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Wetter summers mitigated temperature stress on Rocky Mountain forests during the last interglacial warm period

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Key Points:

- Subfossil wood from the last interglacial was analyzed to assess ecohydrological response of fir and spruce to previous warm period.
- Isotopic analysis of subfossil samples show summer rain was a more critical component of the trees' water source during the interglacial.
- Access to and use of summer rain retained favorable growing conditions for the trees despite higher evaporative stress during warm period.

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Abstract

Rising summer temperatures are expected to increase tree mortality rates across the western United States. Here, we analyze subfossil wood samples from Colorado dating to the last interglacial to assess the response of two common conifers to a previous warm period. The trees experienced comparable growth rates and water use efficiency during the interglacial relative to modern despite evidence from model simulations of a ~30% increase in evaporative demand during the peak of the growing season. High-resolution isotopic analysis of the wood samples show an enrichment in the late season cellulosic $\delta^{18}O$ relative to modern samples, which we find was associated with increased reliance on summer rain. The data are consistent with other proxy data and climate model simulations showing the interglacial was associated with wetter summers across the western US. We propose enhanced summer rain during this warm period compensated for drought stress imposed by higher evaporative demand.

1 Introduction

Periods of punctuated or sustained warmth have been associated with forest stress and tree mortality events in the observational and historical records of the western US (Adams et al., 2009; Anderegg, Anderegg, Abatzoglou, Hausladen, & Berry, 2013; Smith, Paritsis, Veblen, & Chapman, 2015; Van Mantgem et al., 2009; Williams et al., 2010). Warming generates *hot droughts* (Overpeck, 2013) where the ecological effects of reduced precipitation become amplified through the exponential response of vapor pressure deficit (VPD) to temperature (Breshears et al., 2005; Williams et al., 2013). The increase in evaporative demand on soils and plants leads to a decline in leaf water potential and consequently hydraulic failure (McDowell et al., 2016). The outcome of this is down-regulation of photosynthesis and senescence as well as susceptibility to disturbances including fire and insect attack (C. D. Allen et al., 2010; Clifford, Royer, Cobb, Breshears, & Ford, 2013; Sala, 2009). The direct pathway between rising temperature and forest stress has been documented through controlled manipulation experiments (Adams et al., 2009) and gas exchange measurements taken during periods of temperature stress (McDowell et al., 2016). However, understanding the regional-scale response of forests to warming requires a holistic perspective that considers the broader dynamical changes in the climate system that come with an increase in radiative forcing (Diffenbaugh, Ashfaq, Shuman, Williams, & Bartlein, 2006; Harrison et al., 2003; Pascale et al., 2017). Some of these changes, such as a regional shift towards earlier snowpack melt (Mote, Li, Lettenmaier, Xiao, & Engel, 2018), are expected to exacerbate the direct effects of VPD

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on forest stress (Westerling, Hidalgo, Cayan, & Swetnam, 2006). On the other hand, changes in precipitation patterns such as latitudinal shifts in the jet stream or changes in the northerly penetration of the North American Monsoon, may regionally mitigate the response of forested ecosystems to warming (Bhattacharya, Tierney, & DiNezio, 2017; Wagner et al., 2010; Yin, 2005).

