CO-OCCURRING WYOMING CONIFERS DISPLAY DISTINCT CLIMATE-GROWTH RELATIONSHIPS

LAURA A. DYE[1*], JESSIE K. PEARL[2], LAURA SMITH[3], BETHANY COULTHARD[1], CORI BUTKIEWICZ[4], ZANE COOPER[5], JIM DEGRAND[6], JARED FRIEDMAN[5], INGA HOMFELD[1], HILARY HOWARD[7], LEROY IRONCLOUD[8], and **SHANNON WRAY[9]**

[1] Department of Geosciences, University of Nevada, Las Vegas, Las Vegas, NV 89154, USA

[2] United States Geological Survey, Earthquake Science Center, Seattle, WA 98104, USA

[3] Department of Geography, University of Tennessee, Knoxville, TN 37996, USA

[4] Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Madison, WI 53706, USA

[5] Department of Natural Resources Management and Environmental Sciences, California Polytechnic State University, San Luis Obispo, San Luis Obispo, CA 93407, USA

[6] Department of Geography, Ohio State University, Columbus, OH 43210, USA

[7] Department of Earth and Environmental Systems, Indiana State University, Terre Haute, IN 47809, USA

[8] Stevens High School, Rapid City, SD 57702, USA

[9] Department of Environmental Resource Management, Pennsylvania State University, State College, PA 16801, USA

* Corresponding author: dyel1@unlv.nevada.edu

ABSTRACT

The North American Dendroecological Field Week (NADEF) is an intensive dendrochronology-based research workshop, funded by the National Science Foundation. The 2019 Introductory Group at NADEF developed two precisely-dated tree-ring width chronologies for *Pinus contorta* (Lodgepole Pine) and *Pinus flexilis (*Limber Pine) at Wolf Knob, WY, located within the Greater Yellowstone Ecosystem (GYE)'s Shoshone National Forest. Wolf Knob is a semi-arid, south- to southwest-facing, high-elevation site, making it an ideal location to examine the climate sensitivity of annual tree-ring width increments. Here, we show that two co-located conifer species exhibit distinct climate-growth relationships and therefore may be facing distinct threats in the face of regional climate change. *Pinus flexilis* is much more drought-stressed than *Pinus contorta*, exhibiting stronger overall correlations with both cool- and warm-season precipitation as well as snow meltwaters, whereas *Pinus contorta* exhibits only relatively weak correlations with precipitation and temperature during the late summer. The differing seasonal climate sensitivities of these two co-located *Pinus* species is likely due to microsite conditions and distinct species climate responses, both providing local insight for selecting tree-ring snow proxies in the GYE and further highlighting the importance of site and individual selection in dendroclimatology and dendroecology.

Keywords: Greater Yellowstone Ecosystem, Lodgepole pine, Limber pine, dendroclimatology, fire regimes.

INTRODUCTION

As one of the largest and least fragmented ecosystems located within Earth's temperate zone, the Greater Yellowstone Ecosystem (GYE) is of distinct ecological importance and is particularly susceptible to climatic shifts (Rice *et al.* 2012), where warming temperatures (Sepulveda *et al.* 2015) pose cascading effects on the desiccation of soils and vegetation, fire regimes, as well as ecosystem and wildlife health (Pederson *et al.* 2010). Comprised of ~22 million acres, the GYE provides rich biodiversity, abundant water resources, and is a sanctuary for the largest concentration of wildlife in the contiguous U.S. (NPS 2016).

Consistent with much of the western U.S., the GYE is faced with shifting trends in temperature and precipitation in response to anthropogenic greenhouse gas emissions. In recent decades, the GYE has experienced a -.16°C/decade increase in mean annual temperature (Chang and Hansen 2015), manifested as warming winters and hotter summers (Sepulveda *et al*. 2015), lengthening of summer droughts (Westerling *et al*. 2006), reduced snowpack (Tercek *et al*. 2015), and decreased summer stream discharge (Leppi *et al*. 2012). Taken together, these climatic shifts have begun redefining disturbance regimes throughout the region, including increased forest fire activity (Westerling *et al.* 2006) and severity (Whitlock *et al.* 2003), vulnerability to insect disturbances (Raffa *et al.* 2008; Bentz *et al.* 2010), and vertical advancement of tree line (Grace *et al*. 2002; Hinton 2020), ultimately leading to a higher likelihood of forest mortality and forest type transition (Van Mantgem *et al.* 2009; Logan *et al.* 2010).

