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ANNUAL CLIMATE IMPACTS ON TREE GROWTH AND POST-FIRE
REGENERATION IN PONDEROSA PINE AND DOUGLAS-FIR IN THE
NORTHERN ROCKY MOUNTAINS

By

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B.A. Williams College, Williamstown, MA, 2014

Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Systems Ecology

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Missoula, MT

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Annual climate impacts on tree growth and post-fire regeneration in ponderosa pine and Douglas-fir in the northern Rocky Mountains.

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Abstract

Widespread changes in climate and disturbance regimes, including prolonged drought and increases in the size and frequency of wildfires, have raised concerns regarding forest resilience to environmental change. Dry mixed-conifer forests have persisted for centuries under mixed-severity fire regimes; however, climatically driven increases in the frequency of large wildfires in recent decades may lead to increased tree mortality and declines in post-fire tree regeneration. Climatic warming and increased drought may also impact tree growth, with implications for the carbon cycle. Lower-treeline forests near the edge of their climatic tolerance may be particularly vulnerable to these impacts of future climate warming and increased fire activity.

This thesis includes two studies focused on quantifying the impacts of climate change, climate variability, and wildfires on forest dynamics. In Chapter 1, I compared the accuracy of field-based methods to precise dendrochronological techniques to age ponderosa pine and Douglas-fir seedlings sampled from three study regions across the western U.S. The use of precise dendrochronological tree aging was well justified, as node counts systematically underestimated ring counts, with bias increasing with tree age.

In Chapter 2, I studied the impacts of climate variability on lower-treeline forests in the northern Rocky Mountains of the U.S., by quantifying how post-fire tree establishment and radial growth varied with seasonal climate over the 20th and early-21st centuries. Climatic conditions favoring regeneration differed between ponderosa pine and Douglas-fir, suggesting species-specific responses to future increases in temperature and drought. Radial growth was also sensitive to moisture availability and temperature, but this sensitivity varied over the past century and between life stages. While adult growth was consistently sensitive to moisture availability, juvenile growth, particularly for ponderosa pine, was sensitive to moisture availability during the warmest and driest decades, suggesting that directional shifts in temperature, accompanied by increasing moisture stress, may be changing climate limitations on growth. This research demonstrates the increased vulnerability of post-fire tree regeneration and decreased growth in dry mixed-conifer forests given increases in temperature and drought. Shifts towards conditions unfavorable for regeneration and growth will likely result in shifts in species composition of lower-treeline forests or transitions to non-forested states.

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Table of Contents

ANNUAL CLIMATE IMPACTS ON TREE GROWTH AND POST-FIRE REGENERATION IN PONDEROSA PINE AND DOUGLAS-FIR IN THE NORTHERN ROCKY MOUNTAINS	i
Abstract	ii
Acknowledgements	iii
List of Figures	vi
List of Tables	vi
Chapter I: Accuracy of node and bud-scar counts for aging two dominant conifers in western North America	1
Abstract	1
1. Introduction	2
2. Methods	5
2.1 Study Area	5
2.2 Sampling Design and Field Measurements	6
2.3 Dendrochronology	6
2.4 Accuracy Assessment	7
3. Results	10
4. Discussion	13
4.1 Conclusions	16
Literature cited	18
Tables	30
Table 1	30
Table 2	31
Figure Legends	32
Figure 1	34
Figure 2	35
Figure 3	36
Supplementary materials	37
Chapter II: Annual climate impacts tree growth and post-fire regeneration in low-elevation ponderosa pine and Douglas-fir forest of the northern Rocky Mountains	47
2.1 Abstract	47
2.2 Introduction	49

2.3 Methods.....	53
2.3.1 Study Region	53
2.3.2 Site selection	53
2.3.3 Field Sampling and Measurements	55
2.3.4 Dendrochronology.....	55
2.3.5 Climate Data.....	57
2.3.6 Regeneration Analyses.....	57
2.3.7 Radial growth analyses.....	58
2.4 Results.....	60
2.4.1 Regeneration-climate Analyses.....	60
2.4.2 Growth-climate Analyses.....	61
2.5 Discussion.....	63
2.5.1 Climate and post-fire conifer regeneration.....	63
2.5.2 Climate limitations on conifer growth	66
2.5.3 Implications of future climate change	69
2.6 Literature Cited.....	72
2.7 Tables.....	84
Table 1.	84
Figure Legends.....	85
Figure 1.	88
Figure 2.	89
Figure 3.	90
Figure 4.	91
Figure 5.	92
Figure 6.	93
Figure 7.	94
2.8 Supplementary Materials	95

List of Figures

Chapter 1

Figure 1 Map of study sites.....	28
Figure 2 Node counts as a function of ring counts.....	29
Figure 3 Bias between ring counts and node counts as a function sample age.....	30

Chapter 2

Figure 1 Map of study sites.....	82
Figure 2 Mean climate from 1901-2015.....	83
Figure 3 Seedling age structures.....	84
Figure 4 Tree-core age structure.....	85
Figure 5 Climate-regeneration patterns.....	86
Figure 6 Standardized basal area increment chronologies.....	87
Figure 7 Continuous growth-climate linear regressions.....	88

List of Tables

Chapter 1

Table 1 Accuracy of node counts across varying levels of precision.....	24
Table 2 Results from statistical model predicting node counts.....	25

Chapter 2

Table 1 Global growth-climate correlations.....	78
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Chapter I: Accuracy of node and bud-scar counts for aging two dominant conifers in western North America

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Abstract

Accurately aging trees is critical for understanding tree demography and tree responses to environmental change. Given the proliferation of studies aimed at understanding the effects of climate and disturbance on forest ecosystems, it is important to understand the tradeoffs between field-based age estimates and precise dendrochronological techniques. We assessed the accuracy of age estimates from node counts in the field against precise tree-ring counts at the root-shoot boundary, in 1279 ponderosa pine and 1268 Douglas-fir seedlings sampled from across three study regions in the western U.S. We also assessed the accuracy of age estimates from bud-scar counts in the field against node counts and precise tree-ring counts in a subset of 757 seedlings from the Northern Rockies. Node counts systematically underestimated ring counts by an average of 4.1 years, with bias increasing with tree age. At annual, ± 1 -, ± 2 -, and ± 5 -yr precision, the accuracy of node counts was 5%, 15%, 29%, and 74% across all regions and species, respectively. Similar results were found for bud scars. Given the magnitude of the bias between field-based methods and ring counts, it is critical to select appropriate aging methods, based on the precision required to answer specific ecological questions. To improve the accuracy of field-based age estimates in these species, we provide a tool for correcting for the bias when precise dendrochronological aging is not feasible.

Key Words: nodes, bud scars, conifer seedlings, dendrochronology, *Pinus ponderosa*,

Pseudotsuga menziesii, Rocky Mountains, tree age structures, tree rings

1. Introduction

Ongoing global change, including increased drought stress on trees (van Mantgem et al. 2009, Allen et al. 2010, Williams et al. 2012) and an increased frequency of wildfires and other stand-initiating disturbances (Dale et al. 2001, Westerling et al. 2006, Abatzoglou and Williams 2016), has motivated a renewed interest in understanding patterns of tree establishment and recruitment (e.g. Stevens-Rumann et al., 2017). The resilience of forests to these stressors ultimately depends on the ability of trees to reestablish and survive. Studies of forest demography at varying temporal scales highlight post-disturbance vegetation change (Mast et al. 1998, Bergeron 2000, Turner 2010, Rother and Veblen 2017), shifts in treelines (Kearney 1982, Daniels and Veblen 2003, Coop and Givnish 2007), and climate-driven recruitment and stand dynamics (Savage et al. 1996, League and Veblen 2006). Understanding the pattern and timing of tree recruitment is critical to disentangling the drivers of these processes.

Quantifying the impacts of climate change, climate variability, and disturbances on forest dynamics ultimately requires estimating recruitment dates, and thus tree age. Field-based methods such as node or bud-scar counts are commonly used to provide approximate tree ages, and they have the advantage of being efficient and non-destructive (Sprugel 1976, Millar et al. 2004, Dovčiak et al. 2005, Haire and McGarigal 2010, Urza and Sibold 2013, Harvey et al. 2016). However, node and bud-scar counts are only proxies for true tree age (Urza & Sibold 2013). Cross-dated tree rings, from tree cores or cross sections, provide a more precise method for dating trees (Stokes and Smiley 1968, Telewski and Lynch 1991, Telewski 1993, Speer 2010). However, ring counts provide the age of a tree at sample height, which would underestimate true tree age, unless samples are obtained at the root-shoot boundary. While this

may be accounted for with decadal-scale age classes or age-height adjustments, this limits the scope of ecological questions that can be addressed.

Increasingly, a number of studies are attempting to infer the impacts of seasonal- to annual-scale climate on the establishment and early survival of conifer species from across western North America (League and Veblen 2006, Dobrowski et al. 2015, Donato et al. 2016, Harvey et al. 2016, Rother and Veblen 2017, Tepley et al. 2017). For these purposes, one needs annual accuracy in tree-establishment dates, as even 1-2 years of error could obscure relationships to seasonal or annual climate variability. Aging trees or seedlings with annual accuracy requires counting tree rings at the root-shoot boundary (Telewski 1993), which is time-intensive and usually requires destructive sampling (Bergeron 2000, Rother and Veblen 2017).

Given the proliferation of studies aimed at understanding the effects of climate and disturbance on Western forests, it is important to understand the implications of aging trees using field-based methods versus precise dendrochronological techniques. We assessed the accuracy of age estimates from node counts in the field against precise ring counts at the root-shoot boundary in 2547 samples from two dominant low-elevation conifers in western North America. We sampled 1279 ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) and 1268 Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings and saplings from across three study regions in the western United States (Fig. 1) to assess how the accuracy of node counts varies with species, region, tree age, and vertical growth rates. In a subset of 757 seedlings in the Northern Rockies, we also assessed the accuracy of age estimates from bud-scar counts in the field against node counts and precise tree-ring counts. We expected that node and bud-scar counts would underestimate tree ages based on ring counts, with this difference increasing in

older and faster-growing trees due to loss of lower branches and radial bark growth in older trees.

2. Methods

2.1 Study Area

The study was conducted in three regions across the western continental United States in dry mixed-conifer forests dominated by ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Sampling was conducted in recently burned stands in northern California, the Northern Rockies (Idaho and Montana), and the Southwest (Arizona and New Mexico) (Figure 1a). Across the California study sites, mean annual temperatures range from 8.5 – 15.6 °C, and mean total annual precipitation ranges from 645 to 1870 mm (30-yr normals, 1981-2010) (Daly et al. 2008, PRISM Climate Group 2017). The California region experiences hot, dry summers and cool wet winters. Across the Northern Rockies, mean annual temperatures range from approximately 3.3 to 8.4 °C, and mean total annual precipitation ranges from 318 to 878 mm (30-yr normals, 1981-2010) (Daly et al. 2008, PRISM Climate Group 2017). The Northern Rockies region experiences warm dry summers and cool wet winters. Across the Southwest study region, mean annual temperatures range from 8.0 to 10.0 °C, and mean total annual precipitation ranges from 388 to 667 mm (30-yr normals, 1981-2010) (Daly et al. 2008, PRISM Climate Group 2017). The Southwest experiences snow in winters and rain in late June through September due to the North American Monsoon. Terrain in these study regions is mountainous, often characterized by steep topography.

In all regions, study sites were located in low-elevation montane forest, where ponderosa pine and Douglas-fir are close to the edge of their climatic tolerance. In total, post-fire trees were sampled at 55 sites in ponderosa pine and Douglas-fir dominated forests that burned in years spanning 1992 to 2007. All sites burned at moderate to high severity (as classified by the Monitoring Trends in Burn Severity program), and have N/NE or S/SW aspects. Samples were

collected as part of a larger study investigating the effects of seasonal to annual climate variability on the timing and rate of post-fire conifer regeneration.

2.2 Sampling Design and Field Measurements

At each site we sampled all tree seedlings and saplings (hereafter “juveniles”) in a 60-m long belt transect, with transect width varying from 2-40 m, based on the goal of sampling approximately 30 juveniles per site, distributed in proportion to the on-site species composition. Node counts were recorded for seedlings and saplings as a field-proxy for age (Figure 1b), following a standardized protocol that was implemented by each of the three-member field crew. We counted a node where a set of branches extended from the main stem of the sample, and we added the current year’s leader to the count. After node counts, each sample was cut with a hand saw approximately 10 cm above the root collar, excavated to approximately 10 cm below the root collar, and cut to obtain the root-shoot boundary. Across all 55 sites we collected 2595 tree samples (Fig. 1). At a subset of 17 sites in the Northern Rockies, we counted bud scars in addition to node counts in 757 juveniles to compare accuracy in two common field-based aging methods.

2.3 Dendrochronology

To identify tree germination dates with annual precision, we sampled multiple cross sections above and below the estimated root-shoot boundary on each sample. Specifically, seedlings were cut into consecutive 2.5-cm intervals and sanded with successively finer sandpaper (to 1500 grit) to reveal ring boundaries (Speer 2010). We evaluated growth rings on samples below, near, and above the root-shoot boundary (Telewski 1993, Urza and Sibold 2013, Rother and Veblen 2017) under a 10-40x stereomicroscope. We determined the root-shoot boundary by the first appearance of pith (Figure 1c), and we used the number of rings at this

point as the estimated tree age. While we recorded visual marker years when possible, the young age of the samples did not allow for more formal cross-dating methods. To test the repeatability of our lab protocol, we performed independent recounts on a random subset of 555 samples among three analysts. If analysts disagreed on the number of rings, we either selected the ring count based on a consensus, or discarded the sample from analysis if all three analysts disagreed. For each sample, we scored our confidence level in the ring counts on a qualitative scale of 1 to 4 (1 = lowest confidence; 4 = highest confidence), and restricted any subsequent analyses to samples receiving a 3 or 4 in count confidence. A level 4 confidence was given if all ring boundaries were distinct; a level 3 confidence was given if only a single ring boundary was ambiguous. If more than one ring boundary was indistinct or pith dates were otherwise ambiguous, we removed the sample from the final dataset. Overall, 2547 samples met our confidence criteria, representing approximately 96% of original samples (i.e. all but 93 samples). Given these precautions in precise dendrochronological dating, we considered ring counts as the true age of the sample for subsequent analyses, but recognize that other sources of uncertainty remain.

2.4 Accuracy Assessment

Regression and error analyses were performed to understand the relationship between node counts and ring counts, with the purpose of gauging the accuracy of using node counts to estimate juvenile ages in the field. Differences in years between node counts and ring counts for each region and each species were used to calculate accuracy statistics and assess the potential bias in node counts. Metrics included accuracy and mean error. We also fit linear mixed effects models evaluating the relationship between node counts and ring counts. All analyses were performed in R v3.3.2 (R Core Team 2017).

Accuracy was defined at four levels of precision and calculated as the percent of samples where the absolute value of the difference between node counts and ring counts was $\leq 0, 1, 2,$ and 5 years. We then performed Welch's two-sample t-tests using a Bonferroni correction to test for significant differences in accuracy between species at each level of precision for all regions combined.

Mean error was defined as the average of the difference between ring counts and node counts (ring counts – node counts), which we considered the average bias between the methods (Urza and Sibold 2013). To test for significant differences in bias between species, we performed Welch's two-sample t-tests for all regions combined.

Linear mixed effects models were used to assess the relationship between node counts, ring counts, and species with a random site effect. Sites were treated as each sampling transect, and ranged from one to five sites within a single large fire. Models were performed independently with nodes and rings (i.e. tree age) each as the response variable to first, evaluate the relationship of nodes to the expected explanatory variable of tree age, and second, to provide a tool for predicting tree age given field-based node counts. The models were fitted for each region separately and for all regions combined.

Finally, we developed a linear mixed effects model using the bias (ring counts – node counts) as the response variable with a random site effect and age, species, region, and average vertical growth rate (height/age) as fixed effects to assess whether the bias between the two methods varied independently with these factors. We did not include tree height because tree height and vertical growth rate were collinear. The model included all potential two-way interactions to test whether the relationship between each explanatory variable and bias varied conditionally. Although the data were discrete counts, we used linear mixed effects models

because the data were relatively evenly distributed throughout a wide range of node counts and ages (i.e., 1-24) and the residuals were normally distributed. The random site effect accounts for any variations in these relationships due to local site effects. To account for non-constant variance, our models incorporated a power or exponential variance structure with the explanatory variable sample age or node counts, determined using AIC (Pinheiro and Bates 2000). For all models, we used the Satterthwaite approximation of degrees of freedom using the R package ‘lmerTest’ (Kuznetsova et al. 2016) and evaluated R^2 from a linear regression of predicted values as a function of observed values in each model.

3. Results

We analyzed 2547 samples in total, 1279 ponderosa pine and 1268 Douglas-fir, with ring-count based ages varying from 1 to 24 yr. Ring counts at the root-shoot boundary were robust to validation by random independent recounts, with a mean (sd) difference in ring-count based ages among three analysts of 0.298 (0.461) years.

The accuracy of node counts depended strongly on the level of precision considered, and varied among regions and species. For both species and all regions combined, accuracy was 5% when attempting annual precision, but increased to 15%, 29%, and 74% for +/- 1-, +/- 2-, and +/- 5-yr precision, respectively (Table 1). Accuracy was significantly higher for Douglas-fir than ponderosa pine across levels of precision, except for in the Southwest, where accuracy was higher for ponderosa pine than in Douglas-fir (Table 1, Supplementary Table A.1). California tended to have higher accuracy than the Northern Rockies or the Southwest, except for at annual precision (Table 1). For example, accuracy at 5-yr precision was 90% in California, 76% in the Southwest, and 66% in the Northern Rockies.

Node counts consistently underestimated ring counts (Figs. 2, 3), by an average of 4.1 years across all regions and for both species, with a maximum bias of 17 years. Underestimation of tree age varied significantly among individuals, for example, samples with three nodes ranged from 2 to 24 years old. Consistent with trends in accuracy, bias (mean error) differed significantly between species ($t = 13.09$, $df = 2330$, $p < 0.001$), with higher values in ponderosa pine (mean = 4.8 years) compared to Douglas-fir (mean = 3.4 yr) across all regions. While node counts were positively correlated with ring counts across all samples ($0.71 \leq R^2 \leq 0.84$), slopes from linear mixed effects models were significantly less than 1 (Table 2, Supplementary Table A.2). Species significantly affected the slope of this relationship; for example, in all regions

combined, node counts underestimated ring counts by 32% in Douglas-fir samples and 47% in ponderosa pine samples (Table 2).

Bias in node counts increased with sample age, with a significant species, region, and growth rate effect (Supplementary Table A.4). While species, region, growth rate, and a random site effect all explained variability in bias, sample age had the greatest effect on bias. Bias increased by 0.59 years for every additional year in sample age for ponderosa pine, and by 0.40 years in Douglas-fir, consistent with trends in accuracy (Fig. 3). After accounting for sample age and growth rate, bias was greatest in the Southwest for both species, followed by the Northern Rockies and California. Bias was greatest in ponderosa pine for the Northern Rockies and the Southwest, but showed less bias than Douglas-fir in California. Growth rate had the opposite effect on bias as did sample age, with decreasing bias with higher growth rates (Supplementary Fig. A.1). All two-way interactions, excluding species by growth rate, were also significant ($p < 0.05$), indicating that bias is conditional on complex interactions among these factors (Supplementary Table A.4). For example, bias increased with sample age faster in the Southwest than in the Northern Rockies or California. Furthermore, bias increased with sample age faster in slower-growing individuals.

Bud-scar counts exhibited similar patterns in bias and accuracy compared to node counts in a subset of 757 juveniles from the Northern Rockies (Supplementary Table A.5). In the subset of juveniles from the Northern Rockies, and at annual precision, both node and bud-scar counts were accurate 7% of the time. At +/- 5-year precision, bud scars were accurate 63% of the time, while node counts were accurate 65% of the time. While average bias was significantly greater in bud-scar counts (4.9 yr) compared to node counts (4.7 yr), these differences were negligible. Bias introduced by the two methods also differed significantly by species; ponderosa pine

showed greater bias than in Douglas-fir for both bud-scar counts (6.6 vs. 2.9 yr) and node counts (5.8 vs. 3.3 yr).

4. Discussion

Our results highlight and quantify the varying accuracy associated with using node and bud-scar counts to estimate tree age of two dominant low-elevation conifers of western North America. Node counts systematically underestimated tree age across all regions, in both ponderosa pine and Douglas-fir, with the inaccuracies increasing with tree age. If the precision is relaxed, for example to ± 5 years, then the accuracy of node counts increases significantly. Our findings thus highlight the important tradeoff between accuracy and the precision in tree-age estimates. Whether node counts or the more time-intensive methods of ring counts at the root-shoot boundary are most appropriate will depend on the given ecological question.