Recent modeling studies have shown that the North American Monsoon (NAM) is likely to weaken with increased radiative forcing (Pascale et al., 2017) and observational studies have noted declining summer rain across the broader western US in recent decades (Holden et al., 2018). These changes would exacerbate ecosystem stress and the susceptibility to disturbance because even though summer rains often yield significantly less of the total annual water than winter precipitation, these small water inputs during the growing season are critical for maintaining sufficient soil moisture late in the summer (Berkelhammer, Stefanescu, Joiner, & Anderson, 2017; Kerhoulas, Kolb, & Koch, 2017). However, the historical and projected changes in summer rain contrast with proxy records that have noted the strength of NAM is positively coupled to global temperatures (e.g. (Barron, Metcalfe, & Addison, 2012; Bhattacharya, Tierney, Addison, & Murray, 2018; Murray, 2012)). While these results may seem to contradict one another, it is important to note that even if the broader NAM circulation system responds positively to warming, its regional manifestation (i.e. local rainfall amounts) may be heterogenous due to localized land-surface feedbacks and changes in other atmospheric circulation regimes. For example, simulations from Diffenbaugh et al. (2006) noted that warming during the mid-Holocene enhanced summer precipitation in the central and northern parts of the Rocky Mountains due to an increase in easterly moisture sources from the Gulf of Mexico. In other words, there were regional increases in summer rain that were not necessarily coupled to the strength of the monsoonal circulation. Because of the challenges and uncertainties of modeling precipitation in topographically complex regions like the western US, paleoecological records from other warm periods provide critical constraints on the coupled response of climate and forests to warming.

The last interglacial period (~116-130 ka) was the most recent period in Earth's history when temperatures in the western US were likely to have been persistently warmer than today and thus presents a potential window into the ecological response to warming (Lunt et al., 2013; Otto-Bliesner et al., 2013; Pedersen, Langen, & Vinther, 2017). Recent downscaled climate model simulations for North America indicate that during the warmest periods of the last interglacial (i.e. the Eemian period at 125 ka), growing season (JJAS) temperatures were ap-

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proximately 1-3°C warmer than today in the southern Rocky Mountains (Fig. 1) (Insel & Berkelhammer, 2021). The warmer summer temperatures and increased incoming shortwave radiation manifested in growing season canopy temperatures that were 2-4°C warmer during June and July and an increase in canopy VPD of up to 0.5 kpa (~30% increase) relative to modern (Fig. 2). These temperature changes were likely similar or greater to those that occurred during the Medieval Climate Anomaly when there was high levels of stress on forests across the region (Williams et al., 2013). The combined effects of higher VPD and lower pCO_2 (which was similar to pre-industrial concentrations) (Kleinen, Brovkin, & Munhoven, 2016), would have resulted in photosynthetic declines relative to modern conditions (Fig. 2). However, the climate model simulations also indicate the Rocky Mountains of Colorado and Wyoming experienced a ~15-20% increase in summertime precipitation (Fig. 1) indicating there were opposing influences of wetter summers yet higher evaporative demand associated with persistently warmer conditions. Winter precipitation was largely unaffected by the different orbital forcing throughout the interglacial and therefore was not likely to have had a critical impact on ecosystems during this period (Insel & Berkelhammer, 2021).

To assess how the competing affects of both higher summer precipitation and evaporation-demand influenced forest stress, we analyzed a unique collection of exceptionally preserved interglacial subfossil wood samples that were collected outside of Snowmass, Colorado (Mahan et al., 2014; Miller, Miller, & Jackson, 2014). Earlier analyses on these samples showed the wood assemblage was dominated by *Abies* and *Picea* (like today) and that growing conditions were similar, if not slightly more favorable, relative to today (Brown, Nash, & Kline, 2014). This interpretation of the climate from the wood samples was also supported by analysis of coeval plant macrofossil (Strickland, Baker, Thompson, & Miller, 2014) and insect assemblage (Elias, 2014) that also suggest the presence of similar climate conditions as today. Building from this work, we generated high resolution records of oxygen and carbon isotope ratios of the subfossil wood following similar approaches as Jahren and Sternberg (2008) and Schubert and Jahren (2015) to assess how the forests responded ecohydrologically to the forcing of higher temperature and precipitation during this period.