One way to benchmark modern climate and ecological shifts is to use long-term tree-ring records to reconstruct past climate and ecological disturbance (Fritts 1976). In high-elevation (>2400 m) semi-arid forest communities, such as those within the GYE, annual tree-ring increments are often

highly sensitive to environmental conditions and forest dynamics, such as climate, disturbance, and competition (Hinton 2020). A rich history of broad-scale paleoclimate and paleoecological work exists within the GYE and surrounding Rocky Mountain region, including records derived from lake sediments (Fall *et al.* 1995), pollen (Lynch 1998; Whitlock 1993), terrestrial sediments (Pierce *et al.* 2004), diatoms (Bracht *et al*. 2008), ice cores (Naftz *et al.* 2002), and other proxy records (Krause *et al*. 2015; Krause and Whitlock 2013; Mensing *et al.* 2012; Whitlock *et al.* 2003) that provide a multi-millennial context for past environmental conditions. Tree-ring based climatological (Wise 2010; Graumlich *et al*. 2003; Gray *et al*. 2007) and ecological (Romme and Despain 1989; Littell 2002; Higuera *et al*. 2011, Rinaldi *et al.* 2021) reconstructions provide the highest-resolution (annual) context for changes within the GYE over the past two millennia. While these records have contributed to the development of a palaeoclimatological and paleoecological framework of the GYE, very few climate-sensitive, high-elevation tree-ring datasets exist within the region (Hinton 2020). High-elevation forest communities are most sensitive to shifting temperature and precipitation patterns (Diaz *et al.* 2003), thus in a region where much of the elevation remains > 2200 m, high-resolution records which capture recent environmental shifts are needed. The goal of this study is to evaluate the potential of *Pinus contorta* (Lodgepole pine) and *Pinus flexilis* (Limber pine) for future climate reconstructions in the region. To do this we develop multi-centennial chronologies from these two co-located conifer species, and quantify and compare climate responses between the species

MATERIALS & METHODS

Site Selection

The GYE is a semi-arid region that spans from 1400 to over 4200 m in elevation situated in northwest Wyoming, and is host to multiple habitat types including those dominated by *Pinus contorta* and *Pinus flexilis* (Figure 1). Average annual temperature (precipitation) within the SNF range from 8 degrees C (254 mm/year) at low elevations (~ 1402 m) to -12 degrees C (1525 mm/year) at high elevations (~4221 m; Rice *et al.* 2012).

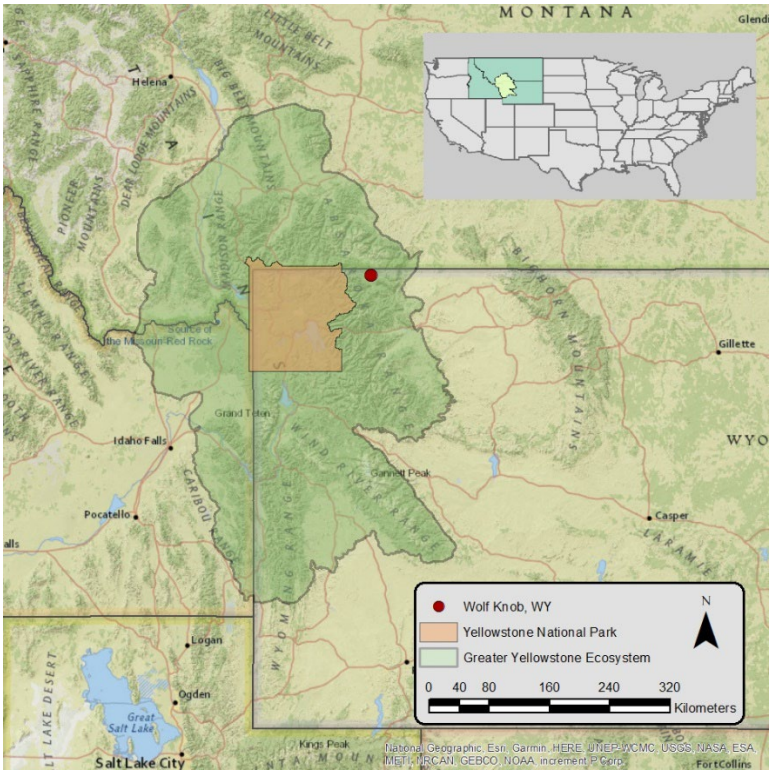


Figure 1. Location of Wolf Knob study site (44.946°N, 109.6497° W).

We selected our study site, Wolf Knob (located within the SNF), based on its relatively high altitude (2682 m), sheer south/southwest facing slopes, and rocky cliff characteristics. Based on

the dendrochronological principle of limiting factors (Fritts 1976), we anticipated the shallow, rocky soils on this high elevation granitic gneiss outcrop to host mature, climate sensitive trees that may have survived lowland fires.

Tree-Ring Data and Chronology Development

Two or three cores from 26 *Pinus flexilis* and 24 *Pinus contorta* trees were taken with an increment borer following standard dendrochronological procedures (Stokes and Smiley 1968). The sampled trees are within approximately 30 meters of the summit elevation (2682 m) on the south/southwest-facing slope at Wolf Knob. We selected mature trees that exhibited few signs of disturbance from insects or fire, minimal canopy competition, and DBH larger than juvenile, understory trees (>15 cm) (Fritts 1976). We recorded the locations of each sampled tree with a GPS, as well as a measurement of diameter at breast height (DBH). Samples were stored in paper straws and transported to the A.L. Mickelson Field station in Cody, WY, where they were mounted on wooden mounting boards and surfaced with progressively finer sandpaper until a fine polish was achieved and uni-cellular rings were visible under the microscope.

