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Impacts of growing-season climate on tree growth and post-fire regeneration in ponderosa pine and Douglas-fir forests

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Abstract. We studied the impacts of climate variability on low-elevation forests in the U.S. northern Rocky Mountains by quantifying how post-fire tree regeneration and radial growth varied with growing-season climate. We reconstructed post-fire regeneration and radial growth rates of *Pinus ponderosa* and *Pseudotsuga menziesii* at 33 sites that burned between 1992 and 2007, by aging seedlings at the root–shoot boundary. We also measured radial growth in adult trees from 12 additional sites that burned between 1900 and 1990. To quantify the relationship between climate and regeneration, we characterized seasonal climate before, during, and after recruitment pulses using superposed epoch analysis. To quantify growth sensitivity to climate, we performed moving regression analysis for each species and for juvenile and adult life stages. Climatic conditions favoring regeneration and tree growth differed between species. Water deficit and temperature were significantly lower than average during recruitment pulses of ponderosa pine, suggesting that germination-year climate limits regeneration. Growing degree days were significantly higher than average during years with Douglas-fir recruitment pulses, but water deficit was significantly lower one year following pulses, suggesting moisture sensitivity in two-year-old seedlings. Growth was also sensitive to water deficit, but effects varied between life stages, species, and through time, with juvenile ponderosa pine growth more sensitive to climate than adult growth and juvenile Douglas-fir growth. 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 juvenile ponderosa pine in recent decades. Changing sensitivity of growth to climate suggests that increased temperature and water deficit may be pushing these species toward the edge of their climatic tolerances. Our study demonstrates increased vulnerability of dry mixed-conifer forests to post-fire regeneration failures and decreased growth as temperatures and drought increase. Shifts toward 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 regeneration; tree rings.

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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). 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 require understanding the underlying controls of tree establishment, growth, and survival.

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 (Chambers et al. 2016, Johnstone et al. 2016, Tepley et al. 2017, Stevens-Rumann et al. 2018). In dry mixed-conifer forests of western North America, 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, as germination and survival require energy and moisture (Dobrowski et al. 2015, Rother et al. 2015, Harvey et al. 2016, Stevens-Rumann et al. 2018, Davis et al. 2019*a*). Several studies highlight abundant regeneration, both following and independent of wildfire, occurring during cooler- and/or wetter-than-average 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 changes in seed availability and warm and dry conditions (Welch et al. 2016, Stevens-Rumann et al. 2018, Kemp et al. 2019, Davis et al. 2019*a*). Observed and potential declines in post-fire regeneration are of increasing management concern, requiring managers to decide if, where, and when post-fire management interventions, such as plantings, should occur.

Once trees are established, radial tree 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 and 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 from 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 change over time, due to climate variability and prolonged periods of cool/wet or warm/dry conditions (Carrer and Urbinati 2006, Hayles et al. 2007, Olivar et al. 2015). For example, increasing precipitation variability, along with underlying directional trends in temperature, may alter growth sensitivity due to underlying physiological thresholds being crossed and/or an increased frequency of extreme climate conditions (Carrer and Urbinati 2006, Hayles et al. 2007). Local conditions, such as competition or changes in microclimate, can also alter 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 development of conifer forests, our study addressed the following questions in low-elevation forests of the U.S. northern Rocky Mountains (hereafter "Northern Rockies"): (1) How does growing-season climate affect post-fire conifer regeneration? (2) How has growth sensitivity to growing-season climate varied between 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 climatic changes resulting in conditions closer to species' climatic tolerances for growth.

Methods

Study region

The study was conducted in the Northern Rockies of Idaho and Montana in dry mixed-conifer forests dominated by ponderosa pine and Douglas-fir (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; Wang et al. 2016).

Climate has changed significantly across the study area over the past century. For example, growing-season temperatures increased from a mean (SD) of 12.1(0.7)°C during the period 1901–1930 to 13.1(0.7)°C in 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 in 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 (Appendix S1: Fig. S1). The 1960s and 1970s exhibited comparatively low climatic variability (Appendix S1: Fig. S1).

Site selection

Sites were separated into two sampling units: (1) 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"); (2) 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). 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 were necessary to obtain areas that had not experienced fires in more recent decades. Thus, our sample sites are specifically located where we would expect species to be closest to their climatic limits for tree establishment and growth, and therefore be most sensitive to climate change. Our sample sites are not intended to be representative of all mixed-conifer forests.

