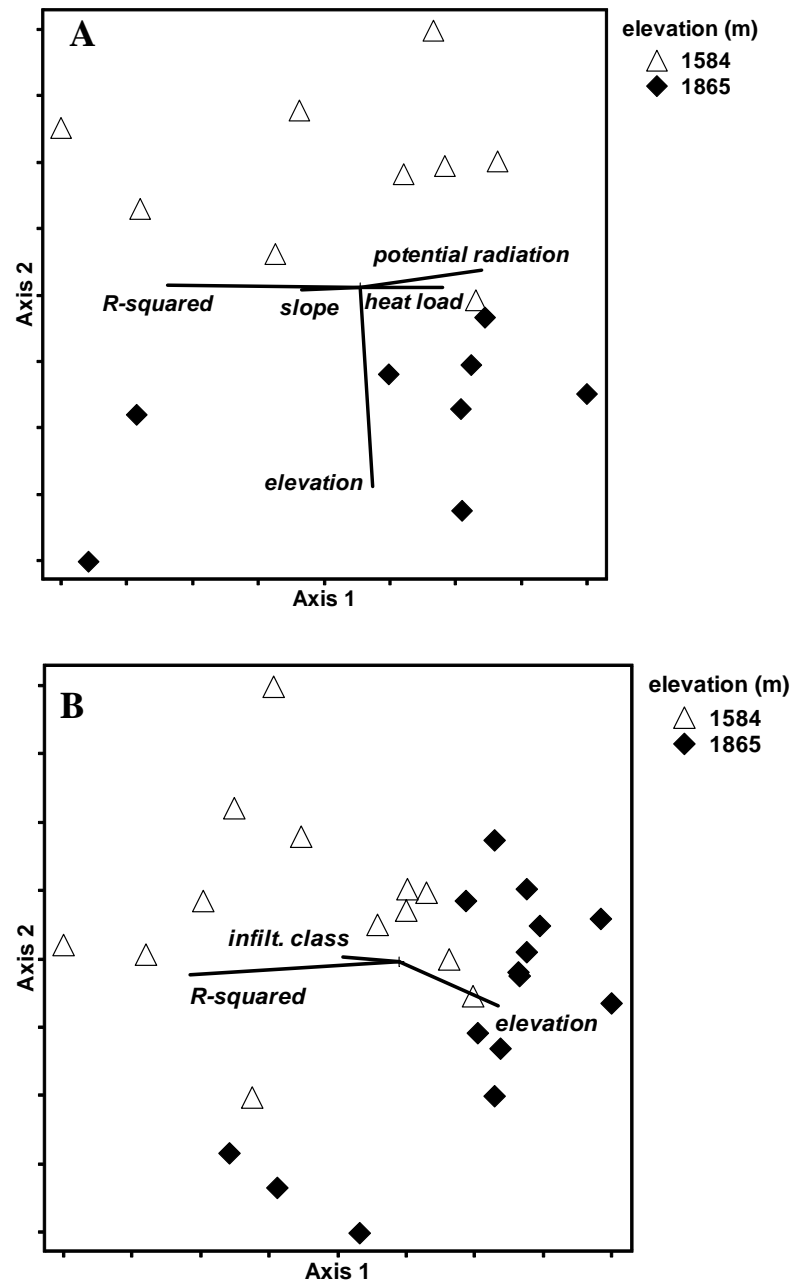
PCA of western juniper site chronologies extracted 9 axes that explained significantly more variation than by chance alone, but only the first two axes were interpreted to identify primary environmental relationships with growth. The cumulative variance represented by the first two principal components was 35.4%. Western juniper growth at the site level was most strongly correlated with elevation ( $r = 0.45$  with axis 1), site slope ( $r = 0.48$  with axis 2), and potential annual direct incident radiation ( $r = -0.62$  with axis 1) (Figure 9A). In terms of the variance represented ( $R^2$ ) in growth-climate models (Table 3), juniper site chronologies with greater climate sensitivity (greater  $R^2$ ) tended to also have higher Axis 1 scores than sites that were less sensitive climatically. Correlation between axis 1 scores and  $R^2$  values was 0.79. PCA of western juniper soil-based chronologies was similar to the analysis of site chronologies in that the first two axes cumulatively represented slightly less variation than site chronologies (29.4%) and 9 axes of significance were extracted that represented more variance than expected by chance alone. The soil-based biplot ordination of PCA axes 1 and 2 (Figure 9B) was similar to that of western juniper site chronologies in that potential radiation was again negatively correlated with axis 1 scores ( $r = -0.60$ ) and climate-growth model  $R^2$  was strongly, positively correlated with axis 1 scores ( $r = 0.86$ ). Elevation and slope did not correlate as much with PCA scores in the soil-based analysis when compared to site-based analyses. In terms of specific soil features identified by PCA as potentially affecting western juniper annual growth processes, only soil infiltration was correlated



**Figure 9.** Joint plot of an ordination of western juniper site (A) and soil-derived (B) chronologies from a Principal Components Analysis. Points represent chronology sampling units for each analysis. Vector lines represent site environmental variables that correlate with the pattern of site ordination. The vector labeled R-squared shows the high correlation between axis 1 and growth-climate model  $R^2$  (Table 3, Appendix D). pot. rad'n. = potential radiation, infiltr. class = soil infiltration classification

with ordination scores (Figure 9B). Soil surface and subsurface textures as well as fragment composition were not strongly correlated to axis 1 and 2 scores.