Total ring widths were scanned at 2400 dpi using a high-resolution scanner and measured at 0.001 mm precision using either a Velmex measuring stage and Tellervo measurement software (Brewer 2014) or the visual analysis program CooRecorder (Cybis Elektronik 2010). Due to difficult ring-width patterns, these two measurement techniques were used interchangeably (Stockton *et al.* 2011); when narrow or faint ring-width patterns were undetectable with the high-resolution core images, we proceeded with the Velmex measuring stage. Annual growth increments were crossdated using the skeleton plot and list methods (Fritts 1976; Yamaguchi 1991), and

crossdating was confirmed statistically using the program COFECHA (Holmes 1983). As part of the NADEF program, all members of the Introductory Group participated in crossdating. Thus, crossdating of each core was confirmed by at least two independent scientists. Previously crossdated *Pinus contorta* samples from the Between Two Knobs site (44.931, -109.640; Gentry *et al*. 2017) were utilized as a reference in the crossdating process. Tree-ring measurement series were detrended (Cook 1985) with a two-thirds smoothing spline using the Dendrochronology Program Library (dplR) package (Bunn *et al.* 2008) in R programming language (R Core Team 2020), and standardized using a bi-weight robust mean to estimate the final chronology (Cook and Kairiukstis 1990). We selected this detrending method based on its ability to remove non-climatic growth trends yet preserve more common forest dynamics (Cook and Peters 1981). We calculated a suite of diagnostic statistics to evaluate the quality of the chronologies, including inter-series correlation (Fritts 1976), Expressed Population Signal (EPS; Briffa 1999), mean sensitivity (Fritts 1976), and mean total r-bar (Briffa 1999; Table 1). EPS is a statistical measure used to evaluate how well the sample size captures the hypothetical population growth signal (Wigley *et al.* 1984). Lastly, autocorrelation function tests (Blackman-Turkey method; Percival and Walden 1993) were conducted for each chronology to classify the spectral and autocorrelation properties of these sites.

Climate-growth relationships

To determine which, if any, climate parameters have a significant relationship to *Pinus flexilis* and *Pinus contorta* growth at Wolf Knob, we calculated full and partial correlation coefficients between each chronology and local precipitation (nearest grid point taken from Global Precipitation Climate Centre gridded precipitation product; GPCC v7.0; Schneider *et al*. 2016) and temperature (nearest grid point taken from Climate Research Unit; CRU v4.01; Harris *et al.* 2014), datasets using the seasonal correlation (SEASCORR) procedure developed by Meko *et al.* (2011).

147 We tested individual monthly and seasonal precipitation and temperature records integrating 1, 3,
148 9, and 12 months, within a 14-month window starting in the September prior to the growth year
149 and ending in October when conifer growth typically becomes dormant (Vaganov *et al*. 2006).
150 Significance was estimated using exact simulation (Percival and Constantine 2006). Additionally,
151 to determine if the *Pinus flexilis* and *Pinus contorta* chronologies have a significant relationship
152 with snowpack, Pearson's correlation tests were conducted with 50-year moving windows between
153 each chronology with regional reconstruction of mean Snow Water Equivalent (SWE) developed
154 by Coulthard *et al*. (2019), modeled SWE (Coulthard *et al*. 2019), as well as winter (sum of prior
155 December, January and February) precipitation (nearest grid point taken from GPCC v7.0;
156 Schneider *et al*. 2016), over the common periods between the two records of 1730-1980, 1900-
157 2015, and 1892-2016, respectively. Bonferroni corrections and autocorrelation adjustments were
158 made for all series being compared, to ensure the relationships were not spurious (Snedecor and
159 Cochran 1989).
160