Across all regions combined, the bias introduced by node counts was greater in ponderosa pine than in Douglas-fir (Fig. 2). On average, node counts underestimated tree age by 4.8 years in ponderosa pine, and 3.4 years in Douglas-fir. Greater bias in ponderosa pine is consistent with other work suggesting that field-based age proxies are less reliable for faster-growing species, partially due to bark growth (Urza and Sibold 2013). Furthermore, bias increased with sample age for both species, indicating decreasing reliability for older juveniles. These patterns are consistent with previous findings showing decreasing reliability of bud scars as age increased in several subalpine conifer species, and particularly in faster-growing species (Urza and Sibold 2013). Older ponderosa pine juveniles tended to lack lower branch nodes, presumably having lost them over time, which could explain the increasing error with age and the higher bias in ponderosa pine than in Douglas-fir. While field-based methods are suggested to be more accurate for smaller and slower-growing juveniles, we found that bias increased with sample age faster in slower-growing individuals, suggesting that slower-growing individuals may not produce as clear annual nodes because of physiological limitations and/or poor growing

conditions. While this pattern was statistically significant, growth rate explained little of the variability in bias. Instead, this pattern may be explained by the poor relationship between age and growth rate across all regions and suggests that age rather than size is the most important factor in determining the accuracy of node counts.

Bias introduced by node counts was greatest in the Southwest and lowest in California (Table 2), after accounting for age and average growth rates, but accuracy varied among regions across each level of precision (Table 1). It is unclear why the Southwest showed greater bias in estimating tree age, but climatic differences between these regions may contribute to differences in the production and maintenance of clear annual branch nodes. The Northern Rockies included samples from older trees, relative to those from the Southwest and California, which likely accounts for the greater overall bias in this region when age is not considered. We did not detect any obvious or consistent morphological differences in branch nodes between samples from different regions, but seedling morphology of both species is known to vary geographically (St Clair et al. 2005, Grant et al. 2017). Other factors such as soil conditions and herbivory may also influence the production of clear annual branch nodes.

While previous studies have used bud-scar counts in place of node counts as a more reliable field-based proxy for age (Urza and Sibold 2013, Harvey et al. 2016), we found that the bias from bud-scar counts was similar to the bias from node counts (i.e., 4.7 vs. 4.9 yr). Overall, bud-scar counts only differed from node counts by an average of 0.78 yr (Supplementary Table A.5). Therefore, we suggest that our results based on node counts generally hold for age estimates based on bud-scars.

Given the magnitude of the bias between field-based age estimates and ring counts, we have little confidence in using node or bud-scar counts as annually precise estimates for juvenile

age. Studies requiring annual precision, as well as +/- 1-yr or +/- 2-yr precision, ultimately require the more precise dendrochronological techniques. When feasible, destructively sampling juveniles and counting rings at the root-shoot boundary (Telewski 1993) will provide substantially more accurate establishment dates than using field-based methods. Studies requiring annually resolved age structures, such as those investigating annual-scale patterns of post-fire regeneration and the effects of seasonal or annual climate variability on regeneration, may miss important patterns or identify false patterns if based on field-based age estimates. In contrast, for studies in which 10-yr bins (i.e., +/- 5-yr precision) around the true tree age are appropriate, node counts were accurate in 74% of the samples across both species and all regions. Despite uncertainties in field-based methods, they still provide useful data for reconstructing stand dynamics, treeline shifts, tree encroachment, disturbance history, and tree responses to decadal-scale climate variability, provided they are interpreted at the appropriate level of precision (Mast et al. 1998, Miller and Halpern 1998, Savage et al. 2013, Harvey et al. 2014, Meunier et al. 2014, Donato et al. 2016).

Our empirical dataset can also be applied to improve the accuracy of field-based methods to estimate tree age. We provide a tool for correcting for the bias introduced by node counts when precise dendrochronological aging is not feasible, applicable to the species and regions included in our dataset. This tool allows for coarse age corrections when node counts are being used to estimate tree age, and it can be used in two ways. First, we provide a function for estimating mean predicted age from a given node count collected in the field by entering species (i.e. "PIPO" or "PSME"), node count, and region. Our function uses the fixed effects of the linear mixed effects models with tree age as a function of nodes, species, and their interaction (Supplementary Table A.2). This correction reduces but does not eliminate bias. For example,

we predicted tree age from species and node counts in across all regions combined for a 20% testing dataset using the remaining 80% to fit our model, as a demonstration of how accuracy measures would change. At annual precision, accuracy of estimated ages increased from 9% to 21%. At +/- 1- and +/- 2-yr precision, accuracy increased from 19% to 40%, and 26% to 59%, respectively. Finally, at +/- 5-yr precision, accuracy of age estimates increased from 65% to 81%. This simple tool improves accuracy at all levels of precision, as well as significantly reduces the average bias (ring counts – node counts) from the true tree age (mean bias = 0.08 yr) (Supplementary Fig. A.2). To account for the variability in bias, the model results can be combined with the prediction intervals to make age corrections that include variability around the mean, by randomly selecting from a normal distribution centered on the regression line at a given node count and using the standard deviation calculated from the 95% prediction interval (Supplementary Table A.3).

While our work emphasizes the overall higher accuracy of age estimates based on ring counts, our field and dendrochronological methods are also subject to important uncertainties. Variable degrees of secondary and tertiary branching, as well as herbivory, may have contributed to inaccuracies in our field-based node counts. Despite our confidence in our ability to determine the establishment years using tree rings, our inability to cross-date such young samples precludes us from fully accounting for missing or false rings. However, missing rings, more likely in sites near the edge of their climatic tolerance, would decrease the bias observed between ring counts and node counts. Finally, all sampled seedlings established following moderate to high severity fire. Patterns of bias could be different in unburned areas.

4.1 Conclusions

Our study reveals a consistent underestimation of tree age when using field-based node or bud-scar counts, with decreasing reliability as age increases. The empirical dataset presented here can be used to help correct for some, but not all, of this bias when precise dendrochronological aging is not feasible. Future studies are needed to quantify the relationship between node counts, bud-scar counts, and ring counts in additional conifer species, as well as along additional biophysical gradients. Ecological studies of forest demography should consider the level of precision required to gauge the appropriateness of using field-based versus precise dendrochronological aging techniques.

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Tables

Table 1. Accuracy of node counts across varying levels of precision. Accuracy is expressed as the percentage of samples with node-count estimated ages that matched ring counts, within +/- 0, 1, 2, and 5 yr. Mean age for each subset of samples is shown with standard deviation in parentheses.

Region		Precision (+/- yr)				
		Age (yr)	+/- 0 yr	+/- 1 yr	+/- 2 yr	+/- 5 yr
All Regions	All (n = 2547)	10.9 (5.4)	5%	15%	29%	74%
	PIPO (n = 1279)	10.7 (6.2)	4%	13%	23%	66%
	PSME (n = 1268)	11.2 (4.4)	6%	18%	35%	83%
California	All (n = 639)	8.8 (4.2)	4%	20%	37%	90%
	PIPO (n = 316)	8.0 (4.7)	2%	23%	38%	84%
	PSME (n = 323)	9.6 (3.5)	5%	16%	36%	95%
N. Rockies	All (n = 1389)	12.6 (5.9)	5%	14%	27%	66%
	PIPO (n = 658)	13.5 (6.6)	3%	7%	14%	52%
	PSME (n = 731)	11.9 (5.0)	7%	21%	39%	79%
Southwest	All (n = 519)	8.9 (3.3)	6%	12%	24%	76%
	PIPO (n = 305)	7.5 (3.2)	8%	14%	27%	76%
	PSME (n = 214)	10.0 (2.3)	3%	8%	18%	78%

Table 2. Results from linear mixed effects models predicting node counts as a function of sample age, species, and their interaction as fixed effects, with site as a random effect. The 95% confidence intervals are shown in parentheses. Ponderosa pine serves as the reference level species for all estimates. R^2 values are from linear regressions of predicted values as a function of observed values for each model.

Region		Estimate	df	t-value	R^2
All Regions	Intercept	0.50 (0.18, 0.81)	2483	3.07	0.76
	Age	0.47 (0.44, 0.49)	2483	41.03	
	Species	-0.13 (-0.40, 0.15)	2483	-0.92	
	Age:Species	0.17 (0.14, 0.20)	2483	10.91	
California	Intercept	-0.19 (-0.66, 0.28)	625	-0.79	0.84
	Age	0.59 (0.55, 0.64)	625	25.71	
	Species	0.43 (0.03, 0.84)	625	2.11	
	Age:Species	0.07 (0.01, 0.13)	625	2.29	
No. Rockies	Intercept	0.92 (0.27, 1.37)	1347	2.94	0.75
	Age	0.44 (0.41, 0.48)	1347	25.76	
	Species	-0.27 (-0.76, 0.22)	1347	-1.10	
	Age:Species	0.20 (0.15, 0.24)	1347	9.23	
Southwest	Intercept	0.66 (0.36, 0.96)	505	4.30	0.71
	Age	0.38 (0.35, 0.41)	505	23.49	
	Species	-0.91 (-1.37, -0.46)	505	-3.94	
	Age:Species	0.26 (0.21, 0.31)	505	9.46	

*Bold t-values were statistically significant at $p < 0.05$.

Figure Legends

Figure 1. Sampling sites in low-elevation dry mixed-conifer forests that burned between 1992 and 2007 across the western continental United States (a). Pink areas indicate all fires that occurred from 1984-2014 from the Monitoring Trends in Burn Severity dataset. (b) Nodes visible on a seedling sample in the field. (c) Annual rings at the root-shoot boundary visible using a 1200 dpi scanner.

Figure 2. Node counts as a function of ring counts for samples from (a) California, (b) Northern Rockies, (c) Southwest, and (d) all regions. Black triangles and regression line are for ponderosa pine (PIPO) samples; grey circles and regression line are for Douglas-fir (PSME) samples. All points are jittered for visual clarity. R^2 values are from linear regressions of predicted values as a function of observed values for linear mixed effects models of node counts as a function of sample age, species, and their interaction, with site as a random effect. The 1:1 line is shown in grey. The $y = 1.5x$ and $y = 0.5x$ lines are shown in dashed gray to correspond with 50% over/underestimation.

Figure 3. Bias between ring counts and node counts as a function of sample age from (a) California, (b) Northern Rockies, (c) Southwest, and (d) all regions. Black triangles and regression line are for ponderosa pine samples; grey circles and regression line are for Douglas-fir samples. All points are jittered for visual clarity. Regression lines are from a linear mixed effects model of bias (ring counts - node counts) as a function of sample age (yr), species, region, vertical growth rate (cm/yr), and their two-way interactions with site as a random effect. The species: growth rate interaction was not significant and therefore excluded from the final model.

Growth rate was held constant at the median value of 4.25 cm/yr for prediction. R^2 from a linear regression of predicted values as a function of observed values was 0.68.

Figure 1

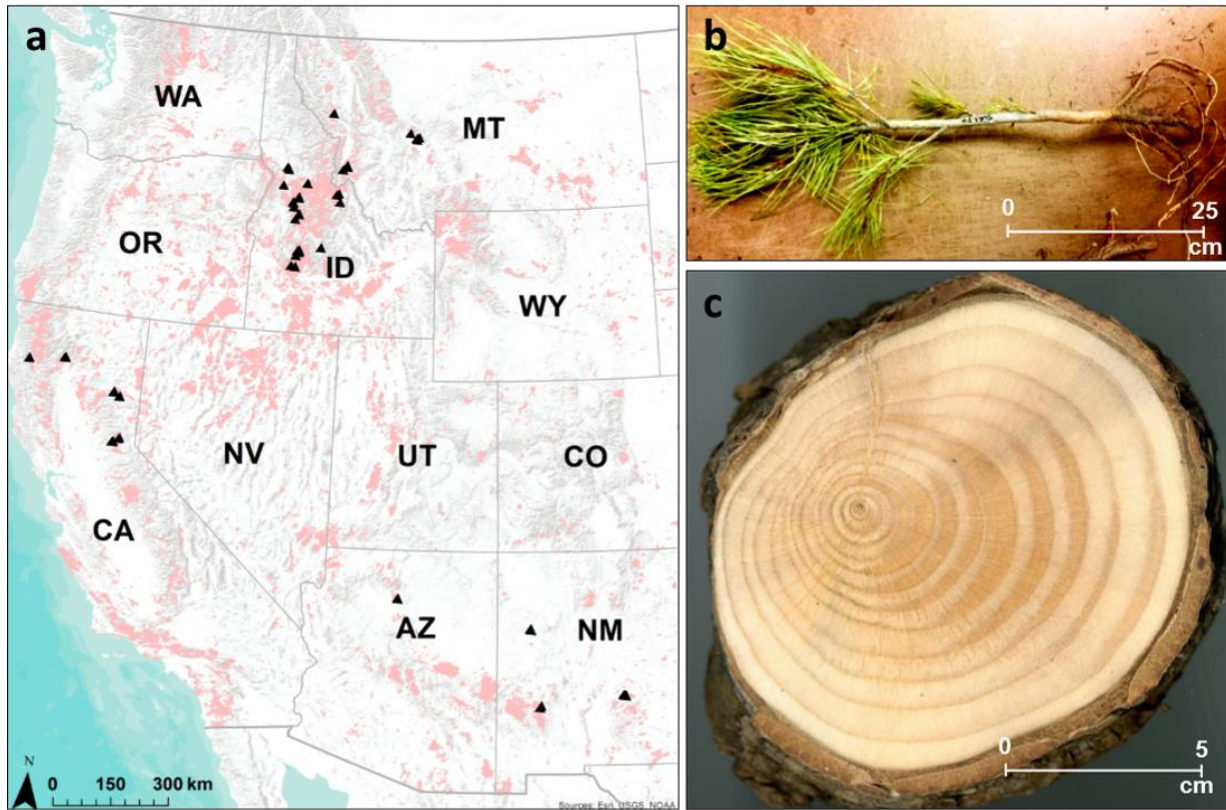


Figure 2

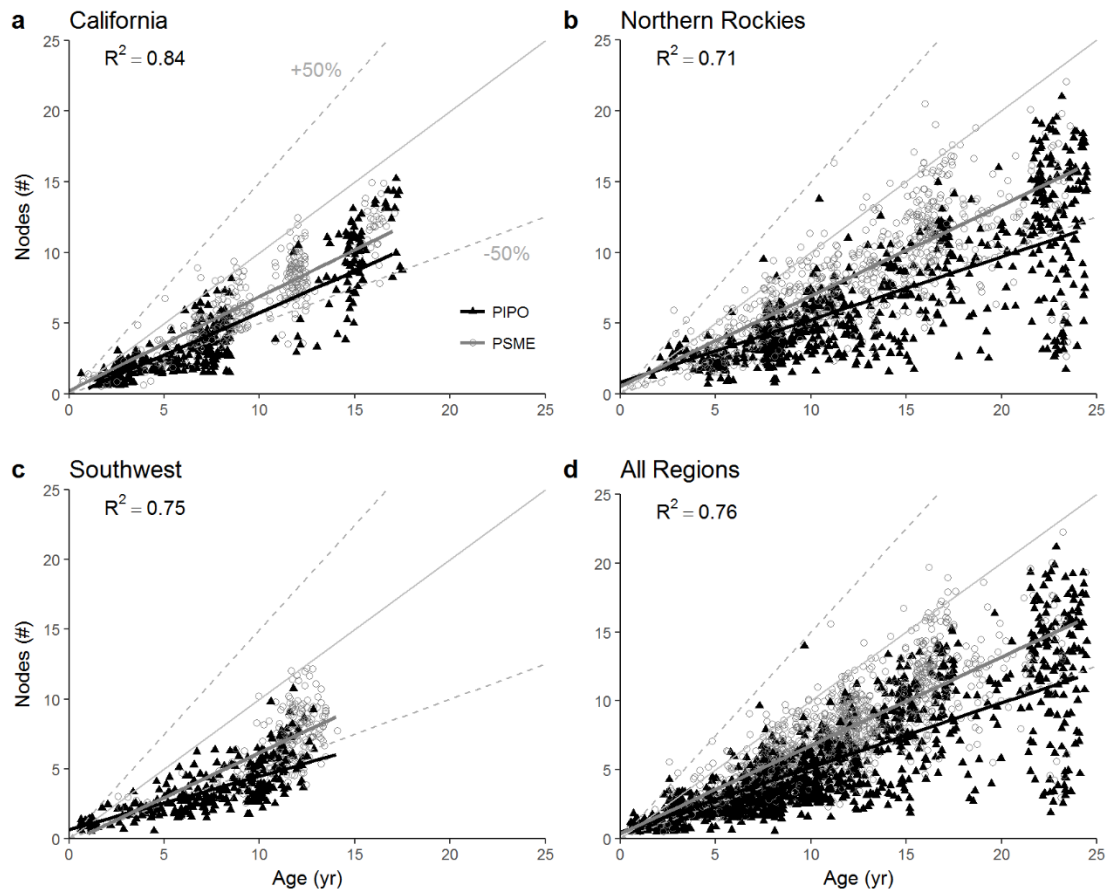
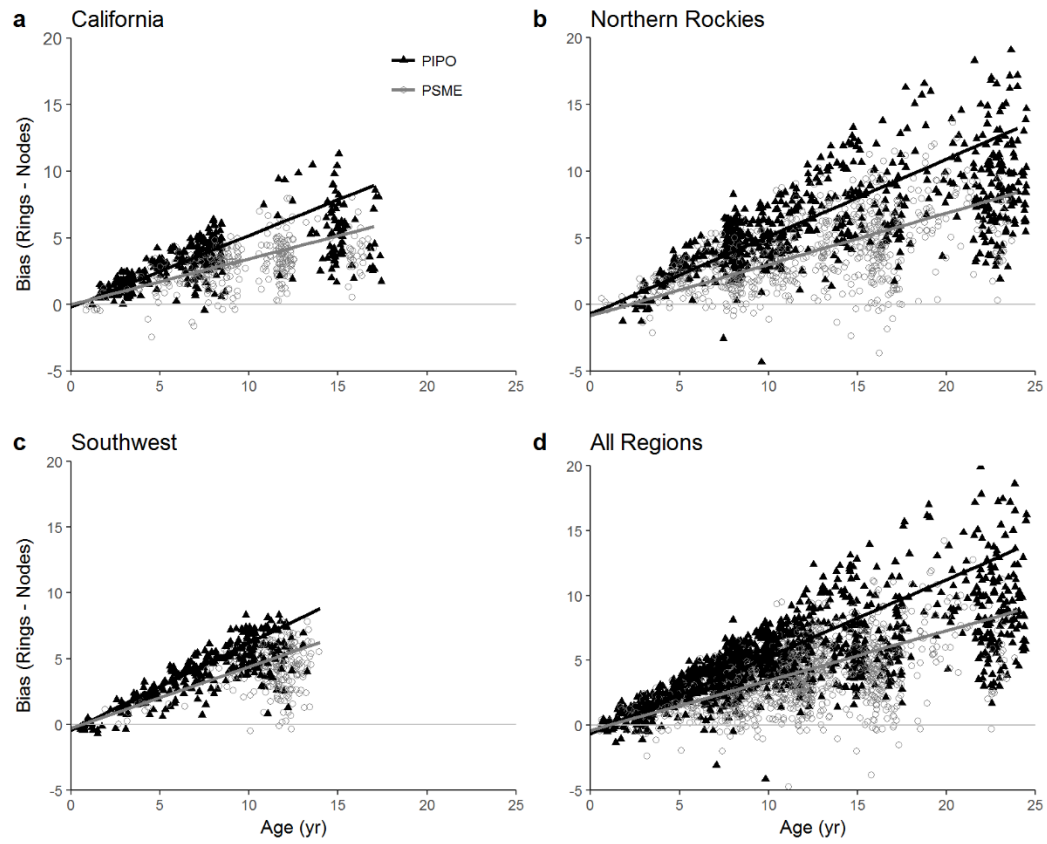


Figure 3



Supplementary materials

Appendix A.

Table A.1. Results from Welch's two-sample t-tests using 95% confidence testing whether the mean accuracy at varying levels of precision was significantly different among species for all regions combined. P-values were adjusted using a Bonferroni correction for an overall $\alpha = 0.05$.

Precision	t-value	df	p-value
+/- 0 yr	-2.49	2438	0.393
+/- 1 yr	-3.41	2497	0.037
+/- 2 yr	-6.81	2500	<0.001
+/- 5 yr	-10.76	2415	<0.001

Table A.2. Results from linear mixed effects of sample age as a function of node count, species, and their interaction (when significant at $p < 0.05$) as fixed effects, and a random site effect. 95% confidence intervals are shown in parentheses. Ponderosa pine serves as the reference level species for all estimates. R^2 values are from linear regressions of predicted values as a function of observed values for each model.

