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Climate and ecological disturbance analysis of Engelmann spruce and Douglas fir in the greater Yellowstone ecosystem

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ABSTRACT

The effects of anthropogenic climate change are apparent in the Greater Yellowstone Ecosystem (GYE), USA, with forest die-off, insect outbreaks, and wildfires impacting forest ecosystems. A long-term perspective would enable assessment of the historical range of variability in forest ecosystems and better determination of recent forest dynamics and historical thresholds. The objectives of this study were to (1) develop tree-ring chronologies for Engelmann spruce and Douglas fir growing at the study location, (2) correlate the annual ring widths of each species to monthly climate variables, (3) examine the instrumental climate data for regimes shifts in the mean state of variables, and (4) determine when ecological disturbances occurred through a quantification of growth releases. Finally, we discuss both climate-growth relationships and growth releases in the context of climate regime shifts and known forest disturbances. Engelmann spruce and Douglas fir showed some similar climate responses using moving correlation analysis including negative correlations between ring width and June – August current year temperature and previous growing season temperature. Regime shift analysis indicated significant ($p < 0.05$) shifts in minimum and maximum GYE temperature in the latter half of the 20th century. Disturbance analysis indicated that both tree species responded to wildfire and insect outbreak events with growth releases in up to 25% of the trees. Disentangling the influence of climate regime shifts and forest disturbances on the climate-growth relationships can be difficult because climate and forest disturbances are intricately linked. Our evidence indicates that regime shifts in monthly climate variables and forest disturbances as recorded by growth releases can influence the ring width response to climate over time. Trees are key to providing a long-term perspective on climate and ecological health across the GYE because they integrate both climate and ecology in their annual ring widths.

Introduction

Climatic changes, including increasing temperatures, result in glaciers melting at a faster rate, reductions in snowpack, and changing streamflows in the intermountain region in the United States (Vose et al., 2017). The effects of anthropogenic climate change can already be seen in the Greater Yellowstone Ecosystem (GYE) with forest die-off, insect outbreaks, and wildfires (Gonzalez et al., 2018; Hansen and Phillips, 2018) impacting forest ecosystems. For example, warmer than average temperatures in winter and fall combined with low summer precipitation has enabled mountain pine beetles to overwhelm alpine forests causing tree mortality (Buotte et al., 2016). The productivity of forests depends on multiple factors including climate, soil, and disturbances that are altered due to climate change (Grier et al., 1989). Forest disturbances, like wildfires, have shaped the landscapes of the GYE creating changes in nutrient cycling (Griffin et al., 2011), forest structure (Romme et al., 2011), and tree species composition (Clark et al., 2017). The 1988 Yellowstone fires were a foundational event shaping the landscape, and ecologists have developed a repository of knowledge on the response of the ecosystem (Romme et al., 2011). However, the intense study of the GYE in response to one event neglects some of the long-term changes to forest ecosystems. One challenge to the management and adaptation of forest ecosystems is the limited amount of long-term climatological and ecological observations. The Yellowstone Vital Signs Monitoring Project seeks to build baseline data for key metrics of the ecosystem to determine how waterways, vegetation, animals, and climate change over time (Ray et al., 2019). Keane et al. (2009) have emphasized the use of the historical range and variability in landscape management and the application of ecological research to guide decision making. Further, reference conditions derived from ecological research can be used to evaluate current conditions and provide targets for forest

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restoration to build more resilient ecosystems (Swetnam et al., 1999; Tinker et al., 2003). To develop baseline data on forests' response to disturbances and climatic changes, we need a long-term perspective to better determine if recent forest dynamics are within the normal range of variability. Trees are natural recorders of past environmental events. They are fixed on the landscape for decades to centuries, enduring drought, heat waves, wildfires, and insect outbreaks. Dendrochronological analysis in forested areas is crucial to understanding the dynamic relationships between climate, forest disturbance, and annual tree growth in the presence of climate change (Speer, 2010).

The GYE encompasses roughly 7.7 million ha and consists of national parks, national forests, wildlife refuges, and state and privately owned land in the northwest corner of Wyoming, USA, with portions of the region extending into Idaho and Montana (Hansen and Phillips, 2018). The northeastern region of the GYE, the Shoshone National Forest, where the current study was conducted, comprises a mosaic of public and private land outside of the national park. The management of this ecosystem can be difficult due to the differing goals of the organizations that own portions of this land. Yellowstone National Park, established in 1872, is at the center of this ecosystem, and prior to its establishment there was little European settlement in the region (Clark, 1999). The GYE is a crucial ecosystem for large herbivores (e.g., American bison (*Bison bison*) and elk (*Cervus canadensis*)) and predators (i.e., reintroduced wolves (*Canis lupus* Linnaeus)) that have been extirpated from much of North America (Yellowstone Center for Resources, 2018). The ecosystem contains abundant biodiversity due to the wide range of habitats including forests, meadows, hydrothermal, and high-alpine areas (Yellowstone Center for Resources, 2018).

Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominate much of the mid- to upper-elevation forests in the GYE from 1000 to 3000 m, with Engelmann spruce most common at higher elevations and Douglas fir most common at lower elevations. Engelmann spruce is prominent throughout the Rocky Mountains and is a major component to high-elevation forests (USDA Natural Resources Conservation Service, 2020). The geographic range of Engelmann spruce includes Alberta and British Columbia, Canada, at the northernmost boundary, extending south to Arizona and New Mexico, USA, at the southernmost boundary. Engelmann spruce is a shade tolerant species with a life span of approximately 300 years that favors cool temperatures and adequate soil moisture (USDA Natural Resources Conservation Service, 2020). Douglas fir is a fire-resistant species with the ability to withstand low-intensity fires (Baysinger et al., 2017). The northernmost geographic range for Douglas fir encompasses Alberta and British Columbia, Canada, and the southernmost range extends to Arizona, New Mexico, and Mexico. Douglas fir is a drought-tolerant species that favors full- or part-time sun and requires well-drained soils (USDA Natural Resources Conservation Service, 2020). This species is widespread in mixed conifer and evergreen forests with a life span of approximately 500 years (Steinberg, 2002). Wildfires in the Shoshone National Forest portion of the GYE have occurred on average every 47 years in lower elevation forests and approximately every 100 years at higher elevations (Brown et al., 2020a). Climate change is lengthening the growing season in the intermontane region of the US with higher temperatures during the summer and more frequent droughts driven by declines in winter snowpack (Vose et al., 2018). We anticipate that the effect of these climatic changes on Engelmann spruce and Douglas fir tree growth will be negative because of decreasing moisture and increasing evapotranspiration during the growing season. Climate-related changes, such as increased temperatures and changing streamflows, can already be observed throughout the GYE (Coulthard et al., 2019) and are expected to drive ecosystem changes (Gonzalez et al., 2018). Increased monthly temperatures and droughts have led to larger wildfires and caused insect outbreaks to increase in frequency and severity (Yellowstone Center for Resources, 2018). Altered fire regimes have been reported in the GYE due to climate change (Turner et al., 2003), and from June to September 1988, a series of wildfires burned 45% of the GYE (Parmenter et al., 2003). Additionally, climate change is driving current insect outbreaks such as western spruce budworm (*Choristoneura occidentalis* Freeman), an insect that attacks both Engelmann spruce and Douglas fir. Spruce budworm is characterized as one of the most destructive insects in conifer forests (Brookes et al., 1987). Insect infestations from spruce bark beetles (*Ips typographus* Linnaeus), Douglas fir beetles (*Dendroctonus pseudotsugae* Hopkins), and mountain pine beetles also have been reported in the Shoshone National Forest, Wyoming, where this study took place (Rice et al., 2012). Climate change increases susceptibility to insect outbreaks because of the stress induced on trees from drought and an increase in other disturbances (Gonzalez et al., 2018; Hansen and Phillips, 2018). By studying the impacts of climate and disturbances on a forest-stand scale, we can better understand the landscape-scale impacts of these ecosystem changes.

Better understanding of how trees have responded to past changes in climate and forest disturbances and to place current and future changes in the context of past variability is crucial. A long-term perspective is needed to understand forest ecosystem dynamics, and dendrochronology is uniquely positioned to address such temporal questions. Here, we use tree-ring data to provide ecological information that can be used to expand upon the paleoenvironmental understanding of the GYE. The objectives of this study were to (1) develop tree-ring chronologies for Engelmann spruce and Douglas fir growing at the study location, (2) correlate the annual ring widths of each species to monthly climate variables, (3) examine the instrumental climate data for regimes shifts in the mean state of variables, and (4) determine when ecological disturbances occurred through a quantification of growth releases. Finally, we discuss both climate-growth relationships and growth releases in the context of climate regimes shifts and known forest disturbances.

Data and methods

Study area

The study was conducted within the Shoshone National Forest situated within the Greater Yellowstone Ecosystem (Fig. 1). The Shoshone National Forest was established in 1891 and consists of approximately 980,000 ha and ranges in elevation between 1402 and 4207 m (United States Department of Agriculture, 2020). The average annual temperature in this region is 5.2 °C and monthly temperatures range from 18.9 °C in July to −7.5 °C in January (NOAA National Centers for Environmental Information, 2019). The average annual precipitation in this region is 380 mm, and monthly precipitation ranges from 58 mm in May to 20 mm in February (NOAA National Centers for Environmental Information, 2019). The study site (~4 ha), Stacked Rock (SRS), is a steep rocky outcrop with a southwest-facing slope and an elevation of 2682 m. The highest density of trees persists at lower elevations below the outcrop. Forests in the GYE are composed of a variety of tree species, including lodgepole pine (*Pinus contorta* Douglas ex Loudon), whitebark pine (*Pinus albicaulis* Englem.), limber pine (*Pinus flexilis* James), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Additionally, forest composition includes Douglas fir and Engelmann spruce, which are the species examined in this study. Nutrient poor soils with low water retention are found at high elevations in the GYE; nutrient rich soils with greater water retention are found in valleys (Parmenter et al., 2003).

