Wetter summers mitigated temperature stress on Rocky Mountain forests during the last interglacial 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 δ^{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.

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Key Points:

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

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15 Abstract

Rising summer temperatures are expected to increase tree mortality rates across the western 16 United States. Here, we analyze subfossil wood samples from Colorado dating to the last in-17 terglacial to assess the response of two common conifers to a previous warm period. The trees 18 experienced comparable growth rates and water use efficiency during the interglacial relative 19 to modern despite evidence from model simulations of a $\sim 30\%$ increase in evaporative demand 20 during the peak of the growing season. High-resolution isotopic analysis of the wood samples 21 show an enrichment in the late season cellulosic δ^{18} O relative to modern samples, which we 22 find was associated with increased reliance on summer rain. The data are consistent with other 23 proxy data and climate model simulations showing the interglacial was associated with wet-24 ter summers across the western US. We propose enhanced summer rain during this warm pe-25 riod compensated for drought stress imposed by higher evaporative demand. 26

1 Introduction

Periods of punctuated or sustained warmth have been associated with forest stress and 28 tree mortality events in the observational and historical records of the western US (Adams et 29 al., 2009; Anderegg, Anderegg, Abatzoglou, Hausladen, & Berry, 2013; Smith, Paritsis, Ve-30 blen, & Chapman, 2015; Van Mantgem et al., 2009; Williams et al., 2010). Warming gener-31 ates hot droughts (Overpeck, 2013) where the ecological effects of reduced precipitation be-32 come amplified through the exponential response of vapor pressure deficit (VPD) to temper-33 ature (Breshears et al., 2005; Williams et al., 2013). The increase in evaporative demand on 34 soils and plants leads to a decline in leaf water potential and consequently hydraulic failure 35 (McDowell et al., 2016). The outcome of this is down-regulation of photosynthesis and senes-36 cence as well as susceptibility to disturbances including fire and insect attack (C. D. Allen et 37 al., 2010; Clifford, Royer, Cobb, Breshears, & Ford, 2013; Sala, 2009). The direct pathway 38 between rising temperature and forest stress has been documented through controlled manip-39 ulation experiments (Adams et al., 2009) and gas exchange measurements taken during peri-40 ods of temperature stress (McDowell et al., 2016). However, understanding the regional-scale 41 response of forests to warming requires a holistic perspective that considers the broader dy-42 namical changes in the climate system that come with an increase in radiative forcing (Dif-43 fenbaugh, Ashfaq, Shuman, Williams, & Bartlein, 2006; Harrison et al., 2003; Pascale et al., 44 2017). Some of these changes, such as a regional shift towards earlier snowpack melt (Mote, 45 Li, Lettenmaier, Xiao, & Engel, 2018), are expected to exacerbate the direct effects of VPD 46

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 52 to weaken with increased radiative forcing (Pascale et al., 2017) and observational studies have 53 noted declining summer rain across the broader western US in recent decades (Holden et al., 54 2018). These changes would exacerbate ecosystem stress and the susceptibility to disturbance 55 because even though summer rains often yield significantly less of the total annual water than 56 winter precipitation, these small water inputs during the growing season are critical for main-57 taining sufficient soil moisture late in the summer (Berkelhammer, Stefanescu, Joiner, & An-58 derson, 2017; Kerhoulas, Kolb, & Koch, 2017). However, the historical and projected changes 59 in summer rain contrast with proxy records that have noted the strength of NAM is positively 60 coupled to global temperatures (e.g. (Barron, Metcalfe, & Addison, 2012; Bhattacharya, Tier-61 ney, Addison, & Murray, 2018; Murray, 2012)). While these results may seem to contradict 62 one another, it is important to note that even if the broader NAM circulation system responds 63 positively to warming, its regional manifestation (i.e. local rainfall amounts) may be heteroge-64 nous due to localized land-surface feedbacks and changes in other atmospheric circulation regimes. 65 For example, simulations from Diffenbaugh et al. (2006) noted that warming during the mid-66 Holocene enhanced summer precipitation in the central and northern parts of the Rocky Moun-67 tains due to an increase in easterly moisture sources from the Gulf of Mexico. In other words, 68 there were regional increases in summer rain that were not necessarily coupled to the strength 69 of the monsoonal circulation. Because of the challenges and uncertainties of modeling pre-70 cipitation in topographically complex regions like the western US, paleoecological records from 71 other warm periods provide critical constraints on the coupled response of climate and forests 72 to warming. 73

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 & Berkel-80 hammer, 2021). The warmer summer temperatures and increased incoming shortwave radi-81 ation manifested in growing season canopy temperatures that were 2-4°C warmer during June 82 and July and an increase in canopy VPD of up to 0.5 kpa (~30% increase) relative to mod-83 ern (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 85 the region (Williams et al., 2013). The combined effects of higher VPD and lower pCO_2 (which 86 was similar to pre-industrial concentrations) (Kleinen, Brovkin, & Munhoven, 2016), would 87 have resulted in photosynthetic declines relative to modern conditions (Fig. 2). However, the 88 climate model simulations also indicate the Rocky Mountains of Colorado and Wyoming ex-89 perienced a ~15-20% increase in summertime precipitation (Fig. 1) indicating there were op-90 posing influences of wetter summers yet higher evaporative demand associated with persistently 91 warmer conditions. Winter precipitation was largely unaffected by the different orbital forc-92 ing throughout the interglacial and therefore was not likely to have had a critical impact on 93 ecosystems during this period (Insel & Berkelhammer, 2021). 94