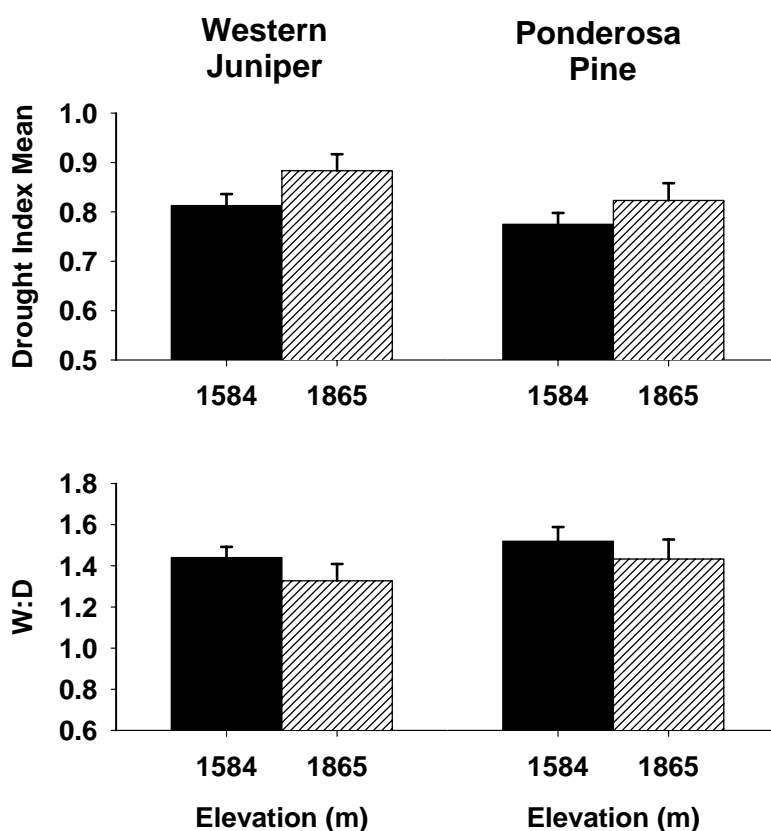
PCA of ponderosa pine site chronologies extracted 10 axes that explained significantly more variation than by chance alone. The ordination of PCA axis 1 and 2 pine site scores was similar to the findings for western juniper, and these two axes represented 39.9% of the variance in the original growth matrix. In terms of environmental gradients, pine site scores partitioned most strongly by elevation ( $r = -0.86$  with axis 2, Figure 10A). Potential annual direct incident radiation also was correlated with the ordination pattern of ponderosa site chronologies ( $r = 0.68$  with axis 1), as well as site heat load index ( $r = 0.56$  with axis 1) and site slope ( $r = -0.47$  with axis 1). Pine chronologies also tended to partition along axis 1 according to climatic sensitivity of sites, based on climate-growth model  $R^2$  ( $R^2 = 0.74$ , Figure 10A). PCA of ponderosa pine soil-derived chronologies had similarities to the analysis of site chronologies in that the first two axes cumulatively represented 35.0% of the variance and 10 axes of significance were extracted that represented more variance than expected by chance alone. The soil-based biplot ordination of PCA axes 1 and 2 (Figure 10B) was similar to that of pine site chronologies (Figure 10A) in that elevation again was related to the patterns of growth similarity within soil-derived pine chronologies. Climatic sensitivities as determined by climate-growth model  $R^2$  also were strongly correlated with axis 1 ( $r = -0.87$ ). PCA ordination of pine soil chronologies (Figure 10B) was also similar to the ordination of western juniper soil chronologies (Figure 9B) in that soil infiltration classification was associated with growth patterns.



**Figure 10.** Joint plot of an ordination of ponderosa pine site (A) and soil-derived (B) chronologies from a Principal Components Analysis. Points represent chronology sampling units for each analysis. Vector lines represent site environmental variables that correlate with the pattern of site ordination. The vector labeled R-squared shows the high correlation between axis 1 and growth-climate model  $R^2$  (Table 3, Appendix E). infiltr. class = soil infiltration classification



Since elevation, slope, and potential annual direct incident radiation are potentially key factors influencing tree growth in the study area, relationships of these three factors were examined for patterns and differences in site chronologies using wet-to-dry year (W:D) ratio and the mean drought index (DRHT) of site chronologies. The mean drought index consistently increased in both juniper and pine growth chronologies at the high elevation sites (Figure 11). W:D also declined at the high elevation sites.