Tree-ring data

We collected tree core samples (two cores per tree unless rot was present) using a 5 mm diameter increment borer from trees greater than 5 cm diameter at breast height (DBH; 1.3 m above ground). DBH has historically been the location of comparative tree size measurement based upon allometric observations of tree growth. We collected 17 core samples of Engelmann spruce and 26 of Douglas fir. The cores were mounted

Fig. 1. Location of the study site (SRS, Stacked Rock Site) in the Greater Yellowstone Ecosystem, Wyoming, USA.

and sanded using progressively finer sandpaper to produce suitable surfaces for determining ring boundaries (Speer, 2010). We visually crossdated all samples using skeleton plots (Stokes and Smiley, 1968). Tree cores were measured using a Velmex (Velmex Inc.) sliding measuring stage with the measurement software Tellervo (tellervo.org). To establish absolute dating, we statistically validated all visual crossdating using the software COFECHA (Holmes, 1983). We used the Dendrochronology Program Library in R (*dplR*) package to create chronologies (for climate-growth analysis) for Engelmann spruce and Douglas fir from the raw ring width measurements (Bunn, 2008). A two-thirds smoothing spline was applied to remove non-climatic noise and age-related growth trends (Cook and Peters, 1981). An autoregressive model was applied to the time series to remove temporal autocorrelation and produce residual chronologies for each species that were then used for further analysis. The expressed population signal (EPS), interseries correlation, and mean sensitivity were calculated for each chronology. The EPS measures how similar growth is across the site, and a value above 0.85 indicates that the chronology is representative of the stand-level signal (Wigley et al., 1984). Interseries correlation is the average of the correlations between each core and the master chronology. Mean sensitivity measures the fluctuation in tree-ring width from year to year.

Climate data

To examine the growth response to climate, mean monthly minimum temperature, maximum temperature, and total monthly precipitation data were downloaded from the National Centers for Environmental Research for Wyoming climate division 1 for the period 1895–2017 (https://www.ncdc.noaa.gov/cag/divisional/mapping; NOAA National Centers for Environmental Information, 2019). Regime shift analysis was conducted on monthly climate variables to identify statistically significant changes in the mean state of climate over time (Rodionov, 2004). Shifts were identified using a running t-test ($p < 0.05$) in which 20-year windows of climate observations were compared for a given monthly climate variable. For example, the temperature from 1900 to 1920 would be compared to the temperature from 1901 to 1921. A significant change in the mean state would indicate a regime shift. Analysis ended 10 years prior to the end of the series to prevent spurious shifts from being identified.

Climate-tree growth relationships

Climate-growth relationships were analyzed in the *treeclim* package in R (Zang and Biondi, 2015). The program analyzes the relationships between the climate data and tree-ring chronologies using moving windows to determine how climate-growth relationships might change over time (Biondi and Waikul, 2004). We correlated each monthly climate variable with the Engelmann spruce and Douglas fir ring-width chronologies. We used the EPS (>0.85) to help determine the period of climate-growth and disturbance analyses discussed below. A moving interval with a 35-year window was used to analyze climate-growth relationships from 1930 to 2017 for the Engelmann spruce chronology and 1896 to 2017 for the Douglas fir chronology. We analyzed monthly climate data from the previous May extending through the current October (e.g., May 1901 to October 1902) to determine if a lag effect of climate was present and to capture responses in two growing seasons. The moving window began with the earliest year and then incremented one year at a time. The correlation ($p < 0.05$) between a tree-ring chronology and a monthly climate variable was recalculated using 1000 bootstrapped runs for each 35-year window to generate confidence intervals.