To assess how the competing affects of both higher summer precipitation and evaporation-95 demand influenced forest stress, we analyzed a unique collection of exceptionally preserved 96 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 98 the wood assemblage was dominated by Abies and Picea (like today) and that growing con-99 ditions were similar, if not slightly more favorable, relative to today (Brown, Nash, & Kline, 100 2014). This interpretation of the climate from the wood samples was also supported by anal-101 ysis of coeval plant macrofossil (Strickland, Baker, Thompson, & Miller, 2014) and insect as-102 semblage (Elias, 2014) that also suggest the presence of similar climate conditions as today. 103 Building from this work, we generated high resolution records of oxygen and carbon isotope 104 ratios of the subfossil wood following similar approaches as Jahren and Sternberg (2008) and 105 Schubert and Jahren (2015) to assess how the forests responded ecohydrologically to the forc-106 ing of higher temperature and precipitation during this period. 107

108 2 Methods

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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,

106.9648°W) (Fig. 1). The samples were previously dated to the last interglacial using Optically-112 Stimulated Luminescence (Mahan et al., 2014). We hereafter discuss the growing conditions 113 for these trees with respect to the simulated climate during the Eemian period of the last in-114 terglacial (125 ka). However, we note that there remains significant uncertainty regarding their 115 precise age within the interglacial (~2-4 ka, Mahan et al. (2014)). In consideration of the age 116 uncertainty in the samples, we hereafter refer to the samples as *interglacial* but refer to results 117 from the climate simulations as *Eemian*. While the climate of the interglacial was not homo-118 geneously warm, we note that the increased summer temperatures and precipitation that are 119 the key climate features of the Eemian simulations were also present in 130 ka and 120 ka sim-120 ulations (Insel & Berkelhammer, 2021; Scussolini et al., 2019). 121

The wood samples were preserved with sufficient integrity to identify ring boundaries 122 and key anatomical features (Figs. S1-S5). As such, Brown et al. (2014) were able to confirm 123 that the wood samples were dominated by Abies and Picea, like today. We utilized samples 124 of these genus' from the archive at the Denver Museum of Nature and Science. Each sample 125 was sanded, scanned and sliced along the growth axis such that each annual ring was broken 126 up into between 5-16 samples (Barbour, Walcroft, & Farquhar, 2002; Belmecheri, Wright, Sze-127 jner, Morino, & Monson, 2018; Jahren & Sternberg, 2008; Szejner et al., 2018) (Fig. S6). The 128 cellulose was extracted from the wood slices using the Brendel Method and the δ^{18} O of the 129 cellulose (i.e. $\delta^{18}O_{cellulose}$) was determined by pyrolysis-GC-IRMS using a TC/EA with a ce-130 ramic reactor kept at 1400°C that was coupled with a ConFlo II interfaced to a ThermoFisher 131 Delta Precision Isotope Ratio Mass Spectrometer. The method of sample preparation, isotope 132 analysis and calibration was identical to that presented by Berkelhammer et al. (2020) and the 133 details are thus only provided in the supplement. In total, 985 subfossil wood samples were 134 analyzed that yielded 143 annual tree ring cycles (Fig. S7). The isotopic ratios of the subfos-135 sil wood were compared against published modern Abies lasiocarpa and Picea engelamannii 136 samples that were collected near the shores of the modern Ziegler Reservoir (Berkelhammer 137 et al., 2020) (Fig. 1). In total, 1206 modern samples were analyzed and they were distributed 138 over 135 annual rings. 139

¹⁴⁰ A subset of wood samples were also analyzed for δ^{13} C to assess differences in water use ¹⁴¹ efficiency between time periods (Van de Water, Leavitt, & Betancourt, 1994; Ward et al., 2005). ¹⁴² The cellulose was extracted from the wood using the same method as with $\delta^{18}O_{cellulose}$ and ¹⁴³ the $\delta^{13}C_{cellulose}$ was measured by combustion-GC-IRMS at Northern Illinois University. Sam-¹⁴⁴ ples 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).

