

Article

Dendroclimatic Analysis of Sierra Nevada Mixed Conifer Species between Different Diameter Size Classes

Andrew Hirsch ¹, Sophan Chhin ^{1,*} and Jianwei Zhang ² 

¹ Division of Forestry and Natural Resources, West Virginia University, 322 Percival Hall, 1145 Evansdale Dr, Morgantown, WV 26506, USA

² United States Department of Agriculture—Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA

* Correspondence: sophan.chhin@mail.wvu.edu; Tel.: +1-304-293-5313

Abstract: Climate change is expected to lead to higher temperatures in the Mediterranean region of northern California in the Sierra Nevada. Dendroclimatic studies typically focus on large, old trees, but there relatively limited understanding on how climatic sensitivity can vary with trees of different size classes. We collected tree increment cores and compared radial growth responses of small (20.32 to ≤ 40.64 cm), medium (40.64 to ≤ 60.96 cm), and large (> 60.96 cm) diameter mixed conifer species in the Sierra Nevada to different climate variables (temperature, precipitation, and climate moisture index (CMI)). The most common tree species encountered were white fir (*Abies concolor* (Gord. & Glend.) Lindl.), followed by sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* Dougl. Ex P. & C. Laws), and incense cedar (*Calocedrus decurrens* (Torr.) Florin). One of the most coherent responses from all diameter groups and across all species was the positive response to increasing minimum winter temperatures. All diameter groups and species also responded positively to precipitation and CMI at some point in the analysis period, which is the seasonal window of April of the prior year to October of the current year of ring formation. Perhaps the most notable difference when comparing the three diameter groups to climate was the higher occurrence of negative responses to the temperature of the previous year from the largest diameter group, as well as the higher number of negative responses to temperature in general. These results suggest that larger trees may be more sensitive to future climate projections compared with smaller trees and they may carry those effects into the next year. The use of dendroclimatology to assess how mixed conifer species in the Sierra Nevada responded to past climate is a key resource that can be used to infer how trees may respond to a future changing climate.

Keywords: dendrochronology; mixed-conifer forest; restoration; Sierra Nevada; diameter size



Citation: Hirsch, A.; Chhin, S.; Zhang, J. Dendroclimatic Analysis of Sierra Nevada Mixed Conifer Species between Different Diameter Size Classes. *Forests* **2023**, *14*, 489. <https://doi.org/10.3390/f14030489>

Academic Editor: Cristina Nabais

Received: 27 January 2023

Revised: 20 February 2023

Accepted: 24 February 2023

Published: 28 February 2023



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1. Introduction

Climate change is expected to alter many different aspects of the current climate, with temperatures being one of the most notable changes especially in the Mediterranean region of northern California. It is expected that global surface temperatures will rise under all future climate change emission scenarios, otherwise called Shared Socioeconomic Pathways (SSPs) [1]. SSPs are characterized by the underling socioeconomic trends of each scenario and the level of radiative forcing resulting from the scenario (in watts per square meter, or $W m^{-2}$) [1]. Relative to 1850–1900, the global temperature in 2081–2100 is expected to increase by 1.0 °C to 1.8 °C under the low emissions scenario (SSP1-1.9), 2.1 °C to 3.5 °C under the intermediate emissions scenario (SSP2-4.5), and 3.3 °C to 5.7 °C under the very high emissions scenario (SSP5-8.5) [1]. These temperature increases, paired with the lack of any distinct changes in precipitation patterns projected to occur in California in the future [2], may be harmful to the future health of California's forests. In terms of precipitation changes, one climate model projects slightly wetter winters, whereas another

projects slightly drier winters [2]. A cascading effect on forest ecosystems reliant on spring moisture from snowpack melting may also occur due to earlier spring melting and the general loss of snowpack that is likely to occur under all emission scenarios [2]. On top of this possible domino effect from earlier snowmelt, if temperatures rise into the medium warming range, the risk of wildfires occurring in California could increase by as much as 55%—almost double that of the lower warming range [2]. Although there are many risks and concerns regarding a future changing climate, mitigating these threats to our ecosystems requires analyzing and managing multiple facets of our natural resources—including analyzing previous effects of climate variables on tree growth. Doing so can provide insight on how trees may respond to these changes in the future and assess forest vulnerabilities to climate change and how we can adaptively manage our forests to be best suited for future conditions [3]. This raises the question as to whether smaller trees will respond as strongly as larger trees do to the climate variables often looked at in dendroclimatology.

Examining climate sensitivity across different diameter size classes is important, since it has been found that large and small trees may have different responses to climate variables, whether it be age dependent or size dependent [4,5]. Furthermore, younger trees may exhibit more complex growth since they are usually being influenced by a higher number of environmental factors in the understory [6,7]. Szeicz and MacDonald [8] found that, in the western Northwest Territories, Canada, older white spruce (*Picea glauca* (Moench) Voss) responded negatively to previous summer temperatures, whereas the younger trees did not. They attributed general differences in growth responses to physiological changes that occur as trees age, such as changes in the root, shoot, and cambial growth patterns [8]. This change in growth patterns may be causing the larger trees to be more dependent and affected by previous years' growing conditions. For example, large trees have a larger stem and root system than small trees (and therefore more tissue for storing nutrients), so they may be more negatively affected if previous summer conditions inhibit their ability to grow and store a large amount of nutrients for the following year. The relationship between tree size and leaf area is typically associated with the stage of stand development: larger trees typically have a higher leaf area before canopy closure, but then show an age-related decline in leaf area after canopy closer (e.g., [9,10]). In addition, respiration demands generally increase as trees age [11], so higher temperatures would amplify those increased respiration demands, i.e., causing more photosynthate to be used for respiration and therefore less for storage. An increased rate of respiration is expected in more exposed higher canopy leaves [12], which older/larger trees would likely contain.

Previous research in northern California that looked at the growth responses of trees between 15 and 92 cm in DBH (diameter at breast height) found, in general, winter precipitation (positive correlation) and summer temperatures (negative correlation) were the most important predictors of annual ring width variation for the six coniferous species studied (*Pinus ponderosa* Dougl. Ex P. & C. Laws, *Pinus lambertiana* Dougl., *Pseudotsuga menziesii* (Mirb.) Franco, *Abies concolor* (Gord. & Glend.) Lindl., *Abies magnifica* A. Murr., and *Calocedrus decurrens* (Torr.) Florin) [13]. Another study, conducted in Plumas County in the northern Sierra Nevada region, looked at the same coniferous trees (except *Abies magnifica*) but only for DBHs greater than 76 cm [14]. This study found that a higher minimum winter temperature (positive correlation) was one of the most important predictor variables followed by a higher maximum summer temperature (negative correlation) and log transformed precipitation of the current year or the year prior (positive correlation) [14]. Interestingly, a study conducted in the Mediterranean climate region of Italy on Douglas firs with an average DBH of 73 cm had similar findings, in which growth was negatively correlated with maximum temperatures in July of the current year and October of the previous year [15]. The Castaldi et al. [15] study also had a similar finding to Bigelow et al. [14], in which growth was positively correlated with winter temperatures of the current year of growth. Since the northern Sierra Nevada region of California is also in a Mediterranean climate, the results from the study conducted in Italy being similar to the results from

the California studies may not be surprising. Research in other areas that compiled data from many temperate regions found that trees responded positively to increased summer temperatures [16], which is generally not the case for the Sierra Nevada and Mediterranean regions [13–15]. This is likely because the summers in Mediterranean climates are usually much drier, with most of the yearly precipitation occurring in the winters [14,15]. Therefore, due to different climate patterns and tree species (among other factors), it is difficult to assert that growth responses in one climate can occur in another.