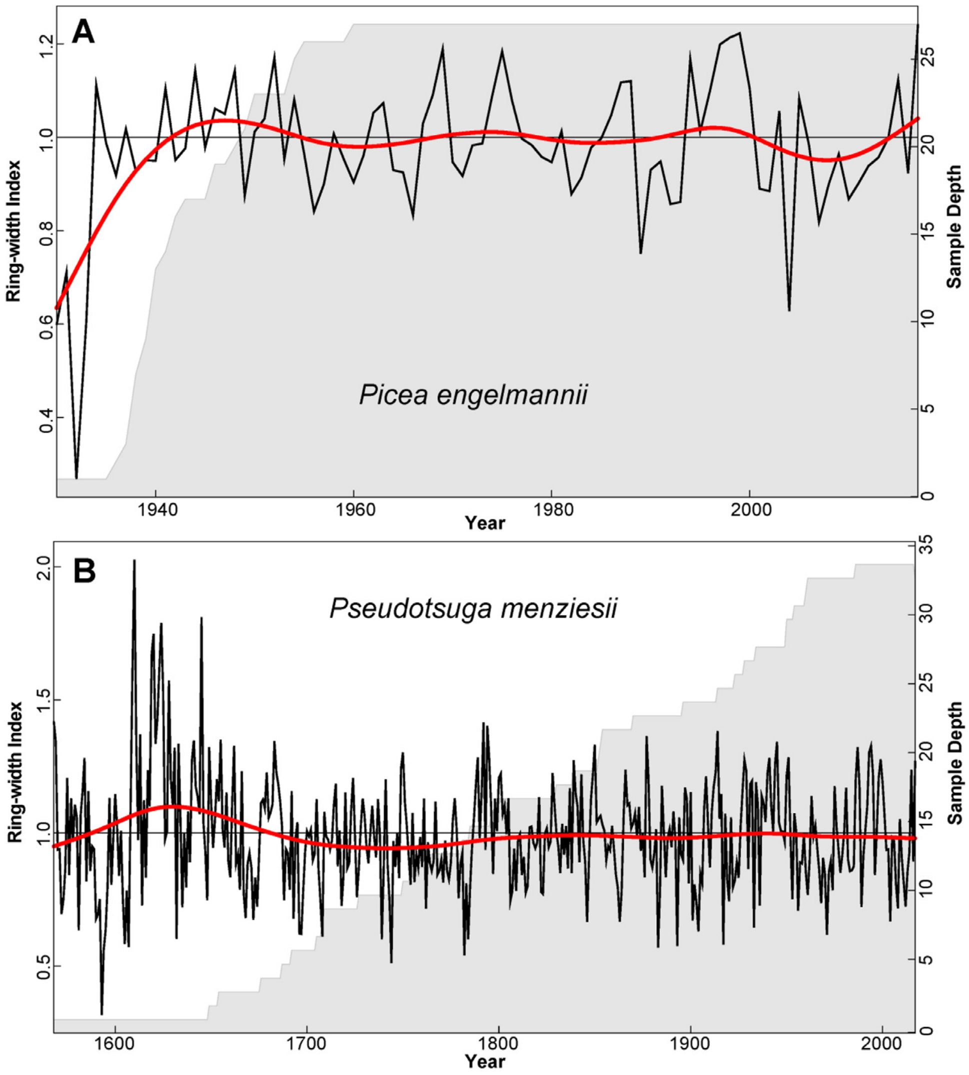

Fig. 2. Residual tree-ring chronologies, represented by the black lines, and the smoothing spline, represented by the red line for a) Engelmann spruce and b) Douglas fir. The sample depth is represented by the gray shaded area. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Disturbance

In addition to climate, ecological disturbances (e.g., wildfires, insect outbreaks) may impact tree growth in the GYE (Speer, 2010). The radial-growth averaging technique was used to identify growth releases for the raw ring-width measurements for Engelmann spruce and Douglas fir (Nowacki and Abrams, 1997). The analysis was run in the *TRADER* package in R (Altman et al., 2014). To detect a growth release, the percent growth increase from 15 years before a given year was compared to 15 years after the year of interest. Releases had to last at least 5 years, have a 25% increase in growth, and be at least 10 years apart to be detected. To determine possible causes of releases, growth release years are discussed in the context of climate regime shifts, and known fire events (Brown et al., 2020a) and insect outbreaks (Lee et al., 2018) generated from previous research.

Results

Tree-ring chronologies

The Engelmann spruce chronology extended from 1930 to 2017, with an EPS of 0.896 overall, an interseries correlation of 0.56, and a mean sensitivity of 0.18 (Fig. 2A). However, the EPS for Engelmann spruce fell below 0.85 in 1947 indicating that climate-growth and disturbance results prior to this year should be interpreted with caution. The Douglas fir chronology extended from 1568 to 2017, with an EPS of 0.896 overall, an interseries correlation of 0.59, and a mean sensitivity of 0.26 (Fig. 2B). The EPS for Douglas fir remained above 0.85 until 1722 allowing for a full analysis of climate-growth relationships in the 20th and 21st centuries. Both tree-ring chronologies experienced increased variability towards the beginning of the chronology due to lower sample size.