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. (2008) 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,

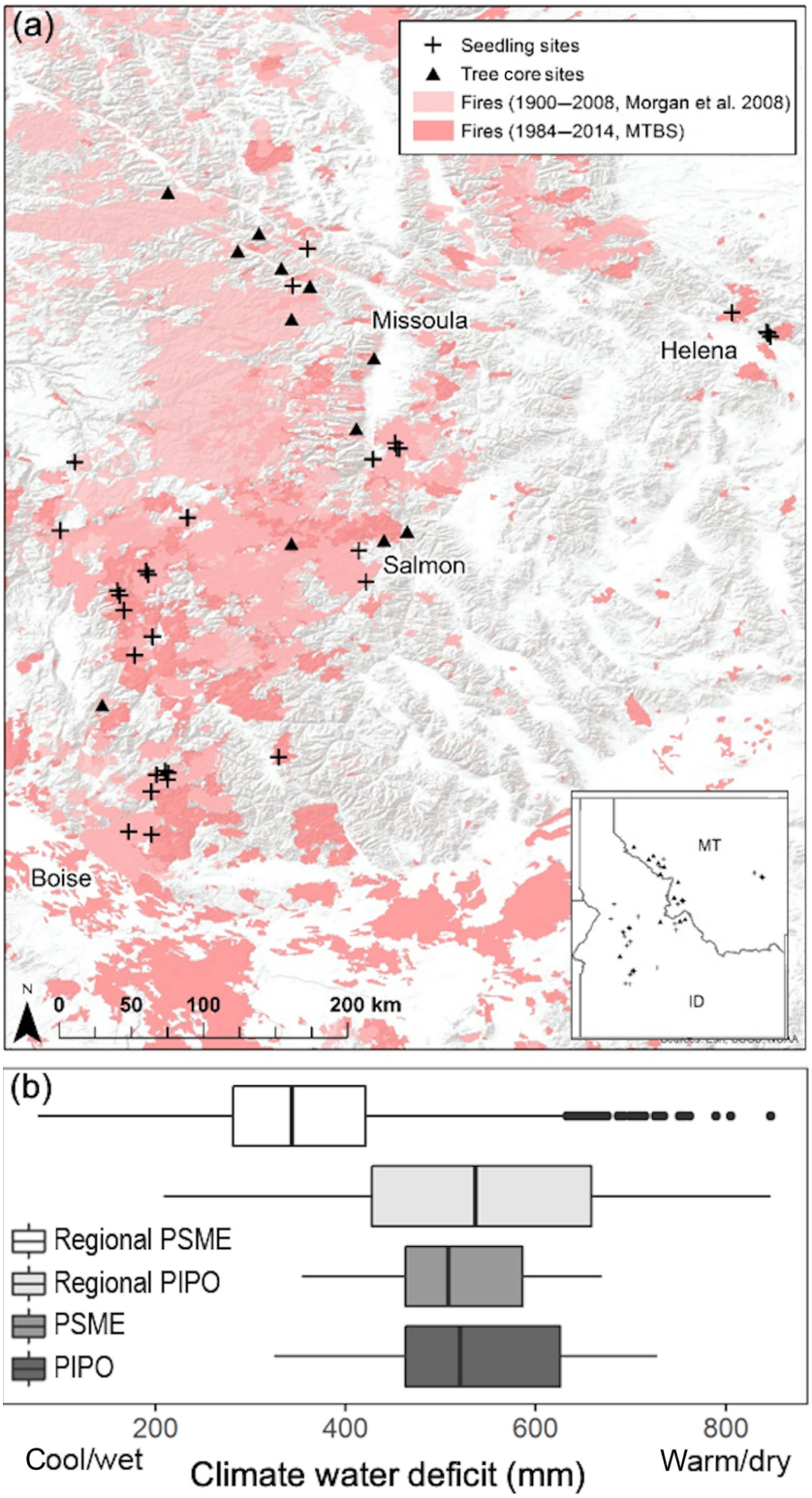

Fig. 1. (a) Sampling sites in low-elevation dry mixed-conifer forests that burned between 1900 and 2007 across

(Fig. 1. *Continued*)

the western continental United States. Dark pink areas indicate all fires that occurred from 1984 to 2014 from the Monitoring Trends in Burn Severity dataset; light pink areas indicate all fires that occurred from 1900 to 2008 from the Fire Atlas (Morgan et al. 2008). (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).