Mérian and Lebourgeois [4] found that, in the Mediterranean climate region of France, shade-tolerant species (*Abies alba* Mill. and *Fagus sylvatica* L.) had a significantly different response to summer drought between small and large trees, with large trees being more affected by summer drought periods. They attributed this occurrence to the possible increase in canopy heterogeneity in areas with more shade-tolerant species. In other words, since shade-tolerant species can persist better in low light, there may be larger gaps between the upper, large diameter, and lower, small diameter crowns—causing the smaller diameter trees to be protected more due to differences in microclimatic conditions such as buffered temperature variations [4]. Vieira et al.'s [5] study, which was also conducted in a Mediterranean climate (Portugal), found that earlywood (i.e., springwood) of young trees was more sensitive to climate influence, whereas the older trees were more sensitive in the latewood (i.e., summerwood) portion of growth. Though these two studies found differences between small and large/young and old trees in Mediterranean climates, this type of direct comparison study is still yet to be conducted in the northern Sierra Nevada region of California.

The use of dendrochronology and dendroclimatology principles helps to build our understanding of tree responses to climate as well as how trees may respond to a future changing climate. Knowing how trees may respond to future climate can help to build better adaptive management plans that can try to account for those future changes.

The objective of this study is to examine the effect of climate on northern Sierra Nevada tree species (ponderosa pine, sugar pine, white fir, and incense cedar) and compare the growth responses of three diameter size classes to different climatic variables. Considering the findings of studies conducted in other Mediterranean climate regions, we hypothesize that: (1) species in the largest diameter group will respond differently to climate variables than the smallest diameter group, especially for shade tolerant species; and (2) large trees will show more lagged responses to growth due to their ability to store more food reserves than smaller trees.

2. Methods

2.1. Study Site

The study took place in the Lassen National Forest in the northern Sierra Nevada range of California, United States, at an average elevation of 1530 m with the following geographic coordinates: latitude = 40.1900 degrees and longitude = −121.3110 degrees (Figure 1). The Lassen National Forest is in the M261 Sierran Steppe–Mixed Forest–Coniferous Forest–Alpine Meadow Province ecoregion [17]. This region of California is described as having warm, dry summers and cool, moist winters, with most of the yearly precipitation generally happening in the winter (between October and March) and representing 83% of the annual precipitation for Lassen National Forest for the period of 1969–2014. Also, most precipitation happening at higher elevations in the winter comes in the form of snow and becomes an important resource for moisture as snow melts during the growing season [13]. The main soils found in this region are ultisols on mountain slopes with humid air, dry alfisols at lower elevations, and entisols in the narrow floodplains and alluvial fans of the valley (USDA Forest Service 1999). The vegetation in this ecoregion contains montane forests and the most common tree species encountered were white fir (*Abies concolor*—ABCO), followed by sugar pine (*Pinus lambertiana*—PILA), ponderosa pine (*Pinus ponderosa*—PIPO), and incense cedar (*Calocedrus decurrens*—CADE) [17] (Figure 2). Other associated species in the montane forest zone include Jeffrey pine (*Pinus jeffreyi*), Douglas fir (*Pseudotsuga menziesii*),

and red fir (*Abies magnifica*) [17]. Ponderosa pine, sugar pine, and incense cedar all start their radial growth around mid-April and continue to put on radial growth for around 147, 129, and 136 days, respectively [18]. White fir starts radial growth slightly later around early May and continues to put on radial growth for around 108 days [18]. Ponderosa pine is the most shade intolerant [19], sugar pine has intermediate shade tolerance [20], incense cedar is shade tolerant [21], and white fir is the most shade tolerant of these species [22]. The stands in the study area (total area of 50.9 ha) have an uneven-aged structure. In general, temperature has been attributed as one of the main environmental factors controlling the start of conifer growth in the Sierra Nevada, whereas water availability is the main factor controlling the ending of the growing season [23].