Climate data

Many significant ($p < 0.05$) regime shifts in the monthly climate data occurred over the past century (Table 1). For minimum temperature, shifts to warmer mean temperatures occurred in the late 20th century in all seasons. Maximum temperature shifts showed similar warming patterns across seasons. Precipitation regime shifts showed less consistent patterns in the mean state but significant downward shifts in precipitation occurred in February, March, and November during the latter half of the 20th century. Precipitation in May and June showed higher means in the late 20th century.

Climate-tree growth relationships

The Engelmann spruce correlation analysis showed a significant positive correlation ($p < 0.05$) between tree growth and previous August precipitation that was mostly consistent over the period of analysis

Table 1
Regimes shifts in monthly climate variables, minimum temperature (Tmin), maximum temperature (Tmax), and precipitation (PCP).

	Tmin			Tmax			PCP		
Month	Year	Direction	*p*-value	Year	Direction	*p*-value	Year	Direction	*p*-value
Jan	1989	up	0.001	1998	up	0.001			
Feb	1924	up	0.005	1990	up	0.04	1916	down	0.006
	1990	up	0.007				1936	up	0.008
							1963	down	0.04
Mar	1947	down	0.009	1947	down	0.01	1973	up	0.004
	1972	up	0.001	1966	up	0.001	1999	down	0.008
Apr	1999	up	0.004	1985	up	0.001			
May	1985	up	0.001				1978	up	0.04
Jun	1931	up	0.08	2006	up	0.001	1992	up	0.02
	1986	up	0.001						
Jul	1928	up	0.001	1916	up	0.007			
	1944	down	0.001						
	1998	up	0.001						
Aug	1934	up	0.008	1929	up	0.001			
	1962	down	0.01	1963	down	0.001			
	1980	up	0.003	1995	up	0.001			
	1998	up	0.02						
Sep	1997	up	0.001	1930	up	0.005			
				1957	down	0.001			
				1997	up	0.001			
Oct	2003	up	0.001						
Nov	1962	up	0.009	1998	up	0.005	1982	up	0.001
	1998	up	0.02				2005	down	0.008
Dec	1991	up	0.001						

(Fig. 3A). Also, the current June and July and previous July precipitation showed positive correlations with growth but the relationship was not consistent over time. We do caution that the results prior to 1947 for Engelmann spruce might be influenced by juvenile growth effects as evidenced by the decline in the EPS. For maximum temperature, a significant negative correlation ($p < 0.05$) existed between Engelmann spruce growth and previous August maximum temperature that was consistent over time (Fig. 3B). The current June and July maximum temperature had negative correlations with growth, but the coefficients were only significant in the middle to late 20th century. For minimum temperature, a negative correlation was found between Engelmann spruce growth and previous May through August minimum temperature, but the correlations only became significant in the most recent decades (Fig. 3C).

The Douglas fir correlation analysis showed a significant positive correlation ($p < 0.05$) between tree growth and previous July through September and current June and July precipitation, with the current year relationships most time stable (Fig. 3D). For maximum temperature, a significant negative correlation existed between Douglas fir tree growth and previous June through August and current June and July. The previous August maximum temperature correlations were most time stable. Also, Douglas fir showed a positive correlation between tree growth and previous November and December maximum temperature that appeared to fade somewhat in recent decades (Fig. 3E). For minimum temperature, a significant negative correlation existed between Douglas fir tree growth and previous July and August minimum temperature in recent decades (Fig. 3F). Other less time stable correlations can be seen with minimum temperature including significant positive correlations with previous October and November minimum temperature.

Disturbance

For Engelmann spruce, disturbance analysis was conducted starting in 1947 because the EPS dropped below 0.85 indicating a decline in signal strength of the chronology ($N = 14$ trees; Fig. 4). Engelmann spruce experienced growth releases in 1960, 1962, 1967, and 1979. For each growth release, 5 – 6% of the trees showed the event. For Douglas fir, the EPS dropped below 0.85 in 1722 at which point we recorded the first release dates ($N = 7$ trees; Fig. 4). Douglas fir experienced the largest growth releases (>10% of trees showing release) in 1723, 1785, 1787, 1901, 1906, and 1985. Many smaller release events (<10% of trees showing release) were detected throughout the period of analysis. The maximum percentage of trees for either species with growth releases was 25%; the minimum percentage was 4 – 5%. In the contemporary period, the majority of growth releases only had 4 – 6% of trees responding. Disturbance was lacking for Douglas fir from the 1940s to the 1970s. However, Engelmann spruce experienced three growth releases during this period. Both species experienced a growth release in 1979. We compared our release dates to know dates of wildfire and insect outbreaks source from previous research (Table 2; Brown et al., 2020a; Lee et al., 2018).

Table 2
Known wildfire (Brown et al., 2020a) and insect outbreak (Lee et al., 2018) events near the Greater Yellowstone Ecosystem, Wyoming.