Region		Estimate	t-value	df	R^2
All Regions	Intercept	7.37 (6.55, 8.18)	17.76	2483	0.84
	Nodes	0.64 (0.61, 0.68)	34.01		
	Species	-0.44 (-0.86, -0.03)	-2.08		
	Nodes:Species	-	-		
California	Intercept	7.12 (5.54, 8.89)	8.44	625	0.90
	Nodes	0.41 (0.36, 0.46)	17.07		
	Species	0.12 (-0.40, 0.63)	0.45		
	Nodes:Species	-	-		
No. Rockies	Intercept	9.53 (8.30, 10.75)	15.30	1347	0.81
	Nodes	0.54 (0.49, 0.58)	21.57		
	Species	-1.95 (-2.64, -1.26)	-5.55		
	Nodes:Species	0.06 (0.00, 0.12)	1.99		
Southwest	Intercept	4.85 (4.26, 5.44)	16.17	505	0.69
	Nodes	0.86 (0.77, 0.95)	18.50		
	Species	3.96 (3.16, 4.76)	9.58		
	Nodes:Species	-0.53 (-0.64, -0.42)	-9.32		

*Bold values indicate significance at $p < 0.05$.

Table A.3. The 95% prediction intervals for linear mixed effects models of ring counts as a function of node counts, species, and their interaction as fixed effects, and a random site effect in each region and for all regions together. The mean prediction, lower (LL), and upper (UL) limits of the prediction interval are provided for each number of nodes. The number of nodes for which there are prediction intervals is limited to the range of node values in each region in our data.

Nodes (#)	All Regions					
	Mean	PIPO		Mean	PSME	
		LL	UL		LL	UL
0	7.37	1.71	13.03	6.93	1.26	12.59
1	8.01	2.60	13.43	7.53	2.11	12.95
2	8.66	3.47	13.84	8.14	2.95	13.33
3	9.30	4.34	14.26	8.75	3.79	13.71
4	9.95	5.20	14.70	9.36	4.61	14.10
5	10.59	6.05	15.14	9.96	5.42	14.51
6	11.24	6.88	15.59	10.57	6.22	14.92
7	11.88	7.71	16.04	11.18	7.01	15.34
8	12.52	8.54	16.51	11.79	7.80	15.77
9	13.17	9.35	16.98	12.39	8.58	16.21
10	13.81	10.16	17.47	13.00	9.35	16.65
11	14.46	10.96	17.95	13.61	10.11	17.11
12	15.10	11.75	18.45	14.22	10.87	17.56
13	15.74	12.54	18.95	14.82	11.62	18.03
14	16.39	13.32	19.46	15.43	12.36	18.50
15	17.03	14.09	19.97	16.04	13.10	18.98
16	17.68	14.86	20.49	16.65	13.83	19.46
17	18.32	15.62	21.02	17.25	14.56	19.95
18	18.97	16.38	21.55	17.86	15.28	20.44
19	19.61	17.14	22.08	18.47	16.00	20.94
20	20.25	17.88	22.62	19.08	16.71	21.44
21	20.90	18.63	23.17	19.68	17.42	21.95
22	21.54	19.37	23.72	20.29	18.12	22.46

Table A.3 continued.

Nodes (#)	California					
	Mean	PIPO		Mean	PSME	
		LL	UL		LL	UL
0	7.21	2.47	11.96	7.33	2.58	12.08
1	7.62	3.39	11.86	7.71	3.47	11.94
2	8.04	4.26	11.81	8.08	4.31	11.86
3	8.45	5.08	11.81	8.46	5.09	11.83
4	8.86	5.86	11.86	8.84	5.84	11.84
5	9.27	6.59	11.95	9.22	6.54	11.90
6	9.69	7.29	12.08	9.59	7.20	11.98
7	10.10	7.96	12.23	9.97	7.84	12.10
8	10.51	8.61	12.41	10.35	8.44	12.25
9	10.92	9.22	12.62	10.73	9.03	12.42
10	11.33	9.82	12.85	11.10	9.59	12.62
11	11.75	10.39	13.10	11.48	10.13	12.83
12	12.16	10.95	13.37	11.86	10.65	13.07
13	12.57	11.49	13.65	12.23	11.15	13.31
14	12.98	12.02	13.95	12.61	11.65	13.58
15	13.39	12.53	14.25	12.99	12.13	13.85
16	13.81	13.04	14.57	13.37	12.60	14.14
17	-	-	-	-	-	-
18	-	-	-	-	-	-
19	-	-	-	-	-	-
20	-	-	-	-	-	-
21	-	-	-	-	-	-
22	-	-	-	-	-	-

Table A.3 continued.

Nodes (#)	Northern Rockies					
	PIPO			PSME		
	Mean	LL	UL	Mean	LL	UL
0	9.53	1.84	17.21	7.57	-0.11	15.26
1	10.06	2.84	17.28	8.17	0.95	15.39
2	10.60	3.81	17.38	8.77	1.98	15.56
3	11.13	4.75	17.51	9.37	2.99	15.74
4	11.67	5.67	17.66	9.96	3.97	15.96
5	12.20	6.57	17.84	10.56	4.92	16.20
6	12.74	7.44	18.04	11.16	5.86	16.45
7	13.28	8.30	18.25	11.75	6.78	16.73
8	13.81	9.13	18.49	12.35	7.67	17.03
9	14.35	9.95	18.75	12.95	8.55	17.35
10	14.88	10.75	19.02	13.55	9.41	17.68
11	15.42	11.53	19.31	14.14	10.25	18.03
12	15.95	12.30	19.61	14.74	11.08	18.40
13	16.49	13.05	19.93	15.34	11.90	18.77
14	17.03	13.79	20.26	15.93	12.70	19.17
15	17.56	14.52	20.60	16.53	13.49	19.57
16	18.10	15.24	20.96	17.13	14.27	19.98
17	18.63	15.95	21.32	17.72	15.04	20.41
18	19.17	16.64	21.70	18.32	15.80	20.85
19	19.71	17.33	22.08	18.92	16.54	21.29
20	20.24	18.00	22.48	19.52	17.28	21.75
21	20.78	18.67	22.88	20.11	18.01	22.21
22	21.31	19.33	23.29	20.71	18.73	22.69

Table A.3 continued.

Nodes (#)	Southwest					
	Mean	PIPO		Mean	PSME	
		LL	UL		LL	UL
0	4.85	-2.31	12.01	8.81	1.64	15.98
1	5.71	-0.36	11.79	9.14	3.06	15.22
2	6.57	1.42	11.73	9.47	4.31	14.63
3	7.43	3.06	11.80	9.80	5.42	14.18
4	8.29	4.58	12.00	10.13	6.41	13.84
5	9.15	6.00	12.30	10.46	7.31	13.61
6	10.01	7.33	12.68	10.79	8.11	13.46
7	10.87	8.60	13.14	11.12	8.85	13.39
8	11.73	9.80	13.66	11.45	9.52	13.37
9	12.59	10.95	14.22	11.78	10.14	13.41
10	13.44	12.05	14.84	12.10	10.72	13.49
11	14.30	13.12	15.49	12.43	11.25	13.61
12	15.16	14.16	16.17	12.76	11.76	13.77
13	16.02	15.17	16.88	13.09	12.24	13.94
14	-	-	-	-	-	-
15	-	-	-	-	-	-
16	-	-	-	-	-	-
17	-	-	-	-	-	-
18	-	-	-	-	-	-
19	-	-	-	-	-	-
20	-	-	-	-	-	-
21	-	-	-	-	-	-
22	-	-	-	-	-	-

Table A.4. Results from a linear mixed effects model of bias (ring counts - node counts) as a function of sample age (yr), species, region, vertical growth rate (height/age), and their two-way interactions as fixed effects with site as a random effect. The species by growth rate interaction was not significant and therefore excluded from the final model. 95% confidence intervals are shown in parentheses. Ponderosa pine serves as the reference level species for all estimates. California serves as the reference level region for all estimates. R^2 from a linear regression of predicted values as a function of observed values was 0.68.

Fixed Effects	Estimate	df	t-value
Intercept	0.01 (-0.56, 0.58)	2475	0.04
Age	0.59 (0.55, 0.64)	2475	24.85
Species	0.21 (-0.07, 0.49)	2475	1.45
RegionNR	0.02 (-0.65, 0.70)	52	0.07
RegionSW	-0.16 (-0.93, 0.61)	52	-0.41
Growth rate	-0.04 (-0.08, -0.02)	2475	-3.66
Age:Species	-0.19 (-0.22, -0.17)	2475	-12.99
Age:RegionNR	0.04 (0.00, 0.09)	2475	1.90
Age:RegionSW	0.12 (0.07, 0.17)	2475	4.82
Age:Growth rate	-0.01 (-0.02, -0.01)	2475	-8.80
Species:RegionNR	-0.35 (-0.66, -0.04)	2475	-2.20
Species:RegionSW	-0.07 (-0.43, 0.28)	2475	-0.41
RegionNR:Growth rate	-0.12 (-0.16, -0.08)	2475	-5.83
RegionSW:Growth rate	-0.01 (-0.05, 0.02)	2475	-0.76

*Bold t-values were statistically significant at $p < 0.05$.

Table A.5. Accuracy of node counts and bud-scar counts across varying levels of precision in a subset of samples from the Northern Rockies (n = 757). Accuracy is expressed as the percentage of samples with field-estimated ages that matched ring counts.

Method	Precision (+/- year)			
	+/- 0 yr	+/- 1 yr	+/- 2 yr	+/- 5 yr
Bud Scars	7%	19%	29%	63%
Nodes	7%	17%	25%	65%

Supplementary Figures

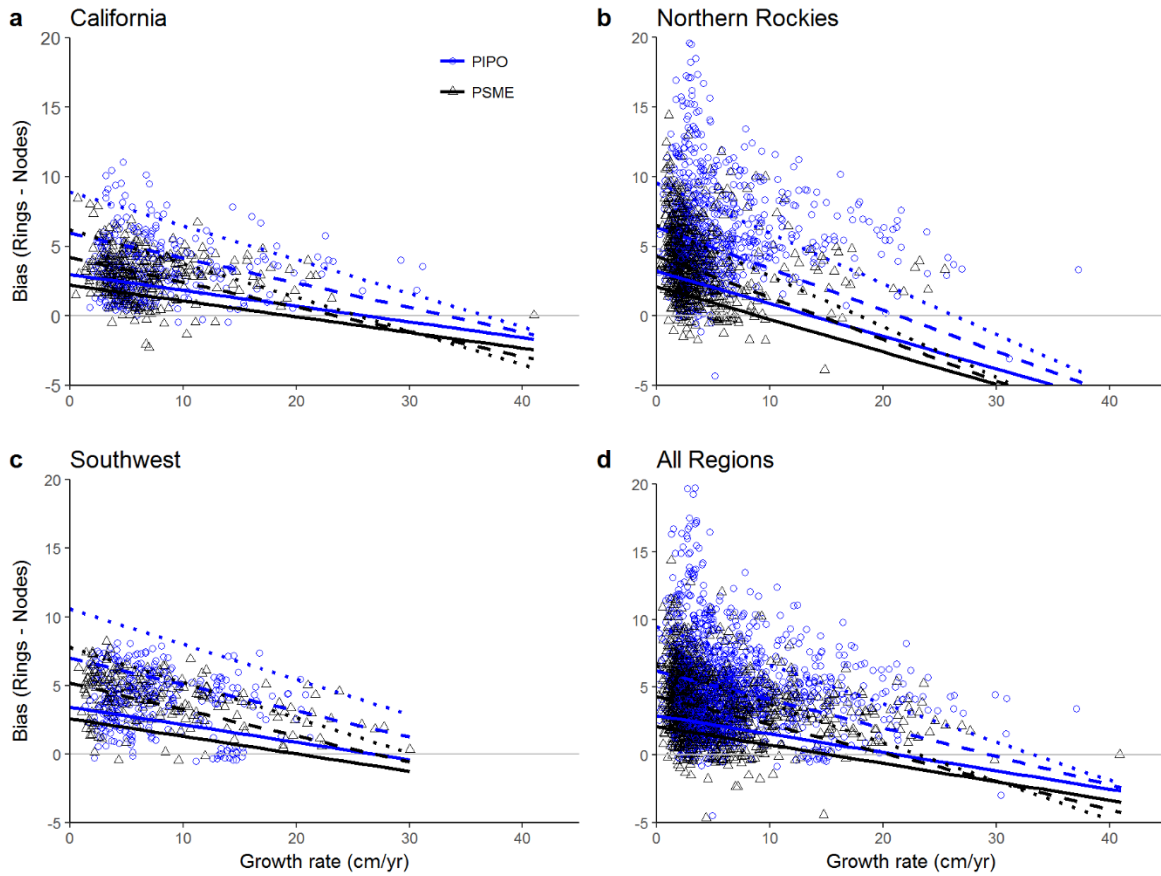


Figure A.1. Bias between ring counts and node counts as a function of growth rate of the samples from (a) California, (b) Northern Rockies, (c) Southwest, and (d) all regions. Blue circles and regression line are for ponderosa pine samples; black triangles and regression line are for Douglas-fir samples. All points are jittered for visual clarity. Regression lines are from a linear mixed effects model of bias (ring counts - node counts) as a function of sample age (yr), species, region, vertical growth rate (height/age), and their two-way interactions with site as a random effect. The species:growth rate interaction was not significant and therefore excluded from the final model. Age was held constant at 5 (solid line), 10 (dashed line), and 15 (dotted line) years for prediction. R^2 from a linear regression of predicted values as a function of observed values was 0.68.

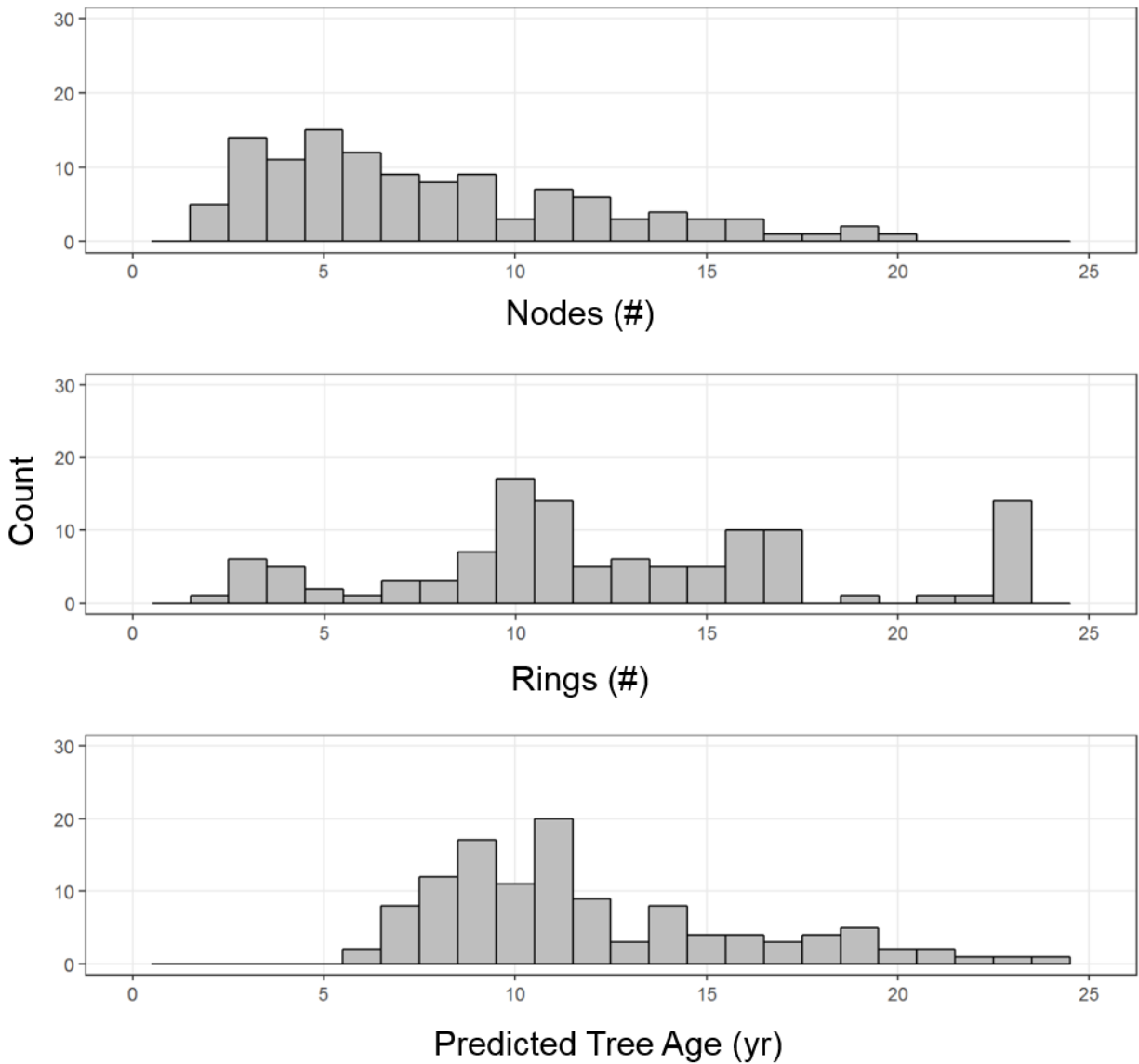


Figure. A.2. Estimated tree age from observed node counts in the field (top panel), precise ring counts (middle panel), and predicted ring counts using our corrective tool (bottom panel).

Estimates are from a 20% holdout dataset for all samples combined across regions and species.

The tool uses a linear mixed effects model to predict tree age as a function of field-based node counts, species, and their interaction as fixed effects, and a random effect of site.

Chapter II: Annual climate impacts tree growth and post-fire regeneration in low-elevation ponderosa pine and Douglas-fir forest of the northern Rocky Mountains

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2.1 Abstract

Low-elevation forests near the edge of their climatic tolerance may be particularly vulnerable to future climate warming and increased fire activity. We studied the impacts of climate variability on low-elevation forests in the U.S. northern Rocky Mountains by quantifying how post-fire regeneration and radial growth varied with annual climate. We reconstructed regeneration rates of *Pinus ponderosa* and *Pseudotsuga menziesii* at 33 sites that burned between 1992 and 2007, using dendrochronology to age seedlings at the root-shoot boundary. We also measured radial growth in seedlings, and in adult trees from 12 additional sites. To quantify the relationship between regeneration and climate, we characterized seasonal climate conditions before, during, and after annual recruitment pulses using superposed epoch analysis. To quantify growth-climate relationships, we performed moving regression analysis from 1901-2015, for each species and for juvenile and adult life stages.

Climatic conditions favoring regeneration and tree growth differed between species, suggesting species-specific responses to future climate change. Water deficit and temperature were significantly lower than average two years prior and during years with ponderosa pine regeneration pulses, suggesting that antecedent and germination-year climate limits regeneration. Growing degree days were significantly higher than average during years with Douglas-fir regeneration pulses, but water deficit was significantly lower one year following pulses, suggesting moisture sensitivity in two-year-old seedlings. Growth was sensitive to water deficit,

but effects varied between life stages, species, and through time. Increasing water deficit corresponded with reduced adult growth of both species. Increases in maximum temperature and water deficit corresponded with increases in juvenile growth of both species in the early 20th century but strong reductions in growth for only juvenile ponderosa pine in recent decades. Changing sensitivity of growth to climate variability suggests that directional increases in temperature and moisture stress may be pushing these species towards the edge of climatic tolerance. Our study demonstrates the increased vulnerability to post-fire regeneration failures and decreased growth in dry mixed-conifer forests, given increases in temperature and drought. Shifts towards unfavorable conditions for regeneration and juvenile growth may alter the composition and resilience of low-elevation forests to future climate and fire activity.

Key words: climate change, conifer seedlings, dendrochronology, growth-climate relationships, *Pinus ponderosa*, *Pseudotsuga menziesii*, Rocky Mountains tree rings, tree regeneration

2.2 Introduction

Widespread changes in climate and disturbance regimes, including prolonged drought and increases in the size and frequency of wildfires, have raised concerns regarding forest resilience to environmental change (Dale et al. 2001, Westerling et al. 2006, van Mantgem et al. 2009, Abatzoglou and Williams 2016, Seidl et al. 2017). Wildfires shape ecosystem patterns and processes by changing vegetation structure and composition, and nutrient and water availability (Neary et al. 2005, Smithwick 2011). Across western North America, many tree species possess traits that are well suited for specific fire regimes, including thick bark that allows survival of low-intensity surface fires, or serotinous cones that allow regeneration after high-intensity crown fires (Lotan 1976, Fowler and Sieg 2004). However, climatically driven increases in the frequency of large wildfires in recent decades (Westerling et al. 2006, Littell et al. 2009, Abatzoglou and Williams 2016) may lead to increased tree mortality and declines in post-fire tree regeneration (van Mantgem et al. 2009, Stevens-Rumann et al. 2018). Further, climatic warming and increased drought frequency may also impact tree growth, potentially reducing net primary productivity enough to alter the global carbon cycle (Allen et al. 2010, Zhao and Running 2010, Restaino et al. 2016). The combined stressors of climate change and increasing fire activity will therefore have complex ecological impacts on forest ecosystems. Quantifying and anticipating these impacts requires understanding the underlying controls on tree establishment, growth, and survival.