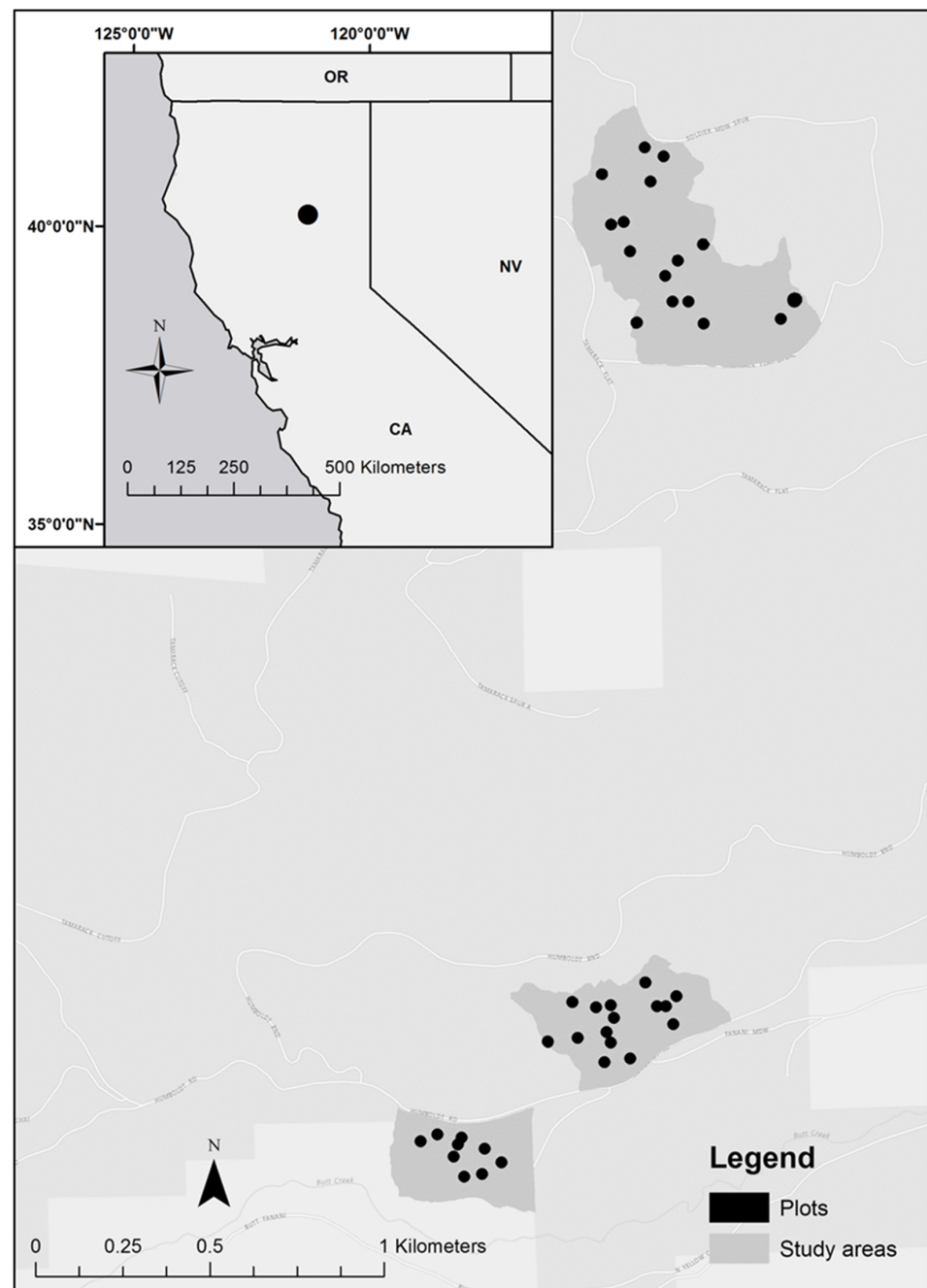


Figure 1. Map of study plots and forest structure at study areas in the southern portion of Lassen National Forest, northern California, southwest of Lake Almanor. Plots are indicated as black dots on the main map.



Figure 2. The most common tree species encountered in the study were white fir (*Abies concolor*—ABCO), followed by sugar pine (*Pinus lambertiana*—PILA), ponderosa pine (*Pinus ponderosa*—PIPO), and incense cedar (*Calocedrus decurrens*—CADE).

2.2. Site Selection and Field Methods

The study sites were selected based on them containing an old-growth pine, which was defined as having a breast height diameter of at least 63.5 cm. A total of 40 plots were selected for the study; 25 of those plots had an old-growth sugar pine as the plot center and 15 plots had an old-growth ponderosa pine as the plot center. Plots were centered on a focal tree, which was the largest pine in the plot. Plots were circular with varying radii: 16 plots had a fixed radius of 9.1 m (plot size = 0.026 ha), 5 plots had a radius calculated from the DBH of the focal tree $\times 12$ (i.e., plot radius range of 8.8–9.1 m and corresponding plot size range of 0.024–0.026 ha), and 19 plots had a radius calculated from the DBH of the focal tree $\times 15$ (i.e., plot radius range of 9.5–18.1 m and corresponding plot size range of 0.028–0.103 ha). The varying plot radii are relevant to other future silvicultural studies conducted in these plots, but for this study they have little impact since differences in plot size have little effect on plot measurements [24]. Within each of the measurement plots, the DBH (minimum DBH of 20.3 cm or greater) and species of all trees were recorded. For every tree in the plot, a single core was taken at stump height (0.5 m), perpendicular to the direction of the slope to avoid compression wood [25]. For each of the focal trees and their two key competitors, a second core was taken opposite the first core at the same height. Competitor trees met at least two out of three of the following criteria: DBH that is at least 1/3 of the DBH of the focal tree; at least 1/3 of the height of the focal tree; and the gap between the competitor tree's crown and that of the focal tree is less than the crown width of the focal tree. It is important to note that Johnson et al. [26] used the data and cores collected on the center and competitor trees to analyze how the growth of the center

and competitor trees differed based on both the competition index and different climate variables. This current study is also using those cores from the center and competitor trees, but it is using the additional singular cores taken on all the other trees in each plot.

2.3. Laboratory Methods and Dendrochronological Analysis

To analyze the growth responses to climate and compare between different species and diameter groups, cores were separated out by species and diameter at breast height (DBH) ranges into 12 distinct groups. Groups were first separated into the 4 main tree species: ABCO, CADE, PILA, and PIPO. The few *Abies magnifica* and *Pinus jeffreyi* Grev. & Balf. that were encountered were grouped with ABCO and PIPO, respectively. Groups were then further broken down by DBH, herein referred to as diameter groups. Diameter Group 1 (i.e., small diameter size) ranged from 20.32 to ≤ 40.64 cm, Group 2 (i.e., medium diameter size) ranged from 40.64 to ≤ 60.96 cm, and Group 3 (i.e., large diameter size) was anything greater than 60.96 cm. Diameter groups were created by referencing the thinning guidelines used for the project area, which specified to keep all healthy pines greater than 40.64 cm within the radial release treatments and to center the radial release treatments around the healthiest pine tree greater than 60.96 cm in each plot (Hood et al. 2018). These guidelines were established to prevent the harvesting of the healthy medium-sized trees as well as to apply the thinning treatments around the healthy larger pine trees. Using these two criteria (species and DBH), 12 distinct groups were created; for example, *Abies concolor* was separated out into ABCO_G1, ABCO_G2, and ABCO_G3, no matter what plot the cores were initially in (since all plots were in the same general area).

Collected cores were dried in the lab and then mounted, sanded, and cross-dated using standard dendrochronological methods as in Speer [25]. Cross-dating was performed by comparing and matching up ring width patterns (primarily narrow rings) using the list method for each species–diameter group [27]. Once visual cross-dating was performed as accurately as possible, ring widths were measured in Coorecorder and then cross-dating accuracy was examined and further improved using the program COFECHA [28]. After cross-dating was finished, ring widths from every species–diameter group were standardized in ARSTAN using the same standardization technique when possible, to remove any noise from competition and other non-climatic factors such as age-related growth declines [29]. Ring widths for all trees within Diameter Group 1 and Group 2 were standardized using a negative exponential distribution with autocorrelation removed. Group 3 trees (ABCO_G3, CADE_G3, and PILA_G3) were standardized using a negative exponential distribution, whereas PIPO_G3 was standardized using an 80-year cubic smoothing spline. It is important to note that PIPO_G2 was not analyzed for growth responses to climate due to it having much lower than the ideal 0.85 expressed population signal (EPS value) [30]. This EPS value is the benchmark for chronology signal strength and the time frame having this EPS value is considered to have a reliably strong chronology signal. For the small- and medium-diameter groups, the EPS value threshold was lowered because these size classes likely exhibit a weaker stand-wide signal since they may be more influenced by microsite factors [31]. Since we are investigating growth–climate relationships and not trying to reconstruct past climate, this is an acceptable EPS value threshold for the smaller trees [31]. Therefore, 11 of the 12 groups, those having an EPS value greater than 0.80 (and 0.85 for the large diameter group), were used for further analysis.

2.4. Dendroclimatic Analysis

To analyze growth responses to climate variables, long-term weather data for the geographic centroid of all plots (Lat 40.1900, Long -121.3110) were gathered from the PRISM Climate Group at Oregon State University [32] for the timeframe of the dendroclimatic analysis (1969–2014). Specific data collected for analyses were the following primary climatic variables: minimum temperature (MIT), maximum temperature (MAT), mean temperature (MET), and precipitation (PPT). These variables were then used to calculate a secondary climate variable, climate moisture index (CMI), so that precipitation

and temperature could be combined to express the moisture regime of the area [33]. Each monthly variable was also converted into 3-month seasonal scales by averaging the temperature variables and summing up the precipitation and climate moisture index variables for the respective three-month periods. A regression model was then created for each species–diameter group’s growth response to each of the climatic variables (monthly and 3-month seasonal scales) using an RScript program developed by Chhin et al. [34]. This program utilizes a stepAIC function that prefers models that minimize Akaike’s information criteria (AIC) values and penalizes models with excessive predictor variables [34]. More specifically, variables were only included in a model if they lowered the AIC value by at least 2 when included [35]. Using the program developed by Chhin et al. [34], growth responses to each of the climatic variables were analyzed from April of the previous year ($t - 1$) through October of the current year (t). The significant variables included in the regression models were then ranked based on their standardized (β) partial regression coefficients; in this case, variables with the highest absolute value coefficient were ranked number one [36].