Western Spruce budworm outbreaks	1833 - 1849
	1896 - 1910
	1931 - 1938
	1974 - 1996
	2014 - 2018
Wildfire Events	1664
	1694
	1706
	1717
	1763
	1785
	1804
	1846
	1873
	1900

Discussion

Engelmann spruce and Douglas fir showed some similar climate responses using moving correlation analysis. Both species had a significant positive correlation between tree growth and previous August precipitation. Additionally, both species had a significant negative correla-

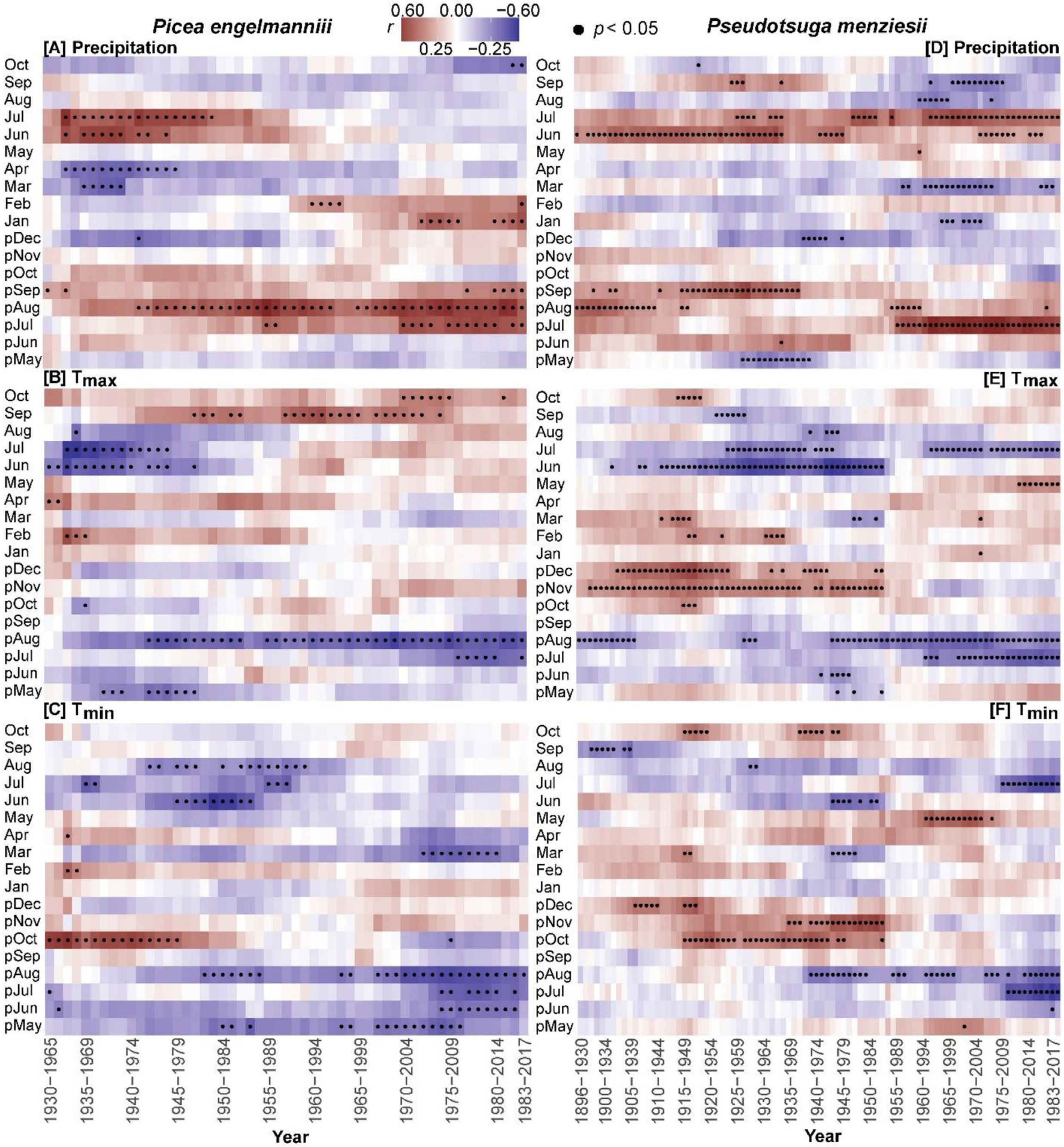

Fig. 3. Moving correlation coefficients for the relationship between precipitation, maximum temperature, and minimum temperature and Engelmann spruce (A-C) and Douglas fir (D-F) tree-ring width chronologies. The values represent the results of a 35-year moving window. Red values represent positive correlations and blue values represent negative correlations. Values with * are significant at the $p < 0.05$ level. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

tion between tree growth and previous August maximum and minimum temperature. Current year June and July precipitation and temperature were correlated significantly with ring width in both species but the strength and significance of the correlations varied over time. A visual inspection of the tree-ring chronologies indicates below average growth in the early part of the 21st century that might be linked to these climate-growth responses where increasing temperatures in the current and previous growing seasons might enhance summer drought (Fig. 2; Table 1). The shift in the growth response to both summer temperature and precipitation indicates that these high-elevation species are currently being impacted by warming temperatures due to climate change. As previous research has shown, warming temperatures and shifts in precipitation are leading to ecosystem-wide changes in the GYE (Gonzalez et al., 2018; Hansen and Phillips, 2018).

