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Key Points:

- Higher evapotranspiration on cooler pole-facing slope than warmer equator-facing slope within an oak savanna in a Mediterranean climate
- Aspect-differences in plant functional groups and phenology drive observed evapotranspiration variability
- Higher evapotranspiration contributes to a drier subsurface on pole-facing slopes

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

A. Donaldson,
amdonald@ucsc.edu

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Author Contributions:

Conceptualization: Amanda Donaldson, David Dralle, Margaret Zimmer

Data curation: Amanda Donaldson

Formal analysis: Amanda Donaldson, David Dralle

Funding acquisition:

Amanda Donaldson, Margaret Zimmer

Investigation: Amanda Donaldson, Nerissa Barling

Methodology: Amanda Donaldson, David Dralle, Michael E. Loik, Margaret Zimmer

Project administration:

Margaret Zimmer

Supervision: David Dralle, Michael E. Loik, Margaret Zimmer

Visualization: Amanda Donaldson

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Aspect Differences in Vegetation Type Drive Higher Evapotranspiration on a Pole-Facing Slope in a California Oak Savanna

Amanda Donaldson¹ , David Dralle² , Nerissa Barling¹ , Russell P. Callahan^{1,3} , Michael E. Loik⁴ , and Margaret Zimmer¹ 

¹Department of Earth and Planetary Sciences, University of California, Santa Cruz, CA, USA, ²Pacific Southwest Research Station, United States Forest Service, Albany, CA, USA, ³Department of Earth Sciences, University of Connecticut, Storrs, CT, USA, ⁴Department of Environmental Studies, University of California, Santa Cruz, CA, USA

Abstract Quantifying evapotranspiration (ET) is critical to accurately predict vegetation health, groundwater recharge, and streamflow generation. Hillslope aspect, the direction a hillslope faces, results in variable incoming solar radiation and subsequent vegetation water use that drive ET. Previous work in watersheds with a single dominant vegetation type (e.g., trees) have shown that equator-facing slopes (EFS) have higher ET compared to pole-facing slopes (PFS) due to higher evaporative demand. However, it remains unclear how differences in vegetation type (i.e., grasses and trees) influence ET and water partitioning between hillslopes with opposing aspects. Here, we quantified ET and root-zone water storage deficits between a PFS and EFS with contrasting vegetation types within central coastal California. Our results suggest that the cooler PFS with oak trees has higher ET than the warmer EFS with grasses, which is counter to previous work in landscapes with a single dominant vegetation type. Our root-zone water storage deficit calculations indicate that the PFS has a higher subsurface storage deficit and a larger seasonal dry down than the EFS. This aspect difference in subsurface water storage deficits may influence the subsequent replenishment of dynamic water storage, groundwater recharge and streamflow generation. In addition, larger subsurface water deficits on PFS may reduce their ability to serve as hydrologic refugia for oaks during multi-year droughts. This research provides a novel integration of field-based and remotely-sensed estimates of ET required to properly quantify hillslope-scale water balances. These findings emphasize the importance of resolving hillslope-scale vegetation structure within Earth system models, especially in landscapes with diverse vegetation types.

Plain Language Summary Understanding how much water leaves hillslopes as evapotranspiration (i.e., evaporation and plant water use) is important for predicting water storage and movement within hillslopes. Small differences in solar radiation between adjacent hillslopes that face opposite directions can produce contrasting plant water use and hillslope water storage patterns. However, previous studies have focused on landscapes with trees on either hillslope. It remains unclear how the combination of differences of solar radiation and plant type (i.e., grasses and trees) influence evapotranspiration and water storage within hillslopes that face opposite directions. Here, we combined on-site measurements and remote-sensing data to show that in central coastal California, a hillslope with oak trees that received less direct sunlight had higher evapotranspiration than a hillslope with grasses that received more direct sunlight. Importantly, we suggest that the cooler hillslope with oak trees may be drier and have lower groundwater recharge than the warmer hillslope with grasses, which is opposite the findings of studies with trees on both hillslopes. Our findings highlight the critical need for forest managers and modelers to consider hillslope-scale vegetation types to more accurately predict groundwater recharge, streamflow generation, and vegetation health within oak savannas.

