Canopy structure modulates the sensitivity of subalpine forest stands to interannual snowpack and precipitation variability

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Abstract. Declining spring snowpack is expected to have widespread effects on montane and subalpine forests in western North America and across the globe. However, the effect of this forcing at the species and hillslope scale are difficult to predict from remote sensing or eddy covariance. Here, we present data from a network of sap velocity sensors and xylem water isotope measurements from three common subalpine tree species (*Picea engelmannii*, *Abies lasiocarpa*, *Populus tremuloides*) across a hillslope transect in a subalpine watershed in the Upper Colorado River Basin. We use these data to compare tree- and stand-level responses to the historically high spring snowpack but low summer rainfall of 2019 against the low spring snowpacks but high summer rains of 2021 and 2022. From the sap velocity data, we found that only 40% of the trees showed an increase in cumulative transpiration in response to the large snowpack year (2019), illustrating the absence of a common response to a major decline in snowpack. The trees that benefited from the large snow year were all found in dense canopy stands - irrespective of species - while trees in open canopy stands were more active during the years with modest snow and higher summer rains. This pattern reflects how persistent access to soil moisture recharged by snowmelt in topographically-mediated convergence zones shapes stand density. These locally dense canopies also experience high levels of summer rainfall interception that reduce summer precipitation inputs to the soil perpetuating their greater sensitivity to snowmelt inputs. The

results illustrate that the progression towards a low snowpack future will manifest at the sub-hillslope scale in dense stands
15   with significant rainfall interception and high water demands reflecting their historical reliance on snowmelt water.

1   Introduction

Across the mountainous regions of the western US there has been a widespread decline in spring snowpack (Mote et al., 2018).
The spring pulse of snowmelt recharges deep soil layers providing a water source for forest ecosystems that can persist through
the fore summer drought period (Harpold and Molotch, 2015; Wainwright et al., 2020; Sloat et al., 2015; Coulthard et al.,
20   2021). Isotopic and modeling studies have also determined that winter precipitation can continue to act as the primary water
source for subalpine trees for a period of months after the snowmelt pulse (Berkelhammer et al., 2020; Allen et al., 2019;
Martin et al., 2018; Love et al., 2019). A reduction in the magnitude and duration of the spring snowmelt pulse combined with
higher warming-induced increases in evaporative demand have been shown to manifest in these forests as phenological shifts,
increases in mortality, thinning, crown dieback and greater susceptibility to disturbance (Kelsey et al., 2021; Allen et al., 2010;
25   Knowles et al., 2023; Carrer et al., 2023; Cooper et al., 2020).

Despite the broad ecological importance of snowmelt for subalpine forests (Trujillo et al., 2012), utilization of summer rain
may also be critical to the functioning of these ecosystems, particularly in years with less snowmelt (Berkelhammer et al.,
2017; Coulthard et al., 2021). For example, aspen (*Populus tremuloides*) may rely on shallow soil moisture replenished by
30   summer rains to alleviate periods of drought stress (Anderegg et al., 2013). In contrast, subalpine conifers including *picea*,
abies and *pinus* may be less reliant on summer precipitation (Pataki et al., 2000). Although summer rain may only contribute
10-20% of annual precipitation inputs for many areas in the western US, these inputs may be sufficient to increase soil matric
potentials above thresholds that can cause hydraulic damage to trees and thus facilitate an extension of the growing season
(Samuels-Crow et al.). Furthermore, the convective storm systems associated with summer rain locally increase humidity and
35   moisten the surface soils, thus reducing evaporative demand on trees (Strange et al.). While more attention has been given to
declining trends in spring snowpack, summer rain may also be experiencing a decrease or possibly a change in frequency and
intensity though any trends are far less obvious (Holden et al., 2018; Pascale et al., 2017).

In this study, we propose that understanding the response of these forest systems to changes in seasonal precipitation inputs
40   requires a better understanding of the factors that influence the seasonal origins of water used by trees (Allen et al., 2019).
Previous work in subalpine forests has often considered this problem from the perspective of species traits and their impact on
when and where trees extract their water from. For example, Grossiord et al. (2017) showed that co-located piñon and juniper
had opposing belowground responses to water stress manifesting in piñon trees seeking out deeper winter-sourced water during
drought. Simultaneously, aboveground traits influence water use patterns such that species like aspen with lower susceptibility
45   to embolism can maintain high rates of transpiration during drier periods late in the summer (Pataki et al., 2000). On the other
hand, fir species that are susceptible to embolism from air seeding face a higher risk of extracting water from desiccated soils

and during periods with high vapor pressure deficits (VPD). Consequently, they are less likely to remain active during the dry periods that may precede or occur after the arrival of summer rains. These species thus have a tendency for higher relative reliance on snow - when all else is held equal - because the risk of transpiring during periods of low soil moisture outweighs

50   the benefits of access to sporadic rain events (Berdanier and Clark, 2018). While specific plant traits may be a useful predictor of water use, physical characteristics of a stand that emerge through aggregate traits of the individuals also generate impacts on seasonal origins of water sources. As noted by LaMalfa and Ryle (2008), wintertime sublimation was 20% higher in aspen due to the leafless winter canopy while the more open summer canopy relative to conifers increases throughfall of summer rain such that aspen stands may experience 40% higher effective precipitation rates than nearby conifer stands (Thomas, 2016).

55   LaMalfa and Ryle (2008) also note potential differences in physical soil properties such that aspen stands had more porous soils due to increased bioturbation and fine root turnover leading to higher rates of moisture infiltration (Samuels-Crow et al.).

To study the question of source water utilization strictly in terms of ecological dynamics of co-located species has limitations, because those same species have distributions that are generally sensitive to hillslope position (Metzen et al., 2019). Thus,

60   nearby species may experience different temperatures and vapor pressure deficit, depth to groundwater, snowpack buildup, timing of snow disappearance and radiation loading (Brooks et al., 2015; Martin et al., 2018; Molotch et al., 2009; Fabiani et al., 2022; Cooper et al., 2020). In water limited areas, the importance of these factors manifests primarily through hillslope gradients in soil moisture (Famiglietti et al., 1998; Looker et al., 2018). Indeed, despite work showing the importance of summer rain for aspen, as noted above, it is also common to see areas where winter precipitation and groundwater may be of equal or greater

65   importance to the species' water demands illustrating an overriding impact of hillslope context relative to species-specific traits (Love et al., 2019). For example, using sap velocity and water isotope data from an alpine watershed in Montana, Martin et al. (2018) found a measurable increase in reliance on snowmelt by subalpine fir over just a 350 m elevational gradient. They argue that fir trees in the lower elevation plots rely on more snowmelt due to shallower groundwater and lateral near-surface flow both of which are primarily supported by snowmelt inputs. The lower snow-reliant plots are thus more sensitive to annual