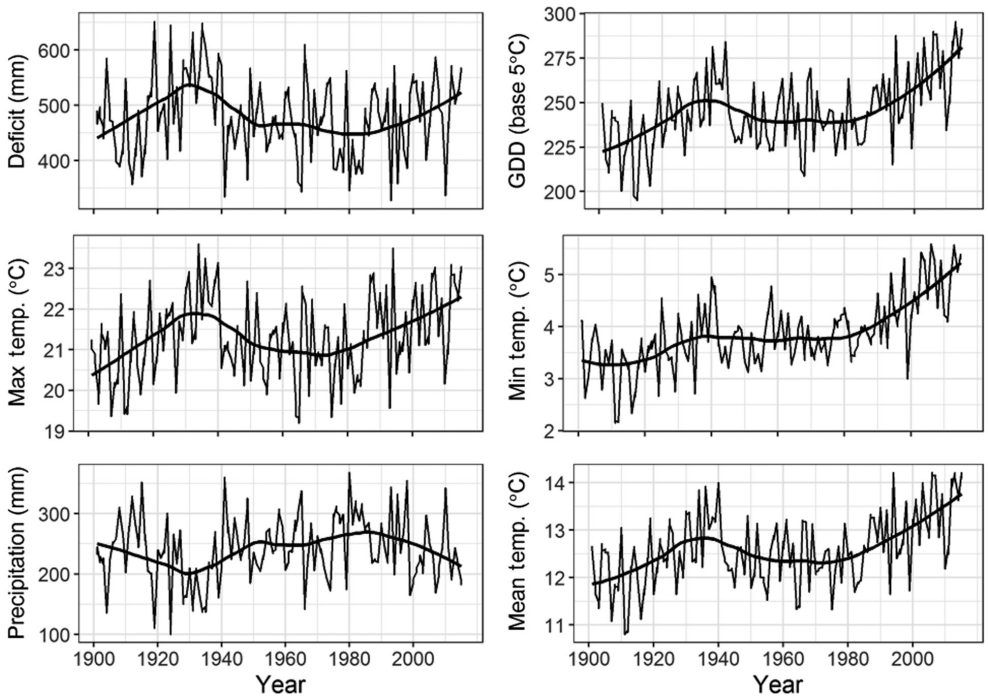

Fig. 2. Mean growing-season climate across all sites from 1901 to 2015. One-kilometer monthly to annual climate data are from ClimateNA (Wang et al. 2016). Monthly climate variables were summarized to the growing season from April to September.

burn severity was estimated based on stand structure. Each site was assessed for distance-to-seed-source and post-fire management. As our study was aimed at specifically sampling post-fire tree regeneration, sites were only included if they were within 100 m of a potential seed source, which was typically either a few adult trees or a small unburned patch; this distance was based on the results of Kemp et al. (2016), who found that the probability of post-fire seedling presence decreased significantly beyond 95 m from the nearest live tree. All sites were also free of post-fire planting or salvage logging.

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 to 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.

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. (2018). 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 10–40× magnification using a Nikon SMZ645 stereomicroscope (Nikon Instruments, Melville, New York, USA). 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 laboratory protocol for aging 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 United States (Hankin et al. 2018). 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 (SD) 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 (SD) 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 (Seiko Epson Corporation, Suwa, Japan). If seedlings were too small for scanning, they were photographed under the microscope at 10–40× magnification using a SPOT Idea CMOS digital camera (Diagnostic Instruments, Sterling Heights, Michigan, USA). Ring widths were measured from the digital images using the computer program CooRecorder and were then exported for further analysis using CDendro (Cybis Dendrochronology, Saltsjöbaden, Sweden). While we recorded visual marker years, the young age of the seedling samples did not allow for more formal cross-dating methods. For tree-core samples, we also performed statistical cross-dating at the site level using COFECHA (Holmes 1983, Grissino-Mayer 2001).

Climate data

We used 1-km resolution monthly climate data generated with the ClimateNA v5.10 software package for the period of 1901–2015 (Wang et al. 2016). 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 calculates water deficit as the difference between reference evapotranspiration, calculated using air temperature data (Hargreaves and Samani 1985), and precipitation; an important limitation of this approach is the assumption that air temperature is the sole driver of evapotranspiration. Thus, this approach does not incorporate important physical processes that also determine evapotranspiration, including

humidity, solar radiation, and wind speed. Despite these limitations, we used ClimateNA to generate historical data because we needed a single dataset that spanned the entire length of our study (i.e., 1901–2015).

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. At each site, we defined a regeneration pulse as any year where ≥20% of total seedlings at a site established (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 consecutive years, we identified only the year with the largest pulse as a regeneration pulse.

To quantify the relationship between regeneration and climate, we compared regeneration pulses to climate conditions using superposed epoch analysis (SEA) in R v3.3.2 (Swetnam 1993, R Core Team 2017). Specifically, we used SEA to

