Contents lists available at ScienceDirect





Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Snowmelt causes different limitations on transpiration in a Sierra Nevada conifer forest



Ava E. Cooper^{a,*}, James W. Kirchner^{b,c,d}, Sebastian Wolf^b, Danica L. Lombardozzi^e, Benjamin W. Sullivan^a, Scott W. Tyler^f, Adrian A. Harpold^a

^a Department of Natural Resources and Environmental Sciences, University of Nevada, Reno 1664 N. Virginia St., Reno, NV 89557, USA

^b Department of Environmental Systems Science, ETH Zürich, Universitätstrasse 16, Zürich 8092, Switzerland

^c Mountain Hydrology Research Unit, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

^d Department of Earth and Planetary Science, University of California, Berkeley, CA 94720, USA

^e National Center for Atmospheric Research, 3090 Center Green Drive, Boulder, CO 80301, USA

^f Department of Geological Sciences and Engineering, University of Nevada, Reno 1664 N. Virginia St., Reno, NV 89557, USA

ARTICLE INFO

Keywords: Sap flow Snow water equivalent Water stress Slope aspect Conifer forest Sierra Nevada

ABSTRACT

Snowmelt is a major source for summer soil water storage that supports tree growth in the Mediterranean climate of the Sierra Nevada, California. The timing and magnitude of snow-water contributions to soil moisture are controlled by energy and water availability that varies based on climate (and thus weather) and topography (i.e. elevation, slope, and aspect). Few studies, thus far, have explored how transpiration rate is affected by differences in the timing and magnitude of snowmelt across years and locations. Here we used meteorological and hydrological measurements on north and south aspects in the Sagehen Creek catchment (Sierra Nevada, California) to investigate the controls on the timing of conifer sap flow, a proxy for transpiration rate, in response to the timing and magnitude of snowmelt. We found that sap flow prior to its seasonal peak in July was largely controlled by air temperature and that spring sap flow was reduced by cloudy conditions. Years with earlier snow disappearance caused earlier peak sap flow, which was nearly coincident with the beginning of soil moisture limitations than years with later snow disappearance. Because Sagehen Creek receives little summer rainfall, years with earlier snowmelt and peak sap flow had more total days with soil moisture limitation on sap flow. Overall, our results suggest that earlier snow disappearance and more spring rain (both expected to result from climate change) will potentially shift the peak of sap flow earlier in the growing season and increase the duration of water limitations during summer. These insights about the timing and duration of water limitations could be used as benchmarks to test physically based models and better constrain predictions of transpiration rates in snow-dominated landscapes similar to the study site.

1. Introduction

Montane forests rely disproportionately on snowmelt in much of the Western U.S. (Hu et al., 2010; Trujillo et al., 2012). Spring snowmelt in the Western U.S. has been starting and ending earlier in the year and occurring at slower rates over the last several decades (Harpold and Kohler, 2017; Harpold and Brooks, 2018; Mote et al., 2018; Musselman et al., 2017). Earlier snow water inputs and shifts from snow to rain will lead to an earlier peak and earlier seasonal recession of soil moisture (Harpold, 2016; Harpold and Molotch, 2015). In areas with limited summer rain, earlier water inputs could increase late-season soil water stress (Harpold, 2016), which would increase the susceptibility of forests to disturbance (Hart et al., 2014;

Westerling et al., 2006). The timing and magnitude of snowmelt are important for early growing season productivity; for example, up to 30% of annual carbon uptake can occur during snowmelt in the Colorado Rockies (Winchell et al., 2016). Understanding forests' ability to shift their growing seasons earlier and withstand correspondingly longer dry seasons is critical for developing forest management strategies, but remains challenging to observe and model. Additionally, our understanding of how snowpack dynamics influence conifer transpiration is insufficient for predicting the effects of climate change on largerscale water budgets that provide critical natural resources.

In the higher elevations of the Sierra Nevada, USA, there is little summer rainfall and high variability in winter snowfall and melt, causing large variations in transpiration rates (Kelly and

* Corresponding author.

E-mail address: avac@nevada.unr.edu (A.E. Cooper).

https://doi.org/10.1016/j.agrformet.2020.108089

Received 18 September 2019; Received in revised form 9 June 2020; Accepted 15 June 2020 Available online 25 June 2020

0168-1923/ © 2020 Elsevier B.V. All rights reserved.



Fig. 1. (a) Location of Sagehen Creek Watershed in California and watershed boundary showing forest cover in green with the location of the study site marked in red, (b) 30 m meteorological tower (square) and sap flow cluster locations (circles) with tree heights in meters and open diamonds marking trees used in this study, (c) April 2016 Airborne Snow Observatory (ASO) snow depth, and (d) May 2016 ASO snow depth (missing data are shown as white). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

Goulden, 2016; Goulden et al., 2012; Royce and Barbour 2001; Tague and Peng, 2013; Trujillo et al., 2012; Urban et al., 2000). Much of what is known about the impacts of snowmelt on forest water use in the Western U.S. relies on studying regions with a cold, continental climate in the Rocky Mountains (Barnard et al., 2017; Bowling et al., 2018; Hu et al., 2010; Knowles et al., 2018; Winchell et al., 2016). Research conducted in the Rockies is largely located in forests of the southern Rockies (Colorado and New Mexico), with a precipitation regime that consists of both winter snow and summer rain. The different timing of water input between Mediterranean and continental climates is reflected in differences in soil moisture and thus differences in the annual patterns of forest productivity or water use (Barnard et al., 2018). In addition to water limitations, energy input and climate variables exert controls on transpiration. The onset of snowmelt is a critical period for vegetation water use because there is sufficient energy to melt snow and potentially drive photosynthesis (Monson et al., 2005; Winchell et al., 2016; Woelber et al., 2018). Field observations suggest that transpiration rates of conifers in a cold, continental climate are limited by cold air temperatures during the period around snowmelt (Moore et al., 2008; Scott-Denton et al., 2013; Winchell et al., 2016). Temperature limitations can be due to a combination of mechanisms, including frozen tree boles that inhibit water transport (Bowling et al., 2018), cold soils (soil temperature < 5 °C) that reduce root hydraulic conductivity (Day et al., 1989; Running and Reid, 1980), and cold needles < 10 °C that might create suboptimal conditions for photosynthesis (Huxman et al., 2003; Monson et al., 2005). Transpiration in conifer forests in the Sierra Nevada is broadly temperature-limited in winter when transpiration is low (Owston et al., 1972), and waterlimited in late summer, when transpiration tapers off as stomatal conductance decreases (Royce and Barbour, 2001). Other research suggests that conifers in the southern Sierra Nevada can maintain transpiration vear-round because the trees are well adapted to low temperatures and have sufficient sunlight to photosynthesize early in the year, even with deep snow cover (Kelly and Goulden, 2016). These previous studies have not continuously measured conifer transpiration, limiting their identification of energy and water limitations and their dependency on snowmelt timing and soil moisture drawdown.