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2.2 Modeling and Statistical Analysis

One of the challenges associated with interpreting historic $\delta^{18}O_{cellulose}$ is that it is sen-152 sitive simultaneously to changes in both VPD and the isotopic ratio of the trees' source wa-153 ter. This can lead to non-unique interpretations as to why the isotopic ratio of cellulose from 154 one period might differ from another. Following our earlier work, we rely on the fact that the 155 annual cycle in $\delta^{18}O_{cellulose}$ is driven firstly by the seasonal cycle in atmospheric VPD that 156 leads to a predictable pattern in the seasonal enrichment of leaf water and subsequently the 157 $\delta^{18}O_{cellulose}$. This pattern can be seen at sites across the western US (Belmecheri et al., 2018; 158 Berkelhammer & Stott, 2009; Szejner et al., 2018). However, the shape of the seasonal cycle 159 can be altered from this expected pattern by changes in the trees' source water. We utilize an 160 objective clustering approach to classify the observed tree ring cycles into dominant patterns 161 (Supplementary Material) assuming that changes in the shape of the cycle are driven by shifts 162 in the seasonal origins of the water used by the tree. This statistical clustering approach was 163 then supported by a mechanistic modeling approach that closely follows that in Berkelham-164 mer et al. (2020) and is further illustrated in Fig. S8. Briefly, climate data from a downscaled 165 (50 km) GCM (Insel & Berkelhammer, 2021) was used to force a canopy model which, fed 166 a biogeochemical model of fractionation associated with photosynthate formation and cellu-167 lose metabolism. The coarse climate model data provides constraints on the climate conditions 168 (humidity, air temperature, wind and radiation) whereas the canopy model translates those con-169 ditions to the leaf-level where isotopic fractionation occurs. The climate data for the modern 170 and Eemian (125 ka) periods were drawn from downscaled 50 km 10-year model simulations 171 run with the RegCM model (Fig. S9) (Insel & Berkelhammer, 2021). 172

3 Results and Discussion

¹⁷⁴ A comparison between the oxygen isotope ratio ($\delta^{18}O_{cellulose}$) of early season wood from ¹⁷⁵ 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 sub-182 fossil wood relative to modern, we followed the method described above where: (1) the ob-183 served seasonal $\delta^{18}O_{cellulose}$ cycles were first clustered into dominant patterns, (2) a biogeo-184 chemical model was used to understand the trees' source water associated with each of the dom-185 inant patterns and (3) a comparison was made between the relative frequency of annual tree 186 rings that fell into each of the clusters. The results from this analysis show that the seasonal 187 cycles in $\delta^{18}O_{cellulose}$ can be classified into three dominant patterns that are similar between 188 time periods (Fig. 4A-F). Samples from both the modern and interglacial periods share the 189 same most prevalent seasonal cycle, that was apparent in $59\pm7\%$ of the modern and $47\pm8\%$ 190 of the interglacial growth rings (Figs. 4A and D). This cycle (i.e. Cluster 1) was character-191 ized by cellulose that was enriched early in the season by $\sim 1\%$ and the isotopic ratio dropped 192 to a minimum of \sim -1‰ (relative to the annual mean) near the end of the growing season. The 193 structure in Cluster 1 can be reproduced when the mechanistic model for cellulose isotope ra-194 tios was forced by the seasonal cycle in either modern or Eemian climate while the trees uti-195 lize a source water whose isotopic ratio does not change during the growing season. These 196 simulations thus account for how the isotopic ratio of cellulose responds to fractionation at the 197 leaf-atmosphere interface while the trees are utilizing a constant source water. We presume 198 this stable water source to be snowmelt that accumulates and remains in the deeper soil lay-199 ers through the summer. This suggests that - like today - snowmelt was the dominant form of 200 source water for the trees during the interglacial, which is consistent with simulations show-201 ing similar winter precipitation rates during the Eemian as today (Insel & Berkelhammer, 2021). 202

²⁰³ The isotopic cycles that fall into Clusters 2 and 3 reflect years when the source water ²⁰⁴ used by the trees was dynamic through the growing season. Seasonal cycles of the form that ²⁰⁵ define the average shape of Clusters 2 and 3 emerge from increased utilization of summer rain, ²⁰⁶ which provides a water source for the trees that is isotopically enriched and variable through ²⁰⁷ the growing season. While we classified the cycles in discrete clusters, it is more accurate to ²⁰⁸ 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 δ^{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 216 from a change in seasonal water sources between time periods, other factors including a change 217 in stomatal conductance associated with higher interglacial VPD might also explain the iso-218 topic enrichment at the end of the growing season. To address this, we also analyzed $\delta^{13}C_{cellulose}$, 219 which is insensitive to the source water used by the trees but provides an independent proxy 220 of whether there were significant changes in water use efficiency that might indicate moisture 221 stress and changes in stomatal conductance under the potentially higher VPD conditions (Leav-222 itt & Long, 1989). The modern and interglacial populations of $\delta^{13}C_{cellulose}$ are offset by ~3%, 223 which can be explained through differences in δ^{13} CO₂ and pCO₂ between modern (-8.3‰ and 224 380 ppm) and interglacial (-6.5‰ and 276 ppm) atmospheres (Fig. 3). The former data were 225 derived from measurements at the Niwot Ridge observatory (Dlugokencky & Thoning, 2021) 226 and the latter from an Antarctic ice core composite (Kleinen et al., 2016) with justification for 227 these values provided in Supplemental Material. When the background atmospheric differences 228 are accounted for (Eqns. S1 and S2), the interglacial ratio of internal carbon dioxide, ci, to 229 external carbon dioxide, ca, falls along a trajectory defined by modern, Holocene and Last Glacial 230 Maximum wood specimens from other coniferous species across the western US (Fig. 3). Fur-231 thermore, unlike $\delta^{18}O_{cellulose}$, we see no difference in the average gradient between early and 232 late season $\delta^{13}C_{cellulose}$ for interglacial and modern periods (Fig 3E). The results from the 233 $\delta^{13}C_{cellulose}$ analysis do not provide evidence of any significant ecophysiological adjustment 234 to the warmer conditions and higher VPD during the interglacial. This result supports the in-235 terpretation that anomalies in late season $\delta^{18}O_{cellulose}$ are a reflection of greater use of sum-236 mer rain by interglacial trees during the latter portion of the growing season (Szejner et al., 237 2018). 238