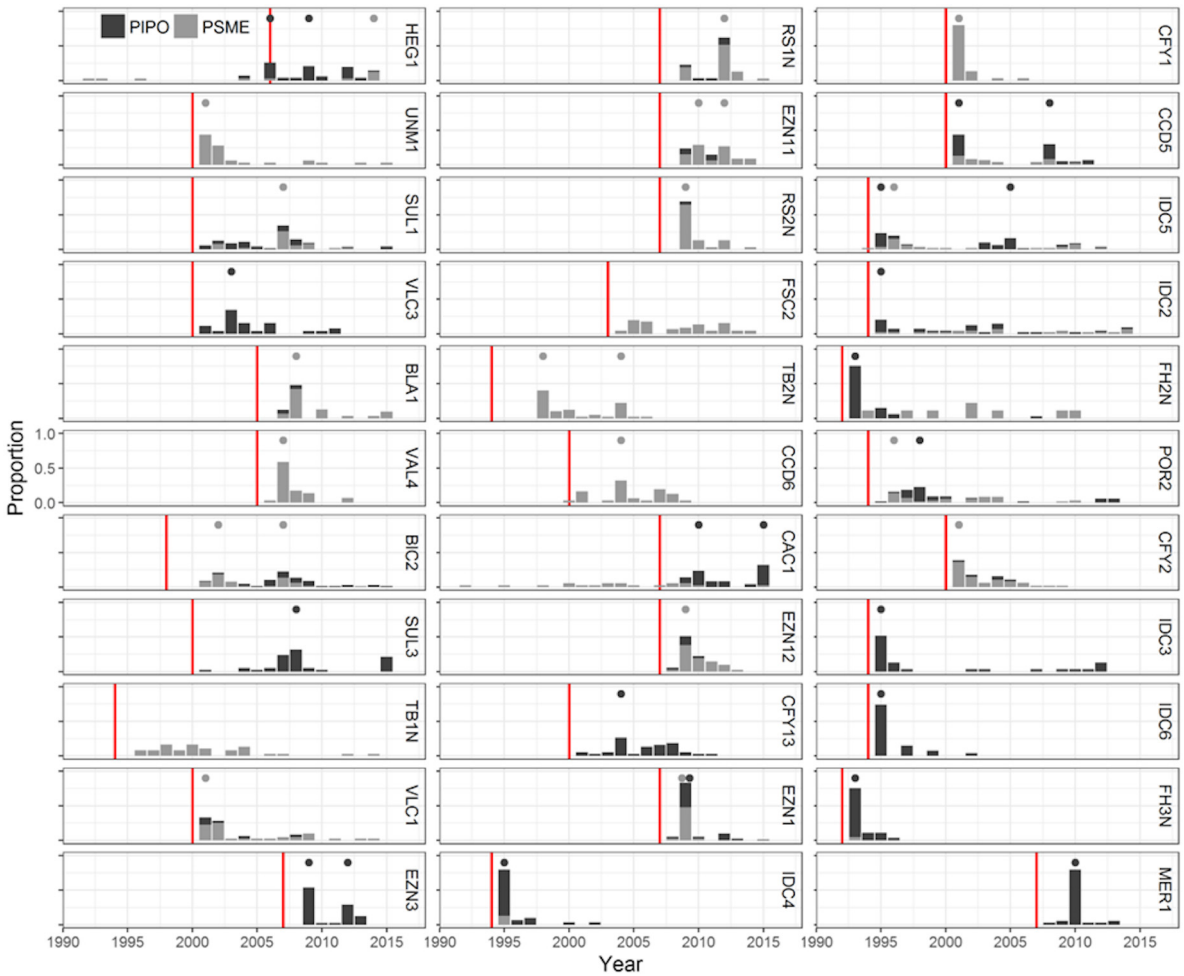

Fig. 3. Age structures and regeneration events at 33 seedling sites. Sites are organized by climatic water deficit using 30-yr deficit normals: lowest (wettest) in the upper left corner and highest (driest) in the bottom right corner. Dark gray bars and circles represent ponderosa pine regeneration and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

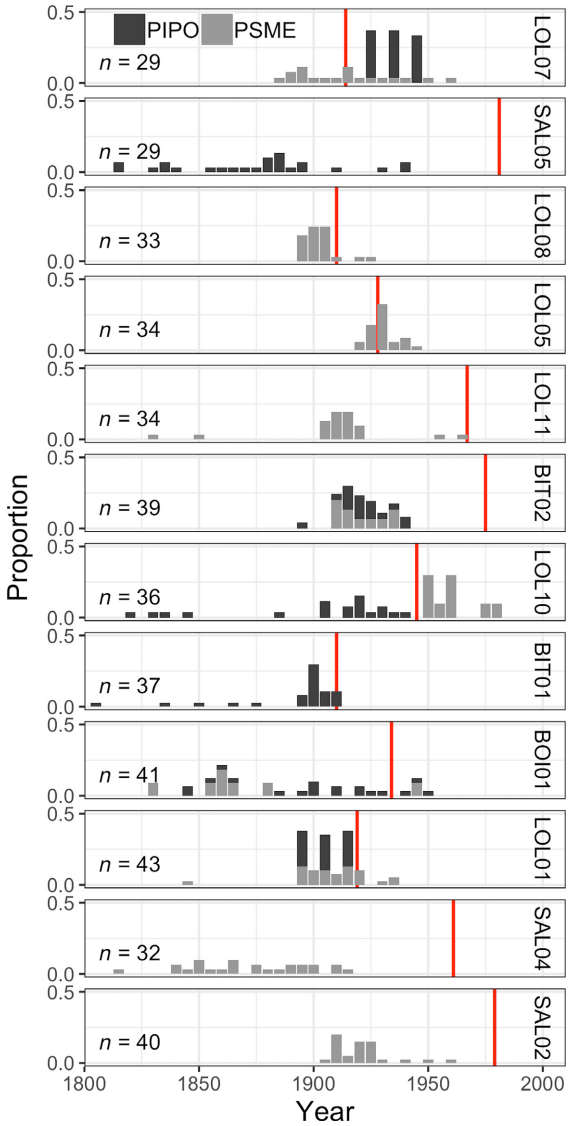

Fig. 4. Age structures at 12 tree-core sites. Sites are organized top to bottom by increasing climatic water deficit (wettest to driest) using 30-yr deficit normals. Dark gray bars represent ponderosa pine regeneration in 5-yr bins, and light gray bars represent Douglas-fir regeneration in 5-yr bins. Red vertical lines are fire years. Note the smaller y-axis range in this figure (0.0–0.5) relative to Fig. 3 (0.0–1.0).

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 using 95% confidence intervals, generated from 10,000 simulations under the null hypothesis of average climate conditions before, during and after regeneration pulses. To account for autocorrelation in the climate record within these simulations, 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 trends 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 yr) from the raw value for each year for each site.