In addition to regional differences in water input timing and limitations on transpiration rates, topography further controls water and energy budgets within a catchment. Elevation can have a profound influence on the amount of precipitation and the timing and duration of snowmelt, which are primary controls on ET (Tague and Peng, 2013; Trujillo et al., 2012). At a given elevation, north-facing aspects accumulate more snow and have later snow disappearance than south-facing slopes (in the northern hemisphere; Elder et al., 1991; Kostadinov et al., 2019: Tennant et al., 2017). The effect of aspect-dependent differences in snow accumulation on transpiration is challenging to observe in space and time, particularly in remote areas. Sap flow systems measure sap flux density (or sap flow) using a variety of heating-based sensors (Steppe et al., 2010) and can provide estimates of transpiration that differ from leaf-level estimates of stomatal conductance from water potential measured in branches or ecosystem-scale ET using eddy-covariance or remote sensing observations. Sap flux density measurements enable the monitoring of tree-scale transpiration measurements across topo-climatic gradients, like elevation or aspect (Barnard et al., 2017; Bowling et al., 2018; Looker et al., 2018). Although the conversion of sap flux density to tree-scale (or stand-scale) transpiration is fraught with assumptions of sap wood area (Looker et al., 2016), sap flow measurements remain one of the few tools capable of making effective measurements in complex terrain typical of high-elevation conifer forests.

Our research objective was to investigate transpiration rates in a montane, Mediterranean climate using sap flow in order to better understand the impact of earlier snowmelt, mediated by topography and climate variability. We used sap flux, meteorological, and hydrological measurements on north and south aspects over three years to investigate controls on the timing and magnitude of transpiration rates in a montane Conifer forest site in the northern Sierra Nevada, USA. We address two questions using empirically focused analyses of our field observations: 1) What controls early season sap flow? 2) How does earlier and more episodic snowmelt predispose a site to late-season water limitations?

2. Methods

2.1. Study site

Sagehen Creek is a 28 km² snow-dominated watershed in the Sierra Nevada of eastern California (39° 25′ 55″ N, 120° 14′ 27″ W; Fig. 1a). It spans an elevation range of 1877 m – 2663 m and has a Mediterranean climate with cold, wet winters and hot, dry summers. Sagehen lies just above the rain-snow transition of the Sierra Nevada and experiences high interannual variability in the amount of snow it receives during the wet, winter months between November 1 and May 1. The mean annual precipitation (calculated between 1981 and 2010) at the upper elevation boundary of Sagehen (USDA SnoTelemetry, SNOTEL site #541; 2541 m) was 120.4 cm. This study was conducted across 3 years: 2016 (average year; 135.4 cm precipitation), 2017 (wet year; 230.6 cm precipitation), and 2018 (drier than average year; 107.7 cm precipitation). Sagehen has a conifer forest of Jeffrey pine (Pinus jeffreyi) and Lodgepole pine (P. contorta) at lower elevations, and White pine (P. monticola) and Red fir (Abies magnifica) at higher elevations. Hillslopes are mantled by shallow, predominantly loamy sand soils developed in weathered volcanic parent material. Lithology is dominated by Tertiary volcanic rocks, overlying several hundred meters of Tertiary volcaniclastic deposits which in turn overlie the granodiorites of the Sierra Nevada batholith (Sylvester and Raines, 2017). We focused our study at the highest elevation (2374 m) meteorological station in Sagehen (called Tower 4 in the basin-wide network). Tower 4 is located on a ridge and we collected data on the north- and south-facing slopes of the ridge (hereafter north site and south site). Both sites have predominantly loamy sand soils except for deeper depths (30 - 50 cm) at the north site which have sandy loam soil. Soil textures were based on United States Department of Agriculture classifications and measured with a hydrometer-based sedimentation method on 2 mm soil. The sites have similar tree species compositions (Red fir and White pine) but the north site has greater stand density (79 trees/hectare versus 26 trees/ hectare at the south site, based on data from Xu et al., 2018).

2.2. Meteorological and environmental data

We collected data from November 1, 2015 to November 1, 2018. Air temperature (8 m and 30 m), relative humidity (8 m and 30 m; HMP50-L Temperature/Relative Humidity; Vaisala Corporation, Helsinki, Finland), solar radiation (30 m; LI200X Silicon Pyranometer; LI-COR, Inc., Lincoln, NE), wind speed (8 m and 30 m; Wind Monitor 05103-L; R.M. Young Company, Traverse City, MI), barometric pressure (30 m; PTB110 Barometer; Vaisala Corporation, Helsinki, Finland), and snow water equivalent (SWE; snow pillow) were recorded every 15 min at a 30 m meteorological tower (called Tower 4 in the basin-wide network) at 2374 m elevation. We established two nearby sap flow clusters that recorded data every 15 min, the north and south sites, approximately 100 m laterally distant from and 5 m lower in elevation than, the location of Tower 4 on the ridgeline (Fig. 1b). The sap flow clusters measured sap flux density (TDP30; Dynamax, Inc., Houston, TX) in Red fir (n = 1 at the north site and n = 1 at the south site) and White pine (n = 4 at the north site and n = 2 at the south site) which were selected to represent the site-average size class (based on diameter at breast height (DBH); 70 cm average DBH at the north site and 83 cm average DBH at the south site). The number of operational sap flow sensors varied between years due to challenges in long-term operation: 7 total sensors in 2016, 7 total sensors in 2017, and 6 total sensors in 2018. At the center of each sap flow cluster we measured soil moisture and soil temperature (10 cm, 30 cm, and 50 cm depths; CS655; Campbell Scientific, Inc., Logan, UT), and snow water equivalent (SWE plates; Trustman, 2016). We used the 15-minute data from Tower 4 and the sap flow clusters to calculate multiple linear regressions (see below) and daily averages for the rest of the analysis. Some short gaps (< 1 day) in data were filled using linear interpolation.

2.3. Sap flux density data and processing

We measured sap flux density with thermal dissipation probes (TDP30; Dynamax, Inc., Houston, TX) installed at ~ 2 m height for observing bole water transport. The thermal dissipation probes return a millivolt difference between the two thermocouples. The millivolt difference between the probes is converted to a temperature difference (Δ T). A zero-flow reference (hereafter baseline; ΔT_{max}) is required to calculate sap flux density from the recorded temperature differences (Eq. (1)).

A comprehensive study by Peters et al. (2018) explored four different methods for determining baseline conditions. The daily predawn method forces every night to baseline conditions; however, some evidence suggests that nighttime sap flux density may be non-zero if the vapor pressure deficit (VPD) is high enough (Snyder et al., 2003). Other baseline correction methods allow for nighttime sap flux density. We chose to use the double regression method, as described by Lu et al. (2004), instead of the moving window (Rabbel et al., 2016) or environment dependent (Oishi et al., 2016) methods. The double regression method accounts for nighttime flow and issues with a drifting zero-flow reference voltage over the growing season.

In the double regression method, ΔT_{max} is calculated over 10-day periods and a linear regression against time is calculated through those values for the entire growing season. If a ΔT_{max} value is below the calculated regression line, it is removed, and the linear regression is recalculated with the remaining points and used as the ΔT_{max} for calculating sap flux density (Lu et al., 2004).