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 242 likely to have a stronger connection to groundwater and thus a greater reliance on snowmelt 243 that recharges the local aquifers (Fig. S11) (Brooks et al., 2015). The trees that make up the 244 modern population were sampled very close to where the subfossil wood likely grew (Fig. 1) 245 and it is not likely there was a sufficient topographic difference to explain a gradient in wa-246 ter sources. Secondly, utilization of summer rain in modern trees tends to increase during pe-247 riods of high snowpack because shallow roots are able to stay active later in the season (Mar-248 tin, Looker, Hoylman, Jencso, & Hu, 2018). The interglacial was associated with compara-249 ble winter precipitation rates (Insel & Berkelhammer, 2021) and snowpack melted off at a sim-250 ilar time in the Eemian relative to modern (Fig. S10). The simulations of the Eemian climate 251 therefore do not support evidence that snowpack persisted later allowing shallow roots to stay 252 active longer. Lastly, an overall increase in summer rain, as indicated by the model simula-253 tions (Insel & Berkelhammer, 2021) and proxy records from the core of the monsoon domain 254 in Arizona (Murray, 2012), both indicate an increase in summer precipitation during the Eemian 255 period which may simply have supplied sufficient moisture to the root zone to allow the trees 256 to remain active later into the summer. Based on the available data and modeling, the latter 257 seems the most plausible explanation. Irrespective of the mechanism driving the increased re-258 liance on summer rain, the utilization of this moisture source emerges as a plausible expla-259 nation for why the trees retained favorable growing conditions during this warm period despite 260 the higher VPD and lower pCO_2 . 261

²⁶² 4 Conclusion

Forest stress in the western US is commonly considered to be driven along one axis as-263 sociated with precipitation variability and its effect on soil moisture and a second axis asso-264 ciated with growing season temperatures and the resulting effects on VPD. During the warmest 265 period of the last interglacial (the Eemian), the Rocky Mountain forests experienced reduced 266 stress along the precipitation axis and increased stress along the VPD axis. Our detailed anal-267 ysis of forest ecohydrology during this multi-decade window ~120,000-125,000 years ago shows 268 how increased summer rain may have compensated for the temperature-related stress leading 269 to growing season conditions that were similar or more favorable than today (Brown et al., 2014). 270 This result highlights the importance of summer rain to tree moisture stress even though it is 271 snowpack that predominantly recharges the region's aquifers and drives streamflow. If future 272 increases in radiative forcing have the effect of increasing monsoonal circulation and summer 273

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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 298 (D-F) wood samples after being distributed into the three clusters. The individual annual cy-299 cles are shown as faint gray lines and the mean and 1 standard deviation around the mean are 300 shown as solid and dotted brown (interglacial) and green (interglacial) lines. (G) The distri-301 bution of Cluster 1 and Clusters 2+3 for the modern and interglacial time periods with uncer-302 tainties defined using a Monte Carlo approach. (H) A set of simulated δ^{18} O cycles where the 303 climate was fixed as the Eemian seasonal climate forcing (i.e. Fig. 2 and S9) but each sim-304 ulation was run with a different source water input based on the relative use of snowmelt (iso-305

- 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 sim-
- ³⁰⁸ ulations 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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Supporting Information for "Wetter summers mitigated temperature stress on Rocky Mountain forests during the last interglacial warm period"

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9 Material and Methods

10 1 Methods

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1.1 Wood samples: Site location and sample processing

The subfossil wood samples were collected from the Ziegler Reservoir site in Snow-12 mass, CO (39.2075°N, 106.9648°W) (Fig. 1). The wood samples are believed to have been 13 deposited along an interglacial lake shoreline. Cross-dating of the samples revealed that 14 the trees likely died in a single event and that the mean interglacial ring widths were sim-15 ilar to nearby modern chronologies but show decreased sensitivity, indicative of reduced 16 stress. For this study, 8 samples were utilized from the archive at the Denver Museum 17 of Nature and Science (Fig. S1-S5). Each annual ring was broken up into between 5-16 18 samples (Fig. S6) and the cellulose was then extracted from the wood slices using a mod-19 ified version of the Brendel Method where samples were subjected to heating in an acetic/nitric 20 acid mix to remove ligning and regins and then a series of ringes with ethanol, water and 21 finally acetone removed the acidic residue (Berkelhammer & Stott, 2012). The samples 22 were then dried in a vacuum oven and stored in a desiccator. The $\delta^{18}O$ of the cellulose 23 $(\delta^{18}O_{cellulose})$ was analyzed by pyrolysis-GC-IRMS using a TC/EA with a ceramic re-24 actor kept at 1400°C that was coupled with a ConFlo II interfaced to a ThermoFisher 25 Delta Precision Isotope Ratio Mass Spectrometer at University of Illinois at Chicago. 26 Reference IAEA cellulose, sucrose and benzoic acid standards were interspersed in each 27 run and used to normalize the data to the VSMOW scale. Uncertainty of $\delta^{18}O_{cellulose}$ 28 based on repeat measurement of reference standards over the course of the analysis was 29 $\leq 0.2\%$. The similarities between the early wood $\delta^{18}O_{cellulose}$ from the modern and sub-30 fossil samples indicate there was likely no preservation bias in the subfossil samples. 31