161 **RESULTS**

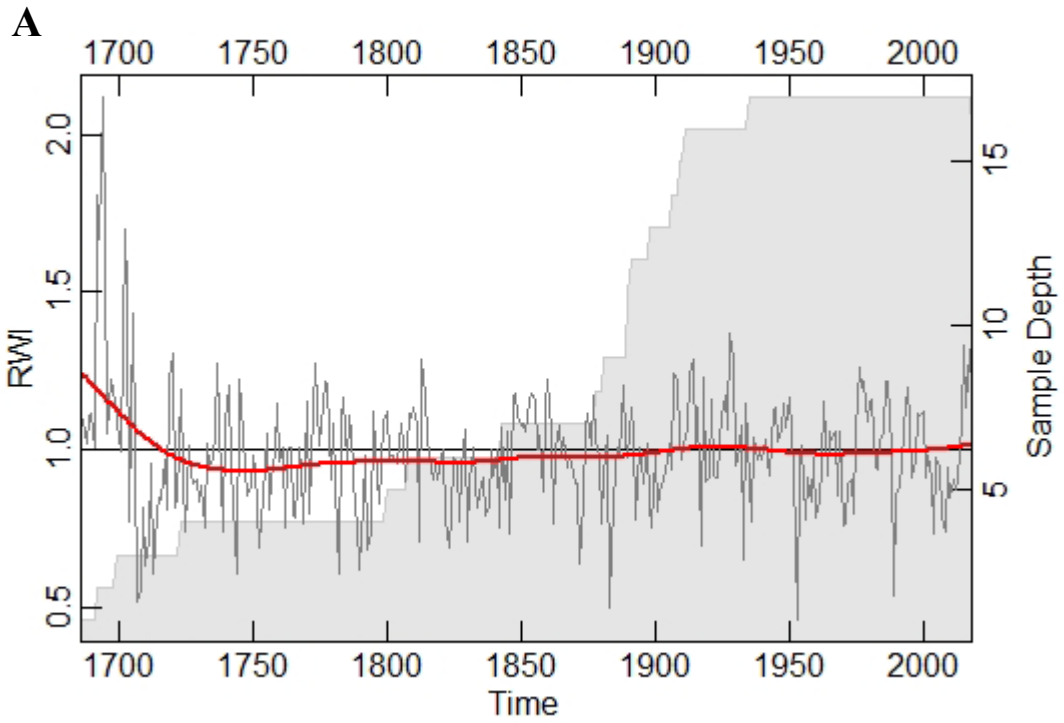
162 *Final Chronology*

163 The final chronologies (Figure 2) are comprised of 17 *Pinus contorta* (A) and 17 *Pinus flexilis* (B)
164 cores, with an expressed population signal (EPS) > 0.67 for each (Table 1). Difficult ring-width
165 patterns (e.g. locally absent rings, ring suppression, lack of anatomical marker years) prevented
166 statistically robust crossdating of all the collected cores, therefore only the samples with precise
167 calendar years were included in the final chronologies. The *Pinus contorta* chronology has
168 temporally consistent EPS values hovering near 0.68 (Table 1) and a larger number of cores

extending into the early 1700s than *Pinus flexilis* (Figure 2 A). The *Pinus flexilis* chronology only has 2 cores which extend earlier than1700, but higher and temporally consistent EPS values (Figure 2 B). Both chronologies have inter-series correlation values over 0.5 and exhibit a shift in (tree-ring width) variance in the early portion of the record, where sample depth drops < 5 samples (Table 1; Figure 2).

Species	Trees	Cores	# cores included in final chronology	Age Range	Series Inter-correlation	Mean Sensitivity	Mean rbar	Mean EPS	EPS >0.80
Pinus contorta	26	54	17	1686-2018	0.502	0.237	0.243	0.689	1894-2018
Pinus flexilis	24	50	17	1569-2018	0.570	0.261	0.326	0.816	1869-2018

Table 1. Summary chronology statistics for *Pinus contorta* and *Pinus flexilis*.


A
1700
1750
1800
1850
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1950
2000
RWI
0.5
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1.5
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Sample Depth
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Time

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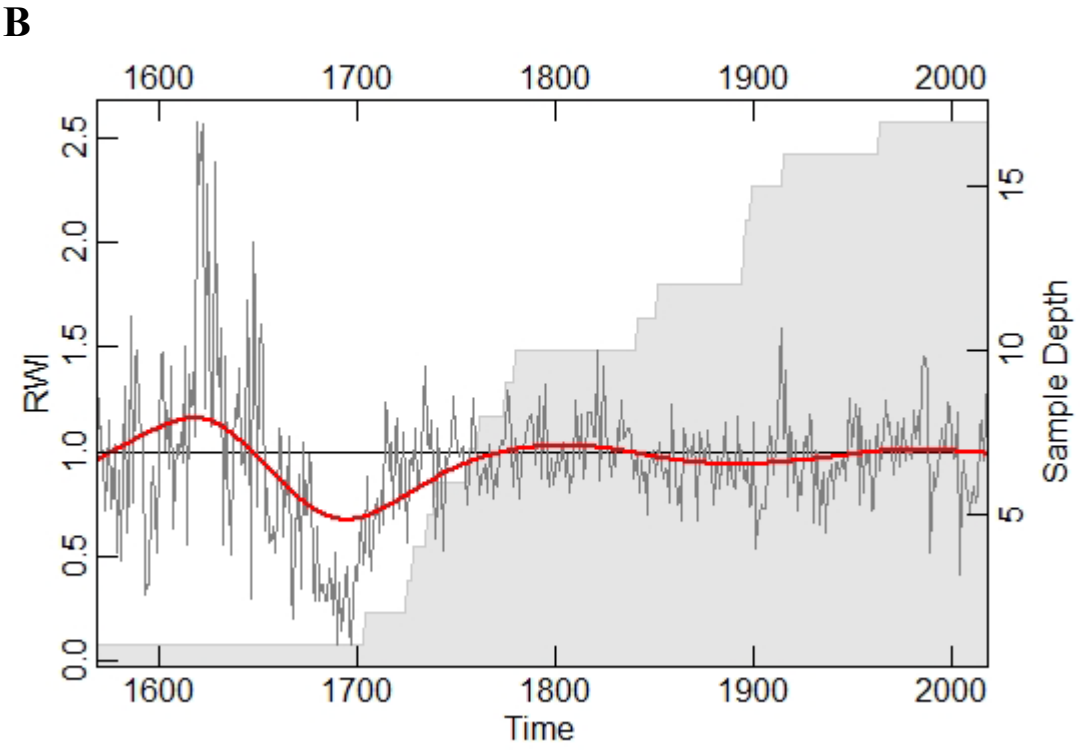
B
1600
1700
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1900
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RWI
0.0
0.5
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1.5
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2.5
Sample Depth
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Time