Recent studies highlight the importance of climate and fire activity on establishment and growth in dry mixed-conifer forests across the western U.S. In particular, the ability of forest ecosystems to return to pre-fire states – forest resilience to wildfire (Holling 1973) - depends upon the interactive effects of numerous abiotic and biotic factors, related to the nature of a fire,

post-fire environmental conditions, and the life history traits of species dominating pre- and post-fire landscapes (e.g. Johnstone et al. 2016). Fire severity and pre-fire forest composition strongly affect rates of post-fire tree establishment by determining post-fire seed availability (Donato et al. 2016, Kemp et al. 2016). Given adequate seed sources, seedling establishment and survival are then particularly sensitive to seasonal and annual climate (Dobrowski et al. 2015, Rother et al. 2015, Harvey et al. 2016, Stevens-Rumann et al. 2018). Germination requires energy and moisture, while subsequent seedling mortality is high during particularly warm and dry growing seasons (Savage et al. 1996, van Mantgem et al. 2009, Williams et al. 2012, Rother et al. 2015). Several studies highlight abundant regeneration, both following and independent of wildfire, occurring during cooler and wetter growing seasons, likely due to the importance of soil moisture and low heat stress (League and Veblen 2006, Rother et al. 2015, Donato et al. 2016, Rother and Veblen 2017). The combined effects of changing climate and fire activity could therefore lead to declines in post-fire regeneration in lower-treeline forests throughout western North America, due to distance seed sources and harsh climate conditions (Welch et al. 2016, Stevens-Rumann et al. 2018).

Once established, radial growth is also limited by temperature and moisture availability, reflecting energy and water demands for photosynthesis and carbon assimilation (Fritts 1965, Carrer and Urbinati 2006, Littell et al. 2008, Lloret et al. 2011). Specifically, water deficit has been shown to strongly limit adult radial growth in Douglas-fir and ponderosa pine (Littell et al. 2008, Adams et al. 2014). However, evidence also suggests that climate conditions limit radial growth in different ways throughout different life stages, for example between juvenile vs. adult trees (Ettinger and HilleRisLambers 2013). Understanding the controls of juvenile radial growth is critical for understanding the future fate of mature trees. For example, higher growth in

juveniles is associated with competitive success and resistance to and recovery following stress events, such as drought (Landis and Peart 2005, Lloret et al. 2011, de la Mata et al. 2017).

The sensitivity of tree growth to climate can also change over time, due to climate variability or prolonged periods of cool/wet or warm/dry conditions (Carrer and Urbinati 2006, Hayles et al. 2007, Olivar et al. 2015). Increasing precipitation variability, along with underlying directional trends in temperature, for example, may alter growth sensitivity due to underlying physiological thresholds being crossed and/or the increased frequency of extreme climate conditions (Carrer and Urbinati 2006, Hayles et al. 2007). Finally, local conditions, such as competition or changes in microclimate, can also modify growth responses to climate over time (Ettinger and HilleRisLambers 2013, Carnwath and Nelson 2016). The possibility of changing growth-climate relationships further complicates our understanding of how future climate may impact tree regeneration, growth, and ultimately survival.

To better understand the effects of climate variability and climate change on post-fire conifer forests, our study addressed the following questions in low-elevation forests of the U.S. northern Rocky Mountain (hereafter Northern Rockies): (1) how does growing season climate affect the rate of post-fire regeneration; and (2) how has growing season climate affected radial growth in juveniles and adults over the last century? We address these questions using precise establishment years and annual growth rings from 1431 seedlings from 33 sites, and annual growth rings from 427 mature trees from 12 sites, from the two dominant lower-treeline species in the Northern Rockies: ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). We expected that cooler and wetter growing-season conditions would be associated with regeneration pulses and higher annual radial growth due to adequate soil moisture and the absence of heat stress (Littell et al. 2008,

Adams et al. 2014, Rother et al. 2015). Further, we expected that these patterns would be more pronounced in juveniles because of their increased sensitivity to environmental conditions (Savage et al. 2013, Dobrowski et al. 2015). Finally, we expected that growth responses to climate would change over the last century due to climate variability and climate change towards conditions closer to species' climatic tolerance for growth.

2.3 Methods

2.3.1 Study Region

The study was conducted in the Northern Rockies of Idaho and Montana in dry mixed-conifer forests dominated by ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Fig. 1). The Northern Rockies experience warm, dry summers and cool, wet winters. Terrain is mountainous, often characterized by steep topography. Mean annual temperature, averaged across all study sites, was 6.1 °C, and mean total annual precipitation was 582 mm, with an average of 175 mm as snow (30-yr normals, 1981-2010) (Daly et al. 2008, PRISM Climate Group 2017).

Climate has changes significantly across the study area over the past century. For example, growing-season temperatures increased from a mean (stdev.) of 12.1 (0.7) °C during the period 1901-1930 to 13.1 (0.7) °C from 1986-2015 ($t = -5.6$, $p < 0.001$) (Fig. 2). Growing-season precipitation also increased, but not significantly, from a mean of 233 (57) mm during the period 1901-1930 to 242 (50) mm from 1986-2015 (Fig. 2). Inter-annual climate variability was high in the early 20th century and late 20th century, relative to the mid-20th century and early 21st century (Fig. A1). The 1960s and 1970s exhibited comparatively low climatic variability (Fig. A1).

2.3.2 Site selection

Sites were separated into two sampling units: (a) 33 sites were used to destructively sample seedlings and saplings that regenerated after fires that burned between 1992 and 2007, including 12 sites previously sampled by Kemp et al. (2016) (hereafter “seedling sites”); (b) 12 additional sites, which burned between 1910 and 1987, were used to sample mature trees (hereafter “tree-core sites”) to establish records of regeneration and growth spanning most of the

20th century (Fig. 1). The suite of sites was designed to allow inference into the mechanisms determining the rate and pattern of post-fire regeneration and tree growth. Sites were limited to those in the warmer, drier portion of the range of ponderosa pine and Douglas-fir, defined as areas exceeding the 40th (tree-core sites) or 50th (seedling sites) percentile of climate water deficit for each species within their geographic range in the Northern Rockies (defined based on 30-yr normal, 1981-2010) (Fig. 1). The lower criteria for tree-core sites was necessary to obtain areas that had not experienced fires in more recent decades.

Landfire 30 x 30 m vegetation-type data were used to select areas classified as ponderosa pine and/or Douglas-fir forests (<https://www.landfire.gov/vegetation.php>) within the Northern Rockies ecoregion. Sites targeting recent fires (1992-2007) burned at moderate or high severity, as classified by the Monitoring Trends in Burn Severity program (Finco et al. 2012). For sites targeting older fires (1910-1990), a fire atlas published by Morgan et al. (2014) was used to sample across a range of fire years spanning 1900 through 1987. As satellite-derived fire severity data are not available for fires prior to 1984, burn severity was estimated based on stand structure. To aid in site accessibility, we included a 1-km buffer around roads for the 33 sites that experienced more recent fires, and a 5-km buffer around roads for the 12 sites representing older fires. Destructive sampling after more recent fires necessitated closer access due to the high volume of sample collection at each site. Given these site requirements, we used a geographic information system (ArcMap 10.4) to randomly assign points within the study area, considered as potential sites. Each potential site was assessed for distance-to-seed-source and post-fire management. To specifically target post-fire regeneration, sites were only included if they were within 100 m of a potential seed source, and all sites were free of post-fire planting or salvage logging. In the case where randomly placed points exceeded this distance threshold, points were

moved to within 100 m of the nearest moderate severity patch in a randomly selected cardinal direction.

2.3.3 Field Sampling and Measurements

Sampling was completed in the summers of 2016 and 2017, from late May to early July. At all sites we used 60-m long belt transects, with transect width varying from 2-40 m, based on the goal of sampling approximately 30 individuals of each species per site. Tree seedlings were cut with a hand saw approximately 10 cm above the root collar, excavated to approximately 10 cm below the root collar, and cut to obtain the root-shoot boundary. Across all 33 seedling sites, we collected approximately 1500 individuals. For tree-core sites, we obtained tree cores at the lowest possible point on the main stem of the tree to minimize corrections needed to account for the age of the tree at core height. If pith was missed in the first core attempt, up to four cores per tree were obtained to reach pith. Trees with severe heart rot or damage were excluded from the sampling effort. In total, we collected tree cores from 427 trees across the 12 sites.

2.3.4 Dendrochronology

For each seedling sample, we prepared multiple cross sections above and below the estimated root-shoot boundary to identify germination dates with annual precision, as described in detail by Hankin et al. (In Press). Briefly, seedlings were cut into consecutive 2.5-cm intervals and sanded with successively finer sandpaper (to 600-1500 grit) to reveal ring boundaries (Speer 2010). We evaluated growth rings on samples below, near, and above the root-shoot boundary (Telewski 1993, Urza and Sibold 2013, Rother and Veblen 2017) at 10-40x using a Nikon SMZ stereomicroscope. The number of rings on the cross section that included the lowest appearance of pith was used to estimate tree age. For tree-core samples, cores were mounted onto wooden

bases and sanded with successively finer sandpaper, up to 600 grit. We then counted growth rings under the microscope, keeping a list of narrow or wide marker rings (Yamaguchi 1990).

To test the repeatability and precision of our lab protocol for ageing seedlings, we performed independent recounts on a random subset of 555 samples among three analysts, including the dataset reported here and additional samples from across two other regions in the western U.S. (Hankin et al. In Press). We scored our confidence level in the ring counts on a qualitative scale of 1 (lowest confidence) to 4 (highest confidence), and restricted any subsequent analyses to samples receiving a score of 3 or 4. If ring boundaries were indistinct or pith dates were otherwise ambiguous, we removed the sample from the final dataset. Given these precautions in precise dendrochronological dating, we analyze seedling ages in one-year bins in subsequent analyses.

Tree-core ring counts were also scored on the same confidence scale outlined above. If more than one core was taken from a single tree, the core with the highest count confidence was used for cross-dating and further analysis. In cores lacking pith, years to pith were estimated using a pith estimation tool available in the computer program *CooRecorder*. In total, 57% of our cores contained pith, and the mean (stdev.) distance to pith was 7.9 mm (12.5 mm). 76% of samples were within 10 mm of pith. Pith dates in tree cores were corrected for missing years due to core height using an age-height relationship developed from the seedling samples. Average (stdev.) core height from among all tree-core samples was 19.6 (7.6) cm.

Once samples were counted, we captured high-resolution images (1200 dpi) of cross-sections and cores for further ring-width analysis, using an Epson Expression 11000XL scanner. If seedlings were too small for scanning, they were photographed under the microscope at 1-7x magnification using a SPOT Idea CMOS digital camera. Ring widths were measured from the

digital images using the computer program CooRecorder, and were then exported for further analysis using CDendro. While we recorded visual marker years, the young age of the seedling samples did not allow for more formal crossdating methods. For tree core samples, we also performed statistical crossdating at the site level using COFECHA (Holmes 1983, Grissino-Mayer 2001).

2.3.5 Climate Data

We used 1-km resolution monthly climate data from ClimateNA for the period of 1901-2015 (Wang et al. 2016). The reference climate grids are based on the Parameter Regression of Independent Slopes Model (PRISM) interpolation method (PRISM Climate Group 2017). Historical data since 1901 are based on the CRU-TS 3.22 dataset (Mitchell and Jones 2005). Monthly climate variables were summarized to the growing season from April to September. Variables included maximum, minimum, and average temperatures, precipitation, growing degree days, and water deficit. ClimateNA defines water deficit as the difference between reference evapotranspiration, calculated using air temperature (Hargreaves and Samani 1985), and precipitation.

2.3.6 Regeneration Analyses

Age structures were developed at annual resolution for seedling sites and using 5-yr bins for adults sampled with tree cores. Age structures were analyzed visually and statistically to identify regeneration pulses (Rother and Veblen 2017). At each site, we defined a regeneration pulse as any year where $\geq 20\%$ of total seedlings at a site germinated, consistent with the threshold used for identifying regeneration pulses in Rother and Veblen (2017). At sites with both ponderosa pine and Douglas-fir present ($n = 9$ out of 33), this was done for each species individually. Based

on this 20% threshold, if a regeneration pulse occurred in two or more years in a row, we identified only the year with the largest pulse as a regeneration event.

To quantify the relationship between regeneration and climate, we compared regeneration events to climate conditions using superposed epoch analysis (SEA) in R v3.3.2 (R Core Team 2017). Specifically, we used SEA to test the null hypothesis that seasonal climate conditions before, during, or after a regeneration event were not significantly different from average. This analysis was used for only seedling sites because of limitations with the resolution of age structures using tree cores, as well as the small number of regeneration pulses at tree-core sites. We assessed statistical significance of the patterns revealed in the SEAs using 95% confidence intervals, generated from 10,000 simulations under the null hypothesis. To account for autocorrelation in the climate record, we randomly reordered climate data in two-year chunks, selecting a random start year in which to begin the grouping for every simulation (Adams et al. 2003). Because of directional shifts in climate in recent decades (Fig. 2), we performed the SEAs using detrended climate anomalies, by subtracting the 30-yr moving mean (i.e., +/- 15 year) from the raw value for each year for each site.

2.3.7 Radial growth analyses

Raw ring widths were graphically examined for anomalies, temporal trends, and age-related growth trends. We standardized ring widths by calculating basal area increment (BAI) with the ‘dplr’ package in R (Bunn 2008, Bunn et al. 2017), and then calculating a z-score for each series (i.e., tree). Site-level chronologies were developed by averaging standardized BAI in a given year across all individuals at a site, producing a mean annual BAI index (hereafter “BAI index”) for each site. Mean chronologies were also developed for each species and each life stage across all sites by averaging the BAI index in a given year across all samples within a given category.

Life stage was defined as either “juvenile,” representing the first 25 years of radial growth, or “adult,” representing radial growth beyond 25 years.

Growth sensitivity to climate for each species and life stage was examined using continuous linear regressions with growth as a function of growing-season climate to understand the strength and direction of climatic effects on growth. We also performed a “global” correlation analysis (i.e., including all years from 1901-2015) to understand overall trends in the significance and sign of climate effects on growth. Moving regressions were performed in 30-year, overlapping windows, starting with the period 1901-1930 and moving in 1-yr increments through the period 1986-2015. We required at least 10 individuals in a given year to perform these analyses, and thus the sample size varied over time. Continuous growth-climate regressions were performed using the mean chronology for each category of species and life stage, with current growing season climate metrics, averaged across all sites that contributed to each mean chronology, using the R package ‘TTR’ (Ulrich 2018). The slopes and 95% confidence intervals from continuous linear regressions reveal if and how growth sensitivity to climate has changed over time, and whether these relationships are significant.

2.4 Results

Approximately 96% of our total samples met our confidence criteria for age estimates. In total, we aged 1431 seedling samples (681 ponderosa pine and 750 Douglas-fir) and 427 tree-core samples (157 ponderosa pine and 270 Douglas-fir). Ring-count based ages varied from 1 to 24 yr in seedlings, and approximately 37 to 277 yr in tree-core samples. Seedling ring counts were also robust to validation by random, independent recounts, with a mean (stdev.) difference in ring-count-based ages among three analysts of 0.298 (0.461) years.

We sampled an average of 43 seedlings per site for our regeneration analyses, and from these we observed regeneration pulses (i.e., > 20% of total site recruitment in one year) at 21 out of 23 Douglas-fir sites and at all ponderosa pine sites (Fig. 3). Ponderosa pine and Douglas-fir regeneration pulses occurred on average 3.3 yr and 3.4 yr after fires (median = 2.5 yr, 2.0 yr), respectively. We sampled an average of 28 trees at each tree-core site, which displayed largely continuous regeneration. Most trees germinated in the early 20th century, even at sites that burned in the mid- or late-20th century (Fig. 4). There was limited evidence of low-severity fire occurring at tree-core sites, including two sites (burned in 1961 and 1979) with charcoal present on several trees to a scorch height of about 0.5 m. There was an average of 1 fire scar per site, typically on ponderosa pine. Little regeneration occurred after seemingly low- to moderate-severity fires at these sites.

2.4.1 Regeneration-climate Analyses

We identified 44 regeneration pulses across the 33 seedling sites (Fig. 3). Ponderosa pine sites tended to have more distinct regeneration pulses than Douglas-fir sites. Climatic conditions concurrent with regeneration pulses differed between species. Growing-season water deficit and temperature metrics (i.e., growing degree days, maximum temperature) were significantly lower

than average two years prior to and during the year of ponderosa pine regeneration pulses ($p < 0.05$) (Fig. 5). In contrast, growing degree days were significantly higher than average during the year of Douglas-fir regeneration pulses, but water deficit and maximum temperatures were significantly below average one year after regeneration pulses ($p < 0.05$). These patterns were largely consistent when using a more conservative 30% threshold to define regeneration pulses, indicating robustness of our results to the definition of a regeneration pulse (Fig. A3).

2.4.2 *Growth-climate Analyses*

Tree-core samples exhibited high intra-site variability in growth patterns. Series intercorrelations from statistical cross-dating at tree-core sites ranged from 0.395 at our southernmost site to 0.691 in one of our northernmost sites. Most samples exhibited periods of slow growth in the 1890s, 1930s, and 1970s (Figs. 6, A4-7). Ponderosa pine adults and Douglas-fir juveniles exhibited rapid growth in the 1950s.

Douglas-fir adult radial growth (i.e., BAI z-score) exhibited stronger correlations with growing-season climate than did adult ponderosa pine, when considering all years combined (Table 1). Douglas-fir adult radial growth was most strongly related to growing-season water deficit ($r = -0.46$), followed closely by growing-season precipitation ($r = 0.45$) (Table 1). Ponderosa pine adult growth was most strongly related to growing-season precipitation ($r = 0.37$), followed closely by mean growing-season minimum temperature ($r = -0.33$). Juvenile growth in both species was most strongly related to growing-season minimum temperature ($r = 0.38$), followed closely by growing degree days ($r = 0.35$ for ponderosa pine, 0.31 for Douglas-fir). Overall, adult growth of both species was more strongly correlated to moisture and temperature, while juvenile growth was more strongly correlated with temperature.

The effect of climate on growth, as indicated by the slope of growth-climate regressions, was relatively static through time for adults of both species; in contrast, juvenile sensitivity to and climatic effects on growth changed significantly through time (Fig. 8). Increased water deficit was consistently related to decreased growth in adult Douglas-fir throughout the 20th and early-21st centuries. Similarly, water deficit consistently related to decreased growth in adult ponderosa pine in the latter half of the study period. An increase of one standard deviation in water deficit corresponded to a -0.2 to -0.4 standard deviation change in growth at varying time periods throughout the 20th and early 21st centuries. The effect of climate on juvenile growth was more temporally variable, with heightened sensitivity in ponderosa pine seedlings (Fig. 8). For example, a one standard deviation increase in water deficit corresponded with 0.2 standard deviation decrease in ponderosa pine juvenile growth during the 1930s and 1940s, and a 0.8 standard deviation decrease in recent decades. However, the same increase in water deficit corresponded with an approximately 0.2 standard deviation *increase* in juvenile ponderosa pine growth in the early 20th century. Growth responses to maximum temperature showed the same temporal pattern. Juvenile Douglas-fir growth was generally less sensitive to climate, and did not exhibit significant shifts over time. Increasing water deficit and maximum temperature corresponded to reduced growth in juvenile Douglas-fir from the 1930s through 1950s, while increasing minimum temperature corresponded to increased growth in the 1960s.

2.5 Discussion

The resilience of lower-treeline forests to the combined stressors of changing climate and fire activity will depend on how climate and fire impact post-fire tree regeneration and growth. Our results highlight the complex effects of growing-season climate on post-fire tree regeneration and radial growth, providing further understanding of the drivers of post-fire forest development in low-elevation forests of the Northern Rockies. While availability of seed sources is a dominant driver of post-fire tree regeneration, the sensitivity of post-fire regeneration and growth to moisture availability and temperature suggest that future changes in climate will lead to overall declines in tree regeneration and growth, even where seed sources are abundant. Our results also suggest that increasing temperatures at lower treeline, coupled with prolonged moisture stress, may lead to species compositional shifts, due to differential effects of climate on regeneration and growth between species.