The comparison between $\delta^{18}O_{cellulose}$ of the modern and interglacial wood took 32 two forms. First, we present a direct comparison between the isotopic ratios of the mod-33 ern and interglacial wood samples. Differences between the populations were assessed 34 for statistical significance using a two-tailed T-test (Fig. 3). Second, we compared the 35 shape of the intra-ring isotopic cycles between the two time periods, which reflects sea-36 sonal variations in the trees' source water and climate conditions (Fig. 4, Fig. S6 and 37 S7). We compared the structure of the seasonal isotope cycles between the two time pe-38 riods by using a clustering algorithm to identify the shape of the most prevalent seasonal 39 cycles and then each annual cycle (143 from the interglacial and 135 from the modern) 40 was uniquely classified as falling into one of the clusters. The optimal choice for the num-41 ber of clusters represents a balance between the maximum reduction of information while 42 sufficiently representing the variability in the population. We chose to use three clusters, 43 which was guided by the analysis and modeling of $\delta^{18}O_{cellulose}$ of modern wood sam-44 ples presented in Berkelhammer et al. (2020). The clustering of seasonal cycles was done 45 by first interpolating all annual cycles to a common 7 sample/year resolution and remov-46 ing the annual mean from each cycle. All the annual cycles from the two time periods 47 were then treated as a single population and a k-means clustering analysis was done to 48

identify the three common structures. Lastly, a T-test was used to assess whether there
 was a difference in the probability of occurrence of any of the clusters between time pe riods.

In addition to the oxygen isotope analysis, a subset of wood samples were also analyzed for δ^{13} C to assess whether there were differences in water use efficiency between periods that manifested through changes in the ratio of internal to external carbon dioxide partial pressures $\left(\frac{ci}{ca}\right)$ (Van de Water, Leavitt, & Betancourt, 1994; Ward et al., 2005). An assessment of $\frac{ci}{ca}$ from δ^{13} C was done using the model of (Farquhar, O'Leary, & Berry, 1982) where:

$$\Delta = \frac{\delta^{13} C_{atmosphere} - \delta^{13} C_{cellulose}}{1 + \delta^{13} C_{cellulose}} \tag{1}$$

58 and

$$\frac{ci}{ca} = \frac{\Delta - a}{b - a} \tag{2}$$

Equation 1 solves for the discrimination against ${}^{13}C$ between the photosynthate 59 and atmospheric CO₂, assuming a 4.4% fractionation associated with diffusion into the 60 leaf (a) and a 27% fractionation associated with carbon fixation (b). In order to solve 61 Equation 1, we used the measured values of $\delta^{13}C_{cellulose}$ and estimated $\delta^{13}C_{atmosphere}$ 62 from the NOAA Global Monitoring Division site at Niwot Ridge, Colorado for the mod-63 ern samples (Dlugokencky & Thoning, 2021) and data from an Antarctic ice core syn-64 thesis (Kleinen, Brovkin, & Munhoven, 2016) for the interglacial samples. We did not 65 apply any offset between the Antarctic ice core $CO_2/\delta^{13}C$ and the gas that was fixed by 66 the trees during the interglacial growing season in Colorado based on the observed sim-67 ilarity between growing season carbon dioxide values measured at Niwot Ridge (382 ppm 68 and -8.15%) and annual average carbon dioxide values measured at the NOAA Global 69 Monitoring Division's South Pole Observatory (381 ppm and -8.18%) for the time pe-70 riod 2000-2014. We also applied a -1.3‰ offset to $\delta^{13}C_{cellulose}$ in Equation 1 to reflect 71 known differences between photosynthate and wood δ^{13} C (Lukens, Eze, & Schubert, 2019). 72 Equation 2 was then used to derive $\frac{ci}{ca}$ based on the Δ values from Equation 1 and an 73 estimate of *ca* from the Niwot Ridge and Antarctic ice data for the modern and inter-74 glacial samples, respectively as shown in Figure 3. 75

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1.2 Climate and Biogeochemical Modeling