1. Introduction

Differences in hillslope aspect, or the direction a hillslope faces, produce subcatchment-scale variability in the delivery of solar radiation to the land surface, which is one of the strongest controls on vegetation distribution and water partitioning within terrestrial landscapes (Chorover et al., 2011; Fan et al., 2019). Equator-facing slopes (EFS; south-facing in the northern hemisphere) with more direct solar radiation have higher air temperature, aridity, and evaporative demand compared to pole-facing slopes (PFS, north-facing in the northern hemisphere (Smith & Bookhagen, 2021)). Current conceptual frameworks depict warmer EFS with higher potential evapotranspiration and subsequently lower infiltration, groundwater recharge, and runoff (García-Gamero

Writing – original draft:

Amanda Donaldson

Writing – review & editing:

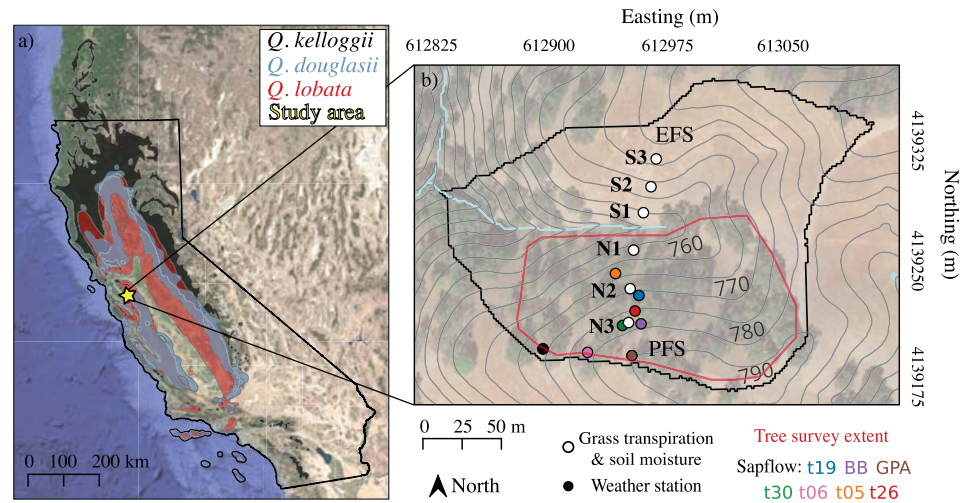
Amanda Donaldson, David Dralle,
Nerissa Barling, Russell P. Callahan,
Michael E. Loik, Margaret Zimmer


Figure 1. (a) Location of study area (yellow star) and approximate natural range of *Q. kelloggii* (black shaded region), *Q. lobata* (red shaded region), *Q. douglasii* (blue shaded region) (United States. Forest Service, 1971). Background is a Google Earth Imagery shaded relief of topography. (b) Study site with instrumentation nests of grass transpiration and soil moisture measurements (white), weather station (black), study trees with sap flow sensors (colors) and tree survey extent (red line). Stream channels are delineated in light blue; contour interval is 5 m and numbers refer to elevation in m above sea level.

et al., 2021; Pelletier et al., 2018; Regmi et al., 2019; Webb et al., 2023). In contrast, cooler PFS are considered to have lower potential evapotranspiration and higher infiltration, groundwater recharge, and runoff (García-Gamero et al., 2021; Pelletier et al., 2018; Regmi et al., 2019; Webb et al., 2023). While this current conceptual model may provide insight into how differences in energy inputs drive hydrologic partitioning, it is unclear if the expected patterns are universal across diverse environments and vegetation types (Brooks et al., 2015; Fan et al., 2019; Zapata-Rios et al., 2016).