2 Methods

2.1 Sample description and isotopic analysis

The analysis presented here is based on a comparison between the stable isotopic ratio of modern and subfossil wood samples from the Ziegler Reservoir site in Snowmass, CO (39.2075°N,

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106.9648°W) (Fig. 1). The samples were previously dated to the last interglacial using Optically-Stimulated Luminescence (Mahan et al., 2014). We hereafter discuss the growing conditions for these trees with respect to the simulated climate during the Eemian period of the last interglacial (125 ka). However, we note that there remains significant uncertainty regarding their precise age within the interglacial (~2-4 ka, Mahan et al. (2014)). In consideration of the age uncertainty in the samples, we hereafter refer to the samples as *interglacial* but refer to results from the climate simulations as *Eemian*. While the climate of the interglacial was not homogeneously warm, we note that the increased summer temperatures and precipitation that are the key climate features of the Eemian simulations were also present in 130 ka and 120 ka simulations (Insel & Berkelhammer, 2021; Scussolini et al., 2019).

The wood samples were preserved with sufficient integrity to identify ring boundaries and key anatomical features (Figs. S1-S5). As such, Brown et al. (2014) were able to confirm that the wood samples were dominated by *Abies* and *Picea*, like today. We utilized samples of these genus' from the archive at the Denver Museum of Nature and Science. Each sample was sanded, scanned and sliced along the growth axis such that each annual ring was broken up into between 5-16 samples (Barbour, Walcroft, & Farquhar, 2002; Belmecheri, Wright, Szejner, Morino, & Monson, 2018; Jahren & Sternberg, 2008; Szejner et al., 2018) (Fig. S6). The cellulose was extracted from the wood slices using the Brendel Method and the δ^{18}O of the cellulose (i.e. $\delta^{18}O_{cellulose}$) was determined by pyrolysis-GC-IRMS using a TC/EA with a ceramic reactor kept at 1400°C that was coupled with a ConFlo II interfaced to a ThermoFisher Delta Precision Isotope Ratio Mass Spectrometer. The method of sample preparation, isotope analysis and calibration was identical to that presented by Berkelhammer et al. (2020) and the details are thus only provided in the supplement. In total, 985 subfossil wood samples were analyzed that yielded 143 annual tree ring cycles (Fig. S7). The isotopic ratios of the subfossil wood were compared against published modern *Abies lasiocarpa* and *Picea engelamannii* samples that were collected near the shores of the modern Ziegler Reservoir (Berkelhammer et al., 2020) (Fig. 1). In total, 1206 modern samples were analyzed and they were distributed over 135 annual rings.

A subset of wood samples were also analyzed for δ^{13}C to assess differences in water use efficiency between time periods (Van de Water, Leavitt, & Betancourt, 1994; Ward et al., 2005). The cellulose was extracted from the wood using the same method as with $\delta^{18}O_{cellulose}$ and the $\delta^{13}C_{cellulose}$ was measured by combustion-GC-IRMS at Northern Illinois University. Samples were normalized to the VPDB scale using internal reference standards. Because the iso-

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tope analysis required larger sample volumes, annual rings were only discretized into early wood and late wood samples (as opposed to the higher resolution of oxygen isotope analysis). In total, 86 subfossil samples were analyzed and 98 modern wood samples. We used the $\delta^{13}C_{cellulose}$ to assess the ci/ca ratio of modern and last interglacial samples based on the approach of Farquhar, O'Leary, and Berry (1982) while utilizing revised carbon fractionation of subfossil woody materials from Lukens, Eze, and Schubert (2019) (Eqns. S1 and S2).