We followed the standard Granier (1985) empirical equation for determining sap flux density (F_d ; cm³ cm⁻² h⁻¹; Eq. (1)) and used the calculated baseline from the double regression for the ΔT_{max} value:

$$F_d = 0.0119^* \left(\frac{\Delta T_{max} - \Delta T}{\Delta T}\right)^{1.231} \tag{1}$$

The sap flow sensors run on 3 V of power supply and we filtered the data for low power supply voltage (< 2.9 V) because lower voltages can cause spikes in the data. We also filtered for data that do not follow a general diurnal pattern (maximum during the day and minimum at night) that is indicative of transpiration. Sensors were deployed in the north- and south-facing sides of trees, but we did not observe substantial differences in sap flow between the different sensor placements. Sap flow sensors work during cold and low-flow conditions (Chan and Bowling, 2017) but the magnitudes of the reported sap fluxes are sometimes questionable. Sap flow sensors are difficult to run for consecutive growing seasons (Moore et al., 2010) and require frequent replacement and repositioning which makes the sensor network expensive and time consuming to maintain. Scaling sap flux density to transpiration using sap wood area would allow for water mass balance calculations and better estimation of water budgets. However, assumptions in sapwood area introduce large errors (up to 130% in Looker et al., 2016) that would make any resulting water budgets unreliable and therefore, raw sap flux densities (units of $cm^3 cm^{-2} hr^{-1}$) are used throughout our analysis.

2.4. Boundary line analysis

Boundary line analysis is a method for determining environmental and physiological limitations on stomatal conductance by finding the upper envelope of the relationship between explanatory variables and stomatal conductance (Chambers et al., 1985). We implemented boundary line analysis on daily average (00:00 - 23:00) sap flux density as a function of the daily averages of different environmental variables (air temperature, vapor pressure deficit, incoming shortwave, and soil moisture). In our analysis, boundary lines represent the maximum predicted sap flux density under a certain environmental variable given optimal conditions of other environmental variables. Unlike a correlation analysis which would reveal the strength of each variable in driving sap flux density, boundary line analysis tells us which of the variables are limiting sap flux density under specified environmental conditions. Due to the proximity of the sites and the height of the tree canopy relative to the height to the ridgeline (5 - 35 m versus \sim 5 m, respectively), we combined the north and south sites for the boundary line analysis because we use the same meteorological data for both sites and the only difference in input to the boundary line analysis is soil moisture. Scatterplots of daily average sap flux densities as functions of daily average environmental variables were grouped into bins of 50 measurements along their x-axes (the environmental variables). For each bin, the 95th percentile value was calculated to delimit the upper envelope. An upper-bound sap flux density value was calculated for each day using linear interpolation across all observed values of the environmental variable based on the 95th percentile values from each bin (see Appendix C for more information). The boundary line for soil moisture has a negative relationship with sap flow above a threshold soil moisture value (7 cm of water in the soil column) that is not consistent with the well-drained soils and the lack of anoxic soil conditions (see Appendix C for further details and sensitivity of this threshold). Because very wet conditions occur only during the Spring in the Mediterranean climate, our boundary line analysis cannot effectively assume all combinations of limiting factors are sampled. The boundary lines allow us to identify which environmental variable will be most limiting under specific environmental conditions. To interpret the boundary lines (see Appendix C), one must first find environmental conditions on the x-axis, and then determine the associated sap flux limitation (y-axis) for each environmental variable (e.g., following the day's x-value to the boundary line and identifying the associated y-axis value). The environmental variable with the lowest corresponding sap flux density is interpreted as the most limiting for that set of environmental conditions.

2.5. Statistical analysis

We performed statistical analyses for early- and late-season sap flux density, as well as the timing of peak sap flux density. Early-season sap flux density is defined as sap flux occurring from one month before peak SWE to the day of peak sap flux density, and late-season sap flux density is defined as sap flux occurring from the day of peak sap flux density to October 1 (the end of the water year). We chose one month before peak SWE to define the start of the early season because little sap flow occurs prior to snowmelt (Fig. 4 and Fig. A5). The dynamic start date to the early season allows us to account for snowpack controls on timing of tree phenology. The day of peak sap flux density was calculated as the midpoint of the 5-day moving window with the highest daily average sap flux density data for each site and year. For the early season, we used a multiple linear regression model (StatsModel OLS, Python, Seabold and Perktold, 2010) on all years of the hourly data for daytime

only (defined as 08:00 - 20:00). Air temperature, VPD, and incoming shortwave radiation were the inputs into the multiple linear regression to predict sap flux density at each site. We standardized sap flux density and all the explanatory variables by subtracting the mean and dividing by the standard deviation for the entirety of the early season for each site and year. Standardized values result in standardized regression coefficients that can be compared between explanatory variables. We calculated the correlation of the day of peak sap flux density with the timing of snow disappearance and with the timing of soil moisture limitations in the boundary line analysis. For the late season, we calculated the duration of soil moisture limitations as the number of days each site showed soil moisture limitations in the boundary line analysis prior to October 1 and calculated the correlation of that value with the timing of snow disappearance and the magnitude of peak SWE.

3. Results

3.1. Snow and soil moisture hydrology

The storage of precipitation as snowpack at peak snow accumulation - which we report as the percentage of annual precipitation $([SWE_{peak}/P_{total}]*100)$ – is a measure of the rain and snowpack ablation occurring over the accumulation season (Harpold et al., 2012). The storage of precipitation differed between the two aspects. The north site stored an average of 43% of annual precipitation as snow at maximum accumulation (SWE $_{\rm peak})$ whereas the south site stored an average of 23% of annual precipitation as snow. The south site stored, on average, 20% less of the annual precipitation as snow than the north site. The sites were most different in the high-snow year, 2017, during which the snowpack on the south site stored 29% less of the annual precipitation as snow than the north site did. The north and south sites had large differences in peak snow water equivalent (SWE), especially in 2017 (difference of 66 cm in SWE), the wettest year of the study. The sites were most similar in the low-snow year, 2018, during which the south site stored 7% less of the annual precipitation as snow than the north site did. 2018 was the lowest-precipitation year (108 cm, Table 1) and snow cover occurred later in the year than in 2016 or 2017. Additionally, 2018 had the warmest DJF average temperature (Table 1) and ablation was occurring in January at both sites, as indicated by the decrease in SWE (Fig. 2d) and the increase in soil moisture (Fig. 2e). Differences in the timing and amount of peak SWE resulted in notable differences in the timing of snow disappearance (Table 1 and Fig. 1c and d). For both sites, the day of snow disappearance occurred latest in 2017 (with day of year (DOY) 167 and 180 for the south and north site, respectively) and earliest in 2018 (41 and 38 days earlier than 2017 for south and north site, respectively) (Table 1). The difference in timing of snow disappearance between sites was similar in all years with an average of 15 days earlier snow disappearance at the south site.