70   snowmelt inputs and presumably sensitive to long term shifts in snowpack dynamics. The dynamic observed by Martin et al. (2018)s supports a view of hillslope ecohydrology where subsurface connections increase downslope and this determines water use patterns in a way that may supersede species traits (Brooks et al., 2015). However, it also should be noted that elevational position along the hillslope may be less important to forest water use than sub-hillslope context such as proximity to local convergence zones where surface connections to groundwater are locally critical to support tree water demand (Hoylman et al.,

75   2018; Graup et al., 2022). In contrast, other studies have found limited differences in water use patterns across the hillslope reflecting multiple interacting influences emerging from species traits, stand properties and hillslope hydrology that ultimately mute gradients in sensitivities to changing precipitation inputs (Fabiani et al., 2022). While hillslope ecohydrology in subalpine regions has received considerable attention in the literature, few studies have considered the interactive effects of species characteristics and sub-hillslope dynamics on water use. We argue this perspective is needed to develop an aggregate view of forest

80   sensitivity to changing precipitation patterns.

In this study we present an interannual analysis of transpiration fluxes (via sap velocity sensors) and water sources (via stable isotope analysis) from a network of sites along a ~500 m hillslope transect in the Upper Colorado River Basin that includes a mixture of fir, spruce and aspen. We consolidate the numerous processes acting across sites by collapsing the measurement

85 clusters along a simple gradient of their canopy density that has been shown to be a useful aggregator of multiple interacting hillslope processes (Metzen et al., 2019). In the absence of disturbance, the density of sapwood to conduct water from an area reflects the long term tree acclimation to available water and sets the peak rates of water use (Graup et al., 2022; Tor-Ngern et al., 2017; Pataki et al., 2000). In snow dominated montane and subalpine areas of the western US, stand density thus may reflect snowmelt access because summer rain alone is insufficient to support high rates of water use and investment in conduct-

90 ing wood tissue (Goodwin et al., 2023). Within this context, we first test two fundamental hypotheses: (1) the seasonal origin of water used by trees influences a stand's sensitivity to changes in precipitation seasonality and (2) that canopy structure is a reflection of the source of water accessible to the trees in that stand. The results suggest the presence of a feedback where stands that have access to reliable snowmelt sources become dense leading to persistence of spring snowpack and higher rates of summer rain interception which perpetuate increasingly higher sensitivity and vulnerability to changing snowmelt.

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2 Methods

2.1 Sap Velocity network

We installed a network of sap velocity sensors at six sites across a hillslope transect on Snodgrass Mountain in the Upper Colorado River Basin (Figure 1) (Fuchs et al., 2017). Sites were selected to encompass a 500 m total change in elevation,

100 with sites transitioning from a dominance of Trembling aspen (*Populus tremuloides*) at the lowest elevation, to a mixture of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) towards the top. At each site, between four and six trees were instrumented with heat-pulse velocity probes (SFM1; ICT International, Armidale, NSW, Australia) to measure sap velocity every 20 minutes (cm hr^{-1}) using the heat ratio method ((Burgess et al., 2001; Looker et al., 2016)). Sensors were installed on the northern side of each tree in June 2019 and re-positioned on the same tree each spring until 2022, excluding

105 2020 when field work was unable to be conducted due to COVID-19. Bark-depth, sapwood depth, sapwood density and water content were measured in July 2019, with wound diameter also determined following each re-installation, for each tree and used to convert heat-pulse velocity (v_h) to sap velocity (V_s). Sapwood depth was determined on two 5 mm diameters cores taken on the northern and southern sides of the tree at 1.2 m height using an increment borer (Haglof, Langsele, Sweden) and stained with methyl orange to observe a color change to indicate active sapwood, with average sapwood depth calculated for each tree.

110 Data from 2020 were not included in these analyses owing to observations that wounding effects were too severe to keep probes in the same location for multiple seasons and still develop reliable estimates of sap velocity. Heat-pulse velocity measurements were restricted on some trees to the daytime only - when sap velocity typically peaks - to reduce power consumption overnight. Consequently, nighttime data were limited and the focus of our analysis, unless otherwise stated, is on midday patterns.
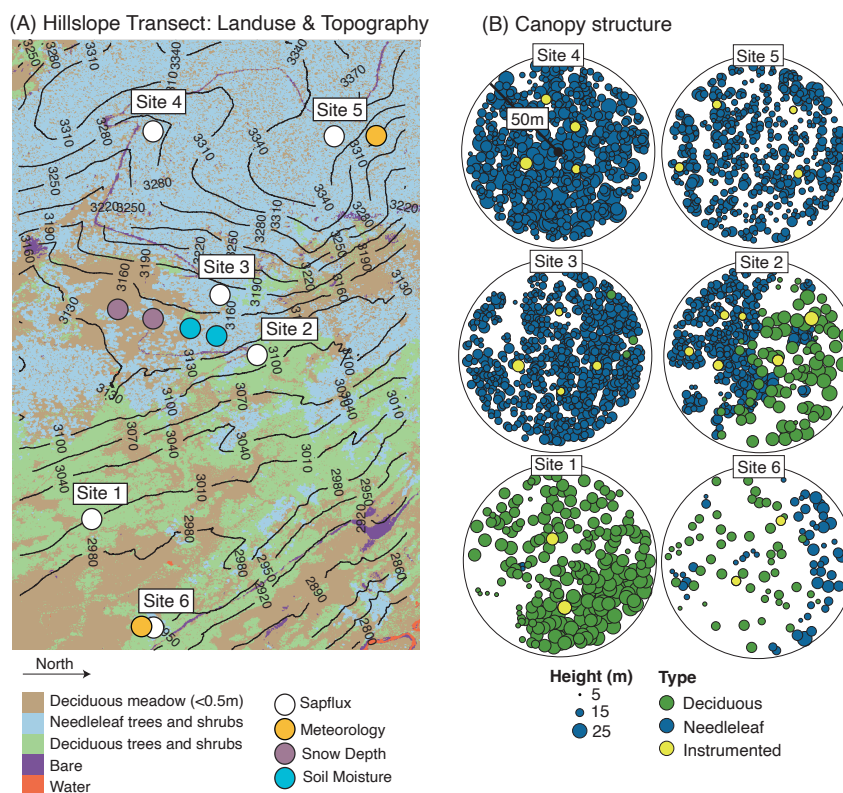
Figure 1. (A) Map of the Snodgrass hillslope showing the six sap velocity clusters and multiple meteorological towers projected over elevation and land use type. (B) Maps of canopy density and tree height for the six plots shown in Panel A. Plots were delineated as 50m radius circle drawn from the center point of the instrumented trees. See Methods for how tree height and individual crowns were delineated.