2.5.1 *Climate and post-fire conifer regeneration*

Post-fire tree regeneration in lower-treeline forests occurred under specific growing-season conditions, suggesting sensitivity of regeneration to ongoing and future climate change. Our study adds to the growing body of literature highlighting the importance of moisture availability for seedling establishment and survival of ponderosa pine (League and Veblen 2006, Rother et al. 2015, Rother and Veblen 2017) and Douglas-fir (Rother et al. 2015, Tepley et al. 2017). Post-fire regeneration pulses of ponderosa pine occurred during cooler and wetter growing seasons (Fig. 5), likely reflecting the moisture demands for germination, or the high rates of germinant mortality under warm and dry conditions (Rother et al. 2015). This is consistent with several studies in low-elevation forests in the southern Rocky Mountains, where

regeneration pulses of ponderosa pine coincided with growing season conditions that were cooler and wetter than average (League and Veblen 2006, Rother and Veblen 2017). Together, these results suggest that ponderosa pine regeneration is moisture limited, even in lower-treeline forests of the Northern Rockies, which are on average cooler and wetter than lower-treeline forests in the southern Rocky Mountains (Stevens-Rumann et al. 2018). These results are consistent with evidence and expectations of reduced tree regeneration with climatic warming (Welch et al. 2016, Stevens-Rumann et al. 2018), as harsh (micro-) climate conditions decrease seedling survival (Rother et al. 2015).

Our results also suggest a potential link between climate and seed production in ponderosa pine, through cooler and wetter climate conditions two years prior to regeneration pulses (Fig. 5). Other studies in the Rocky Mountains have linked seasonal climate to cone and seed production, although climate effects on seed production are highly variable within and between regions (Mooney et al. 2011, Keyes and Manso 2015). Keyes and Manso (2015) found that wetter conditions were associated with both years of higher cone and seed production in the Northern Rockies, consistent with our finding of cooler and wetter conditions two years prior to regeneration pulses. Mooney et al. (2011) also found that cooler, wetter conditions were associated with increased pollen and ovule meiosis in the southern Rocky Mountains, but two years prior to seed production, corresponding to three years prior to a regeneration pulse. In addition, we found warmer- and drier-than-average conditions three years prior to ponderosa pine regeneration pulses, conditions shown to increase reproductive output and initiate cone production in many conifer species (Owens and Blake 1985, Krannitz and Duralia 2004, Roland et al. 2014, Crain and Cregg 2017). However, this pattern at least in part reflects the warm, dry conditions that are associated with regionally extensive burning (Heyerdahl et al. 2008, Morgan

et al. 2008), rather than tree biology, as the median lag between fires and regeneration pulses was three years.

Regeneration pulses of Douglas-fir occurred under different climate conditions than in ponderosa pine. Post-fire regeneration of Douglas-fir coincided with growing seasons with above-average growing degree days, and was followed by a year with cooler- and wetter-than-average growing season conditions (Fig. 5). This result was unexpected, as previous findings have highlighted the importance of above-average moisture availability during the year of Douglas-fir regeneration in low-elevation forests in the southern Rocky Mountains (Rother et al. 2015, Rother and Veblen 2017). The pattern found here is consistent with the importance of moisture availability, but it occurred one year after germination. This may reflect the importance of moisture in limiting second-year mortality in Douglas-fir seedlings (Miller and Halpern 1998, Bai et al. 2000). Further, wetter sites tend to have higher post-fire regeneration densities for Douglas-fir (Tepley et al. 2017), indicating that overall, increased moisture availability promotes Douglas-fir regeneration and survival. Alternatively, variations in species traits between Douglas-fir and ponderosa pine seedlings (Miller and Johnson 2017), or abiotic differences among sites may account for these patterns. For example, water deficit from 1992-2015 was significantly higher at seedling sites dominated by ponderosa pine (mean [stdev.] = 556 [69] mm) vs. Douglas-fir (mean [stdev.] = 495 [75] mm) ($df = 45$, $t = 2.9$, $p = 0.01$) (Fig. 1), suggesting that differences in water balance may explain diverging climate effects on regeneration patterns of each species. The median proportion of trees contributing to pulse years for ponderosa pine and Douglas-fir was not significantly different (Wilcoxon rank-sum test, $p = 0.60$, $n = 22, 24$, respectively), but the higher shade tolerance of Douglas-fir relative to ponderosa pine (Minore 1979) may allow for more continuous recruitment over time. It is

unlikely this pattern reflects biotic competition with ponderosa pine, as the two species co-occurred at only 9 of 33 sites.

While the inferred impacts of climate on regeneration were largely consistent with existing literature, an additional limitation to our interpretation for both species was our inability to cross-date seedling samples, which could lead to underestimations of tree age. However, our definition of a regeneration pulse helps guard against this potential source of uncertainty, as we required at least 20% of the regeneration at a site to occur in a given year to be considered a pulse. We would not expect missing rings to be so pervasive as to mislead identification of clear regeneration pulses.

2.5.2 Climate limitations on conifer growth

Following germination and establishment, tree growth is critical for forest persistence. The sensitivity of growth to climate documented here implies species-specific responses to ongoing and future climate change. Increased moisture availability corresponded to increased growth in adult Douglas-fir throughout the study period (Table 1, Figs. 8, A6), consistent with clear moisture limitations to growth found across the northwestern United States (Littell et al. 2008, Restaino et al. 2016). These findings suggest that moisture demand (i.e., high water deficit) is more limiting to physiological processes than either insufficient or excess energy. Increased moisture availability was also associated with increased growth in adult ponderosa pine in the latter half of the century, but had no significant effects in prior decades. This pattern suggests that moisture limitations on the growth of adult ponderosa pine have increased in recent decades, likely due to increasing drought stress. The sensitivity of ponderosa pine radial growth to moisture availability is consistent with findings from the Colorado Rocky Mountains (Peterson et al. 1993, Adams et al. 2014). For both Douglas-fir and ponderosa pine, declines in

moisture availability likely drive reductions in photosynthesis via stomatal closure (Grieu et al. 1988).

While adult and juvenile growth in both species showed similar sensitivity to moisture availability during distinct time periods, there was striking temporal variability and shifts in the direction of climate effects on juvenile growth from the early 20th century to recent decades. The most prominent pattern was in juvenile ponderosa pine: increased water deficit and maximum temperature were associated with decreased growth from the 1930s through 1950s, and again in recent decades, but these same factors were associated with increased growth in the early 20th century (Fig. 8). The relationship in the 1930 through 1950s and in recent decades is consistent with expectations based on the impacts of climate on adult growth: juvenile growth decreased under warm and dry conditions (Figs. 2, A2). Conditions in recent decades, and projected future changes in climate, are most similar to those of the 1930s and 1940s, in which conditions were warmer and drier than the 1901-2015 average (Figs. 2, A2). To cope with moisture and heat stress, trees would likely reduce their stomatal conductance to prevent increased rates of water loss (Grieu et al. 1988, McMurtrie et al. 1990). This in turn would reduce rates of photosynthesis and carbon assimilation, which are critical for growing roots for water and nutrient acquisition. These results are also consistent with the climate-regeneration patterns we found in ponderosa pine in recent decades, implying that cooler and wetter conditions favor both regeneration and above-average radial growth in juvenile ponderosa pine. During decades with more moderate inter-annual climate variability (e.g., 1950-1970; Fig. A1), juvenile growth was insensitive to temperature and water deficit. Higher growth under warmer, drier conditions in the early 20th century is more surprising, and it may reflect differences in both climate and site characteristics. For example, more open stand conditions after recent wildfires may have facilitated higher

growth in establishing seedlings, relative to seedlings establishing independent of fire or after low- to moderate-severity fires throughout the 20th century. In addition, seedling growth in recent decades may have been more limited by minimum temperatures, which have increased, rather than maximum temperatures. Untangling these two hypotheses is challenging with the current dataset, and it points to the need for more experimental work to complement observational studies.

As with ponderosa pine, increased water deficit corresponded with decreased growth in juvenile Douglas-fir, although these effects were significantly weaker in Douglas-fir relative to ponderosa pine. Cooler maximum temperatures corresponded with decreased juvenile growth during the 1930s-1940s; but, increased minimum temperatures also corresponded with increased juvenile growth from the 1920s through 1970s, suggesting potential energy limitations during the mid-century (Figs. 2, 7). Increased growth with increased minimum temperatures is consistent with findings that warmer spring temperatures favored Douglas-fir growth in low-elevation forests in Germany, presumably by helping compensate for drier summer conditions (Vitali et al. 2018). In more recent decades, growth in juvenile Douglas-fir was insensitive to climate, suggesting that other factors, such as site conditions, may be more limiting. Overall, our results suggest that the seasonality of increased temperatures and moisture stress, relative to the timing of tree growth, as well as site-level abiotic changes, will be critical for anticipating growth response to future changes in climate.

Climate effects on growth for both species were strongest during periods of high climate variability (Fig. A1). While this may be a statistical artifact – where higher variability in an independent variable leads to higher correlations with a dependent variable, even under the null hypothesis of no relationship – it is also consistent with increased sensitivity of growth to

climatic variability, coupled with potential shifts in the relative influence of local biotic factors on growth. Climate effects on juvenile growth were highest in recent decades, a period of high variability in moisture availability and growing degree days (Fig. A1). The greater sensitivity of juvenile ponderosa pine than juvenile Douglas-fir to moisture availability may also reflect higher climatic variability at ponderosa pine sites in recent decades. These results are consistent with Hayles et al. (2007), who found that climate variability was positively correlated with variability in radial growth, likely a result of increased sensitivity to more frequent extreme climate conditions. Periods of growth insensitivity to climate when climate variability is low may likewise indicate that other non-climatic factors have become more limiting to growth, such as local competition or nutrient availability (e.g., Sala et al. 2005).

2.5.3 Implications of future climate change

Our results support expectations for overall declines in tree growth and post-fire tree regeneration in lower-treeline forests of the Northern Rockies (Stevens-Rumann et al. 2018), given projected increases in fire activity and prolonged periods of warm, dry conditions (e.g. Flannigan et al. 2009, Littell et al. 2010, Abatzoglou and Williams 2016). Temperatures are expected to increase under all emissions scenarios throughout the northwestern U.S. and northern Rockies during the 21st century, accompanied by changes in the seasonality of moisture availability (Kirtman et al. 2013, Whitlock et al. 2017). Projected declines in summer precipitation along with rising temperatures and earlier snowmelt will exacerbate growing season drought and likely results in detectable impacts on forested ecosystems.

Given the varying climate limitations for post-fire regeneration highlighted here, the composition of lower-treeline forests will also likely shift, as future climate change favors certain

species over others. Projected increases in temperature and prolonged drought will differentially affect ponderosa pine and Douglas-fir post-fire regeneration and growth, with potentially stronger reductions in growth in ponderosa pine seedlings. Cooler and wetter growing seasons concurrent with ponderosa pine regeneration pulses suggest declines in or failure of post-fire ponderosa pine regeneration at lower-treeline in the Northern Rockies, consistent with expected declines in the Colorado Front Range (Rother et al. 2015, Rother and Veblen 2017) and observations across the western U.S. (Savage and Mast 2005, Welch et al. 2016, Stevens-Rumann et al. 2018). Similarly, stronger reductions in the growth of juvenile ponderosa pine with increasing water deficit and maximum temperature in recent decades, relative to Douglas-fir, suggest that future increases in temperature and water deficit may affect ponderosa pine more so than Douglas-fir. While higher sensitivity of ponderosa pine may result from higher climatic variability at sites that had ponderosa pine vs. Douglas-fir, the magnitude of the difference between species is unlikely explained by differences in climate variability alone. Differences between the sensitivity of ponderosa pine and Douglas-fir to climate are consistent with findings showing greater heat tolerance in Douglas-fir than ponderosa pine seedlings (Marias et al. 2017). Despite potential species-specific responses to future climate change, the overall sensitivity of adult and juvenile growth to water availability and increasing temperatures suggests that future climatic changes will cause overall declines in tree growth at and near lower treeline. Declines in tree growth could lead to lower-treeline forests that experience higher rates of mortality and are less resistant to drought stress (Das et al. 2007, Lloret et al. 2011, Canham and Murphy 2017). Loss of canopy cover through high-severity wildfires will further limit post-fire regeneration and juvenile growth by exacerbating warm and dry conditions (Davis et al. In Press, Von Arx et al. 2013) and removing seed sources (Donato et al. 2016, Kemp et al. 2016).

Given current climate effects on growth and adequate seed sources, post-fire management actions aimed at ensuring forest recovery following wildfire would benefit from promoting microclimates that provide cooler and wetter conditions for seedling regeneration to occur, especially in sites dominated by ponderosa pine. Further, there may be opportunities for pre- and active-fire management to minimize (but not eliminate) the size of high-severity burn patches, and thus distance-to-seed-sources, which would further facilitate post-fire regeneration. Future studies are needed to quantify relationships between climate and growth through time in higher-elevation forests, as well as identify thresholds beyond which regeneration failure will occur. Ecological studies and management actions related to post-fire forest recovery should also consider disturbance and climatic effects on the entire recovery trajectory, both regeneration and growth, to gain a better understanding of forest resilience to future changes in climate and fire activity.

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2.7 Tables

Table 1. Growth – climate Pearson’s correlation coefficients (r) and p-values for adults (>25 yr old) and juveniles (< 25 yr old) from 1901-2015. Growth is the mean standardized basal area increment for all individuals that fall within a given category of species-life stage (i.e. adult ponderosa pine).

	Climate variable	PIPO		PSME	
		r	p-value	r	p-value
Adult	Water Deficit	-0.11	0.26	-0.46	0.00
	Max Temperature	0.22	0.02	-0.30	0.00
	Min Temperature	-0.33	0.00	0.07	0.49
	Precipitation	0.37	0.00	0.45	0.00
	Growing Degree Days	-0.02	0.88	-0.18	0.06
Juvenile	Water Deficit	-0.25	0.01	-0.10	0.30
	Max Temperature	-0.09	0.38	0.17	0.08
	Min Temperature	0.06	0.53	0.52	0.00
	Precipitation	0.20	0.04	0.13	0.16
	Growing Degree Days	-0.01	0.92	0.37	0.00

*Bold values indicate significance at the p = 0.05 level.

Figure Legends

Figure 1. Sampling sites in low-elevation dry mixed-conifer forests that burned between 1900 and 2007 across the western continental United States (a). Pink areas indicate all fires that occurred from 1984-2014 from the Monitoring Trends in Burn Severity dataset. (b) Climatic water deficit (mm) using 30-yr normals at Northern Rockies Forest Inventory and Analysis plots that contain ponderosa pine and Douglas-fir (“Regional”) (David et al. 2018), and at all sampling sites in the Northern Rockies (PRISM Climate Group 2017).

Figure 2. Mean growing season climate across all sites from 1901-2015. One-kilometer monthly to annual climate data are from ClimateNA (Wang et al. 2016). The reference climate grids are based on the Parameter Regression of Independent Slopes Model (PRISM) interpolation method for current climate. Historical data since 1901 are based on the CRU-TS 3.22 dataset (Mitchell and Jones 2005). Monthly climate variables were summarized to the growing season from April to September.

Figure 3. Age structures and regeneration events at 33 seedling sites. Sites are organized by climatic water deficit using 30-yr deficit normals; lowest (wettest) in the upper left corner, highest (driest) in the bottom right corner. Dark grey bars and circles represent ponderosa pine regeneration and events (>20% annual site regeneration), light grey bars and circles represent Douglas-fir regeneration and events (>20% annual site regeneration). Only the largest pulse of multi-year events are included. Red vertical lines are fire years. Regeneration largely occurred within five years after a fire.

Figure 4. Age structures at 12 tree-core sites. Sites are organized top to bottom by increasing climatic water deficit (wettest to driest) using 30-yr deficit normals. Dark grey bars represent ponderosa pine regeneration in 5-yr bins, light grey bars represent Douglas-fir regeneration in 5-yr bins. Red vertical lines are fire years.

Figure 5. Superposed epoch analysis (SEA) results summarizing the average climate anomaly conditions before, during, and after 44 regeneration events from 33 sites. Climate was detrended over the time period using a 30-yr running mean, then annual values were subtracted from the mean to obtain anomaly values. Growing degree days were calculated with a base of 5 °C. Confidence intervals (90%, 95%) were based on 10,000 simulations under the null hypothesis.

Figure 6. Standardized basal area increment chronologies (black lines) for adults and juveniles of ponderosa pine and Douglas-fir individuals across all sites. Grey lines indicate mean growing season climatic water deficit across all sites that contribute to each mean value chronology. Sample sizes for each category are represented below each time series with black accumulation curves.

Figure 7. Slope parameters from linear regressions of growth as a function of climate for each species and life stage (i.e., juvenile vs. adult), for continuous 30-yr windows over the period of analysis. Life stage was defined as either “juvenile,” representing the first 25 years of radial growth, or “adult,” representing any radial growth beyond 25 years. Growth is standardized basal area increment chronologies for adults and juveniles of each species. Climate was standardized using z-scores. Slope values are shown at the center year of each 30-yr window. Grey ribbons

represent 95% confidence intervals around the slope parameter, where bands not overlapping 0 indicate a significant relationship.

Figures

Figure 1.

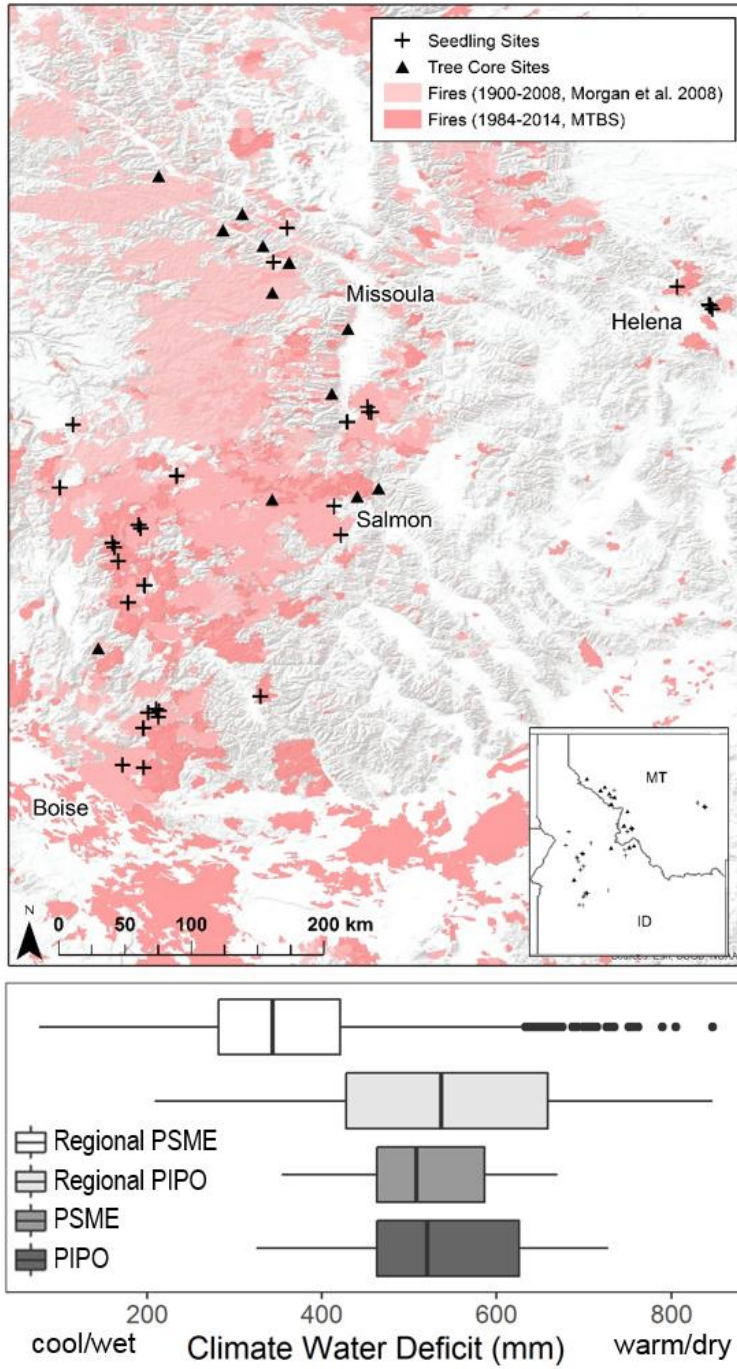


Figure 2.