2.2 Modeling and Statistical Analysis

One of the challenges associated with interpreting historic $\delta^{18}O_{cellulose}$ is that it is sensitive simultaneously to changes in both VPD and the isotopic ratio of the trees' source water. This can lead to non-unique interpretations as to why the isotopic ratio of cellulose from one period might differ from another. Following our earlier work, we rely on the fact that the annual cycle in $\delta^{18}O_{cellulose}$ is driven firstly by the seasonal cycle in atmospheric VPD that leads to a predictable pattern in the seasonal enrichment of leaf water and subsequently the $\delta^{18}O_{cellulose}$. This pattern can be seen at sites across the western US (Belmecheri et al., 2018; Berkelhammer & Stott, 2009; Szejner et al., 2018). However, the shape of the seasonal cycle can be altered from this expected pattern by changes in the trees' source water. We utilize an objective clustering approach to classify the observed tree ring cycles into dominant patterns (Supplementary Material) assuming that changes in the shape of the cycle are driven by shifts in the seasonal origins of the water used by the tree. This statistical clustering approach was then supported by a mechanistic modeling approach that closely follows that in Berkelhammer et al. (2020) and is further illustrated in Fig. S8. Briefly, climate data from a downscaled (50 km) GCM (Insel & Berkelhammer, 2021) was used to force a canopy model which, fed a biogeochemical model of fractionation associated with photosynthate formation and cellulose metabolism. The coarse climate model data provides constraints on the climate conditions (humidity, air temperature, wind and radiation) whereas the canopy model translates those conditions to the leaf-level where isotopic fractionation occurs. The climate data for the modern and Eemian (125 ka) periods were drawn from downscaled 50 km 10-year model simulations run with the RegCM model (Fig. S9) (Insel & Berkelhammer, 2021).

3 Results and Discussion

A comparison between the oxygen isotope ratio ($\delta^{18}O_{cellulose}$) of early season wood from the modern and subfossil samples indicates there were comparable conditions between these

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time periods (Fig. 3A) - as expected from previous analyses (Brown et al., 2014). However, the $\delta^{18}O_{cellulose}$ between these time periods diverges later in the growing season such that the subfossil samples were ~1‰ enriched relative to modern (Fig. 3B). The enriched isotopic values in the latter portions of the interglacial annual growth rings reflect either an increase in the $\delta^{18}O$ of the trees' source water later in the season or an increase in evaporative enrichment of the leaf water (i.e. decrease in stomatal conductance) (Szejner et al., 2018).

To provide a mechanistic understanding of the late season isotopic enrichment in the subfossil wood relative to modern, we followed the method described above where: (1) the observed seasonal $\delta^{18}O_{cellulose}$ cycles were first clustered into dominant patterns, (2) a biogeochemical model was used to understand the trees' source water associated with each of the dominant patterns and (3) a comparison was made between the relative frequency of annual tree rings that fell into each of the clusters. The results from this analysis show that the seasonal cycles in $\delta^{18}O_{cellulose}$ can be classified into three dominant patterns that are similar between time periods (Fig. 4A-F). Samples from both the modern and interglacial periods share the same most prevalent seasonal cycle, that was apparent in 59±7% of the modern and 47±8% of the interglacial growth rings (Figs. 4A and D). This cycle (i.e. Cluster 1) was characterized by cellulose that was enriched early in the season by ~1‰ and the isotopic ratio dropped to a minimum of ~-1‰ (relative to the annual mean) near the end of the growing season. The structure in Cluster 1 can be reproduced when the mechanistic model for cellulose isotope ratios was forced by the seasonal cycle in either modern or Eemian climate while the trees utilize a source water whose isotopic ratio does not change during the growing season. These simulations thus account for how the isotopic ratio of cellulose responds to fractionation at the leaf-atmosphere interface while the trees are utilizing a constant source water. We presume this stable water source to be snowmelt that accumulates and remains in the deeper soil layers through the summer. This suggests that - like today - snowmelt was the dominant form of source water for the trees during the interglacial, which is consistent with simulations showing similar winter precipitation rates during the Eemian as today (Insel & Berkelhammer, 2021).