3. Results

3.1. Stand Characteristics and Chronology Statistics

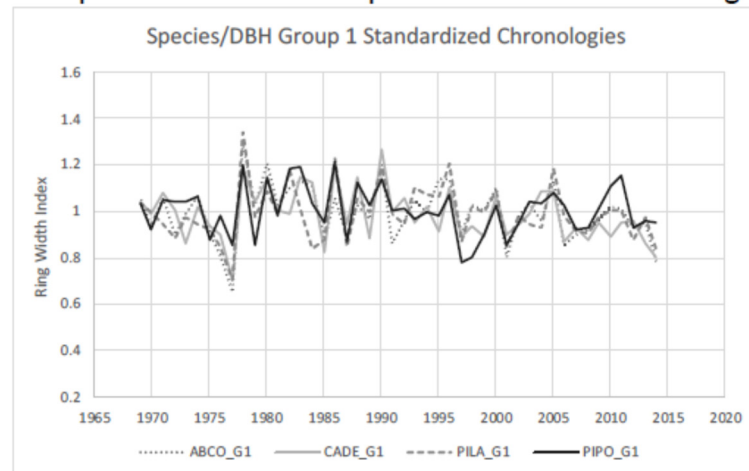
The overall average basal area of the study area was $58.27 \text{ m}^2 \text{ ha}^{-1}$, with sugar pine (PILA) contributing the most ($20.47 \text{ m}^2 \text{ ha}^{-1}$), followed by white fir (ABCO) ($18.11 \text{ m}^2 \text{ ha}^{-1}$), ponderosa pine (PIPO) ($13.87 \text{ m}^2 \text{ ha}^{-1}$), and incense-cedar (CADE) ($5.48 \text{ m}^2 \text{ ha}^{-1}$) (Table 1). The $0.34 \text{ m}^2 \text{ ha}^{-1}$ difference in overall average basal area from the sum of the four main species was due to small amounts of Jeffrey pine (*Pinus jeffreyi*) and/or red fir (*Abies magnifica*) in the sample plots. The overall quadratic mean diameter of the study area was 50.99 cm, with sugar pine (PILA) being the largest (78.89 cm), followed by ponderosa pine (PIPO) (65.14 cm), incense cedar (CADE) (45.02 cm), and white fir (ABCO) (37.40 cm) (Table 1).

Table 1. Average basal area and quadratic mean diameter of the four main species studied and for all species combined. The “All” column total for basal area is slightly higher than the sum of the four main species due to small amounts of Jeffrey pine (*Pinus jeffreyi*) and/or red fir (*Abies magnifica*) in the sample plots.

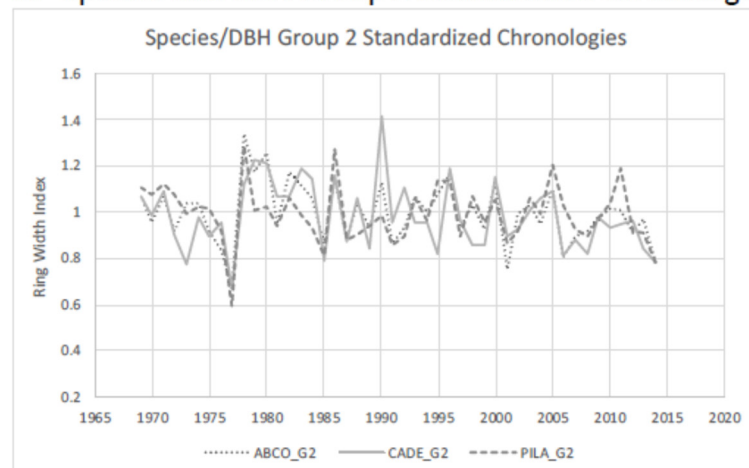
	ABCO	CADE	PILA	PIPO	ALL
BA ($\text{m}^2 \text{ ha}^{-1}$)	18.11	5.48	20.47	13.87	58.27
QMD (cm)	37.4	45.02	78.89	65.14	50.99

The average percentage of missing rings in a species and diameter group was 0.181%, with some groups having no missing rings, and the highest percentage of missing rings being 0.442% (Table 2). Groups having no missing rings usually had a smaller number of trees. All groups had reached an EPS value of 0.80 by 1969 (except PIPO_G2, which was excluded from analyses); most groups had reached an EPS value of 0.85 by 1969, except for CADE_G2 and PILA_G2, which had maxed out at 0.803 and 0.830, respectively, by 1969. Mean sensitivity values ranged between 0.117 and 0.293, with 10 out of the 11 groups being between 0.117 and 0.195. Intercore correlation values were slightly numerically different between the three DBH groups. The average intercore correlation value for DBH Group 1 was 0.252, whereas DBH Group 2 was 0.340 and DBH Group 3 was 0.345. Standardized chronologies are visually represented in Figures 3 and 4. Some key years of growth reduction (relative to the surrounding years) that can be seen in those figures are in 1977, 1985, and 2001. However, the most apparent and drastic growth reduction for those years is in 1977, in which very narrow and missing rings were most commonly found. PILA_G2 and ABCO_G3 had zero missing rings.