Understanding the compounding role of variable solar radiation and plant functional groups (e.g., grass, tree, shrub) on hydrologic partitioning is important for determining the transferability of current expectations of water cycling between hillslopes with opposing aspects (Kumari et al., 2020). The current conceptual model of hydrologic partitioning within aspect-regulated landscapes is largely based on environments where potential differences in actual evapotranspiration (ET) due to variability in plant functional groups are not incorporated (Pelletier et al., 2018; Regmi et al., 2019). Studies in watersheds with similar plant functional groups (e.g., trees) have shown higher transpiration rates on EFS compared to PFS (Bilir et al., 2021; Burns et al., 2023; Holst et al., 2010). However, the diversity in water use strategies (e.g., due to differences in rooting depth) among different plant functional groups and species can result in complex vegetation water uptake patterns between aspects which have lesser known impacts on subsurface water cycling (Armesto & Martinez, 1978; Gutiérrez-Jurado et al., 2013; Hassler et al., 2018; Murphy et al., 2020). Given the importance of vegetation water uptake in driving subsurface hydrologic partitioning, understanding the role of vegetation type is required to accurately forecast water cycling patterns within Earth system models (Fan et al., 2019; Kumari et al., 2020; Marston et al., 2022).

Here, we address these knowledge gaps by quantifying hourly to monthly ET and shallow subsurface water storage between a grass-dominated EFS and an oak tree-dominated PFS in central California. We combined field-based measurements of soil moisture, oak and grass transpiration, tree survey-based transpiration scaling, and remotely-sensed normalized difference vegetation index (NDVI) and ET to determine how hydrologic partitioning differs between hillslopes with opposing aspects and different plant community types.

2. Methods

2.1. Site Description and Instrumentation

The study site (Arbor Creek Experimental Catchment; 37.393, −121.723) ranges from 720 to 790 m above sea level and is located within the University of California, Berkeley operated Blue Oak Ranch Reserve (Figure 1).

This reserve is located within the Mt. Diablo Range, ~24 km northeast of San Jose, California, USA. The local climate is classified as Mediterranean, with hot, dry summers and cool, wet winters and an average 600 mm of precipitation mostly falling as rain between October and April (Donaldson et al., 2023). Soils are loamy and thin (~50 cm) and the dominant rock types are sandstone and shale consistent with the Yolla Bolly Unit and the Great Valley Sequence (Donaldson et al., 2023).

We installed a weather station (ClimaVUE50, Campbell Scientific; Logan, Utah) at the ridge of the PFS to record precipitation at 10-min intervals from 1 October 2020—30 September 2021 (2021 water year). We excavated soil pits at each landscape position (e.g., toeslope, mid-slope, and shoulder) on the PFS and EFS (Figure 1). We monitored soil moisture (ECHO/EC-5, Decagon, Devices Inc. Washington, USA) every 10-min at 10 and 50 cm depths from winter 2020 through September 2021 (start date varied due to sensor installation).

The study site is characterized as a mixed-deciduous oak savanna composed of blue oak (*Quercus douglasii* Hook., Fagaceae), black oak (*Quercus kelloggii*, Newb.), and valley oak (*Quercus lobata*, Nee), with evidence of some extent of hybridization between species (Nixon, 2002). While oaks are largely on the PFS, grasses are across the study site and include species from both native and non-native genera, including *Avena*, *Bromus*, and *Elymus* (Pers. Comm. land steward Zachariah Tuthill).

2.2. Field-Based Transpiration Measurements

We measured plot-scale, surface ET with an open-path, infrared gas analyzer (model LI-7500, LICOR, Lincoln, Nebraska) within a chamber (0.5 m x 0.5 m x 0.5 m) constructed of a polyvinyl chloride pipe frame, covered by Tefzel film with a fan placed inside for chamber mixing (Figure S1 in Supporting Information S1; Huxman et al., 2004). This measurement included both evaporation from the ground surface and grass transpiration, however, we assume that the evaporative flux is negligible, thus we refer to this measurement as “grass transpiration” throughout the manuscript (Arnone & Obrist, 2003; Schlesinger & Jasechko, 2014). We collected measurements weekly at each instrument nest starting when the grass became active after the first rainfall (10 December 2020) to when the grass senescence (10 June 2021), which represented a full grass growing season. We averaged grass transpiration across landscape positions on the PFS and EFS to determine hillslope-averaged grass transpiration for each measurement period. To determine a weekly hillslope-averaged grass transpiration, we assumed each measurement to be representative of the week and multiplied by seven (number of days in the week). To calculate total grass growing season transpiration (December—June), we summed each hillslope-averaged grass transpiration value.