2.2 Water isotope data

115 During the growing season, approximately weekly measurements of xylem water isotopes were made for each of the trees instrumented with sap velocity sensors. Live stems were sampled from the trees, debarked, placed in a sealed bag and frozen as quickly as possible. Water from the stems was extracted cryogenically using a batch distillation method (Berkelhammer et al., 2020). Surface soil samples were collected from a 10 cm depth periodically from each sap velocity site during the field seasons. The soil samples were extracted following the same method as the stem samples. All extracted soil and xylem water
120 samples were analyzed for $\delta^{18}O$ and δ^2H on a Picarro l2140-i analyzer (Berkelhammer et al., 2020).

To understand the source of water within the extracted xylem pool, we utilized additional information on meteoric water inputs to the system. We took advantage of a wide range of isotopic data from this watershed on groundwater, precipitation and snowpack samples which have previously been presented (Berkelhammer et al., 2022; Carroll et al., 2022a). Stem and

125   soil water samples are subject to evaporative enrichment relative to the precipitation inputs, leading to higher values of $\delta^{18}O$ and δ^2H as well as a shallower slope between the two isotopes relative to meteoric inputs. To estimate the sources of water in stems and soils, the measurements need to be projected back to the meteoric water line. We do this following Benettin et al. (2018) and Allen et al. (2019) where evaporation lines are estimated for each sample using measured meteorological data and we solve for the intersection between each sample's evaporation line and the meteoric water line defined by the isotopic ratio

130   of precipitation samples. Lastly, we were cognizant of the possibility for fractionation between δ^2H of the source water and the xylem water that has been noted in a number of recent studies (Chen et al., 2020; Barbeta et al., 2019). To assess this, we compared the soil and xylem water samples during the early period of the summer immediately following snowmelt when we assume soil water would be minimally evaporated with a homogenous profile in the isotopic ratio of the soil water. During this period, we observed equivalent values for stem and soil $\delta^{18}O$ but an offset between stem and soil δ^2H of ∼-6‰ (Figure S2).

135   This is similar to the magnitude of fractionation observed in previous studies (Barbeta et al., 2019) and we therefore apply this value as a correction to all measured stem δ^2H values. Hereafter, we refer to the *stem water* as the estimated isotopic ratio of the source water value following all corrections based on the aforementioned effects. Raw isotopic data are provided in the dataset associated with this publication (Berkelhammer et al., 2022).

2.2.1   Isotopic mixing model

140   To assess the relative proportion of snowmelt in the xylem water sample, we developed a mixing model with three distinct end members. One end member was snowmelt water, whose value was estimated from snowpack and snowmelt measurements with a modest correction for lapse rate across the elevational gradient of our sites (Carroll et al., 2022a). As groundwater from nearby wells in the area was typically hard to distinguish from snowmelt without an additional tracer, we do not attempt to separate the current year's snowmelt from older snowmelt that had recharged the groundwater in previous seasons (Berkelhammer

145   et al., 2020). The second end member is the weighted average of precipitation during the growing season up until the time of sampling. This was developed by combining the date and amount of each rain event with estimates of the isotopic ratio of that rain event. The third end member is the isotopic value of the most recent rainfall event. The justification to separate summer rain into two end members was based on the fact that, on the one hand, growing season rain has a cumulative impact that aggregates in the soil horizon while, on the other hand, the most recent rain event may be present in the near surface soils and immediately

150   taken up by the trees. Early in the growing season, these two precipitation end members were nearly identical but they became distinct later in the growing season as the most recent rainfall event tends to be more enriched than the cumulative inputs (Figure S1). We did not consider travel time and storage within the trees which is a limitation to this mixing model in instances when the most recent rainfall event occurred just days before sampling and therefore would not likely yet be present in the sampled xylem reservoir (Knighton et al., 2020). More sophisticated and higher resolution sampling approaches would help to

155   resolve these dynamics (Seeger and Weiler, 2021). We implemented the mixing model using a Bayesian approach developed in Arendt et al. (2015). We assume Gaussian uncertainty in the xylem water measurement of 1‰ for $\delta^{18}O$ and 8‰ for δ^2H based on repeat measurements from samples of the same tree. These uncertainties are about an order of magnitude larger than analytical uncertainty and represent the cumulative effects of within tree heterogeneity, sampling, storage/transport and

cryogenic extraction. We estimate similar levels of uncertainty for the values of the precipitation and snowmelt end members
based on ranges that emerged from the simulations and measurements of snowmelt and precipitation observed in previous
studies (Carroll et al., 2022b; Anderson et al., 2016).

2.2.2 Seasonal Origin Index

The mixing model described above provides a direct quantifiable estimate of the snowmelt inputs (referred to as *snowmelt reliance* hereafter) to the transpiration stream but the solution to the mixing model is not unique and the designation of the end members is uncertain even with the fairly rigorous isotopic sampling within this watershed. We therefore also estimate the seasonal water use by trees following the seasonal origin index (SOI)(Allen et al., 2019). This approach generates a unitless index of summer or winter water-use based on the distance between the isotopic ratio of a xylem water measurement and the summer and winter end member isotopic ratios. As defined by Allen et al. (2019)s:

$$\text{SOI} = \frac{\delta_{xylem} - \delta_{annualprecip}}{\delta_{annualprecip} - \delta_{winterprecip}}$$

The index is formulated such that a value of 0 indicates an even use of summer and winter precipitation, -1 is the case where the xylem water is indistinguishable from the winter precipitation (snowfall) input and a value of 1 is the case where the xylem water is indistinguishable from the summer rain input. This is an approach that is easier to implement than a mixing model with more than two end members, requires less assumptions, and facilitates unitless comparisons across sites. We used the corrected xylem water values and isotopic end members for winter and summer precipitation as described above. This data is provided as a reference point and validation of the mixing model though we recognize the two are functionally and numerically similar and for simplicity we generally discuss the trees' source water following results from the mixing model (Figure S3).

2.3 Meteorological data

We utilized numerous streams of atmospheric and surface weather data for the analyses and interpretations described in the Results section below. There are 6 meteorological stations on the Snodgrass hillslope transect where the sap velocity measurements were made (Figure 1). These stations - run by three different research groups (i.e. (Simonpietri and Carbone, 2023; Ryken, 2021; Bonner et al., 2022)) - have collected data over different periods of time and have distinct combinations of sensors. We averaged these streams to develop a daily mean temperature and humidity dataset for the hillslope to estimate the evaporative mixing lines described above (2.2.1). To do this, we simply took the daily average temperature based on all available measurements for a given day. We utilized snow depth and snow water equivalent (SWE) from a pair of adjacent forest and meadow stations based on both continuous snow height sensors and periodic snow pits (Bonner et al., 2022) to estimate canopy effects on snow inputs. We utilize daily precipitation for weighting the importance of each precipitation event into the growing season isotopic inputs for the mixing model (Sections 2.2.1 and 2.2.2). We utilized soil water measurements from adjacent conifer and aspen sites to illustrate differences in growing season (MJJAS) rain infiltration between the different canopy types. Lastly, we utilized the long term record of rainfall and snowfall from the Gothic, CO weather station (Faybishenko et al., 2023) to place the years of this study into a climatological context.