A. Species and DBH Group 1 standardized chronologies



B. Species and DBH Group 2 standardized chronologies



C. Species and DBH Group 3 standardized chronologies

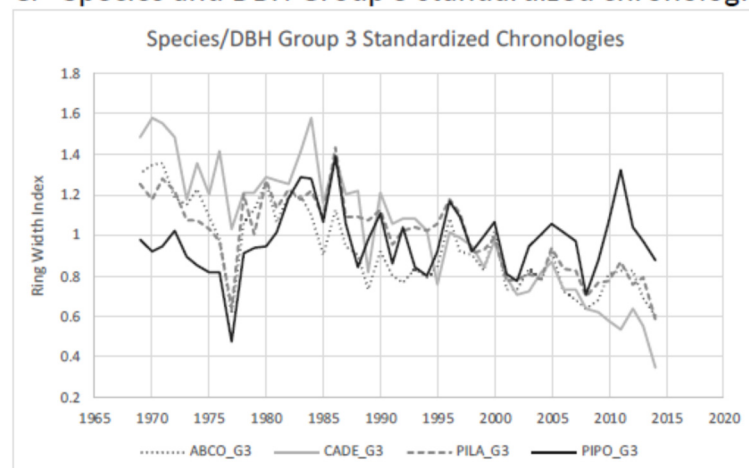
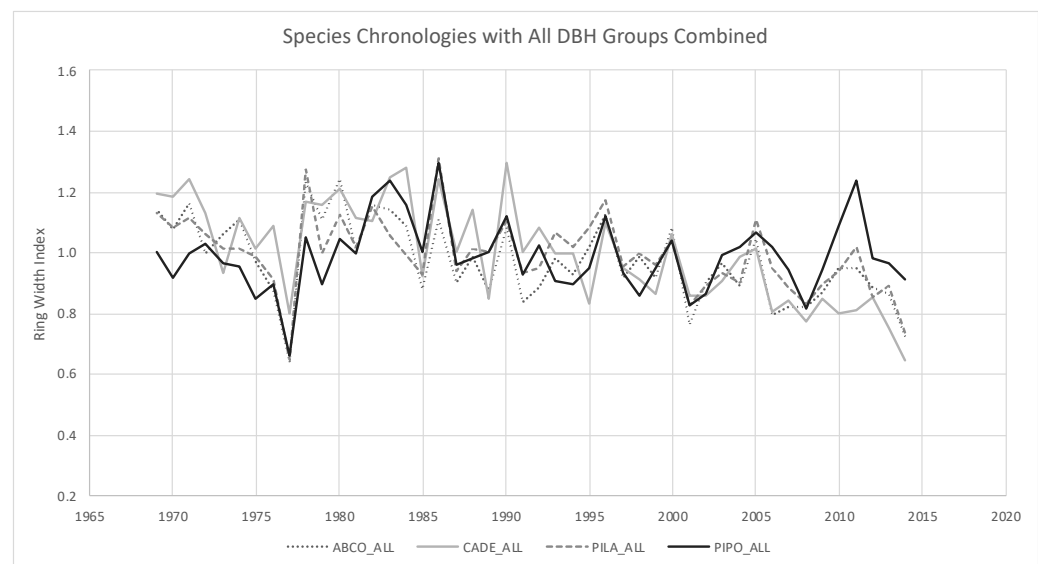


Figure 3. Standardized chronologies for the time frame of the dendroclimatological analysis (1969–2014) for (A) small diameter Group 1, (B) medium diameter Group 2, and (C) large diameter Group 3. ABCO = *Abies concolor*, CADE = *Calocedrus decurrens*, PILA = *Pinus lambertiana*, PIPO = *Pinus ponderosa*. G1 = Diameter Group 1 (20.32 to $\leq$ 40.64 cm, small size), G2 = Diameter Group 2 (40.64 to $\leq$ 60.96 cm, medium size), G3 = Diameter Group 3 ($>$ 60.96 cm, large size). PIPO_G2 is not included because its expressed population signal (EPS) value was too low for dendroclimatological analysis.

Table 2. Statistics for the standardized tree ring chronologies for each species and DBH group.

Species	DBH Group #	Chronology Time Span	# of Trees	Mean Sensitivity	Standard Deviation	Absent Rings (%)	Year EPS Reached 0.80	# of Trees Needed to Reach EPS Value 0.80	Intercore Correlation
ABCO	1	1830–2015	191	0.168	0.171	0.068	1885	15	0.211
CADE	1	1798–2015	40	0.130	0.119	0.131	1925	15	0.221
PILA	1	1876–2015	12	0.163	0.257	0.379	1957	7	0.387
PIPO	1	1819–2015	28	0.293	0.258	0.442	1969	18	0.190
ABCO	2	1851–2015	51	0.195	0.321	0.060	1890	10	0.296
CADE	2	1784–2015	13	0.162	0.150	0.365	1893	9	0.312
PILA	2	1888–2015	7	0.117	0.116	0.000	1950	6	0.411
PIPO	2	1785–2015	9	0.165	0.297	0.062	NA *	NA *	0.222
ABCO	3	1834–2015	15	0.128	0.334	0.000	1879	9	0.319
CADE	3	1812–2015	14	0.160	0.316	0.080	1876	4	0.535
PILA	3	1738–2015	33	0.123	0.209	0.292	1856	12	0.265
PIPO	3	1718–2015	24	0.129	0.169	0.171	1799	12	0.261

Note: DBH Group #: Group 1 (i.e., small diameter size), Group 2 (i.e., medium diameter size), and Group 3 (i.e., large diameter size). * NA values noted because EPS did not reach the 0.80 threshold.

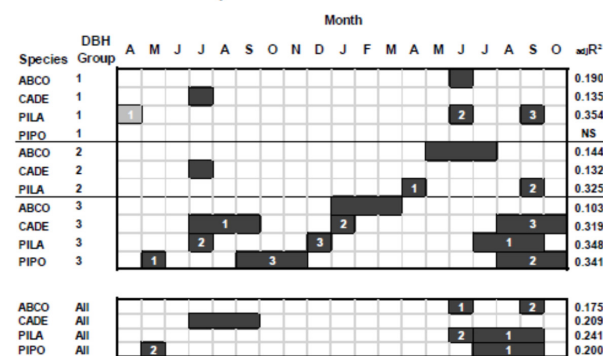
**Figure 4.** Species standardized chronologies with all DBH Groups combined for the time frame of the dendroclimological analysis (1969–2014).

3.2. Growth Responses to Temperature

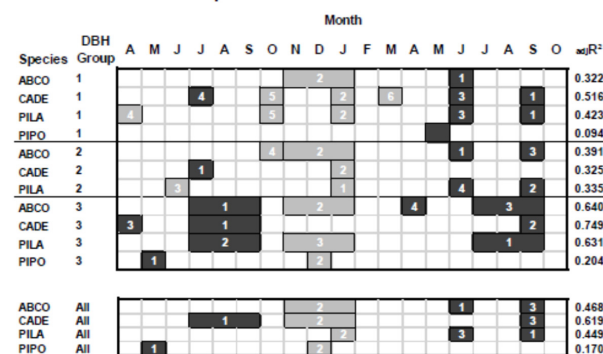
All growth responses to maximum temperature were negative—except for PILA_G1, which responded positively to the max temperature in April of the prior year ($t - 1$) (Figure 5A). In general, there was a more apparent response to maximum temperature from species of Diameter Group 3 (the largest diameter group). Most species–diameter groups responded negatively to maximum temperatures around summer to fall of the current year (if they did respond to maximum temperature), with the largest diameter group showing more of a lagged response to max temperatures in summer to early fall of the previous year. Both ABCO and PILA in Diameter Group 1 (the smallest diameter group) responded negatively to maximum temperatures in June of the current year (t). A negative correlation with maximum temperature in July of the previous year ($t - 1$) was the only predictor variable for CADE_G1, and no predictor variable was found for PIPO_G1. Species in Diameter Group 2 had a very similar response to maximum temperatures compared with Diameter Group 1, however, no positive correlations were found in this group. The main differences between these diameter groups was that ABCO_G2 responded negatively to maximum temperatures for the May–July seasonal period (t) instead of just June (t) and PILA_G2 responded negatively to maximum temperatures in April (t) instead of June (t).