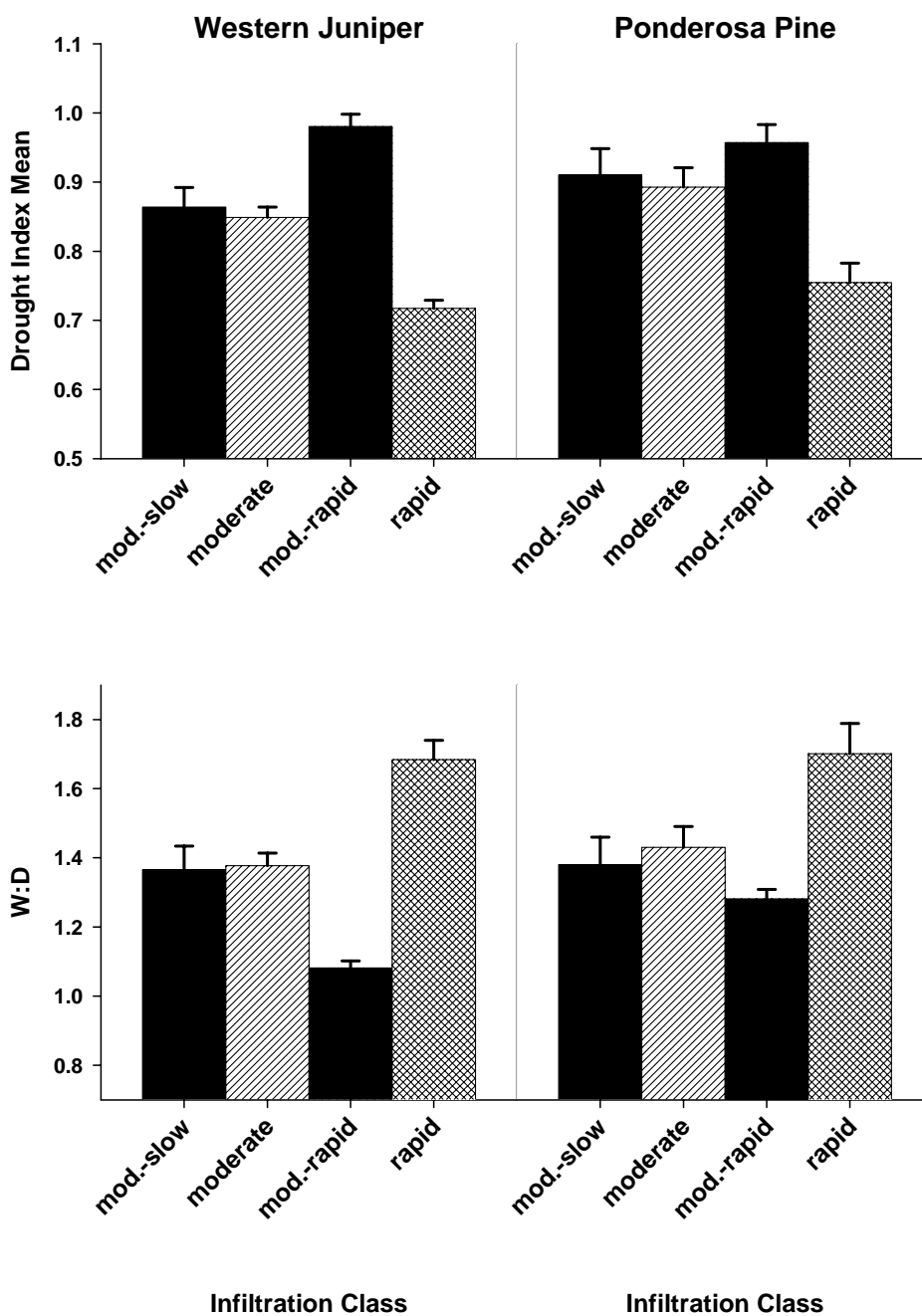
**Figure 11.** Drought index mean of the nine driest years and the ratio of ring-width index of the nine wettest years to the nine driest years (W:D) for western juniper and ponderosa pine site chronologies in relation to elevation. Errors bars are 1 standard error.

Potential annual direct incident radiation was positively associated with the mean drought index of the nine driest years during 1950-2000 for pine site chronologies (Table 4). Mean drought index of juniper site chronologies were not significantly associated with potential annual direct incident radiation. W:D was negatively associated with potential annual direct incident radiation in both western juniper and ponderosa pine. Slope was significantly associated with W:D in western juniper (Table 4). Slope was only weakly associated with mean drought index in both species and the W:D of pine. Neither potential annual direct incident radiation or slope adequately explained a large percentage of the variance in mean drought index or W:D (Table 4).

**Table 4.** Ability of environmental factors associated with dominant patterns in site growth (Figures 9A and 10A) to explain variability in mean drought index (DRHT) and W:D of site chronologies using linear regression. pot'l = potential.

Species	Dependent variable	Environmental variable	Coefficient	P	R <sup>2</sup>
juniper	DRHT	slope	-0.011	0.11	0.16
pine	DRHT	slope	-0.013	0.06	0.21
juniper	W:D	slope	0.032	0.04	0.25
pine	W:D	slope	0.035	0.06	0.21
juniper	DRHT	pot'l. radiation	0.664	0.15	0.13
pine	DRHT	pot'l. radiation	1.094	0.01	0.39
juniper	W:D	pot'l. radiation	-2.002	0.05	0.24
pine	W:D	pot'l. radiation	-2.902	0.01	0.36

Indirect gradient analysis of soil-derived chronologies suggested that infiltration classification would likely be related to juniper and pine climatic sensitivity (Figures 9B and 10B). The rapid infiltration class drought index mean from 1950 to 2000 was considerably reduced compared to any of the other infiltration classes for both western juniper and ponderosa pine soil chronologies (Figure 12, Appendix F, Appendix G), suggesting that tree growth on this soil classification was considerably more drought sensitive. The W:D ratio for western juniper soil chronologies was also significantly greater for the rapid infiltration class (Figure 12, Appendix F), likely reflecting the effect of drought on tree growth. W:D for ponderosa pine displayed a similar pattern to western juniper (Figure 12), and W:D of the moderate-slow and moderate-rapid were significantly less than W:D of the rapid classification (Appendix G). Excluding the moderate-rapid infiltration class, drought index mean tended to decrease with increasing infiltration rate in both species (Figure 12), and W:D had an increasing trend with increasing infiltration rate.