Differences in the percentage of precipitation stored as snow between the aspects were reflected in soil moisture differences between the two sites. The south site had more midwinter snowmelt pulses that were evident in soil moisture in all years, whereas the north site had more distinct diurnal snowmelt pulses after winter, during the spring snowmelt (hourly data, not shown). Peak soil moisture at the north site

Table 1

Climate data for the 3 years of the study. Mean annual, winter (DJF) and spring (MAM) temperatures are from Tower 4. Total precipitation (total P) is reported for the entire site from SNOTEL #541 (2541 m elevation) which experiences comparable totals of precipitation to Tower 4 (see supplemental Fig. A1). Peak snow water equivalent (peak SWE) data are from the SWE plates at each site at Tower 4. Fraction of annual precipitation represented by the peak snow accumulation is reported as [SWE_{peak/Ptotal}]*100%. Day of year (DOY) of snow disappearance is also reported.

Year	Avg. annual temperature (°C)	Avg. DJF air temperature ($^\circ C)$	Avg. MAM air temperature ($^\circ C)$	Total P (cm)	[SWE _{peak} /P _{te} South	_{otal}]*100% North	Snow disappe South	arance (DOY) North
2016	6.1	-1.0	3.7	135	23	50	136	153
2017	6.1	-2.3	3.7	231	17	46	167	180
2018	7.1	0.5	2.9	108	25	32	126	142



Fig. 2. Daily average data from the main 30 m meteorological tower and sap flow clusters (north and south). From the main tower: (a) air temperature (8 m) with 0 °C marked by blue dashed line, (b) vapor pressure deficit (VPD) (8 m), and (c) incoming shortwave radiation (8 m). From the sap flow clusters: (d) snow water equivalent, (e) soil moisture content of top 50 cm of soil (see Appendix B Eqn B.1 for calculation), and (f) site-averaged daily average sap flux density. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

was higher than at the south site in all years (difference of $6.81 \text{ cm H}_2\text{O}$, on average).

3.2. Early season sap flux and boundary line analysis

Early-season sap flux density (i.e. sap flux occurring from one month before peak SWE to the annual peak of sap flux density) was highly variable in all years and ranged from 0.016 cm³ cm⁻² h⁻¹ to 5.3 cm³ cm⁻² h⁻¹ at the south site and from 0.033 cm³ cm⁻² h⁻¹ to 7.5 cm³ cm⁻² h⁻¹ at the north site (Fig. 4, Fig. A4). In all years, sap flux density before its peak was similar between sites in terms of magnitude (Fig. 4) and variability (Fig. 5a). Spring weather patterns resulted in variable spring air temperatures. Sap flux density was also variable during this time period and the coefficient of variation (CV) of sap flux density (r² = 0.95; Fig. 5a). The multiple linear regression during the early season had the greatest explanatory power from air temperature at the south site (standardized regression coefficient = 0.51) and VPD had the greatest explanatory power at the north site (standardized regression coefficient = 0.48; Fig. 5b). Limitations on sap flux density, calculated using the boundary line analysis (Fig. 3), showed general expected relationships with the explanatory variables, with some scatter from a lack of data under certain environmental conditions (i.e. wet soil conditions with high solar radiation). Sap flux density generally follows a linear relationship with air temperature and VPD until reaching an asymptote around 15 C and 1.5 kPa, respectively. The inferred limitation from the boundary line analysis shifted from alternating energy and temperature limitations before peak sap flux density to largely water limitations after peak sap flux density (Fig. 4). Both north and south sites have the same early-season limitations because the same meteorological data were used for each site and we assumed that soil moisture was not the limiting variable when storage was greater than 7 cm of water (there is little sensitivity to this threshold decision; see Fig. C2 in Appendix C).



Fig. 3. Boundary lines are created by plotting daily average sap flux density as a function of different environmental variables and finding the upper envelope of the relationship (black lines). The boundary lines used in our analysis are: (a) air temperature, (b) vapor pressure deficit, (c) incoming shortwave radiation, and (d) soil moisture. We assume that soil moisture does not limit sap flux density when storage is above 7 cm H_2O , which only occurs during energy-limited periods (dashed line in panel d).

3.3. Late season sap flux and boundary line analysis

For both sites and all years, peak sap flux density occurred between DOY 176 and 190. Among the three years, peak sap flux density

occurred latest at the north site in 2017 (DOY 190) and occurred earliest at the south site in 2017 (DOY 176; Fig. 6b). After its peak, sap flux density declined to similar values with no additional rainfall. September and October rainfall supplemented soil moisture and initiated a



Fig. 4. Daily average sap flux density (yellow = south, teal = north). The shaded regions show the 90% confidence interval for sap flux density. The heat maps show the environmental factor most limiting to sap flow for each day. Peak snow water equivalent (SWE) is marked by a triangle and snow disappearance is marked by a circle for each site and year. Data are shown for 2016 (top set), 2017 (middle set), and 2018 (bottom set). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

resurgence in late season sap flux density, as seen in October 2016 (Fig. 4). The boundary line analysis suggests that during the mid to late growing season, the south site reached soil moisture limitations prior to the north site in all years. In 2017, sap flow at both sites experienced soil moisture limitations less often than in the drier years of 2016 and 2018. The boundary line analysis-derived (BLA-derived) timing of soil moisture limitations on sap flow was correlated with the timing of snow disappearance ($r^2 = 0.72$), where the slope of 0.6 days/day represents soil moisture limitation occurring six days earlier for every 10 days earlier that snow disappeared (Fig. 6a). The timing of BLA-derived soil moisture limitations was weakly correlated to the day of peak sap flux density, where peak sap flux density occurred 2.6 days earlier for a 10day earlier shift in the timing of soil moisture limitations on sap flow (Fig. 6b). The duration of BLA-derived soil moisture limitations also correlated with peak SWE ($r^2 = 0.85$) and the day of snow disappearance ($r^2 = 0.79$), where the slope of -0.99 days/day represents an approximately 1 day longer duration of soil moisture limitations for a 1-day earlier snow disappearance (Fig. 7).

4. Discussion

Seasonal patterns in energy (i.e. incoming solar radiation), climate (i.e. air temperature and VPD) and water (i.e. soil water availability) cause a multimodal sap flow regime in high-elevation conifer trees in the northern Sierra Nevada, California (Fig. 4). The relative scarcity of observations of year-round transpiration rates in this geographic area and elevation range (Kelly and Goulden, 2016; Goulden et al., 2012; Owston et al., 1972; Royce and Barbour, 2001; Trujillo et al., 2012) has limited our understanding of the controls on early-season sap flow and the timing and duration of tree-level water limitations. Early in the year, sap flow is highly modulated by the variability in weather patterns (i.e. cold fronts and weather systems). Our results suggest that peak sap flow occurs just prior to water limitations, which are regulated by the timing of snowpack disappearance and the magnitude of snowmelt (Bales et al., 2011; Harpold, 2016; Harpold and Molotch, 2015).

