



## 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,  $\pm 1$ -,  $\pm 2$ -, and  $\pm 5$ -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.

### 1. Introduction

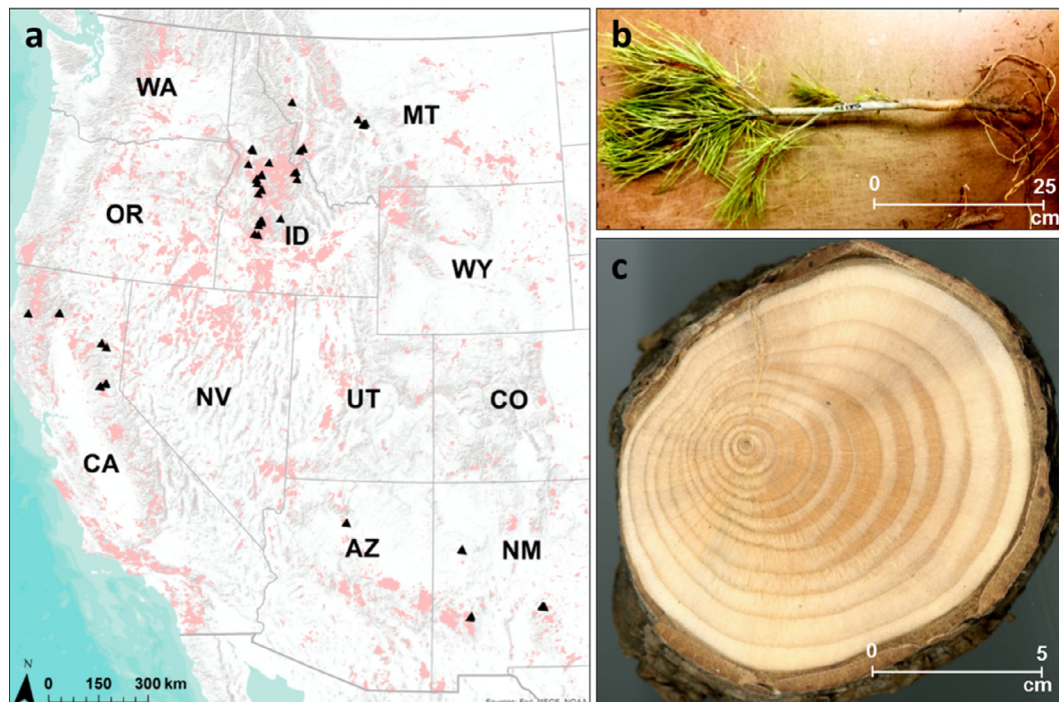
Ongoing global change, including increased drought stress on trees (Allen et al., 2010; van Mantgem et al., 2009; Williams et al., 2012) and an increased frequency of wildfires and other stand-initiating disturbances (Abatzoglou and Williams, 2016; Dale et al., 2001; Westerling et al., 2006), has motivated a renewed interest in understanding patterns of tree establishment and recruitment (e.g. Stevens-Rumann et al., 2018). 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 (Bergeron, 2000; Mast et al., 1998; Rother and Veblen, 2017; Turner, 2010), shifts in treeline (Coop and Givnish, 2007; Daniels and Veblen, 2003; Kearney, 1982), and climate-driven recruitment and stand dynamics (League and Veblen, 2006; Savage et al., 1996). 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 (Dovčiak et al., 2005; Haire and McGarigal, 2010; Harvey et al., 2016; Millar et al., 2004; Sprugel, 1976; Urza and Sibold, 2013). However, node and bud-scar counts are only proxies for true tree age (Urza and Sibold, 2013). Cross-dated tree rings, from tree cores or cross sections, provides a more precise method for dating trees (Speer, 2010; Stokes and Smiley, 1968; Telewski, 1993; Telewski and Lynch, 1991). 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 (Dobrowski et al., 2015; Donato et al., 2016; Harvey et al., 2016; League and Veblen, 2006; 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

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**Fig. 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 to 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.

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) (Fig. 1a). Across the California study sites, mean annual temperatures range from 8.5 to 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 to 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 (Fig. 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 (Rother and Veblen, 2017; Telewski, 1993; Urza and Sibold, 2013) under a 10–40x stereomicroscope. We determined the root-shoot boundary by the first appearance of pith (Fig. 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. Linear mixed effects 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 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.