Our work confirms some previous research on Engelmann spruce across its geographic range showing strong positive correlations with June – August current year temperature and previous growing season temperature (e.g., Hart and Laroque, 2013; Peterson and Peterson, 1994). Similarly, previous research has shown that Douglas fir ring width responds negatively to summer temperature and positively to summer moisture availability from the coastal northwest in Washington and British Columbia, Canada, south into Arizona and Mexico

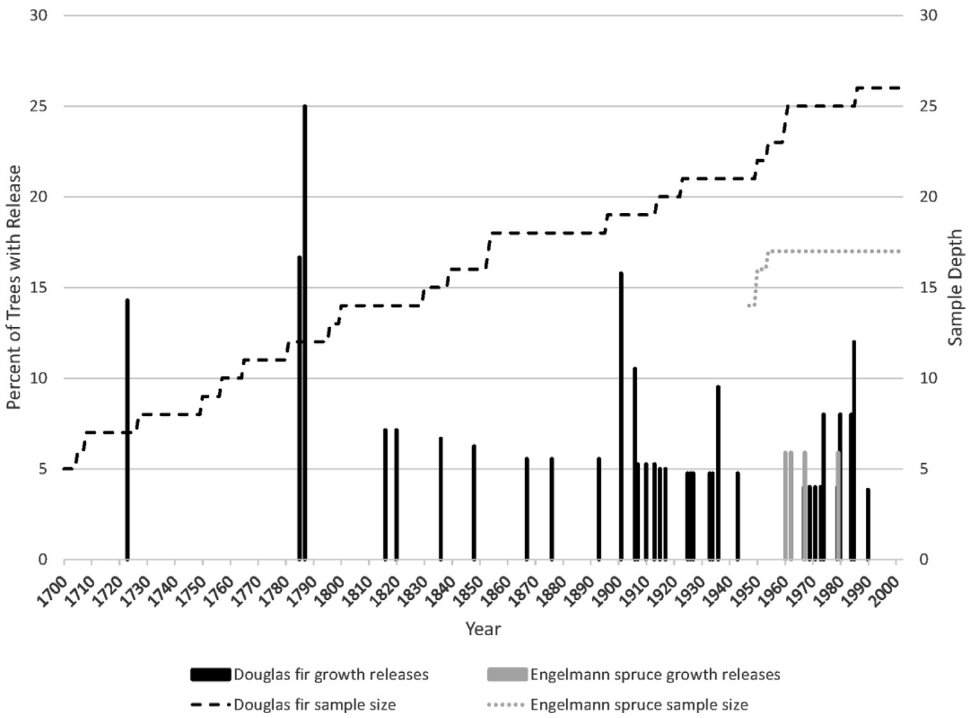

Fig. 4. Disturbance analysis representing growth releases for Engelmann spruce (gray bars) and Douglas fir (black bars). The sample depth is represented by a gray dotted line for Engelmann spruce and by a black dashed line for Douglas fir.

(Biondi, 2000; Chen et al., 2010; Littell et al., 2008; Watson and Luckman, 2002). In a comparison of Engelmann spruce and Douglas fir climate sensitivity in central British Columbia, Wiley et al. (2018) showed Engelmann spruce was more sensitive to changes in summer temperatures than Douglas fir. Our results indicate that both species respond to current and past growing season temperature but we cannot conclude that one species will favor warming temperatures in coming decades. Rather, increases in summer temperatures will lead to higher evapotranspiration and a subsequent decline in tree growth, at least for Douglas fir (Littell et al., 2008).