4.1. What controls early season sap flow?

The north and south sites showed similar early-season sap flow that was controlled by seasonal air temperature and VPD, and was highly modulated by spring weather patterns. The control of air temperature and VPD on early-season sap flow was evident from the multiple linear regression analysis, where air temperature had the highest explanatory power at the south site and VPD had the highest explanatory power at the north site (Fig. 5b, Fig. A2). The difference between the two sites' sap flow correlation with air temperature and VPD likely results from differences in the microclimate between the north and south site due to longer snow cover at the north site and potentially larger diurnal fluctuations in air temperature at the south site. However, we did not have the necessary spatial or vertical coverage in data to analyze these differences. The importance of air temperature is further supported by the boundary line analysis, which predicts that sap flow is more limited by air temperature than VPD during most of the early season (Fig. 4). Our results show the importance of spring weather patterns (Adams et al., 2002; Kelly and Goulden, 2016; Sevanto et al., 2006; Verhoeven et al., 1999) as evidenced by reductions of sap flow to near zero during 2- to 14-day periods of cloudy, cooler temperatures compared to the warmer periods in between (Fig. 4). We see probable interruptions of sap flux (i.e., temporary cessation of water transport in the boles of trees) at times throughout the spring, with air temperatures below 5 °C being the suspected limiting factor, which is consistent with previous research showing that tree water use is low or absent in winter below air temperatures of 5 °C (Goulden et al., 2012; Royce and Barbour, 2001; Stephenson, 1998; Urban et al., 2000). Lower sap flux

densities in spring and fall might also be attributable to temperature limitations that reduce root hydraulic conductivity, as soil temperatures were sometimes >5 °C but never below freezing (Fig. A3; Day et al., 1989; Running and Reid, 1980). It is worth noting that the boundary line analysis is limited by its prediction of a single limiting factor per day and does not account for the potential of interacting variables, but does account for daily, rather than seasonal, variations in environmental variables and therefore appears robust for exploring limitations on sap flow. Air temperature, incoming solar radiation, and VPD are all related via the land surface energy budget and are thus subject to covariation which is not accounted for in the boundary line analysis. However, each variable has important physiological effects and are often included individually as inputs for stomatal resistance models. Larger variability in inter-annual climate (i.e. a more extreme dry year) would have allowed us to investigate differences between sap flow on the north and south sites that were not readily apparent in this threeyear study (e.g. effects of greater stand density at the north site). More years of data collection would allow us to test the statistical difference in soil moisture limitations between wet and dry years and increase the robustness of the boundary line and correlation analyses.

Consistent with evidence from continental climate locations (Bowling et al., 2018; Winchell et al., 2016), air temperature limitations on early season sap flow were dominant over controls from solar irradiance. Changes in spring weather, which is likely to become warmer with an earlier and smaller snowmelt (Karl et al., 1993; Mote et al., 2018), will have important implications for transpiration rates and forest health in the Sierra Nevada. Warmer springs and smaller snowpacks have already been correlated with greater wildfire activity (Westerling et al., 2006; Westerling, 2016) and more insect-caused tree mortality (Paz-Kagan et al., 2017), whereas more frequent spring and summer rainfall would bring cool, cloudy conditions that would reduce spring transpiration rates. Since most predictions for the Sierra Nevada suggest an earlier snowmelt initiation and more sporadic winter snowmelt (Harpold and Brooks, 2018; Musselman et al., 2017), the degree to which drought stress and mortality will increase will likely depend on the physiological adaptability of the vegetation (e.g. rooting depth changes, carbon allocation strategies, etc.; Canadell et al., 1996; Garcia et al., 2016; Jackson et al., 1996), as well as the amount of subsurface plant-available water that will vary based on local critical zone properties (Klos et al., 2018).

4.2. How does earlier and more episodic snowmelt predispose a site to lateseason water limitations?

Our results suggest that earlier snow disappearance led to longer durations of soil moisture limitations on sap flow and these limitations were highly variable between sites and among years. Across the western U.S., the timing of peak soil moisture is highly correlated with snowmelt (Harpold and Molotch, 2015) and in the Sierra Nevada, the timing of soil water stress is better explained by snow disappearance than by total precipitation (Harpold, 2016). Consistent with these previous studies, the timing of soil water limitations derived from our boundary line analysis was correlated with the timing of snow disappearance (Fig. 7a), as well as the magnitude of peak SWE (Fig. 7b). This is because large snowpacks tend to melt later and faster when solar radiation is high, in contrast to small snowpacks that have little cold content and may melt episodically through the winter (more typical of the Sierra Nevada; Harpold and Brooks, 2018). Our study connects aspect-driven differences in snow disappearance and the timing soil moisture dry down to the timing of peak sap flow and duration of soil moisture limitations on sap flow. The linear relationship between snow disappearance and the timing of soil moisture limitations suggests that a 10-day earlier snow disappearance results in a 6 day earlier initiation of soil moisture limitations on sap flow, which is similar to the to the 6.2



Fig. 5. (a) The coefficient of variation (CV) of sap flux density prior to its seasonal peak as a function of the CV of air temperature (AT) prior to peak sap flux density ($r^2 = 0.95$). Points are labeled by site (S = south, N = north) and year (i.e., 16 = WY 2016). (b) Standardized regression coefficients from the multiple linear regression show the relative explanatory power of each of the input variables (yellow = south site, teal = north site; AT = air temperature, VPD = vapor pressure deficit, SW = incoming shortwave radiation). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

day increase in days below wilting point soil moisture (per 10-day earlier snow disappearance) found by Harpold (2016). Both our results and Harpold (2016) imply that much of the limitations observed in transpiration rates are mediated by access to shallow soil moisture. The moderate correlation ($r^2 = 0.46$) between peak sap flow and BLA-derived soil moisture limitations, although not statistically different from

zero at our limited sample size, suggests that snow phenology (i.e. maximum SWE and timing of snow disappearance) may exert some control on the initiation and duration of tree water limitations. This implies that expected changes in snow phenology are likely to shift sap flow earlier and subsequently lengthen durations of water limitations, particularly in drier years. Site differences in soil texture, especially at



Fig. 6. (a) First day of soil moisture limitations as a function of the day of snow disappearance ($r^2 = 0.72$; slope = 0.6 day/day). (b) Day of peak sap flux density as a function of the timing of soil moisture limitations on sap flow calculated from the boundary line analysis ($r^2 = 0.46$; slope = 0.3 day/day).



Fig. 7. (a) Duration of soil moisture limitations on sap flow as a function of the day of snow disappearance ($r^2 = 0.79$; slope = -0.99 day/day). (b) Duration of soil moisture limitations as a function of peak SWE magnitude ($r^2 = 0.85$; slope = -0.69 day/day).

depth, and stem density might further affect stand-level transpiration rates in ways not addressed in this study. Particularly, shifts from snow to rain will result in more similar timing and magnitude of snowmelt between the north and south aspects and differences in stand characteristics (finer soils at depth and higher stand density at the north site) might become more important to the duration of water limitations during longer growing seasons. Lower-elevation conifers (lodgepole pine and Jeffrey pine) likely have different water use strategies than higher-elevation conifers (red fir and white pine) because the lower elevations of catchments have different water availability (e.g. distance to groundwater) and different water partitioning (e.g. whether precipitation is rain or snow). Thus, our results are specific to our study site and further investigation is needed to determine the robustness of these results across elevation gradients. The transferability of our results to other regions is likely to be strongly mediated by both the local microclimate (e.g. precipitation and topography-mediated radiation) and the properties that store water in the subsurface (critical zone). Areas with greater plant-accessible water storage are likely to be buffered against changes in peak sap flow timing and changes in the duration and severity of soil moisture limitations later in the year (Anderson et al., 2014; Broxton et al., 2009; Goulden and Bales, 2019; Hinckley et al., 2014; Pelletier et al., 2018; Zapata-Rios et al., 2016).