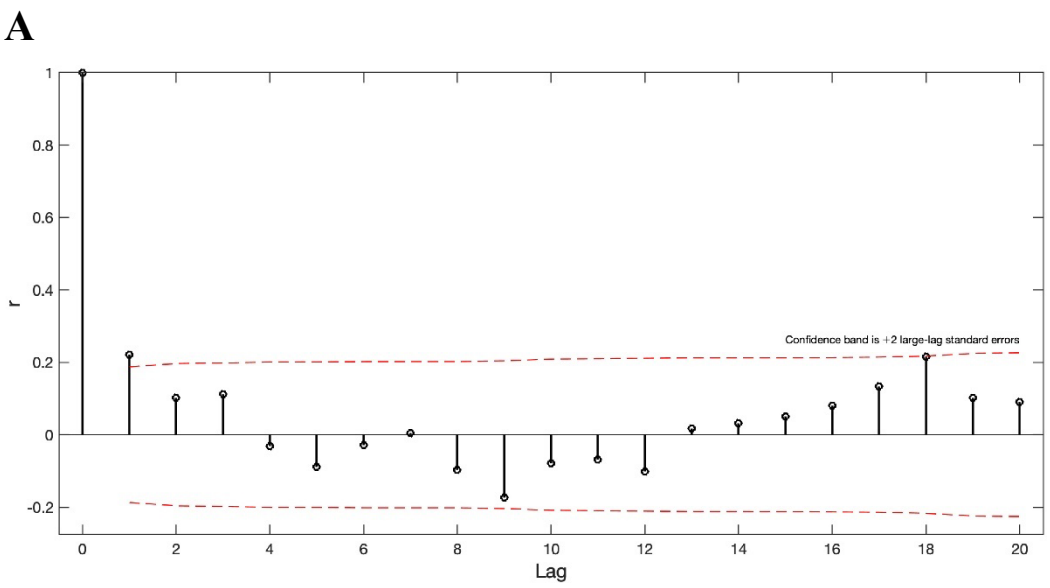
178

179 **Figure 2.** Final detrended chronology with the fitted two thirds spline for (A) *Pinus contorta* and
180 (B) *Pinus flexilis*.

181

182 The *Pinus contorta* chronology has significant ($p < 0.05$) positive autocorrelation structure on the
183 order of 1 (Figure 3 A), whereas the *Pinus flexilis* chronology has persistent autocorrelation
184 structure on the order of 3 (Figure 3 B).

185



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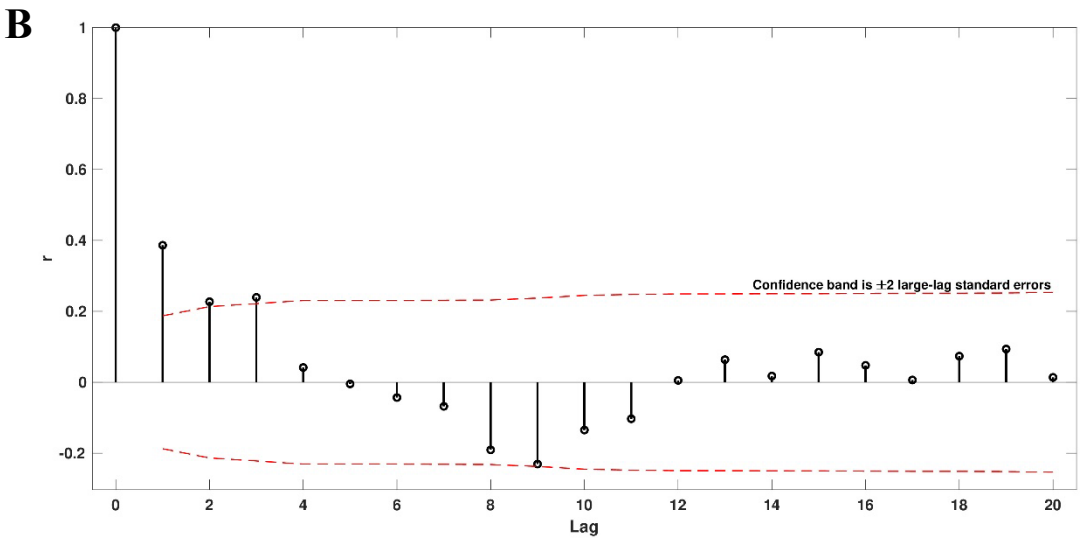