A series of modeling exercises were conducted to provide both local information 77 on the interglacial climate and how that translated into the observed proxy signals (Fig. 78 S8). Firstly, a set of downscaled 50 km 10-year model simulations were run with the RegCM 79 model under both modern and interglacial forcings as described by Insel and Berkelham-80 mer (2021). We focus on the Eemian (125 ka) simulations for the analyses presented here. 81 These experiments were run with model configurations and forcings similar to previous 82 lower resolution simulations (Pedersen, Langen, & Vinther, 2017), but were run with suf-83 ficient resolution to assess differences in snowpack and summer rain in the topograph-84 ically complex Rocky Mountains (Fig. 1). The simulations were not used here to diag-85 nose interglacial climate dynamics, which are discussed in a separate publication (Insel 86 & Berkelhammer, 2021). The results from the GCM simulations were then used to force 87 a canopy model to assess how interglacial climate changes translated to effects on for-88 est ecophysiology. We used the Soil Canopy Observation Photosynthesis Energy Model 89 (SCOPE) (Tol, Berry, Campbell, & Rascher, 2014; Tol, Verhoef, Timmermans, Verhoef, 90 & Su, 2009), which is a 1-D vertical model (40 canopy layers) that solves for the canopy 91 energy budget, thermal properties of the canopy, radiative transfer, sensible and latent 92 heat fluxes, resistance terms (from wind speed and canopy properties) and stomatal con-93

ductance and photosynthesis. Our previous work has shown that this model captures 94 the seasonal cycle of photosynthesis and transpiration for the Ziegler Reservoir grid cell 95 (Berkelhammer et al., 2020) and therefore provides a useful intermediary between the 96 GCM grid cell and proxy. The model was run with a 30-minute time step for the 10-year 97 period during both the modern and interglacial simulations using modeled incoming long-98 wave and shortwave radiation, barometric pressure, vapor pressure, windspeed, atmo-99 spheric CO_2 , canopy height and leaf area index (Supp. Fig 12). From these simulations, 100 we specifically assessed how leaf-level VPD (saturated vapor pressure at leaf - vapor pres-101 sure in free air) and total photosynthesis differed between the modern and warmer con-102 ditions of the interglacial (Fig. 2). A key limitation of this model is that it does not ac-103 count for the effect of soil moisture on stomatal conductance so the results presume soil 104 moisture is the same between time periods and the differences in the simulations emerge 105 from atmospheric forcing. 106

The simulations of both climate and canopy processes were used to force a forward 107 model for $\delta^{18}O_{cellulose}$ that required inputs of transpiration, VPD, stomatal and canopy 108 conductances, leaf temperature and δ^{18} O of the trees' source water ($\delta^{18}O_{source}$) as de-109 scribed below (Fig. S9). The isotope model was used here to assess two aspects of the 110 proxy data: (1) Are observed differences in $\delta^{18}O_{cellulose}$ between the modern and inter-111 glacial the result of changes in climate forcing on leaf-atmosphere exchange vs. changes 112 in $\delta^{18}O_{source}$ and (2) Provide a mechanistic explanation for the observed structure of 113 the annual cycles that emerged from the cluster analysis (Fig. 4). Equations of the mech-114 anistic model for cellulose isotopes are based on those previously published by Barbour, 115 Roden, Farquhar, and Ehleringer (2004); Evans (2007); Keel et al. (2016); Roden, Lin, 116 and Ehleringer (2000) and are provided below. With the exception of $\delta^{18}O_{source}$, the other 117 model inputs were generated from the aforementioned climate and canopy model sim-118 ulations. 119

For the modern period, δ^{18} O of snowpack, groundwater and precipitation in this 120 region are well constrained (Anderson, Berkelhammer, & Mast, 2016; Berkelhammer et 121 al., 2020) but the relative importance of these water reservoirs to support plant growth 122 under both modern and interglacial conditions are unknown and likely to be variable (Fig. 123 S11). To address this, the mechanistic model was run iteratively with numerous $\delta^{18}O_{source}$ 124 inputs that were generated by varying the relative importance of snowpack and summer 125 precipitation as a moisture source. On one end of the spectrum is the condition where 126 the trees relied exclusively on snowmelt, which is isotopically depleted and constant through 127 the growing season. On the other end of the spectrum, is the condition where the trees 128 relied on precipitation, which is isotopically heavier and varies significantly through the 129 growing season. The mechanistic model was run iteratively with inputs between 0-100% 130 reliance on snowmelt (or 100-0% summer rain) and were run in 30-minute timesteps through 131 the 10-year climate model simulations. An ensemble of estimates (based on the variable 132 $\delta^{18}O_{source}$ inputs) were generated for $\delta^{18}O_{cellulose}$ for all timesteps when photosynthe-133 sis was greater than 0 and the air temperature was greater than 6° C (Rossi et al., 2008). 134 Total accumulated photosynthesis for the growing season was then distributed into 7 equal 135 segments and the weighted average of the $\delta^{18}O_{cellulose}$ (weighted by rate of photosyn-136 thesis) was calculated for each segment. Using this procedure we assigned day of year 137 estimates to each segment of cellulose measured. This translated the measurements where 138 the "time" was based on increment in the wood, as in Figure S6, into a calendar day. 139 140 It also has the effect that two sections of cellulose of identical length might represent different lengths of time (Berkelhammer et al., 2020). This procedure ultimately produced 141 modeled annual cycles for $\delta^{18}O_{cellulose}$ of modern and interglacial cellulose that could 142 be directly compared to the observed annual cycles for both time periods (Fig. 4). 143