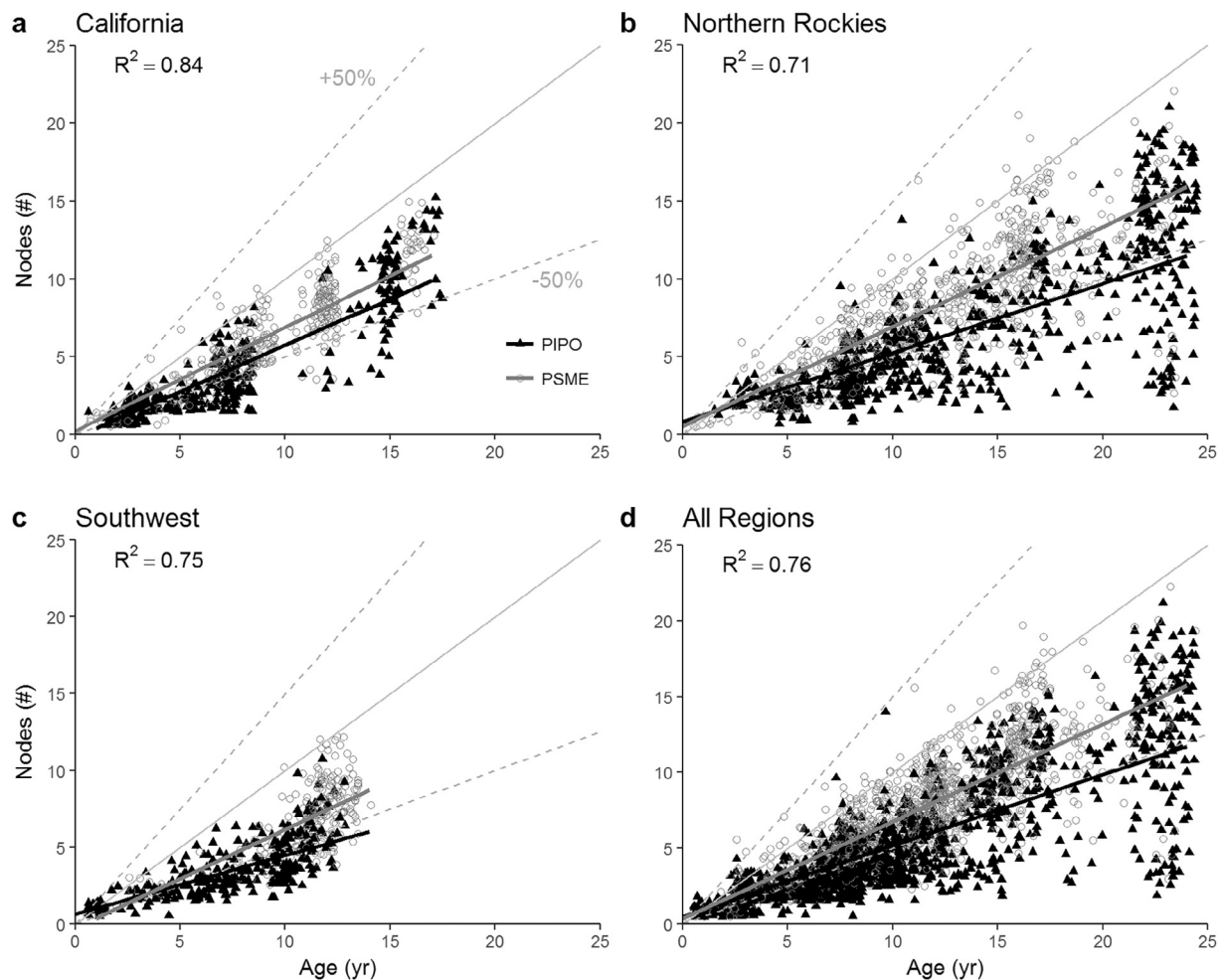
The accuracy of node counts depended strongly on the level of precision considered, and varied among regions and species. For both species and all regions combined, accuracy was 5% when attempting annual precision, but increased to 15%, 29%, and 74% for  $\pm 1,$   $\pm 2,$  and  $\pm 5$ -yr precision, 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 Douglas-fir (Table 1, Supplementary Table A1). 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

**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  $\pm 0, 1, 2,$  and 5 yr. Mean age for each subset of samples is shown with standard deviation in parentheses.

Region		Precision ( $\pm$ yr)				
		Age (yr)	$\pm 0$ yr	$\pm 1$ yr	$\pm 2$ yr	$\pm 5$ 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%



**Fig. 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. The  $R^2$  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  $y = 1.5 \times$  and  $y = 0.5 \times$  lines are shown in dashed gray to correspond with 50% over/underestimation.

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 yr) 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  $< 1$  (Table 2, Supplementary Table A2). 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).