**Figure 12.** Drought index mean of the nine driest years and the ratio of ring-width index of the nine wettest years to the nine driest years (W:D) for western juniper and ponderosa pine soil chronologies in relation to soil infiltration classification. Errors bars are 1 standard error. mod. = moderate

## DISCUSSION

### Climate-growth relationships

The dominant correlation pattern of positive winter-spring precipitation associations followed by a negative summer temperature correlation with growth in both western juniper and ponderosa pine at multiple sites suggests that bole cambial activity in the two species is strongly dependent on recharge of soil moisture content during winter months. In the semiarid climate of central and eastern Oregon, high evaporative demand and large soil water deficits during summer months generally constrain carbon (CO<sub>2</sub>) uptake and assimilation as stomatal conductance is reduced in western juniper (Miller and Schultz 1987, Miller et al. 1992). Photosynthetic output and stomatal conductance in ponderosa pine within the region has also been found to be limited due to the effects of summer drought (Law et al. 2000, Panek and Goldstein 2001). Correlation patterns were similar across changes in elevation, soils, and aspects, providing evidence that interannual variability in soil moisture is a key limiting feature of radial growth at the pine-woodland ecotone.

The generally consistent pattern of tree growth (Figure 3) provides evidence that radial growth of central Oregon western juniper and ponderosa pine is strongly influenced by regional climate patterns. Not only were interannual growth patterns consistent between the two species of interest at each site, but tree growth between sites also tended to track relatively similar patterns. With regard to dendroclimatology theory, this suggests that tree growth is responding to similar limiting factors (Fritts 1976). In terms of climate-growth models, more than half (53%) of the western juniper site

chronologies were influenced the greatest by October to June precipitation, with an additional 29% primarily regulated by spring (April to June) precipitation. These variables (winter-spring and spring precipitation) accounted for approximately one-third to as much as 60% of the total variance in juniper site growth indices. This finding fills in some of the gaps in the habitat range for western juniper and supports previous evidence (Graumlich 1991, Knapp et al. 2001a) that precipitation variation during the winter to spring months is the primary climatic variable associated with radial growth of western juniper in central Oregon. Ponderosa pine site chronologies also tended to be climatically regulated by winter-spring precipitation. A large majority (82%) of pine site chronologies were most strongly linked to winter-spring (October to June) precipitation. Climate models between pine site growth and winter-spring or winter precipitation contained considerable variation in explanatory ability, representing from as little as 8% up to as much as 60% of the variation in pine growth, which supports the concept that local site features can modify the climate-growth relationship.

### **Landscape variations in climate-growth sensitivity**

Site chronologies of both western juniper and ponderosa pine consistently were more sensitive to climate at the lower elevation. High values of W:D indicate increased sensitivity of radial growth to moisture conditions (Fekedulegn et al. 2003). W:D increased and drought means decreased (Figure 11) with the relatively small increase in elevation, indicating that during the time frame of the study higher elevation forests tended to be somewhat buffered against drought. Given the relatively small change in elevation, trends in W:D and drought index mean of both species suggest that tree growth

at higher elevation sites tends to be less sensitive to climate fluctuations than at low elevation sites. This finding is consistent with previous observations in tree-ring studies (Fritts et al. 1965, Watson and Luckman 2002, Adams and Kolb 2005) and dendrochronology theory (Fritts 1976). Trees growing at lower elevations are often subject to higher temperatures and decreased precipitation, and therefore tend to be more precipitation-limited in arid and semiarid environments.

PCA ordinations as well as analyses of W:D and drought index mean also indicated that other local factors affected climatic sensitivity of juniper and ponderosa pine. As expected, sites with greater slopes were to some degree more sensitive to climate fluctuations as measured by W:D and drought index mean (Table 4). While potential annual direct incident radiation was consistently found to be related to PCA ordination patterns (Figures 9 and 10), this relationship was thought to be a spurious observation more related to the fact most sites were predominantly southern aspects (Table 1). The positive relationship between potential radiation and drought index mean for pine suggests that variation in annual radiation load between sites was not likely relevant in terms of drought; a negative relationship between radiation load and the drought index mean would be expected if this were the case. The negative relationship between potential radiation and W:D found for both species is also contradictory. Potential annual direct incident radiation (and heat load index) only reflect annual radiation differences in cloudless conditions and do not account for local topography, cloud cover (McCune and Keon 2002), or canopy structural differences that will affect heat load differences.

Juniper and pine growth at the soils level suggested that trees found on coarse-textured soils classified as rapid infiltration types were more sensitive to drought and generally more climate-responsive. The mean drought index for both juniper and ponderosa pine decreased as infiltration classification increased, with the notable exception of the moderate to rapid infiltration class (Figure 12). For both ponderosa pine and western juniper, the chronologies from the moderate to rapid infiltration classes were from sites DC2 and DC4 (Appendices B and C); these sites were at higher elevation (1865m, Table 1), which possibly acted to buffer these soil growth chronologies against the effects of drought. Models of pine and juniper growth with climatic variables at DC2 and DC4 rarely explained more than 30% of the variance in growth (Table 3, Appendices D and E), which also suggested that climate was not a consistent limiting factor at these sites. Infiltration class did act as a surrogate variable for soil texture and fragment composition. Coarse-textured soils including sandy loams (e.g., site CHE3 map unit 40B: see Table 2) typically constituted the rapid infiltration classification. The increased climatic sensitivity of tree growth on coarse-textured soils (rapid infiltration class) also supports findings that summer soil moisture stress is a major limiting constraint on productivity of central Oregon forests. Sandy soil types generally do not store water efficiently and have a greater percentage of macropores (Brady and Weil 1999), and therefore could be expected to potentially limit tree growth and productivity more than loamy or clayey soil types particularly during severe drought.