5. Conclusions

Our analysis of sap flow at a snow-dominated site in the Sierra Nevada, California led to three important findings about how this montane forest ecosystem might respond to earlier snowmelt and increased winter rainfall. First, hillslopes with identical climates but north- and south-facing orientations showed similar early-season sap flow that was primarily controlled by air temperature and vapor pressure deficit. Warmer springs might shift sap flow earlier in the year, whereas more frequent spring and summer storms (e.g. more frequent cool, cloudy periods) would sporadically reduce sap flow with unknown consequences for late-season and total annual transpiration losses. Second, earlier snow disappearance consistently leads to earlier soil moisture limitations on sap flow and consequently, earlier peak sap flow. This relationship suggests that snow disappearance observations could potentially provide a means for estimating the timing of soil moisture limitations on tree water use (e.g. Harpold, 2016). Third, a 1day earlier snow disappearance timing suggested an additional day of soil moisture limitation on sap flow. Earlier snow disappearance would thus cause longer durations of soil moisture limitations that could have implications for forest carbon budgets and susceptibility to disturbances from fire, pathogens, and insects in ways that are mediated by the subsurface (critical zone) water storage properties (Goulden et al., 2012). The process-based insights from this study can guide future studies of transpiration across topo-climate gradients and inform land surface model process representations to better predict the sensitivity of transpiration to earlier snowmelt.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This project was funded by a Hatch NIFA grant (NEV05293) to A. Harpold. Special thanks to Sagehen Creek Field Station's director, Jeff Brown, and Sagehen's technician Dan Sayler.

Snow and forest lidar data were provided by Tom Painter and the Airborne Snow Observatory (ASO) and the National Center for Airborne Laser Mapping (NCALM). The manuscript benefitted from discussions with Holly Barnard and Naomi Tague. Thanks to the Nevada Mountain Ecohydrology Lab field team that installed and maintained the field sites: Patrick Longley, Rose Petersky, Sarah Petersen, Mackenzie Kohler, Josh Sturtevant, Gary Sterle, Lisa Katz, Matt Newell, Matt Classen, and Sebastian Krogh. Thanks to Brian Morra for assisting with the soil texture analysis.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108089.

Appendix A. Additional figures and tables

Figs. A1-A5, Figs. C1 and C2 and Tables A1-A2



Figure A1. Comparison of accumulated precipitation recorded at SNOTEL #541 (grey dashed line), SWE recorded at SNOTEL #541 (darker blue), and SWE recorded at Tower 4 (lighter blue). SWE measurements at Tower 4 and SNOTEL #541 correspond closely during winter accumulation, justifying the use of SNOTEL precipitation in our calculations of the partitioning of precipitation to SWE.



Figure A2. Multiple linear regression beta coefficients of air temperature (AT), vapor pressure deficit (VPD), and incoming shortwave radiation (SW) showing how much each variable explains sap flow at the south site (yellow) and the north site (teal). The full growing season regression had $r^2 = 0.47$ for the south site and $r^2 = 0.30$ for the north site. The early season (before peak sap flow) regression had $r^2 = 0.74$ for the south site and $r^2 = 0.71$ for the north site. The late season (after peak sap flow) regression had $r^2 = 0.44$ for the south site and $r^2 = 0.19$ for the north site.



Figure A3. Shallow soil temperature (10 cm) for north (dark brown) and south (light brown).) sites. Freezing and 5 °C are marked with the blue and grey dashed lines, respectively.

(B.1)



Figure A4. Sap flux density of individual sensors in 2017 (top panel) and 2018 (bottom panel), the two years during which a tree with a significantly smaller diameter was used at the north site (Table A1). Teal lines are the sensors at the north site and yellow lines are the sensors at the south site. The dashed teal lines show the smallest tree (diameter at breast height = 21 cm).



Figure A5. Sap flow measurements filtered to remove erroneous data lacking a diurnal pattern indicative of transpiration. grey are data that were removed and colors are data that were kept. Data show the trees used at the south site in 2016.

Appendix B. soil moisture calculations

Soil moisture was reported as the total depth of water in the soil column and was calculated from volumetric water content (VWC) at 10, 30, and 50 cm depth, following equation B.1:

Soil moisture =
$$(VWC_{10} * 20) + (VWC_{30} * 20) + (VWC_{50} * 20)$$

Each VWC measurement is treated as the midpoint of a 20 cm thick layer of soil and VWC_{10} , VWC_{30} , and VWC_{50} are the VWC for 10 cm, 30 cm, and 50 cm, respectively. We multiply the thickness of each layer by its VWC and add the values to get the total depth of water in the soil column.

Table A1

S	pecies	(WP	= white	pine,	RF =	red fir)	and	diameter at	breast	height	(DBH)	of trees	used ir	1 the	analysis	5.
				1 /												

Site	Year	Species	DBH (cm)
South	2016	WP	88
		WP	88
		RF	78
	2017	WP	88
		WP	88
		WP	72
	2018	WP	88
		WP	88
		WP	72
North	2016	WP	91
		WP	91
		RF	70
		WP	73
	2017	WP	21
		WP	91
		RF	70
		WP	73
	2018	WP	21
		WP	91
		WP	73

 Table A2

 Site-level tree data from NCALM lidar.

Site	Site average max height (m)	Site average mean height (m)	Site average mean forest cover (%)
South	22.64	16.78	59
North	18.31	11.89	57

Appendix C. boundary line analysis

The environmental variables are defined as air temperature (AT), vapor pressure deficit (VPD), incoming shortwave radiation (SW), and soil moisture (SM). For the boundary line analysis, the daily averages of each environmental variable are sorted and grouped into 18 bins, such that each bin has 50 measurements of the environmental variable and the corresponding sap flux value for that day. We used Python's "describe" function to calculate the 95th percentile of each bin. To avoid over-smoothing the data, the boundary lines were calculated from interpolation (scipy.interpolate.interp1d, Jones et al., 2001) between the 95th percentile values, such that all days had a predicted sap flux density (instead of referencing a single value per bin or a line fitted to the bin points). The jagged lines result from limitations in the quantity of data collected over 3 years. The negative relationship between sap flow and soil moisture at higher soil moisture values is assumed to result from water inputs being out of phase with energy demands in Sagehen's Mediterranean climate. This results in high soil moisture values only occurring during winter and spring, which are energy-limited periods because of low temperatures, low incoming solar radiation, and spring storms. To explore the sensitivity to the assumption that moisture limitations only occur below 7 cm of water storage (Fig. C2). There is relatively little change in the inferences made about limitations on water use based on this assumption.



Figure C1. Example of how to find the limiting variable from the boundary line analysis for April 16 2016, (red) August 8 2016, (blue). The limiting variable is determined by following the day's value of a given explanatory variable up to the boundary line and over to the predicted sap flow value, such that the lowest predicted sap flow is the most limiting variable for that day. For April 16 (red) air temperature is most limiting and for August 8 (blue) soil moisture is most limiting on sap flow.