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 BAI *z*-scores 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 yr of radial growth, or adult, representing radial growth beyond 25 yr.

Growth sensitivity to climate for each species and life stage was examined using temporally continuous linear regressions, with growth modeled 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 to 2015) to understand overall trends in the significance and sign of climate effects on growth. Continuous linear regressions were performed in 30-yr, 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. These analyses were performed

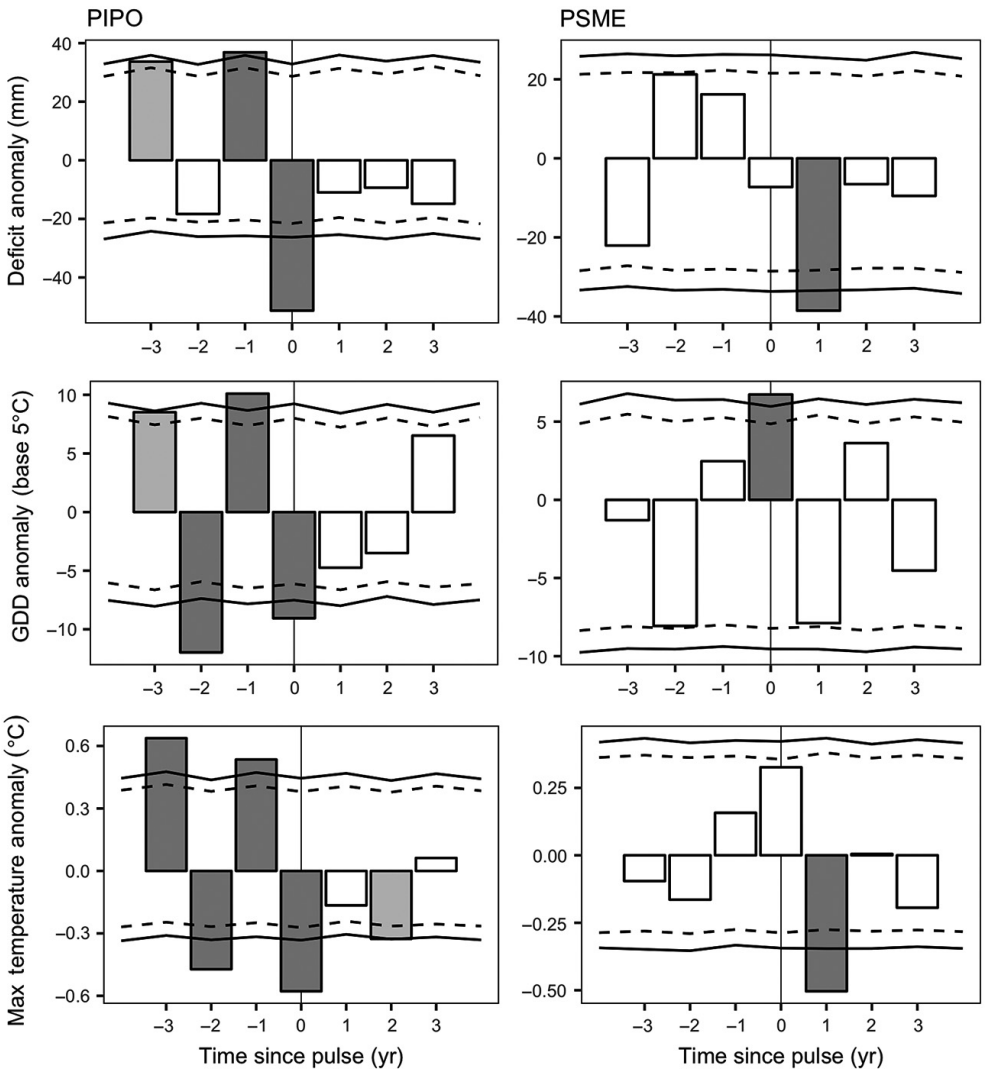

Fig. 5. Superposed epoch analysis (SEA) results summarizing the average climate anomaly conditions before, during, and after 44 regeneration events from 33 sites. Climate was detrended over the time period using a 30-yr running mean, and then, annual values were subtracted from the mean to obtain anomaly 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.

using the mean growth chronology for each category of species (ponderosa pine or Douglas-fir) and life stage (juvenile or adult), 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 had changed over time and whether these relationships were significant.