## **Potential implications**

The consistent climate signal within both species indicated the seasonal limitation of soil moisture within central Oregon forests, particularly at the pine-woodland ecotone, and supports vegetation models that adequately reflect climatic influence on soil water potential effects. Coops et al. (2005) predicted an expansion of the ponderosa pine vegetation type along eastside Cascade slopes and interior Northwest forests during the next century using a physiology-based model (3-PG) with field-based factors that accounted for winter or spring soil water recharge. The findings reported here support the use of soil water recharge to model optimal growing conditions in ponderosa pine. Juniper woodlands and savannas of the interior Pacific Northwest are also generally predicted to increase in range (Bachelet et al. 2001). In a future climate with higher temperatures, however, it will be necessary to also consider more closely the specific drought tolerances of both western juniper and ponderosa pine, particularly at locations where the two species co-occur. At these locations, shifts in vegetation could occur rapidly during short periods of severe drought.

Drought sensitivity of western juniper and ponderosa pine changed as a function of local features including elevation, slope, and soil texture as measured by soil infiltration class. Variations found in climatic sensitivity of pine and juniper support a patch-based dynamic of potential future climate-induced vegetation changes (Neilson 1993) in central Oregon dependent on local environmental features of woodlands and forests. Drought-induced mortality of pinyon pine in the southwestern US has previously been found to be associated with greater tree-ring variation (Ogle et al. 2000), and this

would suggest, based on the findings of this study, that juniper and pine trees at lower elevations with either steep slopes or coarse-textured soils will be more prone to drought-induced mortality and consequent vegetation change. The predicted future shift to warmer temperatures and generally more variable climate in the region (Snover et al. 1998, Snover et al. 2003) can potentially increase the frequency or intensity of drought effects at these extreme sites, causing large and rapid shifts in vegetation type.

Previous large-scale droughts from 1733 to 1980 in central Oregon during PDO warm phases led to severely reduced growth rates regionally in western juniper (Knapp et al. 2004). While it is not clear whether these previous drought events led to region-wide mortality in western juniper or ponderosa pine, recent droughts in the southwestern U.S. have led to increased drought-induced mortality of both pinyon (Breshears et al. 2005) and ponderosa pine (Allen and Breshears 1998). In the recent drought of the southwestern U.S., drought-induced stress led to bark beetle infestations that killed as much as 90% of the dominant tree species (pinyon pine) at some locations (Breshears et al. 2005). Several bark beetle species, particularly of the *Dendroctonus* genus, can lead to tree death in ponderosa pine during periods of stress such as drought (Curtis and Lynch 1965). Insect outbreaks in western juniper typically do not result in tree death except in the most extreme periods of stress (Miller et al. 2005). While growth of both juniper and ponderosa pine displayed similar patterns in response to drought (Figures 11 and 12), morphological adaptations of western juniper, such as protected stomata and thick cuticles (Miller and Schultz 1987), likely would permit juniper to survive future droughts and concomitant insect attacks better than ponderosa pine. Although predicting the

effects of drought or climate change on tree survival in central Oregon woodlands and forests is difficult, managers who seek to restore ecological resilience to fire-suppressed ponderosa pine forests in this region should focus silvicultural efforts and prescriptions for removing the more drought tolerant western juniper on these extreme sites to buffer against drought-induced mortality on the more valuable timber species, ponderosa pine.

## **Conclusions**

Analysis of western juniper and ponderosa pine climate-growth patterns in the Fremont NF of southern Oregon from 1950 to 2000 agreed with previous findings of climate-growth relationships. October to June (winter-spring) precipitation patterns consistently were found to be linked to radial growth of juniper and pine in both correlation and regression analyses. While winter-spring precipitation patterns were the best climatic predictor of radial growth, local environmental features, as expected, did modify and attenuate this climate signal within the tree-ring record of both species. Elevation, slope, and soils all influenced the climate relationship with radial growth of juniper and pine, particularly during drought years. These findings suggest that radial growth of pine and juniper growing at the pine-woodland ecotone in southern and central Oregon is highly dependent on the winter and spring soil recharge, particularly at sites at the extremes. Dynamic and complex responses can be expected in these forests in response to future climate changes.

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**APPENDICES**

**Appendix A.** Summary of site chronology statistics. Table includes number of trees, mean age at core height, number of lag terms used in autoregressive (AR) modeling, and mean sensitivity of the 50-year residual chronology used in analysis. Two radii from each tree were used for chronology development. Site codes beginning with CHE = Chewaucan, CWM = Cottonwood Meadow, and DC = Dent Creek.

<b>Site Code</b>	<b>Species</b>	<b>No. of trees</b>	<b>Mean age (core height)</b>	<b>AR model lag terms</b>	<b>Mean sensitivity (residual series)</b>
<b>CHE1</b>	juniper	21	81.7	5	0.22
	ponderosa	19	82.9	2	0.27
<b>CHE2</b>	juniper	19	80.8	2	0.20
	ponderosa	18	74.7	2	0.22
<b>CHE3</b>	juniper	18	74.3	2	0.27
	ponderosa	22	73.8	3	0.31
<b>CHE4</b>	juniper	13	71.8	2	0.17
	ponderosa	16	80.4	2	0.19
<b>CHE5</b>	juniper	19	86.3	3	0.24
	ponderosa	15	86.4	3	0.29
<b>CHE6</b>	juniper	22	83.1	3	0.30
	ponderosa	21	83.8	3	0.32
<b>CWM1</b>	juniper	17	69.4	2	0.19
	ponderosa	17	73.1	2	0.18
<b>CWM2</b>	juniper	18	68.3	5	0.18
	ponderosa	19	73.5	3	0.19
<b>CWM3</b>	juniper	20	57.6	3	0.19
	ponderosa	21	75.6	2	0.22
<b>CWM4</b>	juniper	18	66.1	2	0.24
	ponderosa	10	109.2	2	0.23
<b>CMW5</b>	juniper	20	94.7	2	0.21
	ponderosa	5	107.7	2	0.23
<b>CWM6</b>	juniper	18	84.7	5	0.23
	ponderosa	22	88.2	2	0.21
<b>DC1</b>	juniper	18	101.3	3	0.18
	ponderosa	17	71.1	4	0.21
<b>DC2</b>	juniper	12	81.5	2	0.14
	ponderosa	17	85.4	2	0.19
<b>DC3</b>	juniper	19	105.4	3	0.22
	ponderosa	13	65.0	2	0.27
<b>DC4</b>	juniper	13	67.9	2	0.13
	ponderosa	14	74.0	1	0.19
<b>DC5</b>	juniper	12	72.3	1	0.21
	ponderosa	9	97.1	2	0.18