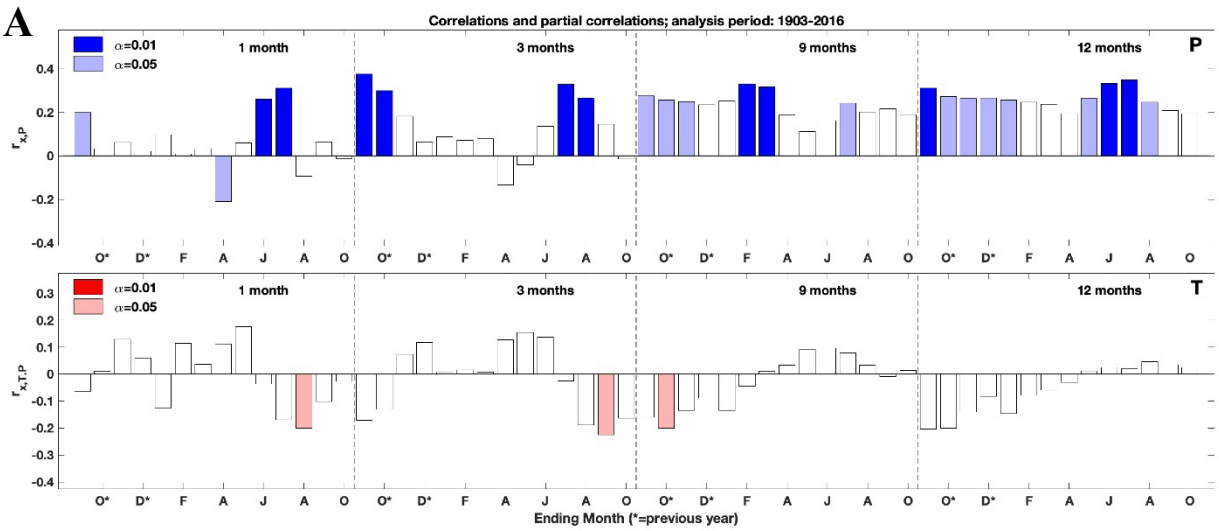
187

188 **Figure 3**: Autocorrelation function plots of the (A) *Pinus contorta* and (B) *Pinus flexilis* and
189 chronologies. Red dashed lines indicate large-lag standard error at the 95% confidence level
190 (Anderson 1976) and r (y-axis) represents the strength of the autocorrelation structure between
191 year t and number of lags (x-axis).

192

193 *Climate-growth relationships*

194 Results of the climate correlation analysis suggest the strongest monthly or seasonal correlation
195 with precipitation is the same for both species in prior-year summer (July-September), although
196 the correlation of *Pinus contorta* to summer precipitation is much weaker than that of *Pinus flexilis*
197 (Figure 4 A and B, Panel 2). The two species' responses to cool-season precipitation are markedly
198 different, however. *Pinus contorta* is only weakly and inconsistently (over time) correlated with
199 precipitation during cool months and seasons (Figure 4 A), whereas *Pinus flexilis* exhibits strong
200 and consistent correlations with cool-season precipitation variables (Figure 4 B, Panels 3-4). Only
201 *Pinus contorta* is statistically significantly ($p<0.05$) correlated with temperature, a weak negative
202 relationship that is restricted to the current late-summer (July-September) in both the prior and
203 current years (Figure 4A, panels 1, 2, and 3).