Species in Diameter Group 3 had a much different response to maximum temperature. All species in Diameter Group 3, except ABCO_G3, responded negatively to maximum temperatures in late summer to fall of the current year (with varying importance). The only growth response from ABCO_G3 was a negative response to maximum temperatures in January–March of the current year. Also, more of a lagged response to maximum temperatures was seen from species in Diameter Group 3, in which they responded negatively to maximum temperatures in varying months throughout the year prior. Responses from each species with all diameter groups combined (i.e., denoted by “_ALL”) tended to follow the same pattern as Diameter Group 3 more so than the other diameter groups.

A. Maximum Temperature



B. Minimum Temperature



C. Mean Temperature

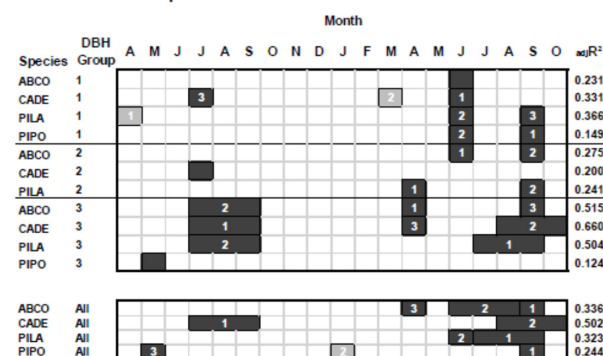


Figure 5. Statistically significant ($p < 0.05$) growth responses to (A–C) by species and diameter group and for each species as a whole (i.e., with all diameter groups combined). Darker coloring indicates a negative correlation with growth, whereas lighter coloring indicates a positive correlation with growth. Numbers indicate the order of importance for that relationship, with 1 being the most important (according to the standardized partial regression coefficients). Explanatory climate variables expressed either for a monthly period or a 3-month seasonal period. NS = no significant variables in the model.

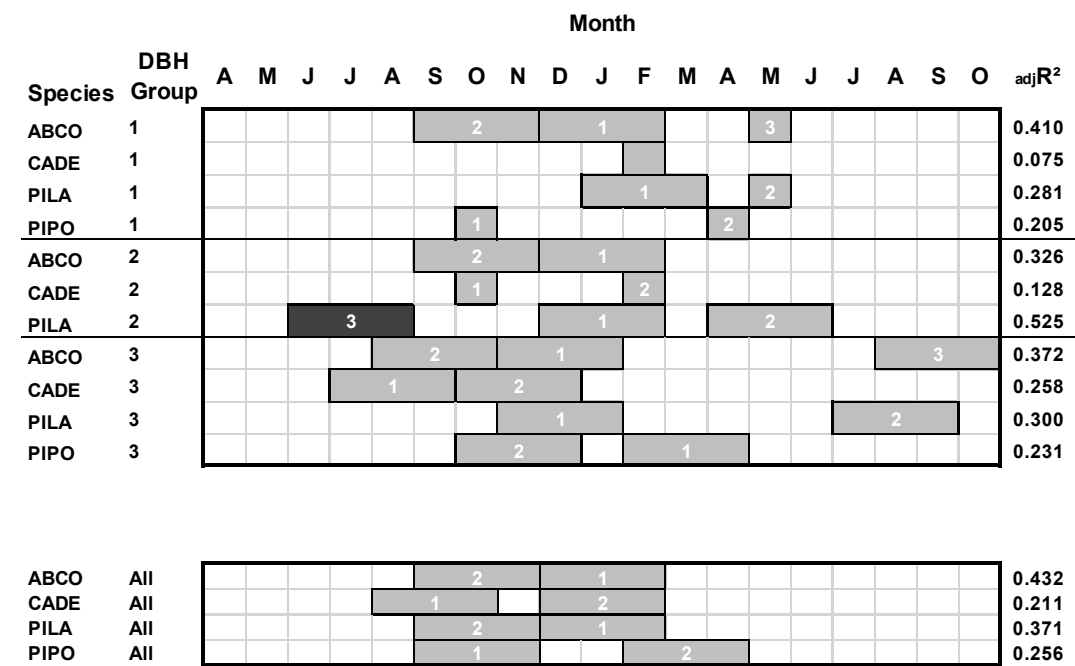
More of a coherent trend across all groups can be observed for the growth responses to minimum temperatures (Figure 5B). Most species and diameter groups responded negatively to minimum temperatures around early summer to early fall of the current year. However, more of a 3-month seasonal response to summer temperatures can be seen for species in Diameter Group 3, specifically ABCO_G3 and PILA_G3. Again, a lagged response was more apparent in Diameter Group 3 than the other diameter groups—with ABCO_G3, CADE_G3, and PILA_G3 responding negatively to minimum temperatures in the 3-month seasonal period of July–September of the previous year ($t - 1$). Perhaps one of the most coherent responses to minimum temperatures from all diameter groups was the positive response to minimum temperatures in the winter leading up to the current year of growth. Most of these positive responses can be seen from November ($t - 1$) to January (t). Something else that stands out in this figure is the positive response to minimum temperatures in April ($t - 1$) for PILA_G1 and in June ($t - 1$) for PILA_G2. When all diameter groups are combined for each species, it is clear that increasing minimum winter temperatures had a positive influence on the growth of all species in at least some portion of the winter months leading up to the current growing season. As seen in the maximum temperature figure (Figure 5A), CADE_ALL and PIPO_ALL also exhibit that lagged negative response to minimum temperatures in July–September ($t - 1$) and May ($t - 1$), respectively.

Mean temperatures had a very similar effect on growth as minimum temperatures; however, no coherent response was seen in the winter months (Figure 5C). In general, species from all diameter groups responded negatively to mean temperatures in summer to early fall of the current year. However, more of a trend arises when looking at mean temperatures. Species in Diameter Group 1 responded negatively to mean temperatures in June (t), whereas species in Diameter Group 3 responded negatively more so in the latter parts of the summer to early fall. As seen in the other temperature variables, a lagged response was more apparent from species in Diameter Group 3. Most of the same growth trends carried over when diameter groups were combined, but the lagged response became less apparent again.

3.3. Growth Responses to Precipitation and CMI

Nearly all growth responses to precipitation were positive (Figure 6A). In general, positive responses to precipitation can be observed between early fall of the previous year and spring of the current year for ABCO_G1, CADE_G1, PILA_G1, and PIPO_G1. Species in Diameter Group 2 had a fairly similar pattern of responses. However, PILA_G2 did have a negative response to precipitation in the June–August ($t - 1$) seasonal period, which was not seen in PILA_G1. ABCO_G3's growth response stayed fairly similar to ABCO_G1 and G2's growth responses, but it also responded positively to precipitation from August–October of the current year—with that seasonal period being the least important predictor of growth. Growth responses to precipitation from CADE_G3 and PILA_G3 seemed to change the most from the two smaller diameter groups. CADE_G3 had a stronger lagged response than CADE_G1 and G2, in which it responded positively and the strongest to precipitation in the July–September seasonal ($t - 1$) period, followed by the October–December seasonal ($t - 1$) period. PILA_G3 had a more lagged response than PILA_G1, in which it responded positively and the strongest to precipitation in the November–January ($t - 1$) seasonal period, followed by the July–September (t) seasonal period. This was a different response than what was seen for PILA_G1, having just one month of overlap in January (t). However, growth responses to precipitation for species in Diameter Group 3 were not as different from Diameter Group 1 as with the other climate variables—with the exception of the positive response to late summer/early fall precipitation by ABCO_G3 and PILA_G3, which was not exhibited in other diameter groups. A clear trend arose when all diameter groups were combined for each species, in which all species generally responded positively to precipitation between early fall ($t - 1$) and early spring (t).