144 1.3 Equations for isotope model of cellulose

The forward model for the isotopic ratio of cellulose is based on the equations described by (Barbour et al., 2004), which are provided below. The isotopic fractionation between liquid and vapor at the leaf boundary is temperaturedependent and referred to hereafter as: $\epsilon_{Temperature}$. To solve for this term, leaf temperature is needed, which was estimated from an energy balance calculation in the SCOPE model. The equation for the temperature-dependent fractionation is as follows:

$$\epsilon_{Temperature} = 2.644 - 3.206 * \frac{10^3}{Temp_{leaf} + 273.15} + 1.534 * \frac{10^6}{(Temp_{leaf} + 273.15)^2}$$
(3)

Isotopic fractionation between the leaf water and atmosphere is not an equilibrium process and requires additional equations to account for kinetic fractionation, referred to as $\epsilon_{Kinetic}$. Kinetic fractionation occurs because of different diffusion rates for the water isotopologues as the vapor passes through the leaf stomata, boundary layers, and across the canopy-atmosphere interface. The approach to estimating these kinetic isotope effects follows the derivation from Lee et al. (2009) where stomatal (gs), boundary (gb) and aerodynamic (ga) conductance terms are extracted from SCOPE:

$$\epsilon_{Kinetic} = \frac{21 * (\frac{1}{gb}) + 32 * (\frac{1}{ga})}{(\frac{1}{qb}) + (\frac{1}{qs})} \tag{4}$$

Isotopic exchange occurs between water vapor and the atmosphere and in order to 158 estimate this effect an estimate of the isotopic ratio of water vapor is needed ($\delta^{18}O_{vapor}$). 159 Traditionally, measurements of the isotopic ratio of water vapor are sparse. We estimate 160 this value using 1000's of water vapor isotope measurements gathered in Gothic, CO, 161 Manitou Experimental Forest, CO (Berkelhammer et al., 2013) and Niwot Ridge, CO 162 (Berkelhammer et al., 2016). From this data we generate an empirical equation that links 163 the isotopic ratio of water vapor with the vapor pressure (e_a) (Berkelhammer et al., 2020). 164 While the specific coefficients of this equation are empirical, it's form follows the clas-165 sic Rayleigh Distillation model thus we used the same equation for both modern and in-166 terglacial simulations: 167

$$\delta^{18}O_{vapor} = \log(e_a) * 8.0787 - 24.3299 \tag{5}$$

The isotopic ratio of water vapor is considered relative to the isotopic ratio of the source water (i.e. $\Delta^{18}O_{vapor}$) because it is the gradient that drives the isotopic exchange:

$$\Delta^{18}O_{vapor} = \delta^{18}O_{source} - \delta^{18}O_{vapor} \tag{6}$$

To estimate the source water for the trees we used isotopic value of precipitation 170 from two nearby National Atmospheric Deposition Program collection sites (Fig. S11). 171 Ten years of weekly data from these sites provide constraints on the seasonal cycle in the 172 isotopic ratio of precipitation (Anderson et al., 2016). We estimate the snowpack source 173 for these trees based on 20 years of data for the April 1 snowpack from the Fourmile Park 174 site (Anderson et al., 2016). A comparison between the isotopic ratio of April 1 snow-175 pack and weekly groundwater samples from a nearby well indicate that snowmelt is the 176 predominant recharge to groundwater. More details of the surface water isotopic values 177 are discussed in Berkelhammer et al. (2020). The iterative model results shown in Fig-178 ure 4 were done by taking the isotopic ratio of precipitation and mixing in a larger frac-179 tion of April 1 snowpack (from 0-100%). A limitation of this approach is that we assume 180 similar isotopic ratios for precipitation for both modern and interglacial, though this is 181 supported by global modeling with an isotope-enabled GCM (Sjolte & Hoffmann, 2014). 182

This is also justified for the isotopic ratio of winter snowpack based on the similarity between modern and interglacial early wood (Fig. 3). We do not have independent constraints on the isotopic ratio of summer rain for the interglacial though we would presume that the enrichment tail at the end of the Clusters 2 and 3 (Fig. 4) would be steeper if the isotopic ratio of interglacial precipitation was significantly higher.