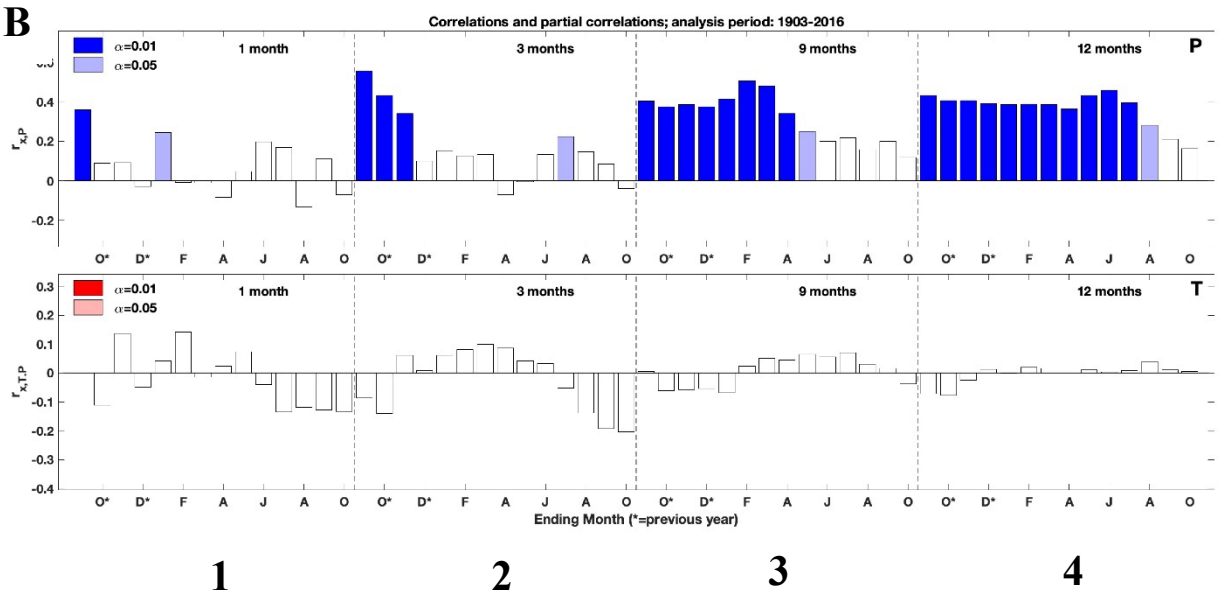


Figure 4. Seasonal correlations and partial correlations using the procedure of Meko *et al*. (2011) of the (A) *Pinus contorta* and (B) *Pinus flexilis* chronologies. The top row in each figure (blue bars) shows correlations between the chronology and monthly and seasonal precipitation. The bottom row on each figure (red bars) shows the partial correlations between the chronologies with monthly and seasonal temperature. The four panels separated by vertical dashed lines are, from left to right for the month indicated: the month ending in the month indicated, the three months ending in the month indicated, the 9 months ending in the month indicated, and the 12 months ending in

the month indicated. Significance levels are determined by exact simulation (Meko *et al*. 2011; Percival and Constantine 2006).

Of the correlations between the chronologies with reconstructed SWE, modeled SWE, and GPCC winter precipitation, only the *Pinus flexilis* and reconstructed SWE exhibit a statistically significant ($p < 0.05$) relationship that is weaker over the full common data period ($r = 0.17$, 1730-1980), but stronger over the last 60 decades ($r=0.45$, 1930-1980, Figure 5).

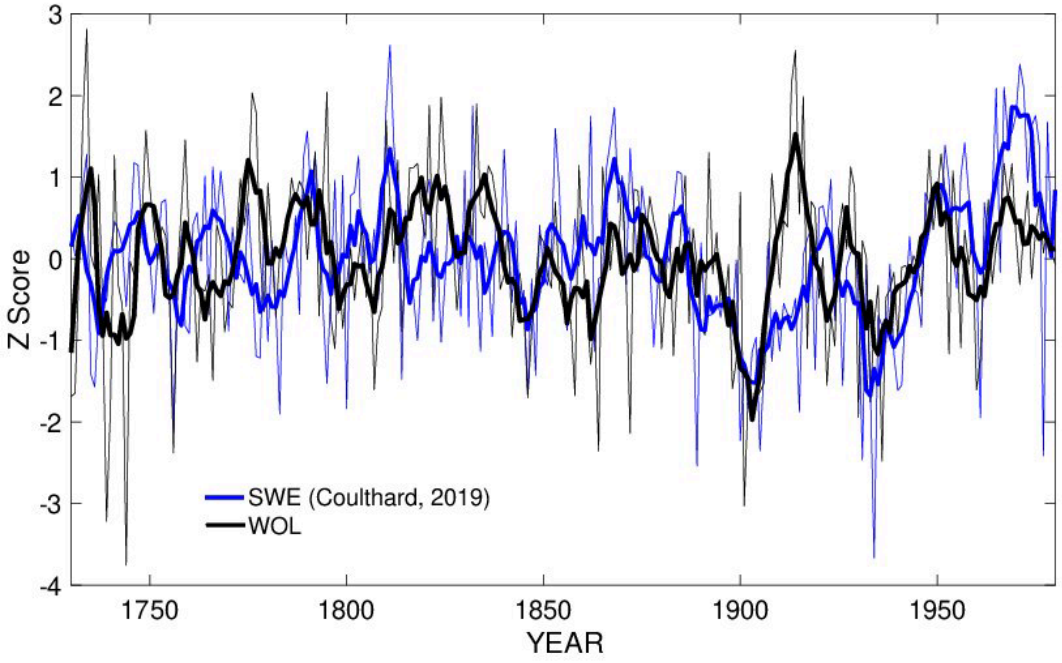


Figure 5. Line plot of the five-year running mean of reconstructed SWE (thick blue line) and *Pinus flexilis* chronology (thick black line) over the 1730-1980 period. Standardized annual values for reconstructed SWE and *Pinus flexilis* chronology are plotted in the thin blue and black lines, respectively.