A Precipitation



B Climate Moisture Index

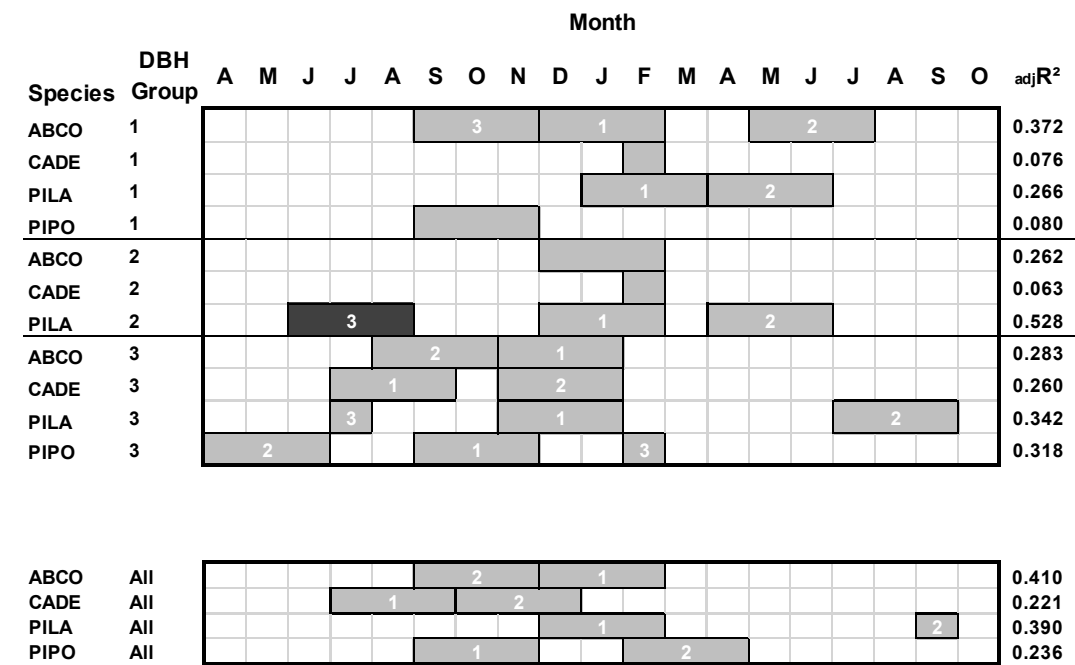


Figure 6. Statistically significant ($p < 0.05$) growth responses to (A,B) by species and diameter size group and for each species as a whole (i.e., with all diameter groups combined). Darker coloring indicates a negative correlation with growth, whereas lighter coloring indicates a positive correlation with growth. Numbers indicate the order of importance for that relationship, with 1 being the most important (according to the standardized partial regression coefficients). Explanatory climate variables expressed either for a monthly period or a 3-month seasonal period.

Growth responses to climate moisture index (CMI) followed a similar pattern as growth responses to precipitation (Figure 6B), with some slight differences.

4. Discussion

4.1. Stand and Chronology Characteristics

The inventory of stand conditions indicates that the study area is dominated by sugar pine but shows that white fir is starting to overtake ponderosa pine due to the past policy of fire suppression in the Western United States [37] (Table 1). Fire suppression has allowed shade-tolerant and fire-sensitive species such as white fir and incense cedar to proliferate in the forest understory. Despite their small diameters, white fir in this study represented a substantial amount of the basal area and can contribute to a higher amount of fuel loading in the understory and, in turn, serve as fuel ladders that can cause fires to transition into the crown region [37] (Table 1). It is important to safeguard these large diameter legacy trees of sugar pine and ponderosa pine with effective silvicultural practices and fire management [38].

Some general findings were likely due to the inherent nature of the climate in the Sierra Nevada. Especially regarding the dramatic decrease in growth around the year 1977 as seen in Figure 2, with a slightly greater decrease in growth perhaps seen for the larger trees. This year (1976 to 1977) is known as one of the worst, if not the worst, drought years in California history [39]. The area of this study was not specifically listed in the report, but it is inferred that the location received less than 60% of the normal precipitation and just 24% of normal natural basin runoff—as compared with 43% natural basin runoff the year prior [39]. Medium-sized sugar pine and the largest diameter white fir had no missing rings, but the pattern is likely associated with tree size and shade tolerance [20,22]. In particular, medium-sized sugar pines were growing in their optimal shade tolerance niche. The lack of missing rings suggests that large white fir have sufficient environmental resources for growth.

4.2. Responses to Temperature

Species in all diameter groups responded positively to increasing winter minimum temperatures, with no distinct difference between diameter groups—highlighting the benefit that trees of all sizes will likely gain from increasing minimum winter temperatures in the future [3]. This positive response to winter minimum temperature is related to the better tree radial growth related to milder winters [12], which was also observed by Bigelow et al. [14].

The general finding that diameter growth decreased due to increasing maximum temperatures in the summer, aligned (Figure 5) with findings from Yeh and Wensel [13] as well as Bigelow et al. [14]. This pattern is not surprising since summer is usually the dry period in the Mediterranean climate of the Sierra Nevada range. Therefore, increasing maximum temperatures would be expected to intensify drought stress, which would subsequently decrease growth. Another notable growth response was the negative response to increasing maximum temperatures in the current summer to early fall from all species in largest diameter group (i.e., #3), except white fir. One possibility that could lead to this negative response would be increased respiration requirements for larger trees as temperatures increase—as well as the general higher respiration demands that are required as trees age [11]. West [11] also suggested that some of this increase in respiration could be due to increases in the maintenance respiration associated with older trees. This distinct difference in growth responses to maximum temperature between the largest and smallest diameter groups was not as apparent with the minimum and mean temperature variables.

One distinct pattern that was observed across all temperature variables was how the largest diameter group had a lagged negative response to temperature (Figure 5). This lagged negative response was to summer temperatures ($t - 1$) for three of the species (ABCO, CADE, and PILA) in Diameter Group 3 and to March ($t - 1$) temperatures for PIPO_G3; this was observed in every temperature variable except for the lack of influence