References

- Adams, W.W., Demmig-Adams, B., Rosenstiel, T.N., Brightwell, A.K., Ebbert, V., 2002. Photosynthesis and photoprotection in overwintering plants. Plant Biol. 4, 545–557. Anderson, S.P., Hinckley, E.-L., Kelly, P., Langston, A., 2014. Variation in critical zone
- processes and architecture across slope aspects. Procedia Earth Planet. Sci. 10, 28–33. Bales, R.C., et al., 2011. Soil moisture response to snowmelt and rainfall in a Sierra Nevada mixed-conifer forest. Vadose Zone J. 10 (3), 786.
- Barnard, D.M., Barnard, H.R., Molotch, N.P., 2017. Topoclimate effects on growing season length and montane conifer growth in complex terrain. Environ. Res. Lett. 12 (6), 64003.
- Barnard, D.M., Hu, J., Goulden, M.L., Litvak, M.E., Barnard, H.R., Knowles, J.F., Molotch, N.P., 2018. Reevaluating growing season length controls on net ecosystem production in evergreen conifer forests. Sci. Rep. 8 (1), 1–10.
- Bowling, D.R., et al., 2018. Limitations to winter and spring photosynthesis of a Rocky Mountain subalpine forest. Agric. For. Meteorol. 252 (December 2017), 241–255.

- Broxton, P.D., Troch, P.A., Lyon, S.W., 2009. On the role of aspect to quantify water transit times in small mountainous catchments. Water Resour. Res. 45 (8), 1–15.
- Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. Maximum rooting depth of vegetation types at he global scale. Oecologia 108, 583–595.
- Chambers, J.L., Hinckley, T.M., Cox, G.S., Metcalf, C.L., Aslin, R.G., 1985. Boundary-line analysis and models of leaf conductance for four oak-hickory forest species. Forest Sci. 31 (2), 437–450.
- Chan, A.M., Bowling, D.R., 2017. Assessing the thermal dissipation sap flux density method for monitoring cold season water transport in seasonally snow-covered forests. Tree Physiol. 37 (7), 984–995.
- Day, T.A., DeLucia, E.H., Smith, W.K., 1989. Influence of cold soil and snowcover on photosynthesis and leaf conductance in two Rocky Mountain conifers. Oecologia 80, 546–552.
- Edler, K., Dozier, J., Michaelsen, J., 1991. Snow accumulation and distribution in an alpine watershed. Water Resour. Res. 27 (7), 1541–1552.
- Garcia, E.S., Tague, C.L., Choate, J.S., 2016. Uncertainty in carbon allocation strategy and

ecophysiological parameterization influences on carbon and streamflow estimates for two western US forested watersheds. Ecol. Model. 342, 19–33.

- Goulden, M.L., Anderson, R.G., Bales, R.C., Kelly, A.E., Meadows, M., Winston, G.C., 2012. Evapotranspiration along an elevation gradient in California's Sierra Nevada. J. Geophys. Res. 117 (3), 1–13.
- Goulden, M.L., Bales, R.C., 2019. California forest die-off linked to multi-year deep soil drying in 2012–2015 drought. Nat. Geosci. 12 (8), 632–637.
- Granier, A., 1985. Une nouvelle methode pour la measure du flux de seve brute dans le tronc des arbres. Ann. des Sci. For. 42, 193–200.
- Harpold, A.A., 2016. Diverging sensitivity of soil water stress to changing snowmelt timing in the Western U.S. Adv. Water Resour. 92, 116–129.
- Harpold, A.A., Brooks, P.D., 2018. Humidity determines snowpack ablation under a warming climate. In: Proceedings of the National Academy of Sciences, , 201716789.
- Harpold, A, Brooks, P, Rajagopal, S, Heidbuchel, I, Jardine, A, Stielstra, C, 2012. Changes in snowpack accumulation and ablation in the intermountain west. Water Resources Research 48.
- Harpold, A.A., Kohler, M., 2017. Potential for changing extreme snowmelt and rainfall events in the mountains of the Western United States. J. Geophys. Res. 122 (24), 13219–13228 13,219-13,228.
- Harpold, A.A., Molotch, N.P., 2015. Sensitivity of soil water availability to changing snowmelt timing in the western U.S. Geophys. Res. Lett. 42 (19), 8011–8020.
- Hart, S.J., Veblen, T.T., Eisenhart, K.S., Jarvis, D., Kulakowski, D., 2014. Drough induces spruce beetle (Dendroctonus rufipennis) outbreaks across nrothwestern Colorado. Ecology 95 (4), 930–939.
- Hinckley, E.L.S., Ebel, B.A., Barnes, R.T., Anderson, R.S., Williams, M.W., Anderson, S.P., 2014. Aspect control of water movement on hillslopes near the rain-snow transition of the Colorado Front Range. Hydrol. Process. 28 (1), 74–85.
- Hu, J., Moore, D.J.P., Burns, S.P., Monson, R., 2010. Longer growing seasons lead to less carbon sequestration by a subalpine forest. Glob. Chang Biol. 16 (2), 771–783. Huxman, T.E., Turnipseed, A.A., Sparks, J.P., Harley, P.C., Monson, R.K., 2003.
- Trushian, L.E., Turinpseed, A.A., Sparks, J.F., Farley, F.C., Monson, K.K., 2005. Temperature as a control over ecosystem CO2 fluxes in a high-elevation, subalpine forest. Oecologia 134, 537–546.
- Jackson, R.B., Canadell, J., Ehringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108, 389–411.
- Jones, E., Oliphant, E., Peterson, P., et al. (2001). SciPy: open source scientific tools for Python, http://www.scipy.org/ [Online; accessed 2019-08-05].
- Karl, T.R., Groisman, P.Y., Knight, R.W., Heim, R.R., 1993. Recent variations of snow cover and snowfall in North America and their relation to precipitation and temperature variations. J. Clim. 6 (7), 1327–1344.
- Kelly, A.E., Goulden, M.L., 2016. A montane Mediterranean climate supports year-round photosynthesis and high forest biomass. Tree Physiol. 36 (4), 459–468.
- Klos, P.Z., et al., 2018. Subsurface plant-accessible water in mountain ecosystems with a Mediterranean climate. WIREs Water 1–14.
- Kostadinov, T.S., et al. (2019). Remote Sensing of environment watershed-scale mapping of fractional snow cover under conifer forest canopy using lidar, 222, 34–49.
- Knowles, J.F., Molotch, N.P., Trujillo, E., Litvak, M.E., 2018. Snowmelt-driven tradeoffs between early and late season productivity negatively impact forest carbon uptake during drought. Geo phys. Res. Lett. 45, 3087–3096.
- Looker, N., Martin, J., Hoylman, Z., Jencso, K., Hu, J., 2018. Diurnal and seasonal coupling of conifer sap flow and vapour pressure deficit across topoclimatic gradients in a subalpine catchment. Ecohydrology 11 (7), e1994.
- Looker, N., Martin, J., Jencso, K., Hu, J., 2016. Contribution of sapwood traits to uncertainty in conifer sap flow as estimated with the heat-ratio method. Agric. For. Meteorol. 223, 60–71.
- Lu, P., Urban, L., Zhao, P., 2004. Granier's thermal dissipation probe (TDP) method for measuring sap flow in trees: theory and practice. Acta Bontanica Sinica 46 (6), 631–646.
- Monson, et al., 2005. Climatic influences on net ecosystem CO2 exchange during the transition from wintertime carbon source to springtime carbon sink in a high-elevation, subalpine forest. Oecologia 146, 130–147.
- Moore, D.J.P., Hu, J., Sacks, W.J., Schimel, D.S., Monson, R.K., 2008. Estimating transpiration and the sensitivity of carbon uptake to water availability in a subalpine forest using a simple ecosystem process model informed by measured net CO2and H2O fluxes. Agric. For. Meteorol. 148 (10), 1467–1477.
- Moore, G.W., Bond, B.J., Jones, J.A., Meinzer, F.C., 2010. Thermal-dissipation sap flow sensors may not yield consistent sap-flux estimates over multiple years. Trees-Struct. Funct. 24 (1), 165–174.
- Mote, P.W., Li, S., Lettenmaier, D.P., Xiao, M., Engel, R., 2018. Dramatic declines in snowpack in the western US. Npj Clim. Atmos. Sci. 1 (1), 2.
- Musselman, K.N., Clark, M.P., Liu, C., Ikeda, K., Rasmussen, R., 2017. Slower snowmelt in a warmer world. Nat. Clim. Change 7 (3), 214–219.
- Oishi, A.C., Hawthorne, D.A., Oren, R., 2016. Baseliner: an open-source, interactive tool