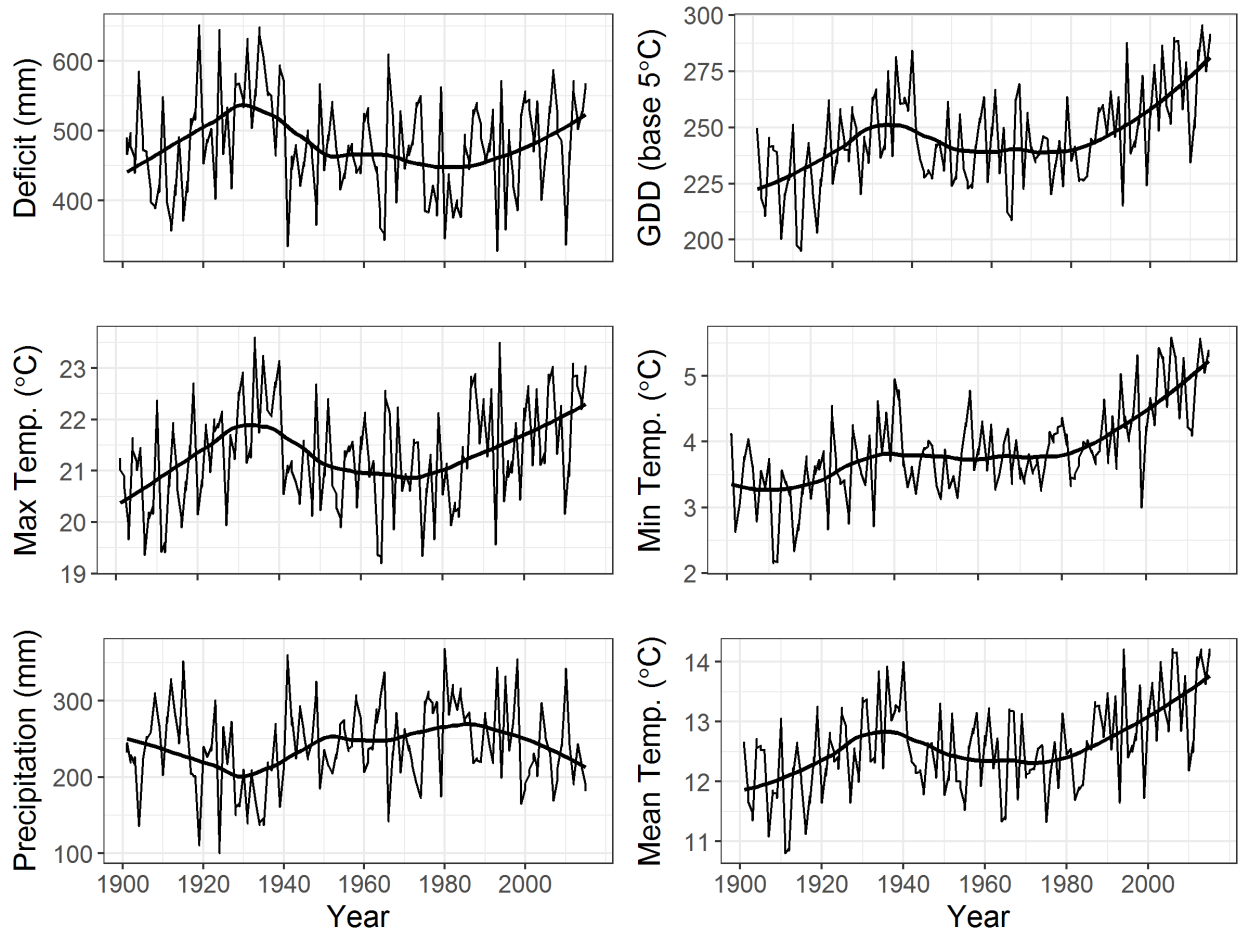


Figure 3.

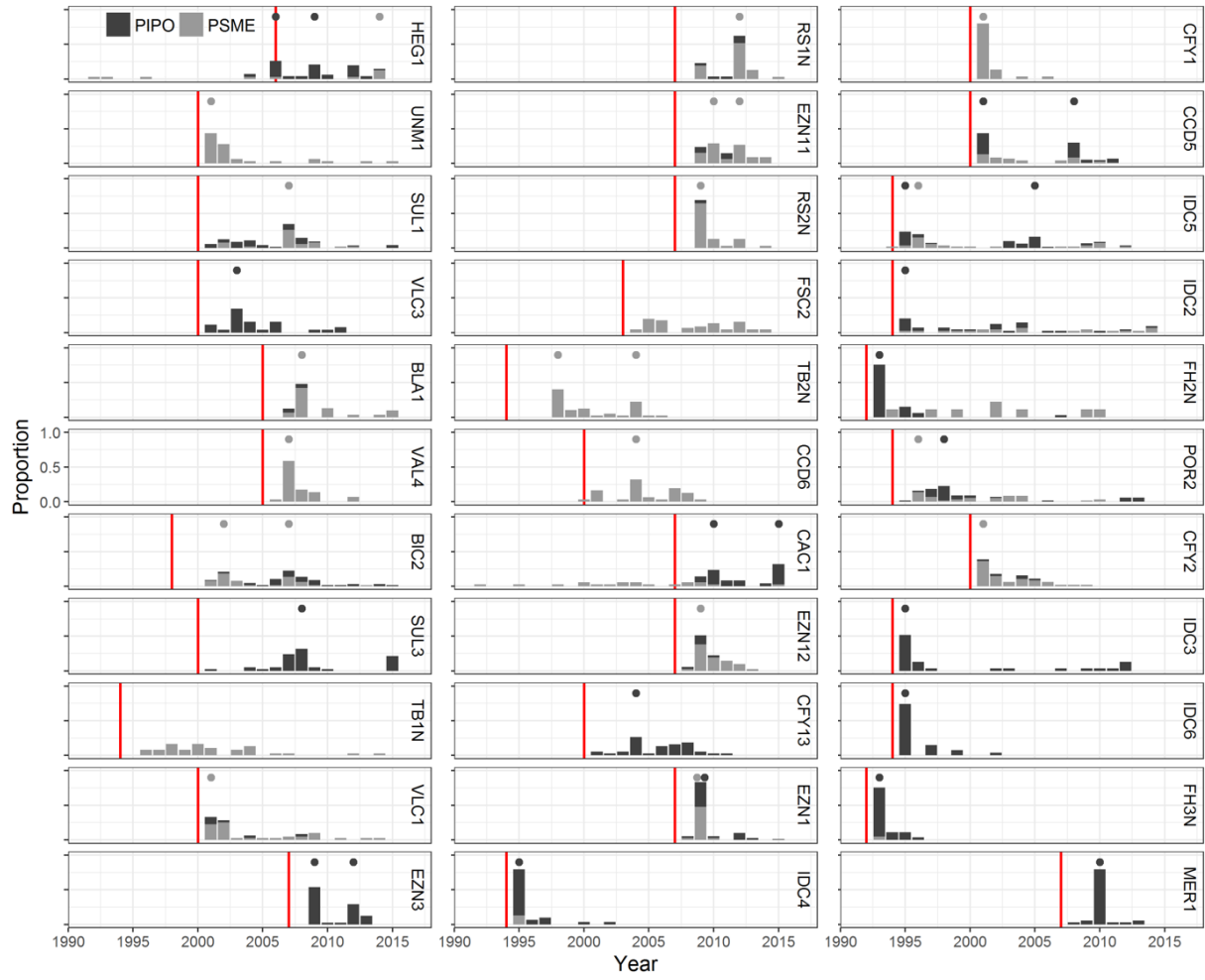


Figure 4.

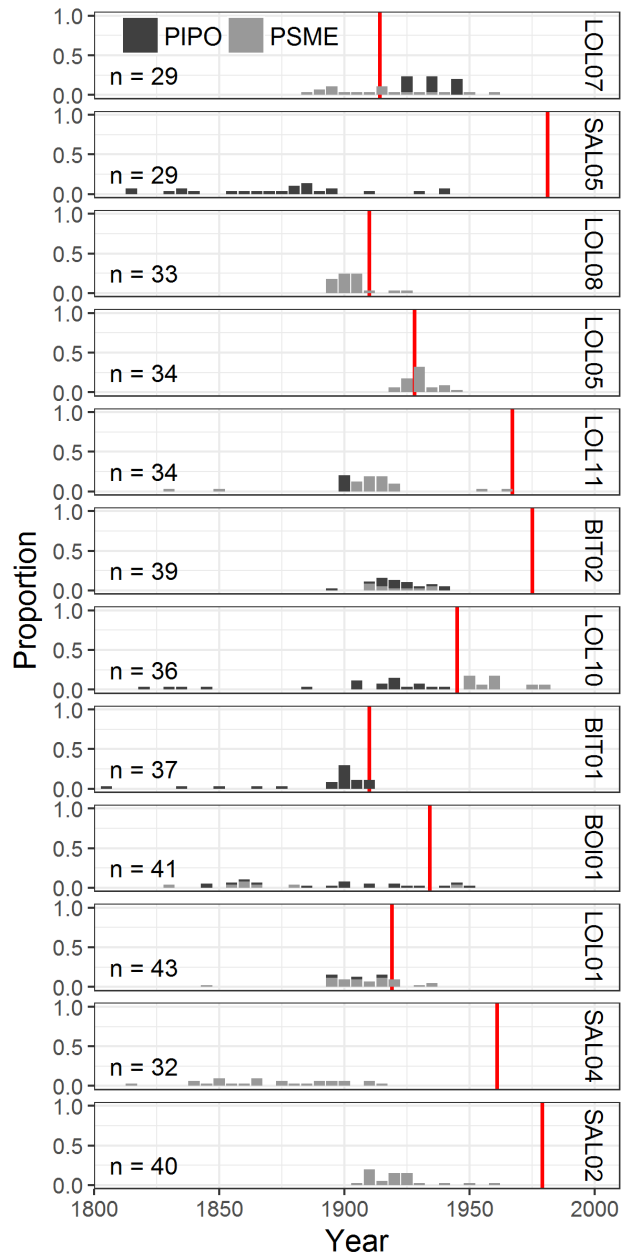


Figure 5.

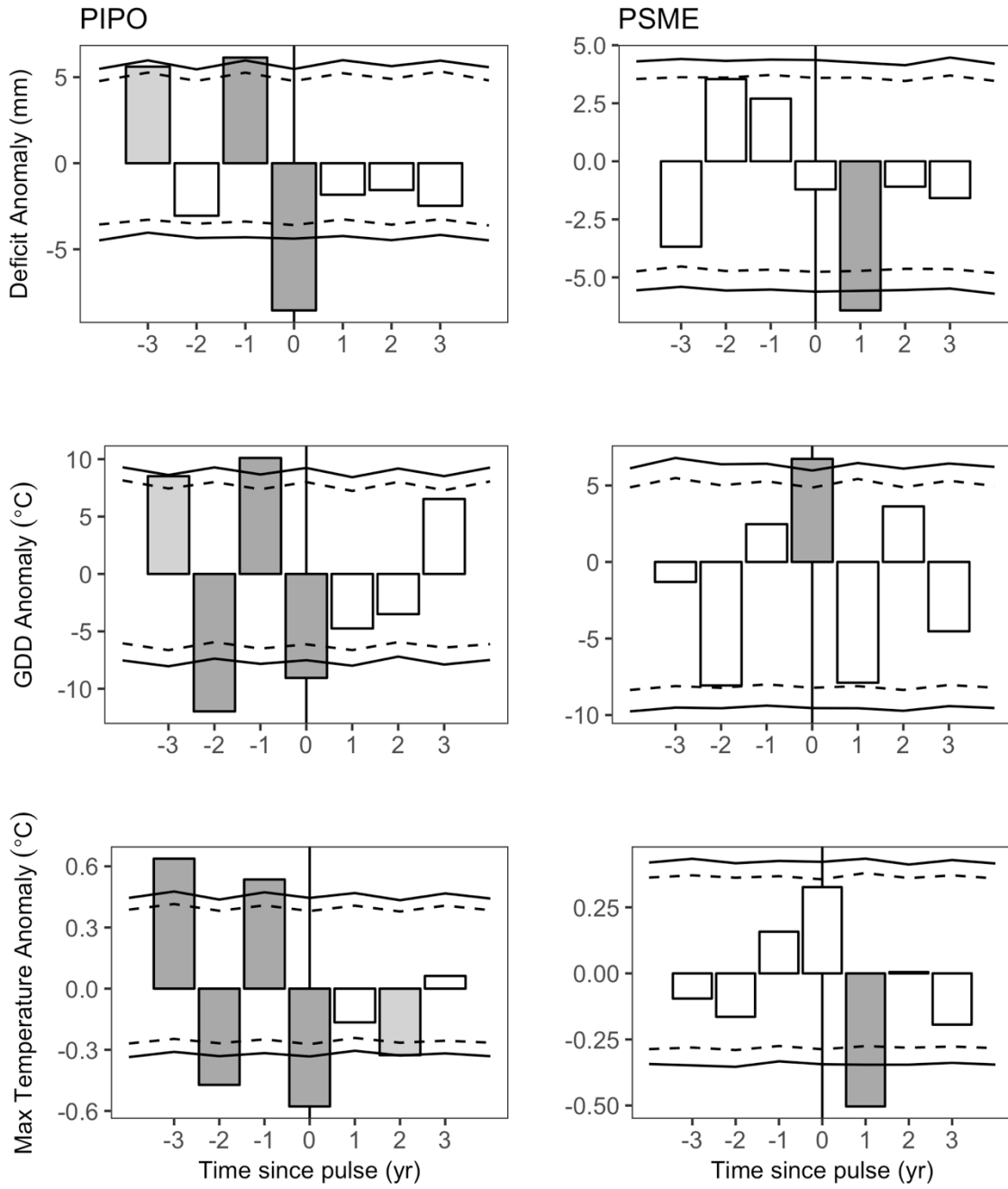


Figure 6.

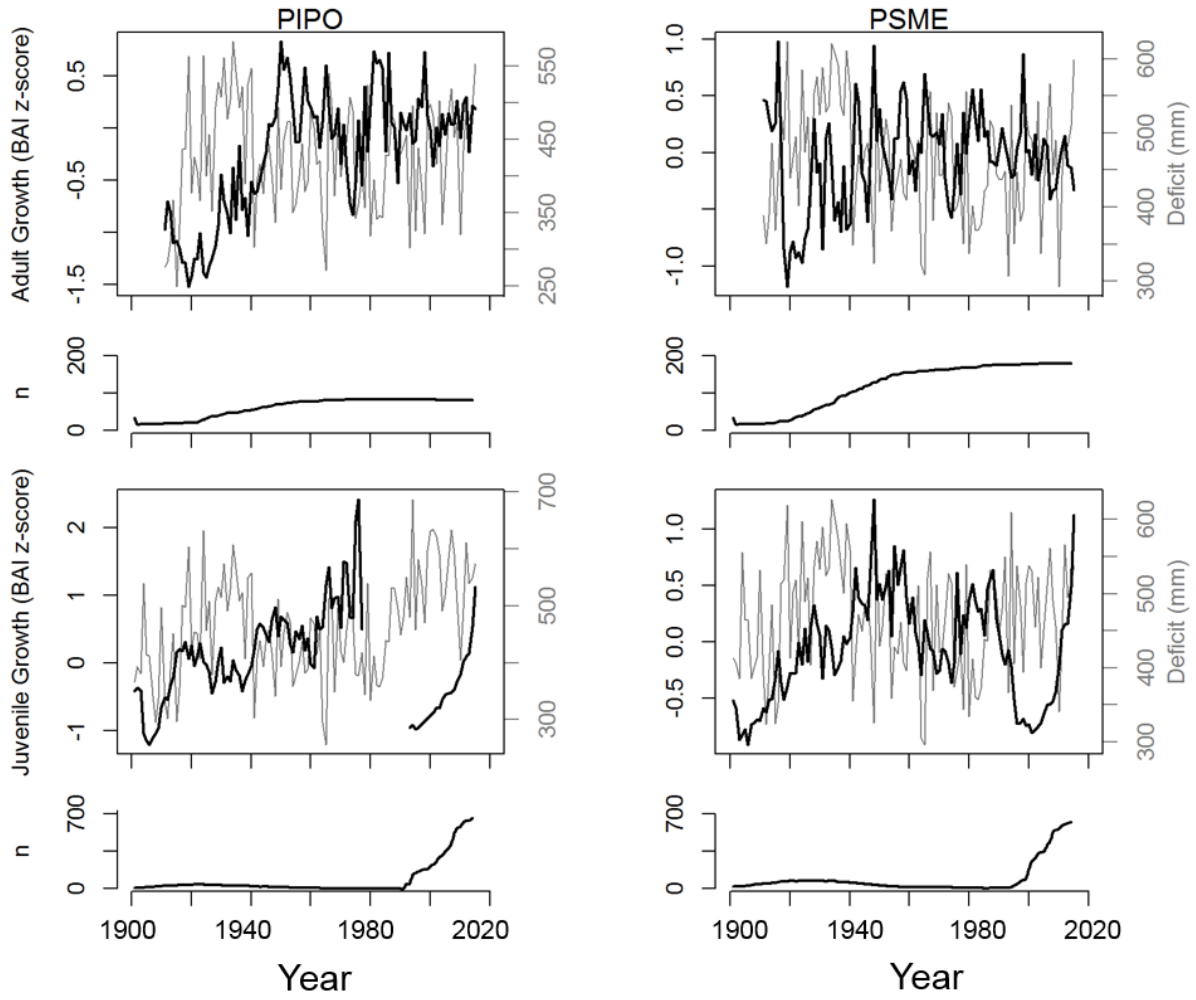
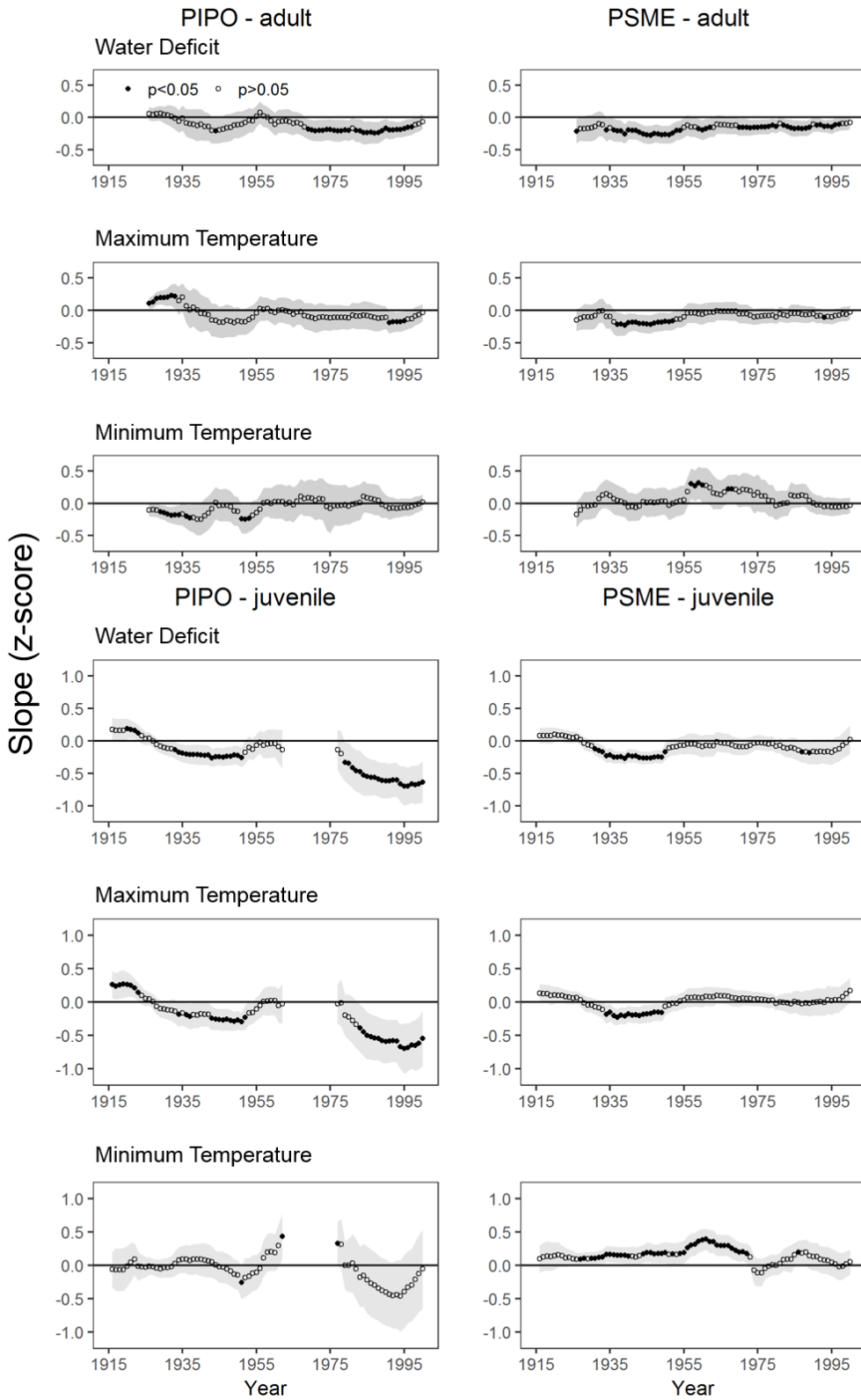


Figure 7.