2.4 Remote sensing and GIS

Canopy structure for each site instrumented for sap velocity was measured using airborne LiDAR scanning (ALS), using the
1-m canopy height model (CHM) and vegetation type data (Goulden et al., 2020). We identified the center point of each cluster
195 of sap velocity probes and captured all trees within a 50 m radius around the center point and classified this tree cluster as a
site or *stand*. For each site/stand, we identified all the tree crowns using the method of Parkan and Tuia (2018) and identified
whether the crown was deciduous (aspen) or coniferous (subalpine fir, Engelmann spruce, or lodgepole pine) based on the land
use classification dataset. We used previously established allometric relationships between tree height and DBH for these tree
species in this region (Hulshof et al., 2015) to estimate the DBH of each crown and then estimated the sapwood area by using
200 our paired measurement of sapwood depth and DBH following the power-law structure developed in Mitra et al. (2020). We
then divided total sapwood area (aspen and conifers) by ground area (fixed at the 50 m radius) to generate a sapwood to ground
area estimate for each site. Lastly, we used a local digital elevational model (Goulden et al., 2020) to estimate the topographic
position index (TPI) for each site (Hoylman et al., 2018).

3 Results

3.1 Sap Velocity Data

Instantaneous sap velocity values displayed diurnal and seasonal cycles for all species that followed expectations based on
previous work in similar montane forest systems in the region (Pataki et al., 2000) (Figure 1). Both conifer species had peak
values early in June during all years but exhibited substantial interannual variations later in the season, such that transpiration
rates dropped to very low levels in August during 2019 but persisted measurably into September and October during both 2021
210 and 2022. These differences reflect the presence of significant summer rainstorms in 2021/2022 relative to 2019. Due to limited
early season site access, we did not generate data to capture the early season water use by the conifers. Based on the fact that
the species displayed nearly peak rates of water use by early June (i.e. day of year 160), we suspect the early growing season
water use was not trivial and is a critical absence in terms of our capacity to close the transpiration water budget (Cooper
et al., 2020). Although the conifers displayed similar average sap velocity values and temporal patterns, we note measurable
215 differences in the behavior between species. For example, the sap velocity of subalpine fir relative to Engelmann spruce was
shifted earlier in the season and showed higher water use during early morning and evening (though with similar midday peak
values for both species). Aspen transpiration began typically in early June following leaf-out with a protracted period of high
transpiration that extended into mid August before showing measurable declines. Transpiration stopped by mid September
ahead of leaf senescence. Despite the shorter period of activity, the peak rates and average sap velocity for aspen were sub-
220 stantially higher during the seasonal period of measurements than both conifer species. However, we did not capture Autumn
through Spring water use by conifers and conifers account for ~60% of the hillslope sapwood (Figure S4) so we estimate that
aggregate hillslope water use was more similar between the conifers and aspens than implied from Figure 2 (Pataki et al., 2000).
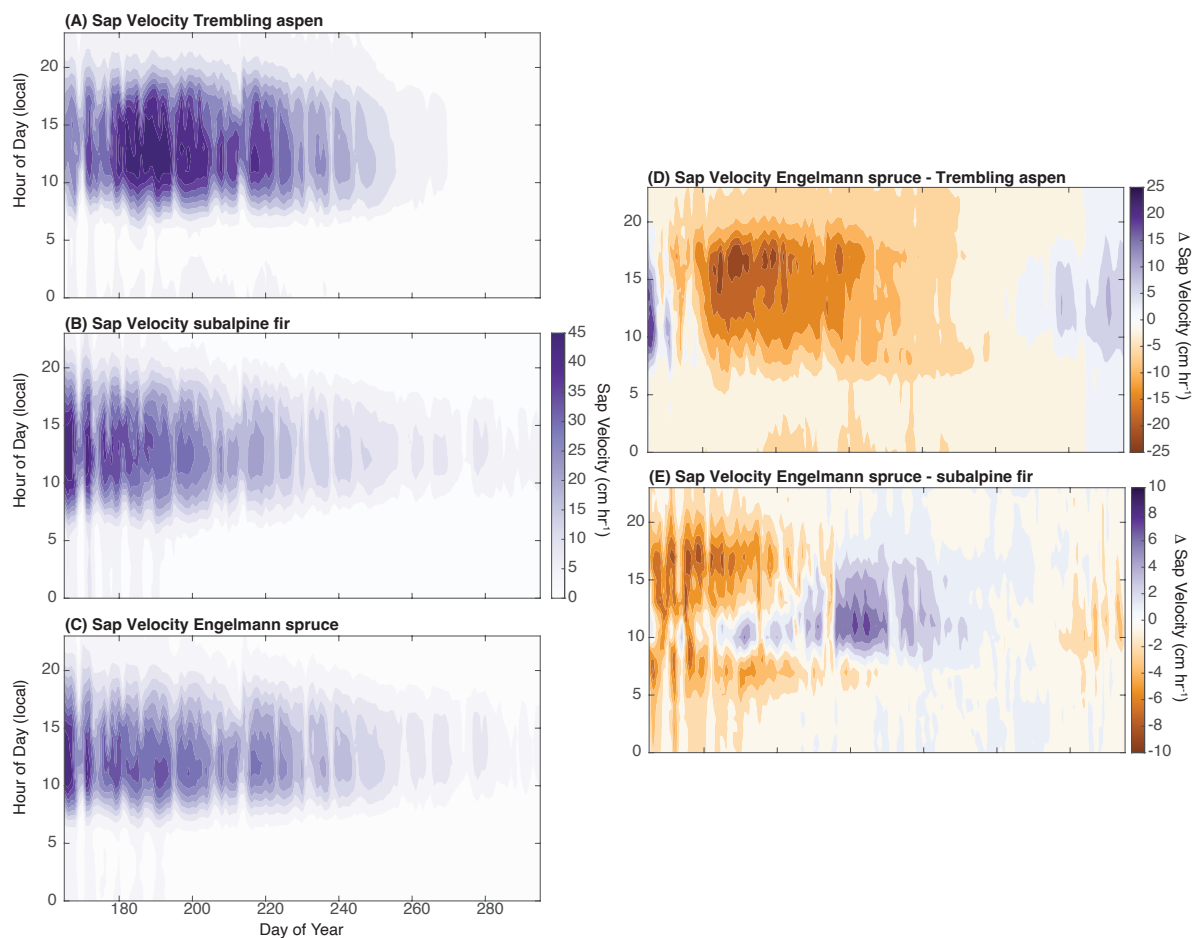
Figure 2. (A) Sap velocity averaged across all Trembling aspen trees between years as a function of Hour of Day (y-axis) and Day of Year (x-axis). (B) As in A but for subalpine fir. (C) As in A but for Engelmann spruce. (D) Differences in sap velocity between Engelmann spruce and Trembling aspen. (E) As in D but for Engelmann spruce and subalpine fir though note differences in scale bar to accentuate the more subtle differences between conifer species.