To quantify oak water use, we installed heat pulse velocity sap flow probes (Edaphic Scientific; Forster, 2019, 2020) within seven mature oak trees at 1.4 m height above ground surface (e.g., breast height) along the PFS of Arbor Creek Experimental Catchment. We chose the instrumented oak trees to include a wide range of landscape positions and sizes (Table S1 in Supporting Information S1). We measured sap flux during the oak tree growing season at 10 mm (outer position) and 20 mm (inner position) within the xylem every 15-min from May to December 2021. To correct for probe misalignment during installation, we assumed zero flow after leaf off (late December 2021) and used a wound correction diameter of 0.2 mm (Burgess et al., 2001). To measure sapwood thickness, we extracted tree cores using an increment borer in August 2021 and identified a shift from translucence to opaqueness, which represented the sapwood to heartwood transition (Quiñonez-Piñón & Valeo, 2018). With these cores, we quantified wood water content and density, which we used to convert heat pulse velocity to sap flux (Burgess et al., 2001). We quantified the radial profile of sap flux in two ways and for the final calculations we assume a constant maximum measured sap flux across the sapwood (see Text 1.2 in Supporting Information S1 for details; Link et al., 2014). To calculate sap flow volumetrically, we multiplied the sap flux by the corresponding sapwood area of the tree.

To scale oak tree sap flow measurements to hillslope-scale transpiration, we performed cruising surveys of every oak tree on the pole-facing hillslope (red outline in Figure 1b). A total of 113 trees were surveyed within the 12,550 m² survey area, which were used to estimate total hillslope-scale oak tree transpiration. We recorded the species and diameter at breast height (DBH) for each tree (Table 2 in Supporting Information S1). Trees that forked below breast height were recorded as two individual trees. We estimated the growing season total sap flow for the surveyed trees using a power law function relating tree diameter to the growing season total sap flow for the instrumented trees. We summed the total sap flow for all trees and divided it by the survey area to quantify a hillslope-scale oak tree transpiration magnitude [mm].

2.3. Remotely-Sensed NDVI and ET

To explore temporal variability in vegetation greenness, we used Google Earth Engine to extract weekly NDVI values from the mid-slope position on the PFS and EFS using images collected from January 2017 to December 2021 on the Copernicus Sentinel-2 mission (10-m spatial resolution). NDVI compares the intensity of reflectance in the visible red and near-infrared spectrum to quantify vegetation greenness (Acker et al., 2014).

We quantified ET at the mid-slope position of our study hillslopes, with remotely-sensed ET products using Python application programming interface to access models from OpenET (Melton et al., 2022). OpenET uses Landsat imagery to estimate monthly ET at 30 m resolution with a variety of approaches, including surface energy balance, Priestley-Taylor, and psychrometry (FAO, 2023) (see Text 1.3 in Supporting Information S1 for details). A multi-model Ensemble ET estimate was calculated by OpenET based on the arithmetic average after removing outliers using the Median Absolute Deviation method (Leys et al., 2013; Volk et al., 2024). While we included the ET results from all models in the Supporting Information S1 (Figure S3), we used the Ensemble model for analyses in this study.

2.4. Subsurface Water Storage Deficit Calculations

We calculated the hillslope-average soil water storage [mm] by integrating soil water content from the surface to the 50 cm depth. We calculated the soil water storage deficit by subtracting the volumetric water content at each timestep from the maximum recorded volumetric water content, assuming the maximum represents a maximum unsaturated water content at field capacity. In addition, we compare this to an estimated subsurface water storage deficit calculated by the total field-based ET measurements on the EFS and the PFS.

Previous studies have shown that oak tree roots can extend beneath the soil, into the unsaturated weathered bedrock, to extract deeper water storage referred to as rock moisture (Hahm et al., 2020, 2022; McCormick et al., 2021). To estimate this deeper storage we calculated the root-zone storage deficit (i.e., soil and rock moisture) from October 2017 to September 2021 using statistically interpolated precipitation data (Oregon State's Parameter-elevation Regressions on Independent Slopes Model daily precipitation) and remotely-sensed ET (Ensemble model from OpenET; described above) following the method by Wang-Erlandsson et al. (2016) and adapted by Dralle et al. (2021). The method used a mass-balance approach to estimate a root-zone storage deficit as a running, integrated difference between fluxes entering and exiting the root zone, assumed to be precipitation and ET, respectively. Here, we estimated the root-zone storage deficit over subsequent water years (2017–2021), where the running deficit represents a lower-bound on the amount of ET supplied from the root zone that has not been replenished by precipitation. Therefore, the root-zone storage deficit represents the minimum amount of vegetation water uptake that is not accounted for by precipitation (refer to Dralle et al., 2021; McCormick et al., 2021; Wang-Erlandsson et al., 2016 for details).