The rate of water loss from the leaf, i.e. transpiration, is driven by the vapor pressure gradient. We estimate the saturation vapor pressure at the opening of the leaf stomata (e_i) as a function of leaf temperature:

$$e_i = 6.112 * e^{\frac{17.67 * Temp_{leaf}}{Temp_{leaf} + 243.5}}$$
(7)

Then, the evaporative enrichment of leaf water relative to the source water was defined using the following variant of the Craig-Gordon Equation where e_a is the vapor pressure of the canopy air:

$$\Delta^{18}O_e = \epsilon_{Temperature} + \epsilon_{Kinetic} + (\Delta_{vapor} - \epsilon_{Kinetic}) * \frac{e_a}{e_i}$$
(8)

A key component of the isotopic enrichment of the leaf water is the Peclet effect, 194 which describes the ratio of advection (i.e. transpiration) of source water towards the 195 stomata and the diffusion of heavy isotopes away from the evaporative surface. We used 196 a fixed effective path length (L) of 0.01 cm, which is a typical value for conifers (Keel 197 et al., 2016). While choice of this value affects the isotope ratio of the cellulose, if we as-198 sume the path length is not changing during the growing season, then the choice of path 199 length would affect the mean isotopic ratio but not the shape or structure of the seasonal 200 cycle. Transpiration was extracted from the SCOPE model and diffusivity (D) was mod-201 eled as function of leaf temperature: 202

$$Peclet = \frac{Path \ Length * Transpiration}{Molar \ Density_{H_2O} * D};$$
(9)

203 and

$$D = 1E - 8 * e^{-0.4 + \frac{1528}{Temp_{leaf} + 273.15} + \frac{-554368}{(Temp_{leaf} + 273.15)}^2}$$
(10)

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The isotopic enrichment of the leaf water $(\Delta^{18}O_{leaf})$ is finally calculated as follows:

$$\Delta^{18}O_{leaf} = \frac{\Delta^{18}O_e * (1 - e^{-1.*peclet})}{peclet}$$
(11)

And then the isotopic ratio of the leaf water $(\delta^{18}O_{leaf})$ is re-defined relative to the source water (Barbour et al., 2004):

$$\delta^{18}O_{leaf} = \Delta^{18}O_{leaf} + \delta^{18}O_{source} \tag{12}$$

It has been suggested that carbonyl exchange of ¹⁸O with water has a temperaturedependence (ϵ_{water}) of the following form (Sternberg & Ellsworth, 2011):

$$\epsilon_{water} = 0.0084. * Temp_{leaf}^2 - 0.51 * Temp_{leaf} + 33.172$$
(13)

Lastly, the isotope ratio of cellulose is presumed to be a mixture between photosynthates formed in the presence of isotopically enriched leaf waters and those oxygen atoms in the photosynthates that subsequently exchange with xylem water during cellulose metabolism. $\delta^{18}O_{source}$ was calculated iteratively based on use of variable mixture of summer precipitation and snowpack and *pe* is the ratio of oxygen atoms in the photosynthates that exchange with xylem water during cellulose metabolism (0.42). We assume this value is constant though recent work has suggested this value may exhibit variability (Belmecheri, Wright, Szejner, Morino, & Monson, 2018):

$$\delta^{18}O_{cellulose} = \delta^{18}O_{source} + (1 - pe) * \Delta_{leaf} + \epsilon_{water}$$
(14)

217 References

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Figure 1. Example of scanned interglacial wood sample. Samples previously described in (Brown et al., 2014).



Figure 2. Example of scanned interglacial wood sample. Samples previously described in (Brown et al., 2014).



Figure 3. Example of scanned interglacial wood sample. Samples previously described in (Brown et al., 2014).



Figure 4. Example of scanned interglacial wood sample. Samples previously described in (Brown et al., 2014).



Figure 5. Example of scanned interglacial wood sample. Samples previously described in (Brown et al., 2014).



Figure 6. Shown are a series of isotopic cycles from annual rings from various samples illustrating some of the individual years included in the Cluster Analysis shown in Figure 4.



Figure 7. Top: All the isotopic data in timeseries form that went into the analyses presented in Figures 3 and 4. As noted by Brown et al. (2014), the wood samples cross date well, which suggest they all died at the same time. Some evidence of this is also visible in the isotopic data but we did not attempt to cross date or line up the samples as we were not concerned with the isotopic cycles of any particular year. Bottom: A zoom into the timeseries from one sample.



Figure 8. A schematic depiction of the modeling framework used to interpret the isotopic ratio of the cellulose.



Figure 9. Timeseries' showing the different forcing data used for the mechanistic modeling. Leaf temperature and photosynthesis are from the canopy model whereas VPD used leaf temperature from the canopy model (to estimate saturation vapor pressure) and atmospheric humidity from the downscaled GCM run with Eemian forcing (Insel & Berkelhammer, 2021).



Figure 10. Spring snowpack for the Snowmass grid cell from the downscaled Modern (top) and Eemian (middle) simulations (Insel & Berkelhammer, 2021). Winter precipitation was comparable between time periods according to the simulations (not shown) and the snow free period in the spring occurred at a similar time between periods. This indicates winter precipitation did not likely impose any significant differences on the forests between these periods.



Figure 11. Timeseries showing precipitation isotopes from two nearby National Atmospheric Deposition Program sites published in (Anderson et al., 2016). These provide estimates of the isotopic ratio of the surface/shallow water source for the trees. A histogram of 20 years of April 1 snowpack isotopic ratios are shown to depict how the snowpack compares with the precipitation. Lastly, the isotopic ratio of weekly groundwater from Gothic from 2015-2017 is shown for comparison against the snowpack (Berkelhammer et al., 2020)