The years during which this experiment were conducted (2019-2022) are plotted in Figure 3 as a function of May 1 snow-
225 pack and JA precipitation. We use May 1 snowpack because this captures the magnitude of the snow reservoir present during the period when conifers were active and could directly utilize inputs from melting snow. We use JA because this covers the peak monsoon period and excludes rainfall inputs in September that occurred after aspen activity ended. We note that over the last 40 years, there appears to be a slight negative relationship between May 1 and JA precipitation as noted previously (Gutzler and Preston, 1997). Using this analysis on precipitation seasonality, 2019 ranks among the highest years for May 1
230 snow and among the lowest years for JA precipitation. In contrast, the period between 2020-2022 was characterized by be-low average May 1 snow and above average JA rainfall, illustrating the strong contrast in precipitation seasonality among the
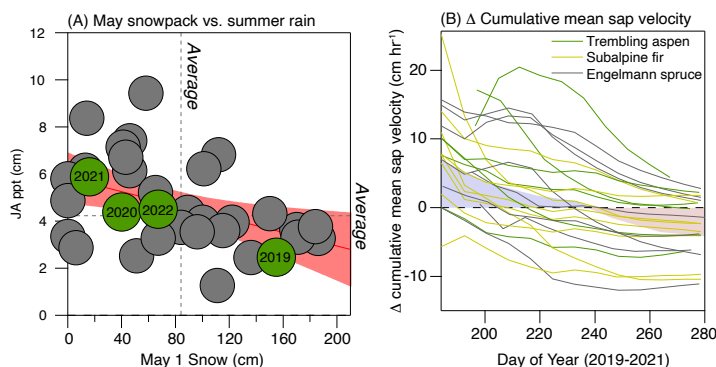
Figure 3. (A) The relationship between May 1 snowpack and July and August rainfall from the nearby Gothic Weather station (Faybishenko et al., 2023). The 4 years encompassing the study are labeled and a trend line with 95% confidence intervals along with the mean values for each seasonal precipitation inputs are indicated on the figure. (B) The difference in cumulatively averaged sap velocity between 2019 and 2021/2022 for each tree that had continuous measurements during each of those three growing seasons. The shaded area is the average of all trees to indicate the mean response between the contrasting precipitation years.

experimental seasons. While we did not include 2020 in our sap velocity analysis, we highlight this year in the figure to emphasize a sustained multi-year difference in precipitation seasonality over the last three years of the experiment relative to 2019.

235   As expected, during the early portion of the growing season most of the trees showed an increase in cumulative average sap velocity in 2019 relative to 2021/2022. However, by the end of the growing season less than half of the trees had retained higher total averaged sap velocity (Figure 3). In fact, averaged across all trees, there was a slight decline in cumulative sap velocity in 2019 relative to 2021/2022. A notable feature of this result is the wide range of responses to changing precipitation seasonality across the trees. This illustrates how the benefits of a historically large spring snowpack like 2019 did not universally enhance
240   water use and - by extension - total vegetation activity. The buffering effect of the more active monsoon seasons of 2021 and 2022 against low snowpack appeared to fully offset the lower snowpack. In more than half the trees, the greater monsoon rainfall of 2021 and 2022 enhanced tree transpiration (Strange et al.).

3.2 Isotopic data

The xylem water samples fall within the expected space to the right of the well-defined Local Meteoric Water Line (Figure 4).
245   The isotopic ratio of the xylem water measurements encompass a range of almost 20‰ in δ^{18}O, indicating a diverse spectrum of water sources across species and the hillslope over the three years of measurements. Based on the results from the mixing model, we estimate that - when weighted by sap velocity - the trees relied on ∼60% snowmelt though this value varied significantly across space and species. This value corresponded to an average Seasonal Origin Index (SOI) of -0.4 (where values less than 0 indicate a preference for winter precipitation use), providing an alternative metric for the preference for snowmelt

as the water source for this population of trees (Figure S3) (Allen et al., 2019). This area of the watershed receives about 80%
of its precipitation as snow based on observations over the last 40 years, implying a preferential reliance on monsoonal rain
compared to aggregated seasonal precipitation inputs to the watershed.

Breaking down this data seasonally, we observed that during June and July snowmelt water was widely utilized with the
importance of summer rain only prominently emerging in samples collected in August (Figure 4). Interestingly, a return to use
of snowmelt as a water source occurs in September indicating a reliance on groundwater or older waters retained in the soil
near the end of the growing season. Sap velocity is generally negligible during this period so the water source in September
is inconsequential to the water budget but may be critical for sustaining low levels of tree activity deeper into the fall after
summer rain inputs have mostly been lost to evapotranspiration. The range of water sources between species generally overlap
indicating broadly similar water sources for the species. However, to properly assess partitioning between species, we focus
on differences in water use between co-located species sampled contemporaneously as discussed below. As expected, we note
a consistent increase in reliance on summer rain in 2021/2022 relative to 2019 across species and time. The one notable ex-
ception to this pattern is the similar interannual use of summer rain in aspens during August. This may reflect the significantly
lower interception rates for aspen (Thomas, 2016) which allowed utilization of the limited summer rain inputs in 2019 that did
not penetrate the conifer canopy and/or the fact that large snowpacks (as in 2019) can enhance summer rain use by allowing
roots to stay active during the fore summer drought (Bailey et al., 2023).

We assess partitioning of water sources between species by filtering the isotopic data to look only at differences in water
sources between co-located species sampled simultaneously. As shown in Figure 5, we can see that all three species utilized
a statistically similar water source for the first part of the growing season but then a partitioning between aspen and conifers
started to emerge in late July (∼day of year 200) and reached a peak in species partitioning in early August. For comparison,
there is never a statistically significant partitioning between Engelmann spruce and subalpine fir. The most obvious interpre-
tation of the difference in water sources between aspen and conifers, emerges by comparing the seasonal cycle in water-use
partitioning against soil moisture data generated from underneath adjacent aspen and conifer crowns (Figure 5). We see that
the increasing reliance on summer rain by aspens corresponds to the periods when summer rains infiltrate under the aspen but
not the conifer stands.