2.8 Supplementary Materials

2.8.1 Appendix A.

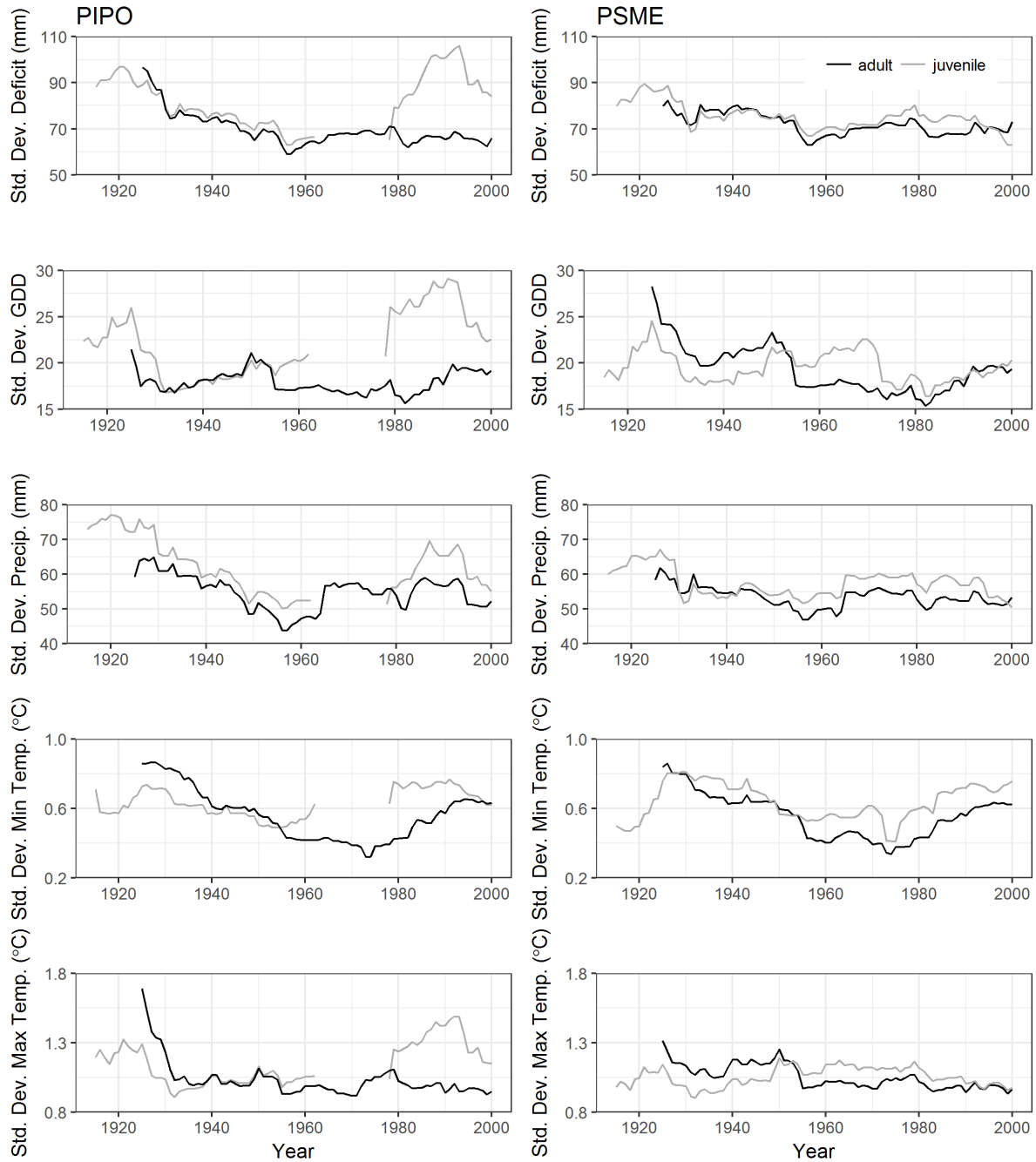


Figure A1. Moving standard deviations of growing season climate through the 20th and early 21st centuries at all sites. Moving standard deviations were determined with a 30-year, overlapping

window starting with the period 1901-1930, and moving in 1-yr increments through the period 1986-2015. Climate data were only included for years in which we have radial growth data, accounting for the gap in climate from 1978 to 1991 at juvenile ponderosa pine sites.

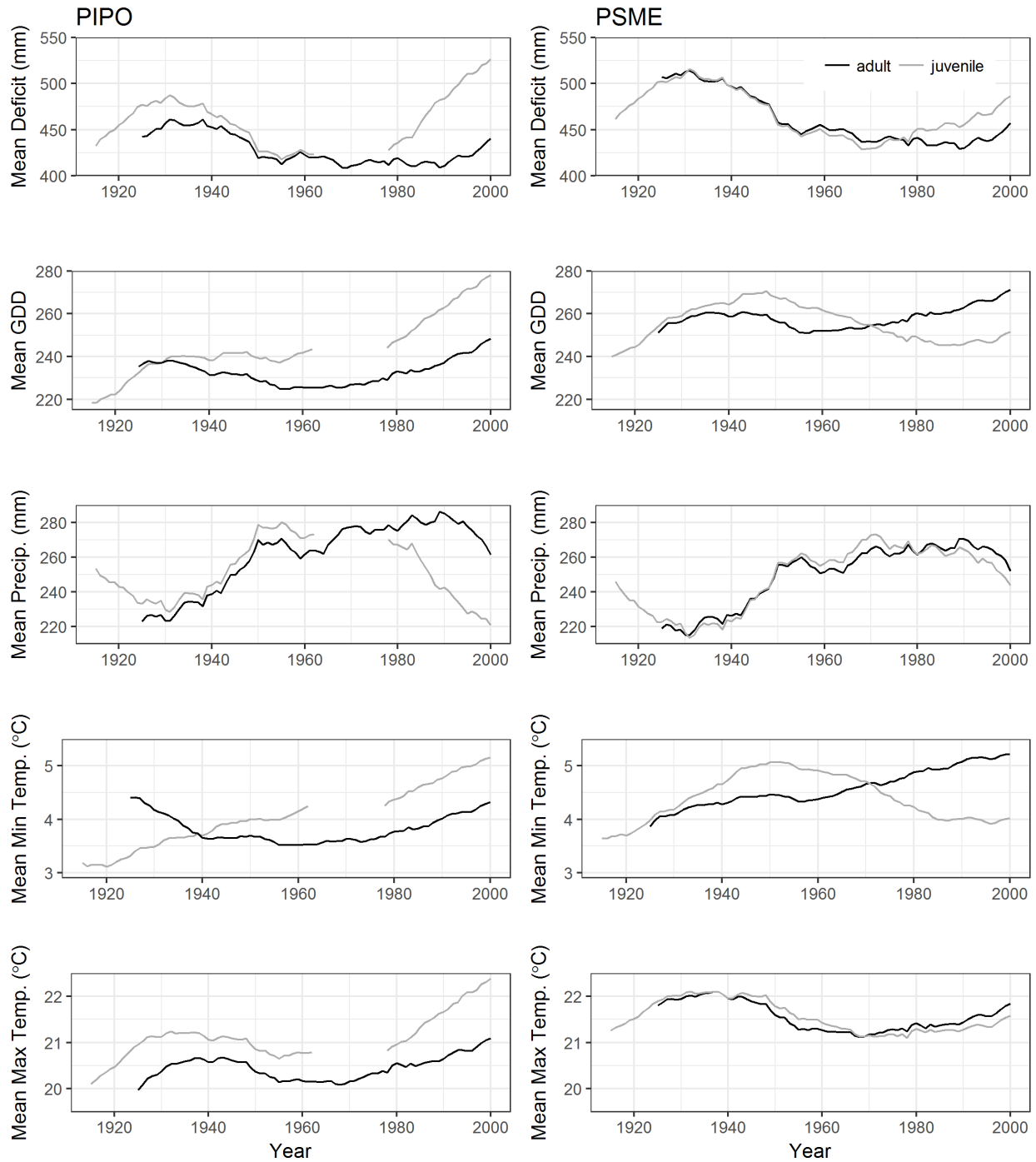


Figure A2. Moving averages of growing season climate through the 20th and early 21st centuries at all sites. Moving averages were determined with a 30-year, overlapping window starting with the period 1901-1930, and moving in 1-yr increments through the period 1986-2015. Climate

data were only included for years in which we have radial growth data, accounting for the gap in climate from 1978 to 1991 at juvenile ponderosa pine sites.

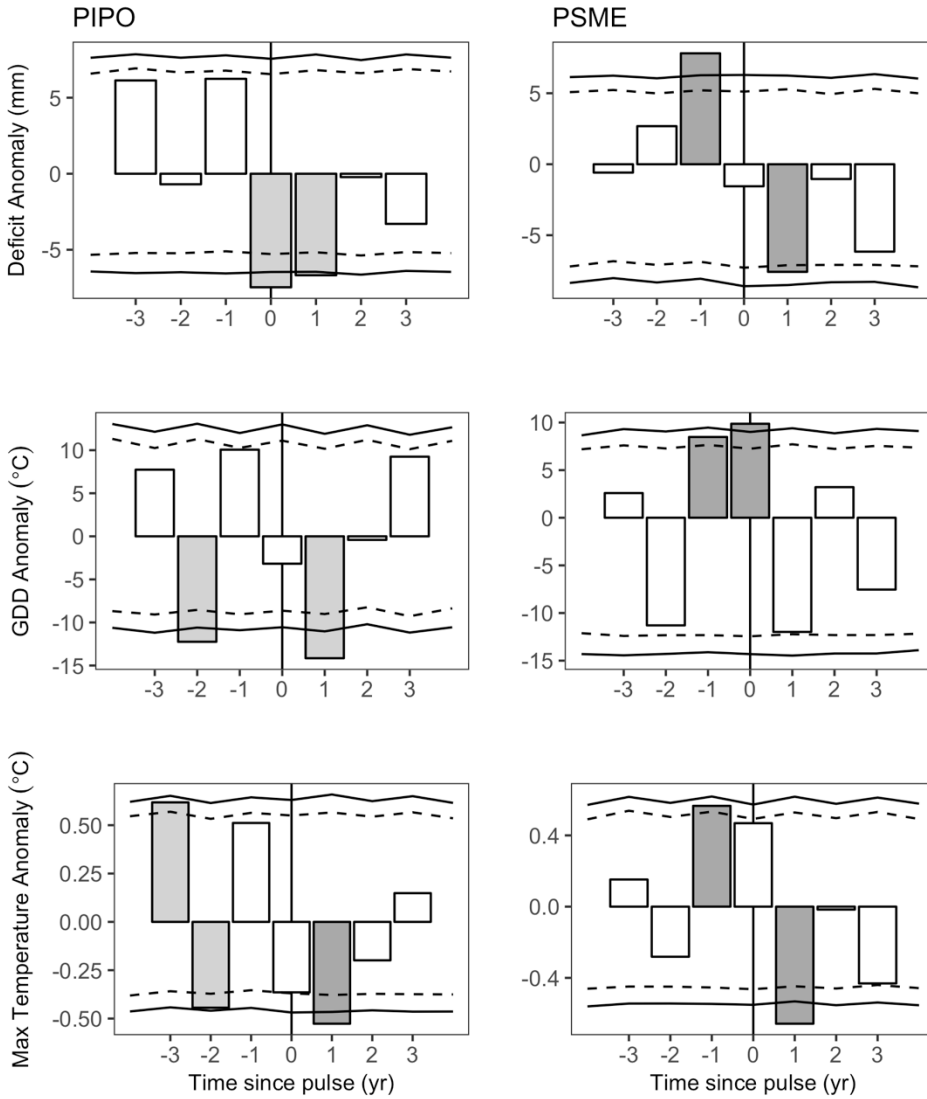


Figure A3. Superposed epoch analysis (SEA) results summarizing the average climate conditions before, during, and after regeneration events (based on 30% regeneration threshold) from 33 sites. Climate was detrended over the time period using a 30-yr running mean. Confidence intervals (90%, 95%) were based on 10,000 simulations under the null hypothesis.

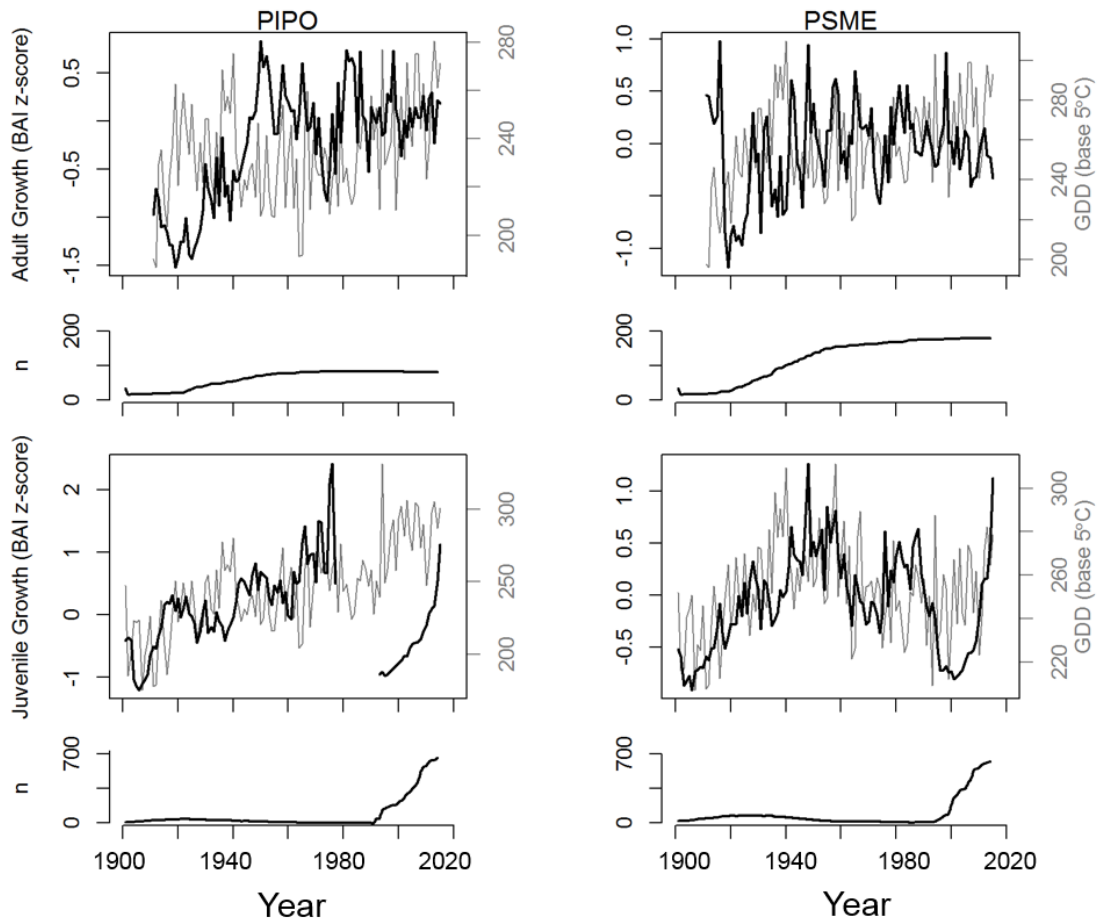


Figure A4. Standardized basal area increment chronologies (black lines) for adults and juveniles of ponderosa pine and Douglas-fir individuals across all sites. Grey lines indicate mean growing season growing degree days (base 5 °C) across all sites that contribute to each mean value chronology. Sample sizes for each category are represented below each time series with black accumulation curves.

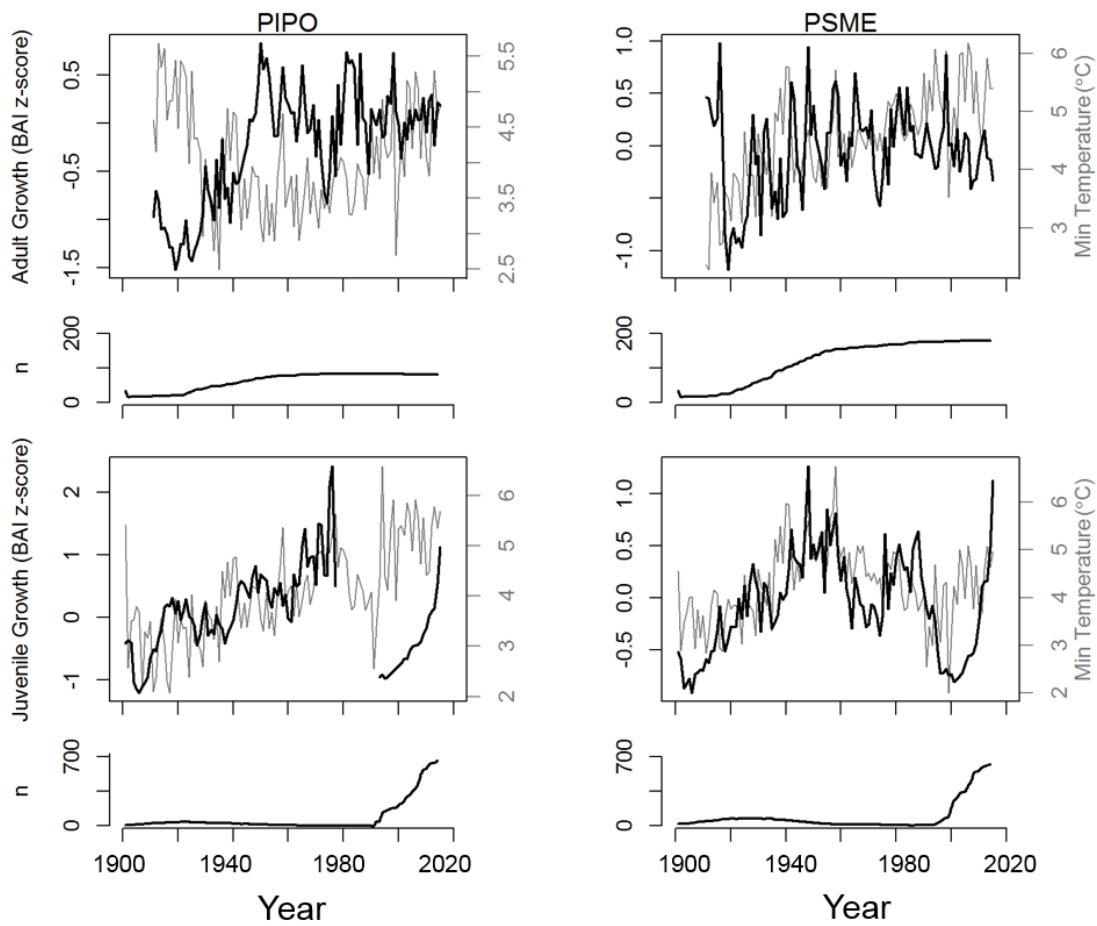


Figure A5. Standardized basal area increment chronologies (black lines) for adults and juveniles of ponderosa pine and Douglas-fir individuals across all sites. Grey lines indicate mean growing season minimum temperature ($^{\circ}\text{C}$) across all sites that contribute to each mean value chronology. Sample sizes for each category are represented below each time series with black accumulation curves.