**Appendix B.** Summary characteristics of juniper soil-based chronologies. Chronologies were based on soil map unit, aspect, or other within-site landscape differences. MS = mean sensitivity of the chronology, AR = autoregressive. See Appendix A for site abbreviations.

<b>Site code</b>	<b>Map unit</b>	<b>Aspect</b>	<b>No. Trees</b>	<b>Infiltration class</b>	<b>AR model lag terms</b>	<b>MS</b>
<b>CHE1</b>	50	N	7	moderate-slow	2	0.32
	53	NE	7	moderate	3	0.18
	62A	NE	7	moderate	3	0.25
<b>CHE2</b>	57	SE	7	rapid	2	0.22
	76B	SE	8	rapid	2	0.22
<b>CHE3</b>	40B	N	8	rapid	2	0.25
	40B	SW	10	rapid	5	0.30
<b>CHE4</b>	62B	S	9	moderate	2	0.16
<b>CHE5</b>	57	SW	9	rapid	2	0.26
	76B	N	6	rapid	3	0.22
<b>CHE6</b>	62A	NW	8	moderate	1	0.31
	63A	NW	6	rapid	2	0.37
	63B	NW	8	rapid	4	0.33
<b>CWM1</b>	67B	S	7	moderate-slow	2	0.17
	67B	S	10	moderate-slow	2	0.21
<b>CWM2</b>	30B	SW	10	moderate-slow	6	0.21
	30B	SW	8	moderate-slow	2	0.19
<b>CWM3</b>	62B	W	8	moderate	2	0.18
	62B	NW	6	moderate	3	0.23
	62B	SW	6	moderate	3	0.19
<b>CWM4</b>	60	S	8	moderate	2	0.25
	60	S	10	moderate	2	0.24
<b>CWM5</b>	60	S	6	moderate	2	0.20
	60	S	7	moderate	2	0.20
	60	S	7	moderate	2	0.24
<b>CWM6</b>	67A	S	9	moderate-slow	5	0.22
	67A	S	9	moderate-slow	5	0.21
<b>DC1</b>	34B	SW	11	moderate	2	0.20
	50	SW	7	moderate-slow	1	0.21
<b>DC2</b>	37B	SE	6	moderate-rapid	2	0.15
	62B	SE	6	moderate	2	0.16
<b>DC3</b>	56B	SE	13	moderate	3	0.22
	56B	NE	6	moderate	1	0.24
<b>DC4</b>	37A	SW	7	moderate-rapid	1	0.15
	37A	SW	6	moderate-rapid	2	0.14
<b>DC5</b>	56B	NE	12	moderate	1	0.21

**Appendix C.** Summary characteristics of pine soil-based chronologies. For two study sites (CHE5 and CWM5), soil map units did not meet the minimum number of tree requirement (at least 6 trees). Chronologies were based on soil map unit, aspect, or other within-site landscape differences. MS = mean sensitivity of the chronology, AR = autoregressive. See Appendix A for site abbreviations.

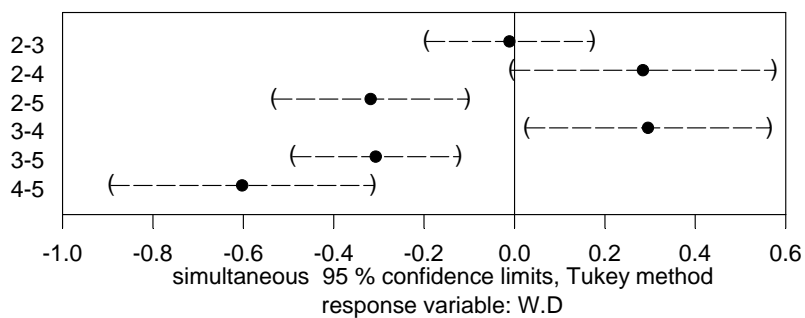
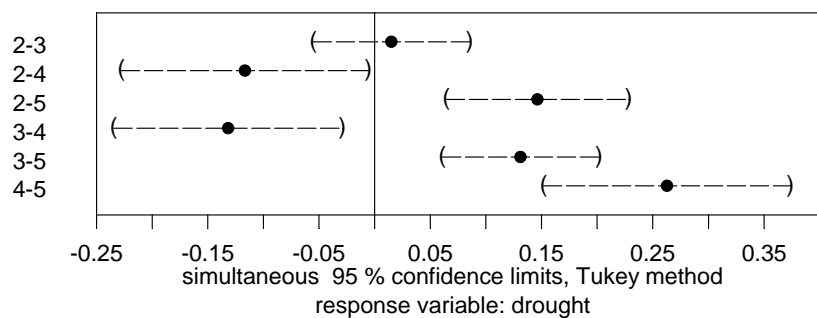
Site code	Map unit	Aspect	No. Trees	Infiltration class	AR model lag terms	MS
<b>CHE1</b>	50	N	7	moderate-slow	2	0.33
	62A	NE	7	moderate	2	0.29
<b>CHE2</b>	57	SE	8	rapid	2	0.23
	76B	SE	6	rapid	2	0.30
<b>CHE3</b>	40B	SW	11	rapid	3	0.36
	40B	N	11	rapid	2	0.28
<b>CHE4</b>	62B	S	10	moderate	2	0.19
	67B	S	6	moderate-slow	2	0.21
<b>CHE6</b>	62A	NW	8	moderate	3	0.31
	63A	NW	8	rapid	1	0.30
<b>CWM1</b>	67B	S	9	moderate-slow	1	0.19
	67B	S	8	moderate-slow	2	0.20
<b>CWM2</b>	30B	SW	9	moderate-slow	1	0.22
	30B	SW	10	moderate-slow	3	0.19
<b>CWM3</b>	62B	W	8	moderate	1	0.23
	62B	NW	7	moderate	2	0.20
	62B	SW	6	moderate	2	0.28
<b>CWM4</b>	60	S	10	moderate	2	0.23
<b>CWM6</b>	67A	S	11	moderate-slow	2	0.21
	67A	S	11	moderate-slow	2	0.23
<b>DC1</b>	34B	SW	13	moderate	4	0.22
<b>DC2</b>	62B	SE	7	moderate	3	0.22
	37B	SE	6	moderate-rapid	2	0.19
<b>DC3</b>	56B	SE	7	moderate	2	0.28
	56B	NE	6	moderate	4	0.23
<b>DC4</b>	37A	SW	7	moderate-rapid	2	0.19
	37A	SW	6	moderate-rapid	1	0.22
<b>DC5</b>	56B	NE	9	moderate	2	0.18