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

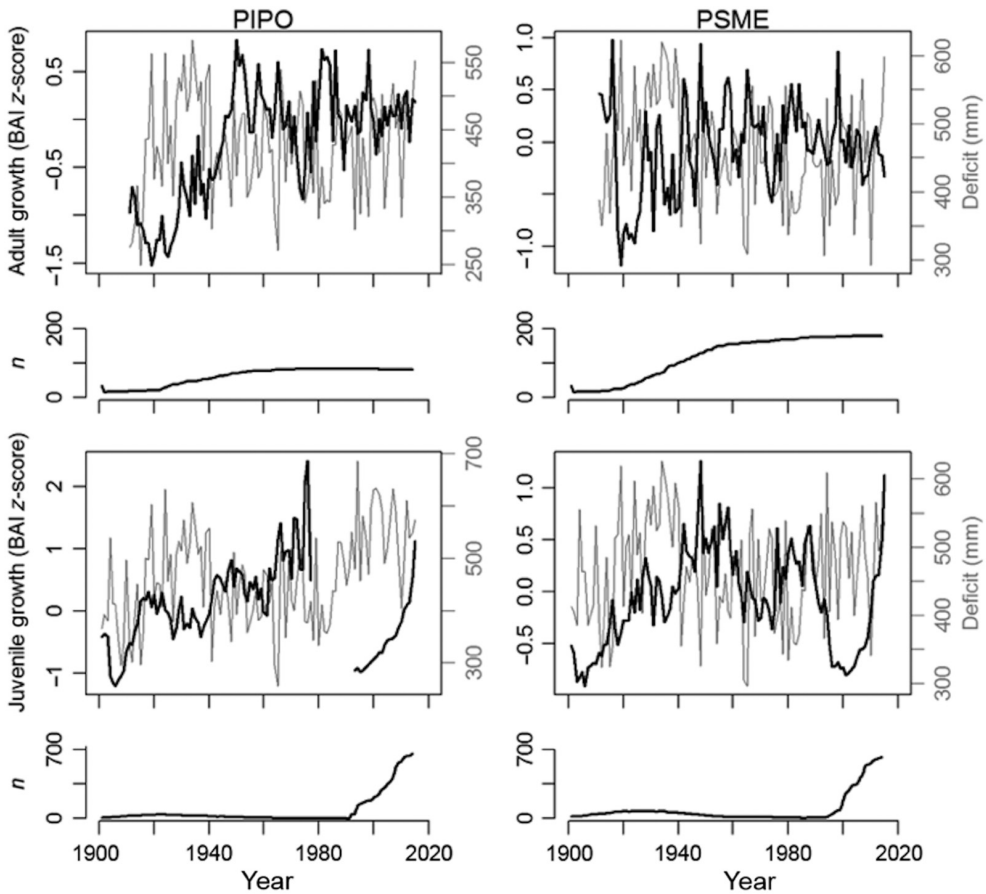

Fig. 6. Standardized basal area increment chronologies (black lines) for adults and juveniles of ponderosa pine and Douglas-fir individuals across all sites. Gray lines indicate mean growing-season climatic water deficit across all sites that contribute to each mean value chronology. Sample sizes for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

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) yr.

We sampled an average of 43 seedlings per site for our regeneration analyses. Across the 33 seedling sites, we identified 44 regeneration pulses (i.e., >20% of total site recruitment in one year), with pulses occurring at all of the ponderosa pine sites and at 21 out of 23 Douglas-fir 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 35 trees at each tree-core site, which displayed largely continuous regeneration across multiple decades in the 19th and/or 20th century. Most trees germinated prior to the timing of fires indicated in the Fire Atlas (Fig. 4), implying that these 20th-century fires were non-lethal (i.e., of low or moderate severity). Additional evidence of non-lethal fire occurring at tree-core sites included an average of one fire-scarred tree per site, typically on ponderosa pine, and charcoal present on several trees to a height of approximately 0.5 m (at two sites with fire dates of 1961 and 1979 in the Fire Atlas).

Regeneration-climate analyses

Climatic conditions concurrent with regeneration pulses differed between species. Growing-season water deficit and temperature metrics (i.e., growing degree days and 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 (Appendix S1: Fig. S3).

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; Appendix S1: Figs. S4–S7). 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 and 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, climatic effects on juvenile growth changed significantly through time (Fig. 7). 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 in one standard deviation in water deficit corresponded to a −0.2 to −0.4 SD 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 greater sensitivity in ponderosa pine seedlings than in Douglas-fir seedlings (Fig. 7). For example, a one standard deviation increase in water deficit corresponded with 0.2 SD decrease in ponderosa pine juvenile growth during the 1930s and 1940s, and a 0.8 SD decrease in recent decades. However, the same increase in water deficit corresponded with an approximately 0.2 SD *increase* in juvenile ponderosa pine growth in the first decades of the 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.

Table 1. Growth–climate Pearson's correlation coefficients (r) and two-tailed P-values for adults (>25 yr old) and juveniles (<25 yr old) from 1901 to 2015.

	PIPO		PSME	
Climate variable	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**

Notes: Growth is the mean standardized basal area increment for all individuals that fall within a given category of species and life stage (i.e., adult ponderosa pine). Bold values indicate significance at the $P = 0.05$ level.