3.3 Integration of isotopic, sap velocity and stand structure data

The response of trees to the hydroclimate differences between 2019 and 2021/2022 can be fairly well predicted by quantifying
the source of water utilized by trees (Figure 6). Specifically, trees with heavy reliance on snowmelt were those that benefited
the most from the large spring snowpack in 2019. The sensitivity of annual tree activity to snow inputs did not clearly map
onto species or elevational position on the hillslope. Instead, we see that the response of trees to the large spring snowpack
of 2019 can best be predicted based on whether a given tree was located in one of the dense stands (i.e. where sapwood to
ground area was ∼38 cm^2 m^2) or open stands (i.e. sapwood to ground area ∼12 m^2 m^2) (Figure 6). We did not intentionally
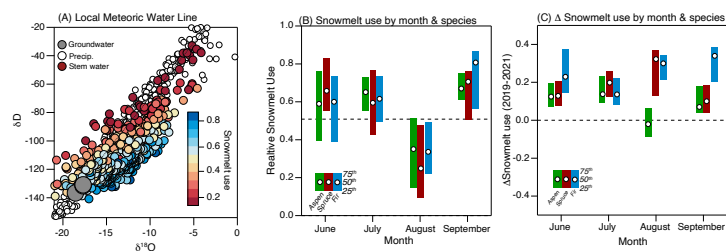
Figure 4. (A) Local meteoric water line for precipitation samples and the three years of collected xylem and soil water samples. Samples are colored based on the inferred snowmelt reliance. (B) Monthly use of snowmelt per species based on all data, where a value of 1.0 corresponds to complete dependence on snowmelt water. We have limited data from September so these should be treated with caution. Snow is important source of water into July but its importance wanes in August. (C) Difference in reliance on snowmelt between 2019 and 2021.
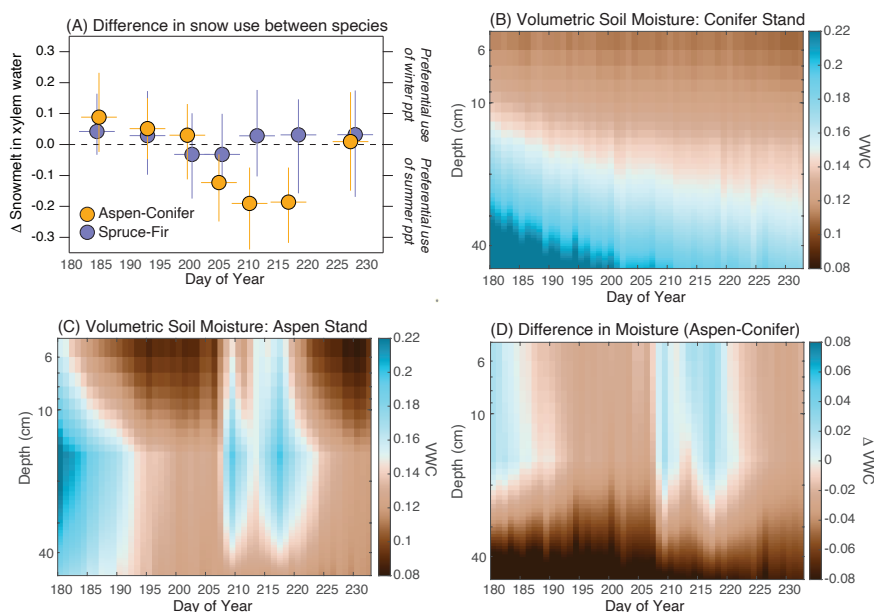
Figure 5. (A) Difference in reliance on snowmelt between Trembling aspen and conifer species (Engelmann spruce and subalpine fir aggregated here), and the difference between the two conifer species. The data were generated by only comparing snowmelt use between co-located and simultaneously sampled stem waters. The data were binned into 10-day windows to capture dynamics that were occurring at the sub-monthly scale. (B) and (C) Volumetric water content under adjacent aspen and conifer stands interpolated from measurements at 5, 15, and 50 cm. Site location is indicated on Figure 1. (D) Difference in volumetric water between aspen and conifer stands illustrating the moistening of soils in late July and August that occurs with a much higher signal under the aspen trees.

aim to test the effect of stand density on water use in our experimental design and so our sites do not occupy a continuum of
285 stand densities but instead incidentally clustered into a group of relatively open or closed canopies. Nonetheless, the effect of
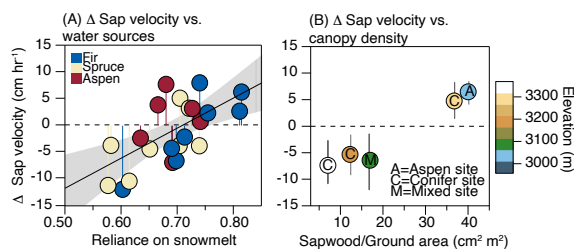
Figure 6. (A) The relationship between differences in averaged sap velocity between 2019 and 2021/2022 vs. the weighted average reliance of each trees use of snowmelt. The positive relationship, which is driven by the conifer species response, implies those trees that rely more heavily on snow are those that were more active during the high snow year of 2019. (B) The differences in sap velocity between years organized by the stand density that each tree fell within. All the trees with increased sap velocity fell within the dense stands.

stand density is highly robust within this population of trees such that virtually every tree in the dense (open) stands all showed increases (decreases) in sap velocity in 2019, irrespective of species and functional traits. Although the positive responses to higher snowfall in 2019 in the dense stands and the negative responses in the open stands are similar for a given sapwood area (Figure 6), the sapwood area is 3-4 times larger in the dense stands so that the total transpiration increase in the dense stands far outweighed the declines in the open stands during 2019 (Figure S6).

While emphasis here has primarily been on drivers of interannual transpiration variability, we also used the merged isotopic and sap velocity data to shed light on whether there were optimal seasonal water utilization patterns over the period of this experiment. To assess this, we compared peak sap velocity values for individual trees - as a proxy for the hydraulic capacity of a tree - against the water source used by the tree. We see from this analysis that use of a diverse mixture of water sources characterized by neither strongly snow- nor rain-dominated led to the highest peak transpiration rates (Figure 7). Those trees with particularly high reliance on either snow or summer rain use (i.e. a more narrow range of water sources) tended to have lower peak transpiration rates than those trees which have mixed water sources albeit with a preference for snow of ∼70%. This, in turn, can be mapped onto the hillslope context as portrayed by the topopgraphic position (TPI) such that sites with lower to moderate TPI values (low slope, convergence zones) exhibited higher individual transpiration capacity than those sites with higher TPIs (i.e. in hilltop areas) (Hoylman et al., 2018).