- for processing sap flux data from thermal dissipation probes. SoftwareX 5, 139–143. Owston, P.W., Smith, J.L., Halverson, H.G., 1972. Seasonal water movement in tree stems. Forest Sci. 18, 266–272.
- Paz-Kagan, T., Brodrick, P.G., Vaughn, N.R., Das, A.J., Stephenson, N.L., Nydick, K.R., Asner, G.P., 2017. What mediates tree mortality during drought in the southern Sierra Nevada? Ecol. Appl. 27 (8), 2443–2457.
- Pelletier, J.D., et al., 2018. Which way do you lean? Using slope aspect variations to understand critical zone processes and feedbacks. Earth Surf. Process. Landforms 43 (5), 1133–1154.
- Peters, R.L., et al., 2018. Quantification of uncertainties in conifer sap flow measured with the thermal dissipation method. New Phytol. 219 (4), 1283–1299.
- Rabbel, I., Diekkrüger, B., Voigt, H., Neuwirth, B., 2016. Comparing ΔT_{max} determination approaches for Granier-based sapflow estimations. Sensors 16 (12), 2042.
- Royce, E.B., Barbour, M.G., 2001. Mediterranean climate effects. I. Conifer water use across a Sierra Nevada ecotone. Am. J. Bot. 88 (5), 911–918. https://doi.org/10. 2307/2657044.
- Running, S.W., Reid, C.P., 1980. Soil temperature influences on root resistance of Pinus contorta seedlings. Plant Physiol. 65, 635–640.
- Seabold, S., Perktold, J., 2010. Statsmodels: econometric and statistical modeling with python. In: Proceedings of the 9th Python in Science Conference.
- Sevanto, S., Suni, T., Pumpanen, J., Grönholm, T., Kolari, P., Nikinmaa, E., Hari, P., Vesala, T., 2006. Wintertime photosynthesis and water uptake in a boreal forest. Tree Physiol. 26, 749–757.
- Scott-Denton, L.E., Moore, D.J.P., Rosenbloom, N.A., Kittel, T.G.F., Burns, S.P., Schimel, D.S., Monson, R.K., 2013. Forecasting net ecosystem CO₂ exchange in a subalpine forest using model data assimilation combined with simulated climate and weather generation. J. Geophys. Res. 118 (2), 549–565.
- Snyder, K.A., Richards, J.H., Donovan, L.A., 2003. Night-time conductance in C3 and C4 species: do plants lose water at night? J. Exp. Bot. 54 (383), 861–865.
- Steppe, K., De Pauw, D.J.W., Doody, T.M., Teskey, R.O., 2010. A comparison of sap flux density using thermal dissipation, heat pulse velocity and heat field deformation methods. Agric. For. Meteorol. 150 (7–8), 1046–1056.
- Stephenson, N.L., 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. J. Biogeogr. 25 (5), 855–870. https://doi.org/10.1046/j.1365-2699.1998.00233.x.
- Sylvester, A.G., and Raines, G.L. (2017). Geologic map of the Independence Lake and Hobart Mills 7.5' Quadrangles, Nevada and Sierra Counties, California, California Department of Conservation, Sacramento, CA.
- Tague, C., Peng, H., 2013. The sensitivity of forest water use to the timing of precipitation and snowmelt recharge in the California Sierra: implications for a warming climate. J. Geophys. Res. 118 (2), 875–887.
- Tennant, et al., 2017. Regional sensitivies of seasonal snowpack to elevation, aspect, and vegetation cover in western North America. Water Resour. Res. 53, 6908–6926.
- Trujillo, E., Molotch, N.P., Goulden, M.L., Kelly, A.E., Bales, R.C., 2012. Elevation-dependent influence of snow accumulation on forest greening. Nat. Geosci. 5 (10), 705–709.
- Trustman, B., 2016. Characterizing spatial and temporal variability of snow water equivalent using pressure sensors. [Thesis]. Univ. Nevada, Reno.
- Urban, D.L., Miller, C., Halpin, P.N., Stephenson, N.L., 2000. Forest gradient response in Sierran landscapes: the physical template. Landsc. Ecol. 15 (7), 603–620. https://doi. org/10.1023/A:1008183331604.
- Verhoeven, A.S., Adams, W.W., Demmig-Adams, B., 1999. The xanthophyll cycle and acclimation of Pinus ponderosa and Malva neglecta to winter stress. Oecologia 118 (3), 277–287.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313, 940–943.
- Westerling, A.L., 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Phil. Trans. R. Soc. B 371, 20150178.
- Winchell, T.S., Barnard, D.M., Monson, R.K., Burns, S.P., Molotch, N.P., 2016. Earlier snowmelt reduces atmospheric carbon uptake in midlatitude subalpine forests. Geophys. Res. Lett. 43 (15), 8160–8168.
- Woelber, B., Maneta, M.P., Harper, J., Jencso, K.G., Gardner, W.P., Wilcox, A.C., Lópezmoreno, I., 2018. The influence of diurnal snowmelt and transpiration on hillslope throughflow and stream response. Hydrol. Earth Syst. Sci. 22, 4295–4310.
- Xu, Q., Man, A., Fredrickson, M., Hou, Z., Pitkänen, J., Wing, B., Ramirez, C., Li, B., Greenberg, J.A., 2018. Quantification of uncertainty in aboveground biomass estimates derived from small-footprint airborne LiDAR. Remote Sens. Environ. 216, 514–528.
- Zapata-Rios, X., Brooks, P.D., Troch, P.A., McIntosh, J., Guo, Q., 2016. Influence of terrain aspect on water partitioning, vegetation structure and vegetation greening in high-elevation catchments in northern New Mexico. Ecohydrology 9 (5), 782–795.