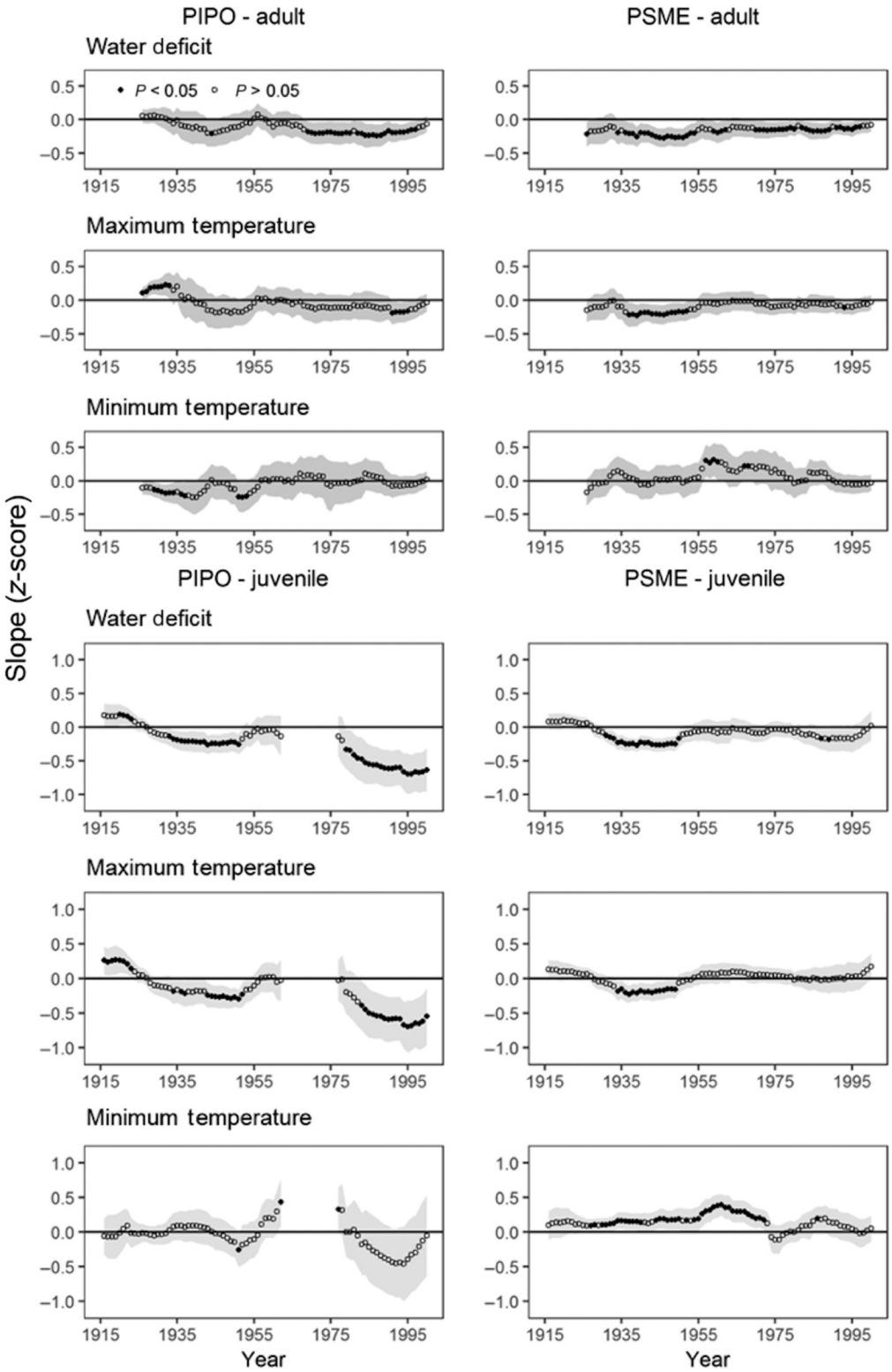

Fig. 7. Slope parameters from linear regressions of growth as a function of climate for each species and life

(Fig. 7. *Continued*)

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 yr of radial growth, or adult, representing any radial growth beyond 25 yr. 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. Gray ribbons represent 95% confidence intervals around the slope parameter, where bands not overlapping 0 indicate a significant relationship.

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 (Kemp et al. 2016), 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.

Our inferences are constrained by two overarching limitations. First, our regeneration analyses are limited by the inability to cross-date our seedling samples, which could lead to underestimating tree age if some samples have missing rings. By analyzing regeneration pulses, however, we minimized the potential impact of any missing rings, since pulses were defined as years with >20% of the regeneration occurring at a given site. Second, while we infer important impacts of climatic water deficit on regeneration and growth, the temperature-based method used here does not incorporate important components of energy balance that affect reference evapotranspiration, and the method ignores edaphic constraints on soil water supply. Consequently, the ClimateNA water deficit metric tracks changes in temperature and can thus mischaracterize changes in evapotranspiration through time (Hobbins et al. 2008). We note, however, that across western North America, temperature-based estimates of potential evapotranspiration are generally consistent in sign with more sophisticated methods (LIG>eld/LIG>eld et al. 2012). Nonetheless, our use of a simplified water-balance metric constrains our ability to infer the specific biophysical constraints on growth and regeneration and their ecophysiological underpinnings.

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, Davis et al. 2019*a*) and Douglas-fir (Rother et al. 2015, Tepley et al. 2017, Davis et al. 2019*a*). It is also one of the first studies to evaluate climatic effects on ponderosa pine and Douglas-fir regeneration pulses independently, allowing for unique inference into species-specific regeneration responses to climate.

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, Kemp et al. 2019, Davis et al. 2019*a*), as harsh (micro-) climate conditions decrease seedling survival (Rother et al. 2015).