4 Discussion and Conclusions

The response of subalpine forests across the western US to changing snowpack and precipitation patterns has significant implications for landscape disturbance, hydrology, water resource management and understanding past climates through dendroclimatology (Cooper et al., 2020; Tague and Peng, 2013; Coulthard et al., 2021; Goeking and Tarboton, 2020; Bentz et al., 2010). Much of the way we have come to understand the sensitivity of forests in the region to precipitation variability is through a handful of longer eddy covariance records (e.g. (Knowles et al., 2015)) and analysis of satellite greenness indices (e.g. (Tru-
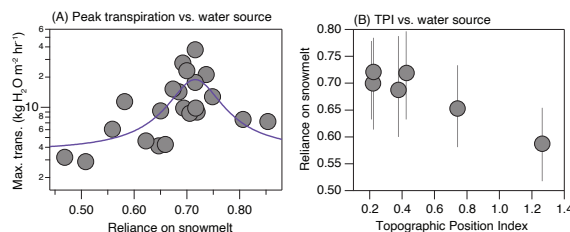
Figure 7. (A) Relationship between peak transpiration reached through the experimental period and the average snowmelt reliance of the tree. A polynomial fit was added to the figure to highlight the structure and location of the optimum value. (B) Relationship between snowmelt reliance and topographic position index (TPI) of each site with the range of snowmelt reliance captured by the error bars. This figure has six sites while the previous figure only has five because we did not have 2019 data from Site 6 to assess differences between years.

jillo et al., 2012)). Yet both these approaches are generally unable to resolve the higher resolution dynamics such as stand and species behavior that are needed to understand aggregate watershed behavior. We thus utilized here a distributed network of sap

310 velocity sensors to understand species and localized transpiration dynamics along with measurements of stem water isotopes to test linkages between ecohydrology and changing precipitation inputs. To a first order, the sap velocity data mirrored results from a similar study in this region over 2 decades earlier (Pataki et al., 2000). Notably, aspens had significantly higher instantaneous sap velocity rates and were more responsive to small summer rain inputs than the subalpine fir or Engelmann spruce trees. The aspen were thus able to sustain high levels of activity through the summer even during a growing season like 2019

315 that experienced a sustained fore summer drought period and weak monsoon (Anderegg et al., 2013; Sloat et al., 2015). On the other hand, many of the individual conifers during 2019 began to show significant declines in water use by early July and showed almost no activity by August even when small rainfall inputs emerged. These differences reflect the higher threshold for embolism and reduced rainfall interception by aspen. We also document measurable differences in seasonality and the diurnal cycles between subalpine fir and Engelmann spruce such that the latter were more active later in the season and had reduced

320 sap velocities during morning and evenings. This was consistent with some previous work documenting a higher sensitivity to vapor pressure deficit and lower sensitivity to soil moisture for Engelmann spruce relative to other common coniferous species (Oogathoo et al., 2020; Pataki et al., 2000). These differences are small relative to those between either conifer species and aspen and will be further analyzed in forthcoming work that includes hydraulic trait measurements of these trees along with process-based modeling.

325

Although the sap velocity patterns between trees of the same species were fairly similar across this population of trees, the trees were located in stands that varied in sapwood density by nearly a factor of 5. Thus, transpiration varied significantly across stands in ways that were not reflected in per tree water use (Figure S6) (Tor-Ngern et al., 2017). In an earlier study that utilized one season of data from this same sap velocity network, Ryken (2021) found that two of the densest sites - cor-

330 responding to Sites 1 and 4 in Figure 1 - displayed transpiration rates that were comparable and/or exceeded latent heat flux
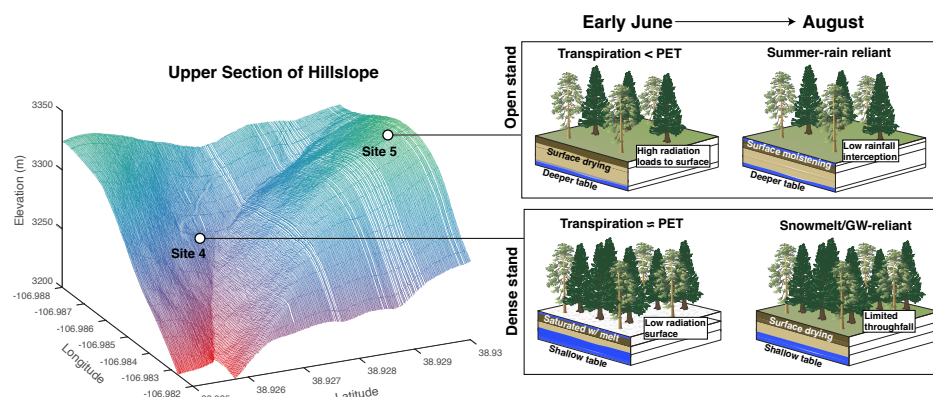
Figure 8. Schematic view on the model proposed here showing the way hillslope position determines water access and stand density and the way this, in turn, influences access to summer rain.

rates from an eddy covariance in the riparian zone at the foot of this hillslope (Ryken et al., 2022). This result suggests that the densest sites in the network were operating in a state during June-July of 2019 when transpiration accounted for virtually all the evapotranspiration (ET) and transpiration was fully energy-limited at least during the early periods of the summer (Figure 8). The forest stands at these sites had developed an optimal sapwood density to move the highest capacity of water that energy

335 inputs would allow. This represents a long term acclimation at a few localized areas of the hillslope where higher amounts of soil moisture or shallow groundwater were present. Because Ryken et al. (2022) had shown that latent heat flux values of the magnitude for a nearby riparian site could only be met by accounting for significant groundwater subsidies to ET we can infer, even without isotopic measurement, that these dense sites (one aspen and conifer) were drawing on groundwater pools or shallow lateral flow recharged by the current or previous seasons' snowmelt (Love et al., 2019; Martin et al., 2018). It is

340 also these sites that have the widest possible range of transpiration rates and are the locations where precipitation inputs to the hillslope are most heavily routed towards transpiration (Faramarzi et al., 2009). Indeed, the increases in water use during 2019 at these sites eclipsed the magnitude of transpiration declines during this year in the more open sites (Figure S6).

We took advantage of intensive isotope sampling to develop a more mechanistic perspective on how species- and stand-level

345 water demands as described above were related to access to specific water sources. One of the most conspicuous results that emerged from the isotopic data is the emergence of sub-seasonal partitioning between the co-located aspen and conifers (Fig. 5). The development of a preference for summer rain by aspen as the growing season progressed was apparent in multiple years and multiple stands and confirms results presented in earlier studies from other sites in the region (Anderegg et al., 2013). The reason for the species-level partitioning can simply be explained by differences in interception of summer rain driven by the

350 fact that conifers have 3-4 time higher leaf area per basal area than aspen (Pataki et al., 2000). This results in up to 40% higher interception by conifers (Thomas, 2016) and manifests clearly here by the fact that the soil moisture under dense conifer stands

was simply non-responsive to smaller summer rain events. This is an important point to make because it implies the partitioning between species does not, per se, require any explanation relating to belowground competition for a common water pool (Berkelhammer et al., 2022) but rather results from differences in aboveground traits relating to leaf area. However, we also

355   acknowledge the possibility of differences in permeability of soils below conifers and aspens (LaMalfa and Ryle, 2008) and/or rooting habitats but this would need to be tested with additional measurements. Another notable but easily overlooked aspect of the aspen-conifer partitioning is that during August the aspens had sap velocity rates that were often double or triple those of conifers while exhibiting 20% higher relative reliance on summer rain. Consequently, both the conifers and aspens were actually transpiring similar amounts of snowmelt water, but the aspens were also mixing summer rain into the transpiration stream.