The isotopic cycles that fall into Clusters 2 and 3 reflect years when the source water used by the trees was dynamic through the growing season. Seasonal cycles of the form that define the average shape of Clusters 2 and 3 emerge from increased utilization of summer rain, which provides a water source for the trees that is isotopically enriched and variable through the growing season. While we classified the cycles in discrete clusters, it is more accurate to imagine that use of summer precipitation as a source water generates seasonal cycles in $\delta^{18}O_{cellulose}$

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that fall along a continuum of patterns (Fig. 4H). For example, Cluster 2 emerges when the trees rely on an even mixture of snowmelt and summer rain while Cluster 3 reflects the conditions where the trees rely on 80% summer rain (Fig. 4). Without better independent constraints on interglacial precipitation $\delta^{18}O$, we do not attempt to provide a quantitative assessment of seasonal water use (e.g. S. T. Allen, Kirchner, Braun, Siegwolf, and Goldsmith (2019)) but simply note that the increased frequency of seasonal cycles of the form in Clusters 2 and 3 likely reflect an increase in the utilization of summer rain during the interglacial.

While the modeling results suggest the late season increase in subfossil $\delta^{18}O_{cellulose}$ emerges from a change in seasonal water sources between time periods, other factors including a change in stomatal conductance associated with higher interglacial VPD might also explain the isotopic enrichment at the end of the growing season. To address this, we also analyzed $\delta^{13}C_{cellulose}$, which is insensitive to the source water used by the trees but provides an independent proxy of whether there were significant changes in water use efficiency that might indicate moisture stress and changes in stomatal conductance under the potentially higher VPD conditions (Leavitt & Long, 1989). The modern and interglacial populations of $\delta^{13}C_{cellulose}$ are offset by ~3‰, which can be explained through differences in $\delta^{13}CO_2$ and pCO_2 between modern (-8.3‰ and 380 ppm) and interglacial (-6.5‰ and 276 ppm) atmospheres (Fig. 3). The former data were derived from measurements at the Niwot Ridge observatory (Dlugokencky & Thoning, 2021) and the latter from an Antarctic ice core composite (Kleinen et al., 2016) with justification for these values provided in Supplemental Material. When the background atmospheric differences are accounted for (Eqns. S1 and S2), the interglacial ratio of internal carbon dioxide, *ci*, to external carbon dioxide, *ca*, falls along a trajectory defined by modern, Holocene and Last Glacial Maximum wood specimens from other coniferous species across the western US (Fig. 3). Furthermore, unlike $\delta^{18}O_{cellulose}$, we see no difference in the average gradient between early and late season $\delta^{13}C_{cellulose}$ for interglacial and modern periods (Fig 3E). The results from the $\delta^{13}C_{cellulose}$ analysis do not provide evidence of any significant ecophysiological adjustment to the warmer conditions and higher VPD during the interglacial. This result supports the interpretation that anomalies in late season $\delta^{18}O_{cellulose}$ are a reflection of greater use of summer rain by interglacial trees during the latter portion of the growing season (Szejner et al., 2018).

Based on a modern analysis of the seasonal origins of water used by conifers at this site, there can be multiple explanations for the increased utilization of summer rain in the last interglacial samples (Berkelhammer et al., 2020). Firstly, the seasonal origins of water used by

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trees can vary with topographic position such that trees near the bottom of a hillslope are more likely to have a stronger connection to groundwater and thus a greater reliance on snowmelt that recharges the local aquifers (Fig. S11) (Brooks et al., 2015). The trees that make up the modern population were sampled very close to where the subfossil wood likely grew (Fig. 1) and it is not likely there was a sufficient topographic difference to explain a gradient in water sources. Secondly, utilization of summer rain in modern trees tends to increase during periods of high snowpack because shallow roots are able to stay active later in the season (Martin, Looker, Hoylman, Jencso, & Hu, 2018). The interglacial was associated with comparable winter precipitation rates (Insel & Berkelhammer, 2021) and snowpack melted off at a similar time in the Eemian relative to modern (Fig. S10). The simulations of the Eemian climate therefore do not support evidence that snowpack persisted later allowing shallow roots to stay active longer. Lastly, an overall increase in summer rain, as indicated by the model simulations (Insel & Berkelhammer, 2021) and proxy records from the core of the monsoon domain in Arizona (Murray, 2012), both indicate an increase in summer precipitation during the Eemian period which may simply have supplied sufficient moisture to the root zone to allow the trees to remain active later into the summer. Based on the available data and modeling, the latter seems the most plausible explanation. Irrespective of the mechanism driving the increased reliance on summer rain, the utilization of this moisture source emerges as a plausible explanation for why the trees retained favorable growing conditions during this warm period despite the higher VPD and lower pCO_2.