The shifting ring width response to climate changes over the past century has been documented in forest ecosystems across the conterminous United States (Maxwell et al., 2016; Patterson et al., 2016; Saladyga and Maxwell, 2015). In high-latitude forests, the shifting growth response to temperature has been labeled the “divergence problem” indicating that the limiting factors to tree growth are shifting in a warming world (Frank and Esper, 2005; Jacoby et al., 2000; Jacoby and D’Arrigo, 1995; Lloyd and Fastie, 2002). Regime shift analyses on the monthly climate data were conducted to help determine the cause of changes in tree growth, and possibly, make predictions in future forest ecosystem change. No shift in August precipitation or temperature was detected as we might expect from the mostly time stable climate-growth correlations. Mean June precipitation and June and July temperature shifted to higher means in the late 20th century. At the same time, the response of Douglas fir shifted from a significant positive correlation with June precipitation to a new significant positive correlation with July precipitation, and shifted from negative correlation with June maximum temperature to a new significant negative correlation with July maximum temperature. This appears to indicate that warming temperatures in June might cause increased evapotranspiration that is mitigated by increased precipitation in June. Conversely, July temperatures have increased without a corresponding increase in July precipitation creating conditions more limiting to tree growth. Finally, a 1985 regime shift for November maximum temperature corresponded with a shifting growth response for Douglas fir to a negative correlation between tree growth and November maximum temperature. The connection between previous year climate and growth can seem counterintuitive, especially for previous November temperature. However, in the Intermountain West, a warmer late fall may delay the accumulation of snowpack and extend the growing season.

Disturbance analysis, in conjunction with climate regime shift analysis, can aid our interpretation of growth responses (Saladyga et al., 2020). Here, we used disturbance analysis to detect significant and sustained growth releases that were triggered by landscape-scale disturbances such as wildfire and insect outbreaks. Beginning with the most recent decades, Engelmann spruce and Douglas fir experienced several growth releases between 1960 and 1990. Previous research indicates that no wildfires burned in the area during this period (Brown et al., 2020a) but an outbreak of western spruce budworm (*Choristoneura freeman*), which attacks both Engelmann spruce and Douglas fir, was detected from 1974 to 1996 (Lee et al., 2018). Engelmann spruce recruitment began in 1930 corresponding with similar recruitment in 1940 occurring at nearby sites (Brown et al., 2020a). While there was no evidence of wildfire during these decades (Brown et al., 2020a), Lee et al. (2018) reported an outbreak of western spruce budworm in the 1930s that might have caused dieback of the dominant Douglas fir on our site, opening space for new establishment.

The growth release chronology for Douglas fir extended back to the early 1700s providing a longer context in which to place forest disturbances. Prior to the 19th century, Native Americans were known to live in the GYE but the extent of their use of the forests is not well known (Johnson, 2010). Sediment charcoal and tree-ring records indicate that wildfires were common (Brown et al., 2020b; Higuera et al., 2010). Douglas fir growth releases in 1785, 1787, 1846, 1901, and 1906 correspond to widespread wildfires in the vicinity (Table 2; Brown et al., 2020a, b). European-American settlement in the GYE was sparse before the establishment of the park in 1872 though several explorations had visited the area (Haines, 1974). Tourism, mining, logging, and ranching began to expand following settlement (Haines, 1974) likely causing forest disturbances that were detected in the growth releases of Douglas fir through the early 20th century. Most recently, Douglas fir experienced a growth release in 1990 as a result of the 1988 Yellowstone fires (Romme and Despain, 1989) but the series of releases from the 1970s to the 1990s can be linked to western spruce budworm outbreaks (Lee et al., 2018).

The recent insect outbreaks coincide with recent temperature increases and regime shifts in monthly climate variables making it difficult to identify a single driver of change in climate-growth responses. For example, the recent shifting climate-growth response documented in Douglas fir may be influenced by (1) a 1985 growth release caused by an insect outbreak favoring survivors, (2) a regime shift in November maximum temperature, or (3) a combination of both climate and ecology. In the eastern United States, an insect outbreak of hemlock wooly adelgid (*Adelges tsugae*) was shown to affect the climate-growth response of eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*) but changes in climate-growth responses could also be linked to regime shifts in climate prior to the outbreaks (Austin et al., 2016; Saladyga and Maxwell, 2015). In western Washington and Oregon, USA, climate is predicted to influence both the severity of drought and insect outbreaks in forests dominated by Douglas fir (Agne et al., 2018).

Conclusion

Disentangling the influence of climate regime shifts and forest disturbances on the climate-growth relationships can be difficult because climate and forest disturbance are intricately linked. Our evidence indicates that both regime shifts in monthly climate variables and forest disturbances as recorded by growth releases can influence the ring width response to climate over time. Nationwide, our forests are experiencing more frequent extreme climate events and a rise in forest disturbances like wildfire and insect outbreaks that are leading to long-term changes in forest structure and function (Vose et al., 2018). With our climate and ecological disturbance research, forest managers in the GYE can better understand how forest ecosystems have changed over the past decades and will change with continued anthropogenic climate changes. Yellowstone National Park has developed a "Vital Signs" monitoring protocol to assess key ecological and climatological signals that have broad ecosystem health implications (Ray et al., 2019). Tracking forest ecosystem vital signs will help to better manage and adapt to climatic and ecological changes. Trees are key to providing a long-term perspective on climate and ecological health across the GYE because they integrate both climate and ecology in their annual ring widths.

Declaration of Competing Interest

The authors declare no competing interests.

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