of maximum temperature on ABCO_G3. Interestingly, Szeicz and MacDonald [8] found very similar results when comparing growth responses between trees less than 200 years old and greater than 200 years old, in which the older trees responded negatively to previous summer temperatures whereas the younger trees did not. They attributed general differences in growth responses to physiological changes that occur as trees age, such as changes in root, shoot, and cambial growth patterns [8]. Similarly, this response may be due to the inherent nature of larger trees having more tissues for storage and therefore being influenced more by the previous season's growth and growing conditions. Furthermore, increased respiration in larger trees due to higher temperatures in the prior year may decrease the amount of stored carbohydrates and therefore cause the lagged negative growth response with temperatures. For example, if a tree experienced a stressful growing season the year prior, it may not have as many reserves for the flush of growth the following year [12], especially for a large tree with more growth and metabolic requirements than a smaller tree. Though this current study found a fairly consistent lagged negative response to summer temperatures ($t - 1$), another study conducted by Bigelow et al. [14] in the Sierra Nevada, which looked at the same four species that are in the current study, did not find any significant lagged responses to previous summer temperatures. However, though Bigelow et al. [14] did not capture that lagged response to summer temperatures ($t - 1$), they did show a similar finding of a lagged negative response from large ponderosa pine (i.e., similar to PIPO_G3) to spring temperatures in the year prior. This lagged negative response was thought to be attributed to vascular embolisms created by early spring drying events in soil that is frozen or dry due to high vapor pressure deficits created from high temperatures; these vascular embolisms could have subsequently resulted in decreases in rates of carbon fixation [14]. However, this is not likely since conifers are fairly resistant to embolisms [40]. Decreases in carbon fixation during the year prior were thought to have caused a decrease in ring width the following year because the trees may not have had as much stored photosynthate to use for the flush of growth occurring in the spring [14]. It is also unclear why large ponderosa pine was the only species to significantly respond negatively to high spring temperatures in the year prior if vascular embolisms are the cause of this lagged response. It is speculated that shade-intolerant trees such as the ponderosa pine have a dominant stature in the canopy at the expense of a harsher, more exposed microclimate with higher solar radiation and temperature stress. This would be in contrast to the more moderated microclimate conditions under the forest canopy in more shaded conditions for the other trees such as the more moderately shade-tolerant sugar pine and the shade-tolerant white fir and incense cedar.

Another main finding from the study was that higher adjusted R^2 values were captured for species in Diameter Group 3 compared with Diameter Group 1—with the exception of a few instances mainly with white fir, in which the adjusted R^2 slightly decreased from Diameter Group 1 to Group 3. These patterns in explained variance were also mirrored in the patterns in intercore correlation, which was typically higher in larger trees of the same species (Table 2). The larger trees also tended to be more influenced at a seasonal scale, whereas the smaller trees were influenced mainly by monthly climatic factors—especially for the temperature variables (Figure 5). The inability to explain as much variation in ring width for the smaller, less mature trees could be attributed to more complex growth since they are usually being influenced by a higher number of environmental factors in the understory, such as competition [6,7]. In this case, smaller, more suppressed trees may be more influenced by edaphic and/or microclimate gradients [41]. This noise (i.e., unwanted growth influences for dendroclimatic analysis) is usually accounted for during analysis in which growth signals are maximized and noise is minimized [7]. However, the higher amount of noise often seen in smaller trees (due to reasons previously mentioned) could be why lower percentages of variation in ring width for smaller trees is explained by the climate variables examined in the current study—even when noise is minimized as much as possible. In other words, this difference is likely because more variation in ring width for smaller trees (versus larger trees) is attributed to other factors not analyzed in this study.

For instance, it is speculated that the overstory trees in the stand could potentially provide nurse-tree effects for the smaller trees that could provide a buffer to microclimatic stress factors such as reducing sun exposure and evapotranspirational water loss [42].

4.3. Responses to Precipitation and Moisture Availability

Another finding that is likely strongly related to climate is that species mainly responded positively to both precipitation and CMI during late fall–winter (Figure 6). This was generally the case for all species and diameter groups, with slightly more adjusted R^2 —on average—accounted for in the larger diameter groups. This positive response commonly occurring around this time of year is likely because most yearly precipitation in the northern Sierra Nevada occurs during the winter. One other finding that commonly occurred across all diameter groups and species was the positive response to minimum temperatures in the winter. This was also found to be a significant predictor variable for the same four species studied by Bigelow et al. [14] in the Sierra Nevada and was speculated to be due to decreases in photoinhibition during warmer winters. Photoinhibition is usually referred to as a light-induced decrease in photosynthesis; however, it can also be attributed to high or low temperature extremes [12,43]. In this case, Bigelow et al. [14] likely speculated that a decrease in photoinhibition may be the reason for increased growth because recovery of photoinhibition is able to occur at warmer, more moderate temperature levels [12]. However, this is unlikely the reason since limited diameter growth is put on before April in the Sierra Nevada [18]. Nonetheless, this finding suggests that trees of all sizes will likely benefit from increasing minimum winter temperatures in the future.

5. Conclusions

This study underscored how climate variables can have differing growth effects on species based on their diameter size and canopy position. One of the most interesting findings from the study was the lagged negative response to temperature variables exhibited by the largest diameter group (DBH Group 3) but not so much by the smaller diameter groups. The largest diameter group also tended to respond more strongly to temperature variables in general. This can likely be attributed to increased respiration in the more exposed higher canopy leaves as well as the general increase in respiration demands and root and shoot size as trees age. Another interesting finding regarding the largest diameter group, in general, was that more variation in ring width was explained by the climate variables used for dendroclimatic analysis in this study. This could be due to the smaller trees having a higher number of environmental factors that influence their growth in the understory, therefore lowering the percentage of variation that could be explained by temperature, precipitation, and CMI. However, there were also some similarities in terms of growth responses to precipitation and CMI across all diameter groups that can likely be attributed to the wet season in the Lassen National Forest occurring around the winter months. Another similarity was that species in all diameter groups responded positively to increasing winter minimum temperatures, with no distinct difference between diameter groups—highlighting the benefit that trees of all sizes will likely gain from increasing minimum winter temperatures in the future.

We recommend that future dendroclimatic studies look to explore other influences on smaller tree growth patterns and may wish to look more closely into microclimatic factors affecting growth in the understory. Using such microclimatic factors, along with the factors already analyzed in this study, may help to explain a higher percentage of ring width variation in those smaller trees.

This study demonstrated the benefits of the dendroclimatic approach to assess how mixed conifer species in the Sierra Nevada responded to past climate and is therefore a key resource that can be used to infer how trees may respond to a future changing climate. The study also contributes to a better understanding of how small-, medium-, and large-sized trees were affected by the historic climate to help us fine-tune our management efforts on the tree sizes we are most interested in managing.

Author Contributions: Formal analysis, A.H.; Funding acquisition, S.C.; Methodology, S.C. and J.Z.; Supervision, S.C. and J.Z.; Writing—original draft, A.H.; Writing—review and editing, S.C. and J.Z. All authors have read and agreed to the published version of the manuscript.

Funding: This work was funded via a grant from the U.S. Forest Service, Pacific Southwest Research Station (Joint Venture Agreements # 14-JV-11272139-016 and 19-JV-11272139-021). This work was also supported by the United States Department of Agriculture (USDA), National Institute of Food and Agriculture (NIFA), McIntire Stennis Project # 1017946, to Sophan Chhin.

Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available until full completion of all project components.

Acknowledgments: We thank C. Johnson, B.-A. Breton, E. Caretti, R. Micklus, K. Minnix, C. Sodergren, and L. von der Linden for providing assistance in field sampling and sample processing. J. Zarlengo, L. Corral, E. Elliot, and H. Van Gieson from the Lassen National Forest, Almanor Ranger District and K. Finley from Pacific Southwest Research Station at Redding provided logistical support. We appreciate the feedback from Jamie Schuler.

Conflicts of Interest: The authors declare no conflict of interest.

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