DISCUSSION

At Wolf Knob, both *Pinus contorta* and *Pinus flexilis* appear to be subject to a significant level of climatological and/or other growth stress, and as a result exhibited a substantial amount of locally absent rings and perplexing ring width patters that presented challenges for crossdating. Therefore, the final chronologies presented here only include the well-dated core samples, to ensure our analyses are derived on precise chronological information.

The requirement of both species for enhanced precipitation in the late summer, as well as the negative response of *Pinus contorta* to warm temperatures during that same season, is consistent with late summer drought-stress observed in many western US forests (Williams *et al.* 2013), although this response is weaker in *Pinus contorta* than in *Pinus flexilis*. Meanwhile, the strong positive correlation between *Pinus flexilis* and cool-season precipitation is a typical water-year drought response exhibited by North American moisture-limited conifer species that rely on snow meltwaters to precondition spring soil moisture availability (Fritts 1971; St. George 2014). This reliance on cool-season precipitation is underscored further by the *Pinus flexilis* relationship to SWE documented in this study.

In short, despite co-occurring at the same site, the two species exhibit different forms and magnitudes of drought stress. Weaker correlations with precipitation indicate *Pinus contorta* is not as strongly water-limited as *Pinus flexilis*, and this is also consistent with *Pinus contorta's* lack of reliance on cool-season precipitation and a sensitivity to rainfall availability only during the late summer, likely only during abnormally long warm/dry growing seasons. Meanwhile strong correlations with precipitation indicate *Pinus flexilis* is relatively more water-limited, relying heavily on snow meltwaters during the early growing season in addition to late summer rainfall at

253 the end of the growing season. In both cases, sustained drought conditions may limit the tree's
254 vital growth-controlling structures (stems, buds, needles, roots) in subsequent years, and thus they
255 may depend on both current and/or prior year precipitation for adequate growth, (Fritts 1971;
256 Coulthard *et al.* 2020).

257 We attribute these contrasting moisture-stress responses to be a result of differing microsite
258 growing locations of each species: the majority of the *Pinus contorta* individuals persisted on flat,
259 less rocky outcrops, while majority of the *Pinus flexilis* individuals tended to prefer the more
260 exposed cliff faces, with shallow and poorly developed soils, where moisture-limitation is
261 typically strongest (Steele *et al.* 1983). Given that both species examined here may be strongly
262 correlated with cool-season precipitation and SWE (Coulthard *et al.* 2020), and/or late summer
263 precipitation/temperature (Williams *et al.* 2013) at other sites throughout western North America,
264 our findings underscore the importance of not only site selection but also microsite and individual
265 selection for dendroclimatological sampling. Our findings also contribute to identifying SWE-
266 sensitive tree-ring proxies in this region, which is of growing importance given the imminent
267 threat of warming-induced snowpack declines in the North American Cordillera (Pederson *et al.*
268 2011) and the projection of a largely snow free (April 1) GYE by 2075 (Chang and Hansen 2015).
269 In this case, we found that *Pinus flexilis* growing in more moisture-stressed microsite conditions
270 serve may serve as SWE proxies while similarly long-lived *Pinus contorta* tree at the same site are
271 not sensitive to SWE.

272 **CONCLUSION**

273 Taken together, these chronologies unveil a multi-centennial history of the GYE climate, and
274 specifically for high-elevation forest communities in northwestern Wyoming. The differing

climate sensitivities seen in these two *Pinus* species underscores the pertinence of declining snowpack, and increasing summer temperatures and drought conditions to high-elevation *Pinus flexilis* and *Pinus contorta* forest communities, respectively. Our findings suggest that each species will likely be faced with dissimilar climate change risks and may even alter their vulnerabilities. For instance, a trend in declining snowpack in the GYE may negatively impact *Pinus flexilis* while *Pinus contorta* may be more resilient to these shifts. Taken together, these high-elevation co-located *Pinus* species prove potentially useful in teasing out species sensitivities to a changing GYE climate, as well as provide forewarning into shifting forest dynamics.

ACKNOWLEDGEMENTS

This project was funded by the National Science Foundation's Geography and Spatial Sciences Program; award # 1759694. A special thank you to the NADEF organizers and the staff of the Northwest College A.L. Mickelson Station, for their hard work and commitment to the ongoing years of this program. We would also like to thank the Introductory group leaders, Dr. Jessie Pearl and Laura Smith, for their guidance, encouragement, and dedication in teaching our group the fundamentals of Dendrochronology.

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