**Appendix D.** Climate-growth models of juniper soil-derived chronologies. Models used the single best climate predictor determined from stepwise analysis of nine composite climate variables. Oct-Junppt = sum of monthly precipitation from October to June, Apr-Junppt = sum of monthly precipitation from April to June, Jun-Augppt = sum of monthly precipitation from June to August, Dec-Febtemp = mean monthly temperature of December to February, and Jun-Augtemp = mean monthly temperature of June to August.

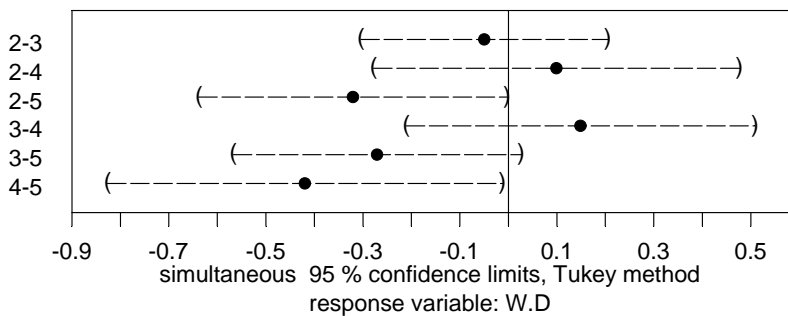
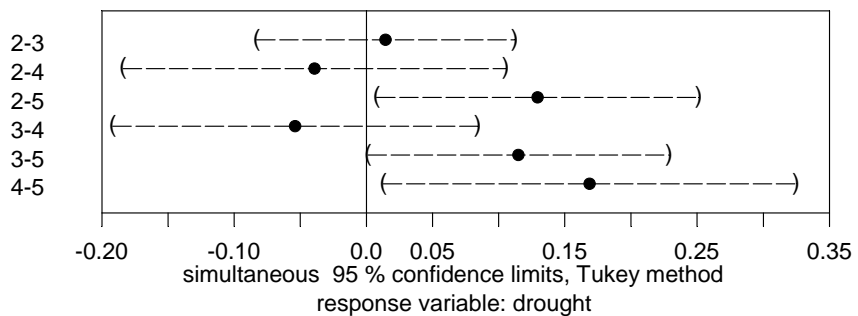
Site code	Map unit	Growth-climate regression model	R <sup>2</sup>
<b>CHE1</b>	50	width = 0.213 + 0.0721(Oct-Junppt)	0.58
	53	width = 0.583 + 0.0372(Oct-Junppt)	0.41
	62A	width = 0.384 + 0.0558(Oct-Junppt)	0.49
<b>CHE2</b>	57	width = 0.478 + 0.0457(Oct-Junppt)	0.50
	76B	width = 0.448 + 0.0498(Oct-Junppt)	0.40
<b>CHE3</b>	40B	width = 0.387 + 0.0552(Oct-Junppt)	0.44
	40B	width = 0.262 + 0.0662(Oct-Junppt)	0.52
<b>CHE4</b>	62B	width = 0.758 + 0.0673(Apr-Junppt)	0.24
<b>CHE5</b>	57	width = 0.324 + 0.0609(Oct-Junppt)	0.55
	76B	width = 0.459 + 0.0486(Oct-Junppt)	0.45
<b>CHE6</b>	62A	width = 0.274 + 0.0652(Oct-Junppt)	0.47
	63A	width = 0.153 + 0.0767(Oct-Junppt)	0.50
	63B	width = 0.144 + 0.0766(Oct-Junppt)	0.52
<b>CWM1</b>	67B	width = 0.602 + 0.0358(Oct-Junppt)	0.32
	67B	width = 0.637 + 0.1116(Apr-Junppt)	0.36
<b>CWM2</b>	30B	width = 0.829 + 0.0859(Jun-Augppt)	0.23
	30B	width = 0.677 + 0.0296(Oct-Junppt)	0.23
<b>CWM3</b>	62B	width = 0.588 + 0.0380(Oct-Junppt)	0.39
	62B	width = 0.839 + 0.0780(Jun-Augppt)	0.17
	62B	width = 0.632 + 0.0326(Oct-Junppt)	0.35
<b>CWM4</b>	60	width = 0.522 + 0.0433(Oct-Junppt)	0.34
	60	width = 0.541 + 0.0425(Oct-Junppt)	0.29
<b>CWM5</b>	60	width = 0.626 + 0.1166(Apr-Junppt)	0.46
	60	width = 0.683 + 0.1039(Apr-Junppt)	0.31
	60	width = 0.528 + 0.1499(Apr-Junppt)	0.45
<b>CWM6</b>	67A	width = 0.667 + 0.1053(Apr-Junppt)	0.27
	67A	width = 0.558 + 0.0397(Oct-Junppt)	0.28
<b>DC1</b>	34B	width = 0.557 + 0.0391(Oct-Junppt)	0.33
	50	width = 0.624 + 0.0341(Oct-Junppt)	0.31
<b>DC2</b>	37B	width = 0.827 + 0.0538(Apr-Junppt)	0.17
	62B	width = 0.771 + 0.0675(Apr-Junppt)	0.28
<b>DC3</b>	56B	width = 0.572 + 0.1342(Apr-Junppt)	0.41
	56B	width = 0.389 + 0.0553(Oct-Junppt)	0.42
<b>DC4</b>	37A	width = 0.582 + 0.0130(Dec-Febtemp)	0.08
	37A	width = 2.995 - 0.0318(Jun-Augtemp)	0.14
<b>DC5</b>	56B	width = 0.845 + 0.0778(Jun-Augppt)	0.25