Our results also are also consistent with a potential link between climate and cone production in ponderosa pine. Specifically, as ponderosa pine has a two-year cone maturation cycle, the observed cooler and wetter conditions two years prior to regeneration pulses (Fig. 5) are consistent with a climate influence on cone initiation (Oliver and Ryker 1990). Keyes and Manso (2015) found that wetter May-August conditions were associated with years of higher cone and seed production in the Northern Rockies, consistent with our finding. Other studies in the Rocky Mountains have linked seasonal climate to cone and seed production, although climate effects on reproduction are highly variable within and between regions (Mooney et al. 2011, Keyes and Manso 2015). 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 2018). 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 for 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 for first-year seedling growth and survival of Douglas-fir in low-elevation forests in the southern Rocky Mountains (Rother et al. 2015). The pattern found here is consistent with the importance of moisture availability, but it occurred one year after germination. This may reflect the influence 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 (Davis et al. 2019*a*). 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 to 2015 was significantly higher at seedling sites dominated by ponderosa pine (mean [SD] = 556 [69] mm) vs. Douglas-fir (495 [75] mm; df = 45, $t = 2.9$, $P = 0.01$; Fig. 1), suggesting that Douglas-fir seedlings sampled here may not be facing the same degree of moisture limitation as ponderosa pine seedlings sampled.

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, Fig. 7; Appendix S1: Fig. S10), 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. 7). The relationship in the 1930s 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; Appendix S1: Fig. S2). 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; Appendix S1: Fig. S2). 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, 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. Higher growth under warmer, drier conditions in the first decades of the 20th century is more surprising and may reflect differences in both climate and site characteristics. For example, seedlings establishing after largely low-severity fires earlier in the 20th century, compared to regeneration following moderate- to high-severity fires in recent decades, may have grown under more closed canopy conditions that coincided with a longer-lasting snowpack.

Increased water deficit also 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 biotic and abiotic conditions, will be critical for anticipating growth responses to future climate change.

Climate effects on growth for both species were strongest during periods of high interannual climate variability (Appendix S1: Fig. S1), consistent with periods of increased sensitivity of growth to growing-season climate. Alternatively, this pattern may be a statistical artifact, as higher variability in an independent variable leads to higher correlations with a dependent variable, even under the null hypothesis of no relationship. Climate effects on juvenile growth were highest in recent decades, a period of high variability in moisture availability and growing degree days (Appendix S1: Fig. S1). 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 climatic factors

not captured in this analysis, or non-climatic factors, have become more limiting to growth. For example, seedling sensitivity to climate could be mediated by competition or nutrient availability, largely independently of climate variability (e.g., Sala et al. 2005). Additionally, our analyses did not consider climate-related factors that occur outside of the growing season, including snowpack depth or frost events. While winter climate variables were not as well correlated with growth in our study as were growing-season metrics (data not shown), changes in snowpack in these low-elevation sites could affect both vulnerability to frost damage during the winter and soil moisture during the early growing season.

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, Kemp et al. 2019), given projected increases in fire activity and prolonged periods of warm, dry conditions (Flannigan et al. 2009, Littell et al. 2010, Abatzoglou and Williams 2016). Temperatures are expected to increase under all emissions scenarios throughout the northwestern United States 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 result 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 the post-fire regeneration and growth of ponderosa pine and Douglas-fir, with potentially stronger reductions in regeneration and growth in ponderosa pine. Our findings suggest declines in 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 United States (Savage and Mast 2005, Welch et al. 2016, Stevens-Rumann et al. 2018). Similarly, higher sensitivity of juvenile ponderosa pine growth to water deficit and maximum temperature in recent decades, relative to Douglas-fir, suggests that future increases in temperature and water deficit may affect ponderosa pine juveniles more so than Douglas-fir juveniles. Differences between the sensitivity of ponderosa pine and Douglas-fir juveniles to climate are consistent with findings showing greater shade and heat tolerance in Douglas-fir than ponderosa pine seedlings (Marias et al. 2017), although the same differences in sensitivity were not apparent for adult growth. 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 (Von Arx et al. 2013, Davis et al. 2019*b*). As high-severity wildfires remove adult trees that exhibit similar growth sensitivity to moisture availability, post-fire forest composition will reflect the more varied species-specific responses to climate conditions highlighted for juveniles in this study, leading to potential shifts in species composition.

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, especially in sites dominated by ponderosa pine. Post-fire planting efforts should consider species-specific climate sensitivities for regeneration and growth to determine the timing and location of these efforts that will maximize seedling success. Future studies are needed to quantify relationships between climate and growth through time in higher-elevation forests, as well as identify climate thresholds beyond which regeneration failure will occur. Considering the entire post-fire recovery trajectory, from post-fire regeneration to

adult growth (Davis et al. 2018), highlights that species-specific responses to climate and fire need to be considered at each stage of forest recovery to better understand, predict, and manage for future forest resilience to changes in climate and fire activity.

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Data Availability

The data and code used in this study are available via the Dryad Data Repository: https://doi.org/10.5061/dryad.gt22vt4.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2679/full