360   By combining the xylem isotope data with sap velocity, we show the aspen, subalpine fir and Engelmann spruce exhibited a similar reliance on one water pool (snowmelt water) while aspen were able to also take advantage of the second pool associated with periodic summer rains. As illustrated by Figure 7, the trees that utilized a mixture of summer and winter precipitation (primarily aspen) were not surprisingly able to achieve the highest rates of instantaneous transpiration.

365   The primary goal of this study was to test whether the sensitivity of widespread Rocky Mountain tree species to changing snowpack is related to reliance on snowmelt as a primary water source (Graup et al., 2022; Tague and Peng, 2013; Strange et al.). Although many studies have independently tracked water sources by trees with stable isotopes spatially (e.g. (Allen et al., 2019)) and changes in tree or forest activity due to differences in precipitation seasonality (e.g. (Berkelhammer et al., 2017; Trujillo et al., 2012)) few studies have actually been able to quantitatively link sources of water and sensitivity to pre-

370   cipitation seasonality across years. Our analysis shows that about 40% of the difference in transpiration of individual trees between 2019 and 2021/2022 can be explained by the seasonal origins of the water used by the trees. We presume some significant amount of the unexplained variance (60%) arises from some combination of analytical uncertainty (e.g. changes in sap velocity installation between years) and specific site and tree traits. The relationship between water sources and sensitivity to seasonal precipitation inputs mapped in a surprisingly simple continuum across stand structure. As discussed above, the

375   diversity of stand structures across the hillslope itself partially represents a long-term acclimation to water availability and specifically access to snowmelt through a combination of direct inputs via infiltration, shallow subsurface flow and access to shallow groundwater recharged by snowmelt. The individual trees thus matured across a gradient of access to snowmelt inputs and the stands reached their observed modern densities at least partially as a reflection of this. The dynamics we observed here are potentially similar to those reported in the Sierra Nevada by Goodwin et al. (2023) who documented an inverse relationship

380   between the isotopic ratio of tree cellulose and stand density. (Though further work is needed to separate how much of the isotopic signal in the cellulose reflects changes in the seasonal origins of source water vs. the impact of open stands on crown conductance or surface evaporation.) We initially interpreted this relationship as a one-way reflection of the hillslope hydrology onto the canopy stand. However, in assimilating the soil moisture and snow data from different locations on this hillslope, we noted that the canopy structure generates a feedback onto a stand's water sources in two key ways:

385   (1) The persistence of snowpack into the growing season increases with stand density though this relationship is non-linear and offset by reductions in peak SWE in dense stands (Dickerson-Lange et al., 2021; Lundquist et al., 2013). Nonetheless, from

measurements made on this hillslope, Bonner et al. (2022) show that beginning around May 1 forested sites have higher SWE relative to open sites over a period that may last as much as 40 days during large snowpack years (Figure S5). This extended period of snowmelt input coincides with an important period of growth and water use especially for conifers which are active early in the spring. The extension of the snow season leads to a kind of snowmelt subsidy.

(2) As stand density increases so too does rainfall interception. This means that as stands mature towards their optimum density their relative reliance on snow increases. We conceptualize this feedback as the hillslope setting the initial access to snowmelt water and a stand density potential, but the resulting canopy structure perpetuates this effect by making the snowmelt-dependent stands increasingly reliant on snowmelt (Figure 8).

Assuming the processes documented here are typical of other subalpine watersheds in the western US, these results imply that sensitivity to historical and future trends in snowpack will be centered on those typically higher density sites that have developed in the context of high reliance on snowmelt. This could and will include denser aspen and conifer stands found in local convergence zones. The dense sites in our network are themselves uncommon in the context of the hillslope with respect to area (Figure S7) but represent a critical component of the interannual changes in water use due to their high peak capacity for water use. While these sites have more access to water and may be more resilient to bifurcation, they are more likely to be vulnerable to dieback and thinning in the likelihood of a low snow future due to the combination of their locally high demands for water coupled with their higher rainfall interception rates (Siirila-Woodburn et al., 2021).

We recognize a number of important limitations of this work that future field and modeling experiments could address. Firstly, we discuss the differences between years (2019-2022) only with respect to changing precipitation seasonality. This is because the differences in snow inputs were the most notable difference between years but use of a more process-based modeling approach would allow us to quantitatively interpret the differences in transpiration not only to changing snowmelt inputs but also to interannual differences in the timing of rain events, VPD and temperature. Also, the design of our network was not intentionally focused on canopy structure and thus we do not have data along a continuum between very dense or open sites. It was thus not possible to infer how stands that fell between the more open and closed end members behaved - which would be needed to scale up towards and aggregated hillslope estimate of transpiration changes to snow input variability. Controlled thinning in experimental plots would be the optimal testbed to explore the continuum of these effects. Furthermore, adding measurements of tree hydraulic properties to link their responses to changes in water access will help to develop an understanding of the variance in behavior that was not driven just by changing snow inputs. In particular, we see some evidence that individual trees with access to diverse water sources can reach the highest peak transpiration rates but the mechanisms for this relationship (e.g. root profiles or root hydraulics) remain unexplored in this study. Despite these limitations, our work links key observations about forest dynamics and changing hydrology that could help guide forest management decisions in such a way to optimize the ecological utilization of summer rain in regions like the southwestern US that receive regular summer rain inputs. Furthermore, the work provides needed benchmarking information for future simulations of coupled ecological

and hydrological processes at the watershed scale.

Data availability. The data associated with this manuscript is available here: https://data.ess-dive.lbl.gov/view/doi:10.15485/1647654 (doi 10.15485/1647654)

425 *Author contributions.* MB wrote manuscript, led analysis of data, assisted with field deployment and design and resource acquisition; GFP edited and wrote manuscript, led field design and data acquisition; CS assisted with editing manuscript and resource acquisition; FZ, WT, LH, JB, KI, AK, MC, KF, WB, MW, MSC, IB, AR, RM, DG, MR, ES and KHW all provided critical data sets for the analysis.

Competing interests. The authors declare that no competing interests are present.

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