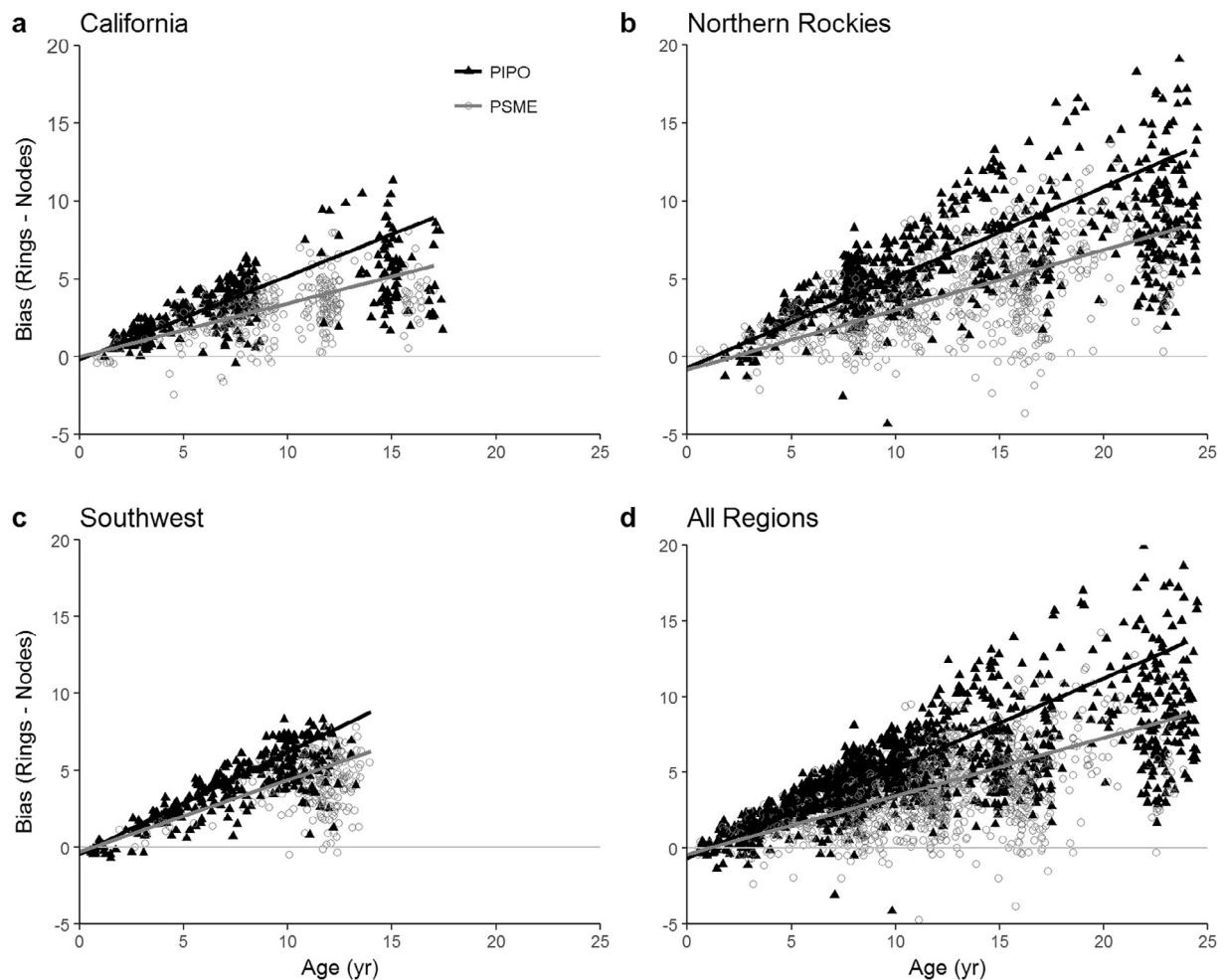
Bias in node counts increased with sample age, with a significant species, region, and growth rate effect (Supplementary Table A4). While species, region, growth rate, and a random site effect all explained variability in bias, sample age had the greatest effect on bias. Bias increased by 0.59 years for every additional year in sample age for ponderosa pine, and by 0.340 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. A1). 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 A4). 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 A5). 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  $\pm 5$ -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



**Fig. 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.

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  $\pm 5$  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

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

<sup>a</sup>Bold t-values were statistically significant at  $p < 0.05$ .

vary geographically (Grant et al., 2017; St Clair et al., 2005). 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 (Harvey et al., 2016; Urza and Sibold, 2013), 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 A5). 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  $\pm 1$ -yr or  $\pm 2$ -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.,  $\pm 5$ -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 (Donato et al., 2016; Harvey et al., 2014; Mast et al., 1998; Meunier et al., 2014; Miller and Halpern, 1998; Savage et al., 2013).

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 A2). This correction reduces but does not eliminate bias. For example, we predicted tree age from species, node counts, and region for a 20% testing dataset using the remaining 80% to fit our models, as a demonstration of how accuracy measures would change. At annual precision, accuracy of estimated ages increased from 9% to 21%. At  $\pm 1$ - and  $\pm 2$ -yr precision, accuracy increased from 19% to 40%, and 26% to 59%, respectively. Finally, at  $\pm 5$ -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) (Fig. A2). 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 A3).

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 for seedlings at the edge of their climatic tolerance, would decrease the bias we observed between ring 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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#### Appendix A. Supplementary results

Supplementary results associated with this article can be found in the online version, at <https://doi.org/10.1016/j.foreco.2018.06.001>.

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