**Appendix E.** Climate-growth models of pine soil-derived chronologies. Models used the single best climate predictor determined from stepwise analysis of nine composite climate variables. Oct-Junppt = sum of monthly precipitation from October to June, Dec-Febppt = sum of monthly precipitation from December to February, Apr-Junppt = sum of monthly precipitation from April to June, and Sep-Novtemp = mean monthly temperature of September to November.

<b>Site code</b>	<b>Map unit</b>	<b>Growth-climate regression model</b>	<b>R<sup>2</sup></b>
<b>CHE1</b>	50	width = 0.215 + 0.0719(Oct-Junppt)	0.51
	62A	width = 0.565 + 0.1007(Dec-Febppt)	0.51
<b>CHE2</b>	57	width = 0.630 + 0.0872(Dec-Febppt)	0.55
	76B	width = 0.438 + 0.0509(Oct-Junppt)	0.30
<b>CHE3</b>	40B	width = 0.066 + 0.0861(Oct-Junppt)	0.61
	40B	width = 0.590 + 0.0965(Dec-Febppt)	0.46
<b>CHE4</b>	62B	width = 2.256 - 0.0273(Sep-Novtemp)	0.10
	67B	width = 0.793 + 0.0585(Apr-Junppt)	0.13
<b>CHE6</b>	62A	width = 0.277 + 0.0646(Oct-Junppt)	0.51
	63A	width = 0.278 + 0.0652(Oct-Junppt)	0.54
<b>CWM1</b>	67B	width = 0.647 + 0.0318(Oct-Junppt)	0.32
	67B	width = 0.661 + 0.0299(Oct-Junppt)	0.26
<b>CWM2</b>	30B	width = 0.776 + 0.0516(Dec-Febppt)	0.23
	30B	width = 0.812 + 0.0416(Dec-Febppt)	0.19
<b>CWM3</b>	62B	width = 0.539 + 0.0418(Oct-Junppt)	0.34
	62B	width = 0.582 + 0.0376(Oct-Junppt)	0.40
	62B	width = 0.363 + 0.0577(Oct-Junppt)	0.47
<b>CWM4</b>	60	width = 0.600 + 0.0361(Oct-Junppt)	0.29
<b>CWM6</b>	67A	width = 0.495 + 0.0462(Oct-Junppt)	0.49
	67A	width = 0.540 + 0.0423(Oct-Junppt)	0.34
<b>DC1</b>	34B	width = 0.526 + 0.0424(Oct-Junppt)	0.31
<b>DC2</b>	62B	width = 0.692 + 0.0272(Oct-Junppt)	0.17
	37B	width = 0.672 + 0.0286(Oct-Junppt)	0.24
<b>DC3</b>	56B	width = 0.252 + 0.0696(Oct-Junppt)	0.60
	56B	width = 0.452 + 0.0491(Oct-Junppt)	0.45
<b>DC4</b>	37A	width = 0.683 + 0.0280(Oct-Junppt)	0.20
	37A	width = 0.639 + 0.0324(Oct-Junppt)	0.20
<b>DC5</b>	56B	width = 0.795 + 0.0483(Dec-Febppt)	0.29



**Appendix F.** DRHT and W:D soil infiltration class mean differences: juniper. Infiltration class mean differences (95% CI) for soil-derived chronologies are from a fixed effects analysis of variance with a Tukey-Cramer adjustment for unplanned comparisons. Confidence intervals that do not contain zero are statistically significant. Soil infiltration classes are coded as follows: 2 = moderate-slow, 3 = moderate, 4 = moderate-rapid, and 5 = rapid.



**Appendix G.** DRHT and W:D soil infiltration class mean differences: pine. Infiltration class mean differences (95% CI) for soil-derived chronologies are from a fixed effects analysis of variance with a Tukey-Cramer adjustment for unplanned comparisons. Confidence intervals that do not contain zero are statistically significant. Soil infiltration classes are coded as follows: 2 = moderate-slow, 3 = moderate, 4 = moderate-rapid, and 5 = rapid.