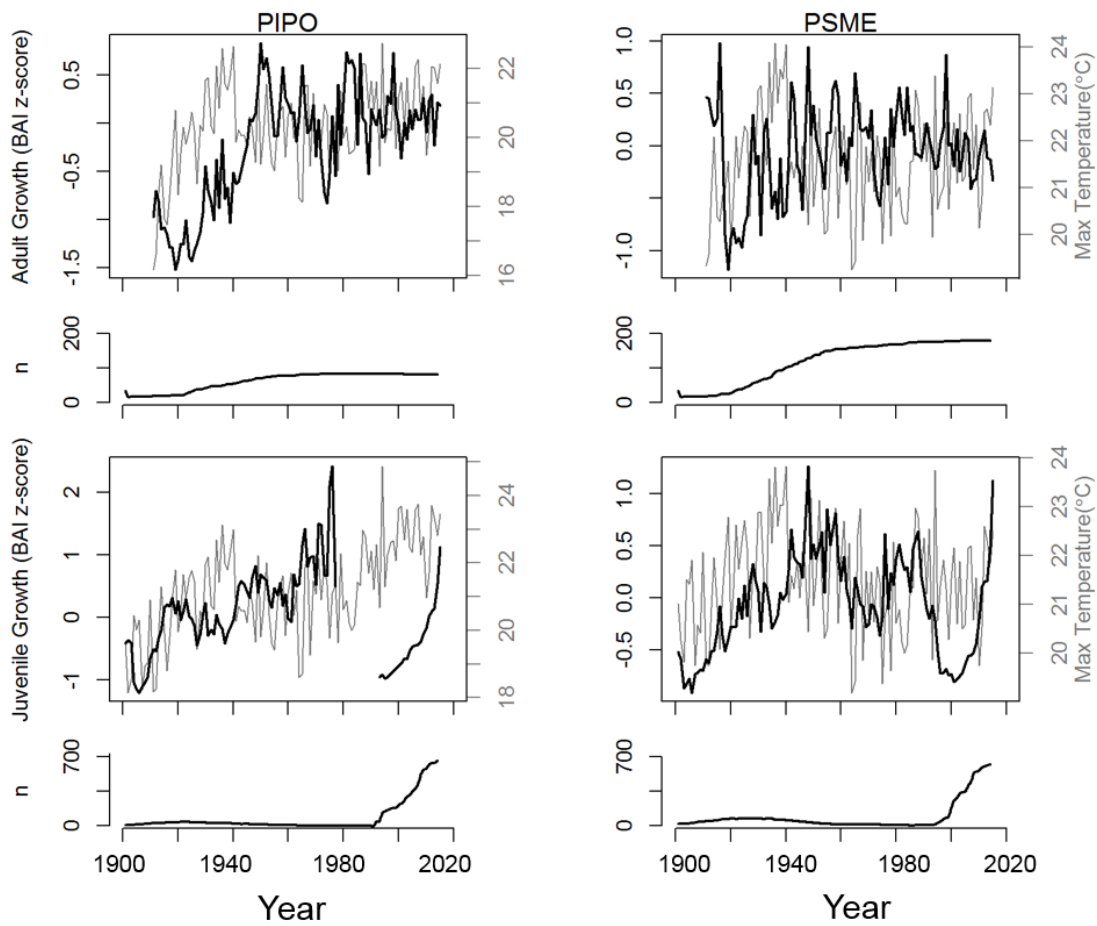


Figure A6. Standardized basal area increment chronologies (black lines) for adults and juveniles of ponderosa pine and Douglas-fir individuals across all sites. Grey lines indicate mean growing season maximum temperature ($^{\circ}\text{C}$) across all sites that contribute to each mean value chronology. Sample sizes for each category are represented below each time series with black accumulation curves.

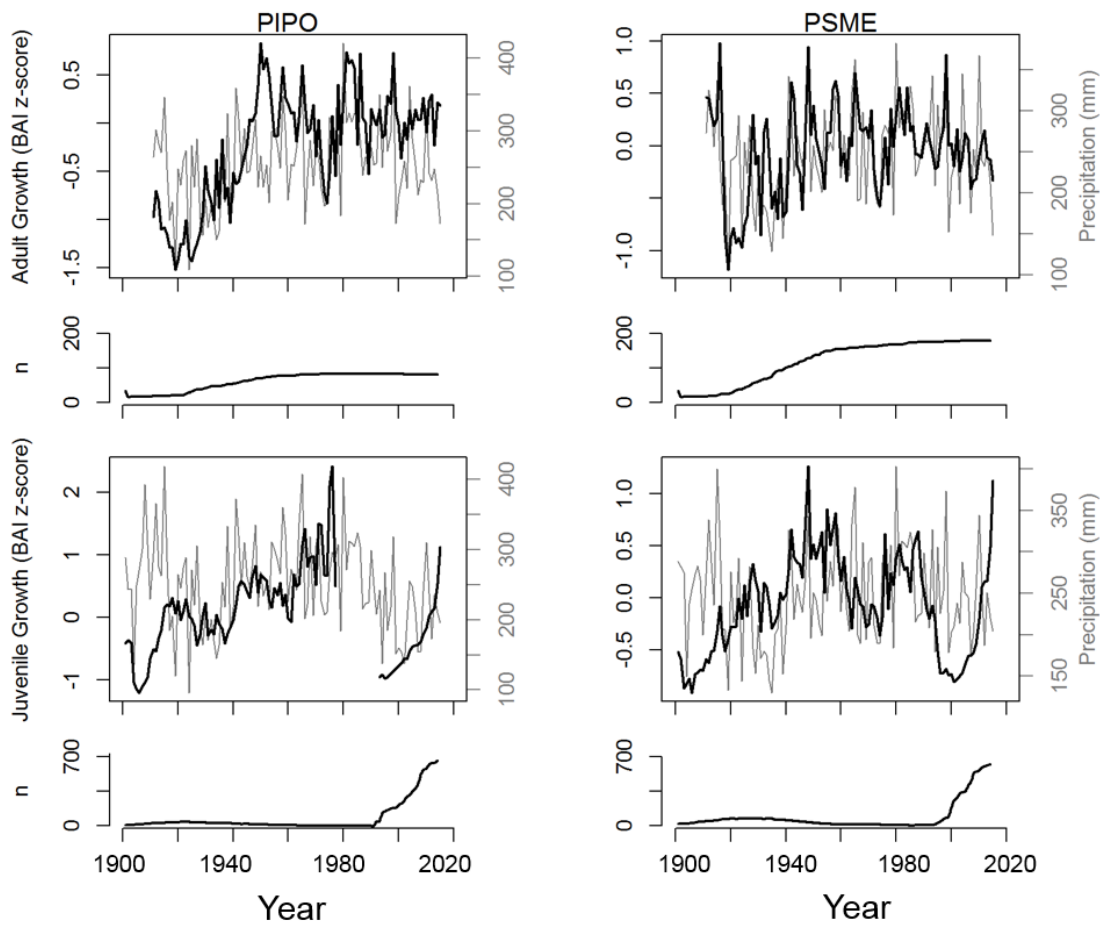


Figure A7. Standardized basal area increment chronologies (black lines) for adults and juveniles of ponderosa pine and Douglas-fir individuals across all sites. Grey lines indicate mean growing season precipitation (mm) across all sites that contribute to each mean value chronology. Sample sizes for each category are represented below each time series with black accumulation curves.

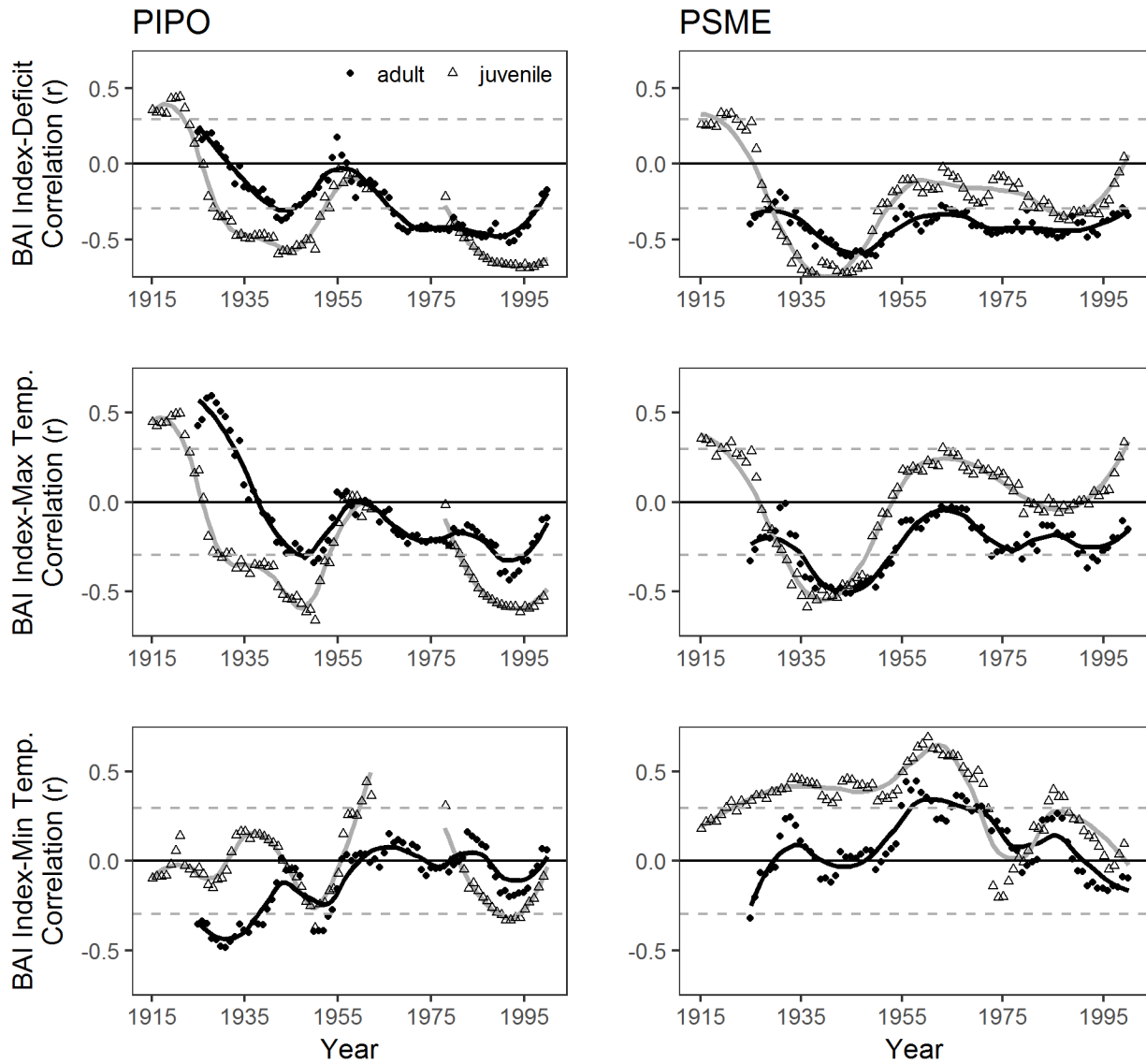


Figure A8. Continuous growth-climate correlations through time for growing degree days and average precipitation for each species and life stage (i.e., juvenile vs. adult). Life stage was defined as either “juvenile,” representing the first 25 years of radial growth, or “adult,” representing any radial growth beyond 25 years. Moving correlations were performed with a 30-year, overlapping window starting with the period 1901-1930, and moving in 1-yr increments through the period 1986-2015.

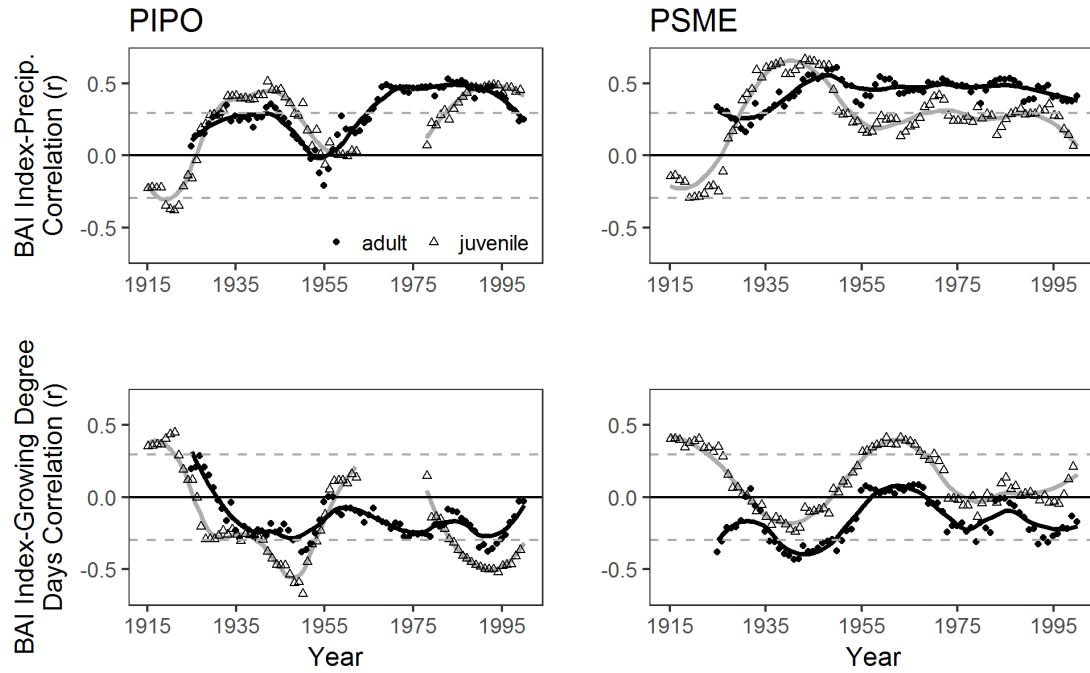


Figure A9. Continuous growth-climate correlations through time for growing degree days and average precipitation for each species and life stage (i.e., juvenile vs. adult). Life stage was defined as either “juvenile,” representing the first 25 years of radial growth, or “adult,” representing any radial growth beyond 25 years. Moving correlations were performed with a 30-year, overlapping window starting with the period 1901-1930, and moving in 1-yr increments through the period 1986-2015.

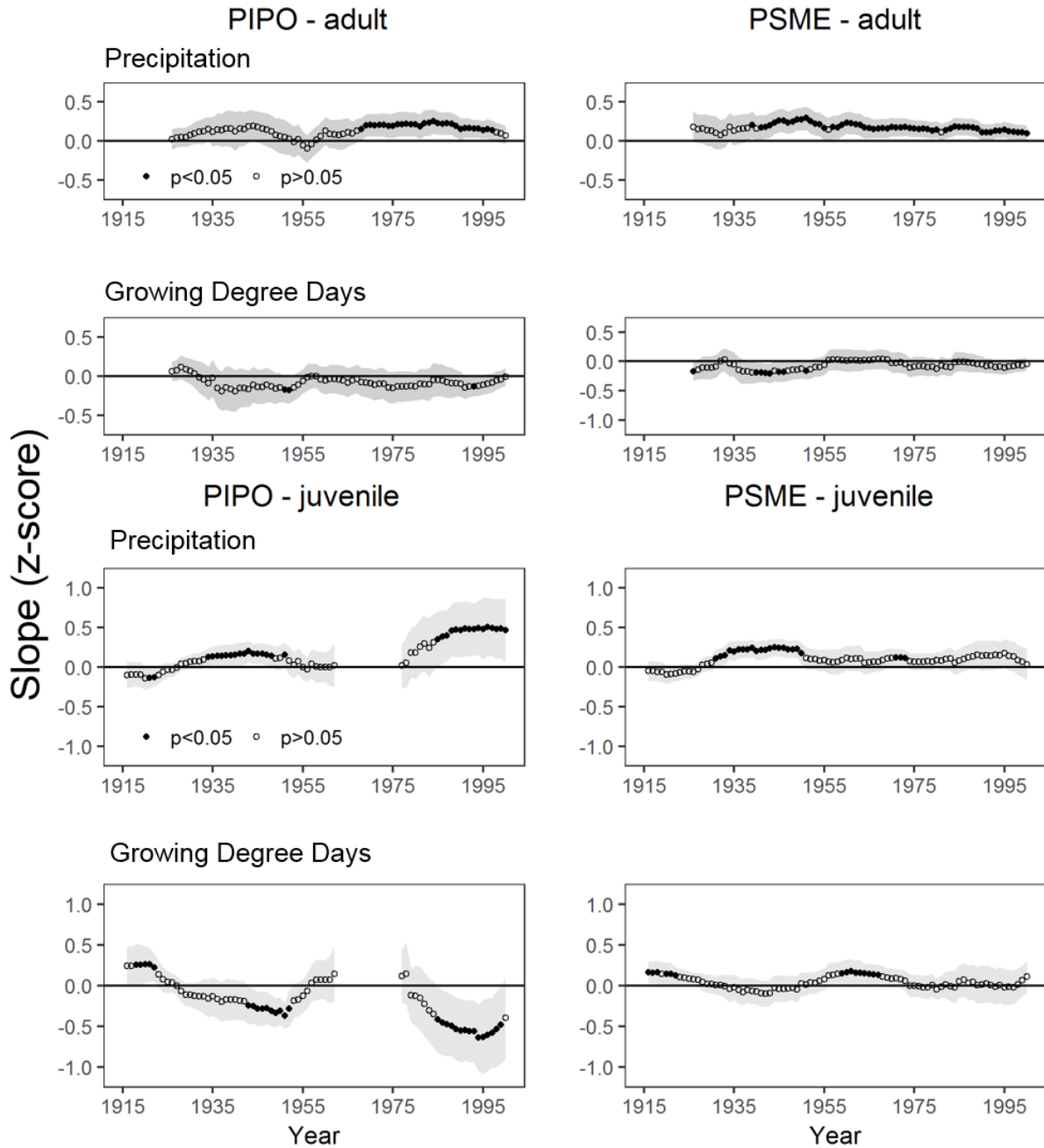


Figure A10. Slopes from continuous linear regressions of growth as a function of climate for each species and life stage (i.e., juvenile vs. adult). Life stage was defined as either “juvenile,” representing the first 25 years of radial growth, or “adult,” representing any radial growth beyond 25 years. Growth is standardized basal area increment chronologies for adults and juveniles of each species. Climate was standardized using z-scores. Moving linear regressions were

performed with a 30-year, overlapping window starting with the period 1901-1930, and moving in 1-yr increments through the period 1986-2015. Slope values are shown at the center year of each window. Grey ribbons represent 95% confidence intervals.

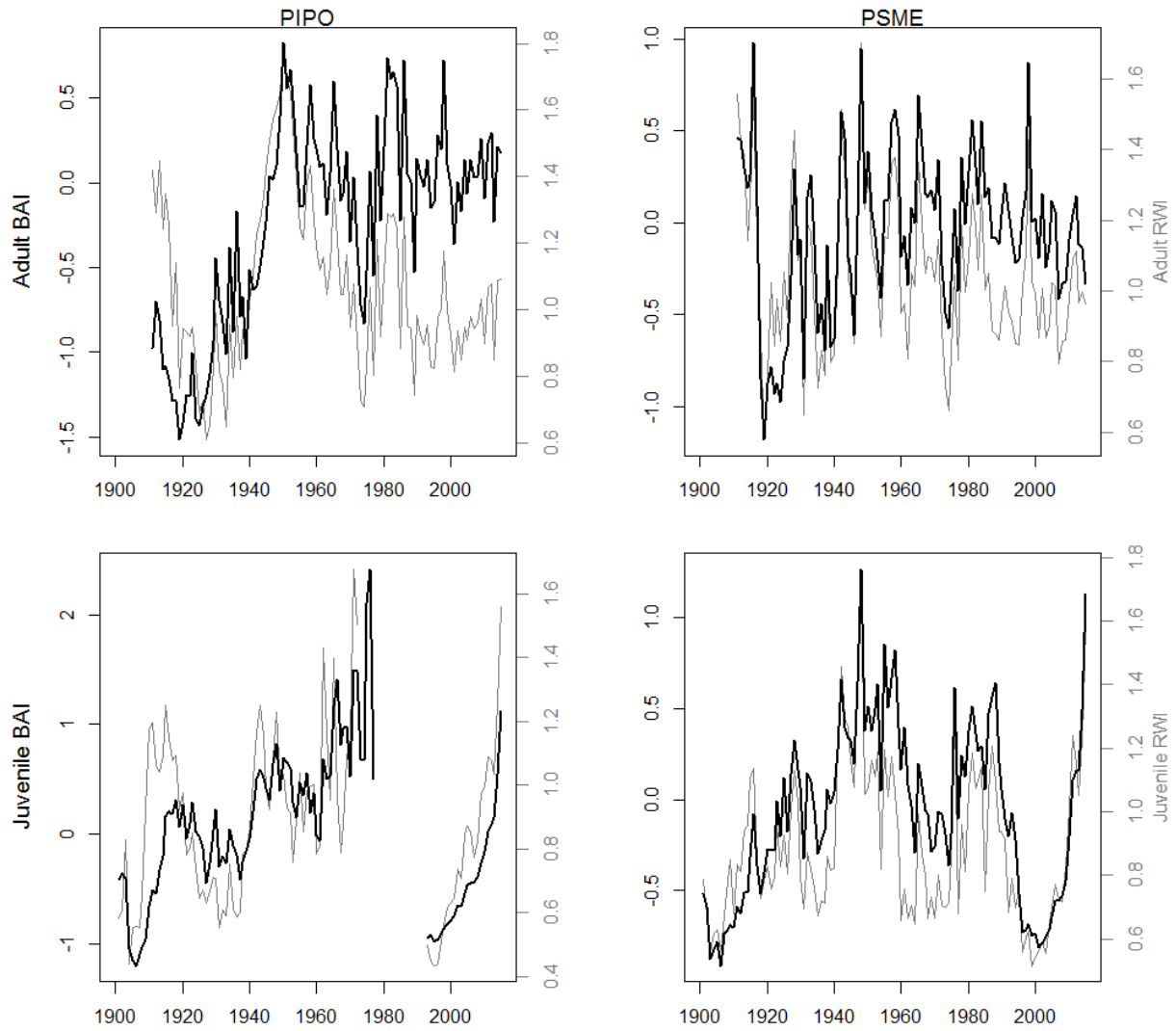


Figure A11. Mean value chronologies using standardized basal area increment (black lines) and detrended and standardized ring widths (grey lines) for adults and juveniles of ponderosa pine and Douglas-fir individuals across all sites.