4 Conclusion

Forest stress in the western US is commonly considered to be driven along one axis associated with precipitation variability and its effect on soil moisture and a second axis associated with growing season temperatures and the resulting effects on VPD. During the warmest period of the last interglacial (the Eemian), the Rocky Mountain forests experienced reduced stress along the precipitation axis and increased stress along the VPD axis. Our detailed analysis of forest ecohydrology during this multi-decade window ~120,000-125,000 years ago shows how increased summer rain may have compensated for the temperature-related stress leading to growing season conditions that were similar or more favorable than today (Brown et al., 2014). This result highlights the importance of summer rain to tree moisture stress even though it is snowpack that predominantly recharges the region's aquifers and drives streamflow. If future increases in radiative forcing have the effect of increasing monsoonal circulation and summer

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rains, then forest ecosystems in this region could be resilient to the moisture stress associated with warming. However, if the observations and modeling of projected declines in summer rain are borne out (Holden et al., 2018; Pascale et al., 2017), then the results presented here portend a more dire context for modern forests than the last period when conditions were as warm as today.

5 Figure Captions

Figure1: (A and B) Downscaled climate model simulations of Eemian (125ka) temperature and precipitation relative to modern Insel and Berkelhammer (2021). (C and D) Maps indicating the broader and local context of the modern and subfossil wood samples (Miller et al., 2014).

Figure 2: Difference in canopy conditions between modern and Eemian climates for the Snowmass grid cell. (A) Difference in daily averaged canopy (leaf) temperature between modern and Eemian from the grid cell nearest the site. (B) Difference in daily average VPD (with respect to leaf temperatures) between modern and Eemian from the grid cell nearest the site. (C) Percentage difference in daily averaged canopy photosynthesis between modern and Eemian. (D) Density map of the relationship between VPD and photosynthesis for all points from the modern and Eemian simulations. The colors are a relative indicator of point density.

Figure3: (A) Difference in δ^{18}O of cellulose between modern and interglacial wood from first half of all growth rings. (B) Difference in δ^{18}O of cellulose between modern and interglacial wood from second half of all growth rings. (C) Difference in δ^{13}C of cellulose between modern and interglacial wood. (D) Relationship between derived *ci* from Equations S1 and S2 measured or reconstructed *ca* from this study (red) and previous studies in California and Nevada Van de Water et al. (1994); Ward et al. (2005). (E) Box and whisper plots showing the difference between early and latewood δ^{13}C for the modern and interglacial samples.

Figure4: (A-F) All the δ^{18}O intra-ring cycles from the interglacial (A-C) and modern (D-F) wood samples after being distributed into the three clusters. The individual annual cycles are shown as faint gray lines and the mean and 1 standard deviation around the mean are shown as solid and dotted brown (interglacial) and green (interglacial) lines. (G) The distribution of Cluster 1 and Clusters 2+3 for the modern and interglacial time periods with uncertainties defined using a Monte Carlo approach. (H) A set of simulated δ^{18}O cycles where the climate was fixed as the Eemian seasonal climate forcing (i.e. Fig. 2 and S9) but each simulation was run with a different source water input based on the relative use of snowmelt (iso-

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topically depleted and unchanging) vs. summer precipitation (isotopically heavier and highly variable through the growing season). Example simulations are pulled from the full set of simulations that correspond to use of mostly snow pack (Cluster 1-like), a mixture of the two sources (Cluster 2-like) and reliance on summer precipitation (Cluster 3-like).

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