3. Results

3.1. Field-Based Estimates of Grass and Oak Transpiration

The EFS consistently had higher weekly grass transpiration than the PFS (Figure 2). The average grass transpiration on the EFS was 3.7 mm/week, while the average on the PFS was 1.9 mm/week. The total growing season grass transpiration was 99 and 50 mm, on the EFS and PFS, respectively. Anecdotally, we observed higher grass density on the EFS compared to the PFS (Figure S2 in Supporting Information S1).

Oak tree transpiration varied across the growing season (Figure 3a). Oak tree leaf development began in April (not entirely recorded due to sensor installation) and transpiration was generally low until a rapid increase in May. Transpiration reached a maximum in June and remained relatively constant until late August/September, when there was a decline. In October, there was an increase in transpiration that coincided with the first precipitation event of the fall, which lasted until December when the oak trees went dormant (Figure 3a).

Average volumetric oak tree transpiration (L/day) was positively correlated with DBH (Figure 3). For example, during oak tree peak water use (June), transpiration varied by DBH from approximately 12 L/day (T30; DBH: 30.6 cm) to 1100 L/day (GPA; DBH: 108.3; Figure 3a). Consequently, total oak tree growing season transpiration generally varied with DBH (Figure 3b). From the smallest tree to the largest tree, the total growing season transpiration magnitude increased from 1,427 L, 13,433 L, 4,373 L, 5,078 L, 12,988 L, 57,962 L, and 147,387 L.

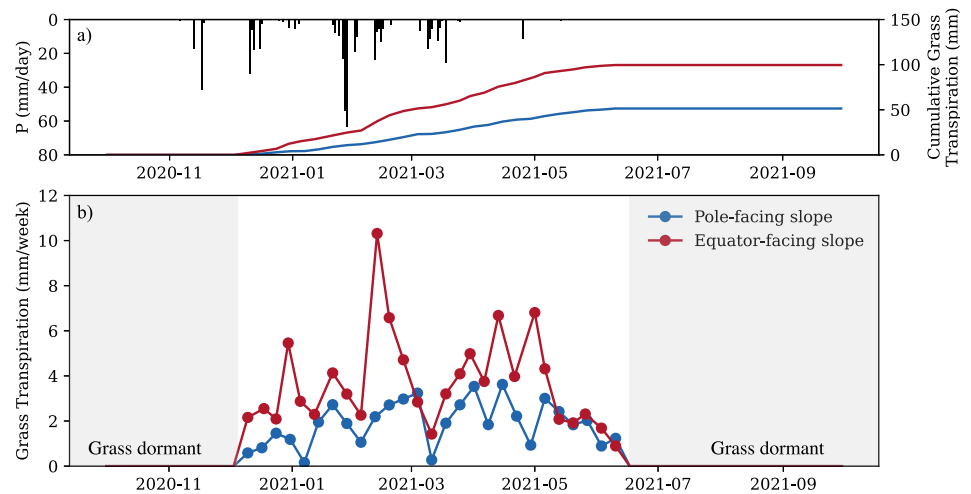


Figure 2. (a) Daily precipitation from October 2020 to September 2021 (black bars) and cumulative grass transpiration for pole-facing slopes (PFS) (blue) and equator-facing slopes (EFS) (red), (b) Slope-averaged weekly grass transpiration measurements for the PFS (blue) and EFS (red). Shaded regions are time periods with no measurements because grasses were dormant.

(Figure 3b). The total hillslope-scale oak tree transpiration for the entire sap flow measurement period (May—December 2021) was 172 and 148 mm for the 2021 water year (May—September 2021).

3.2. Remotely-Sensed NDVI and ET

There were annually consistent seasonal differences in NDVI values between the PFS and EFS (Figure 4a). During the winter season with only grasses actively transpiring (November—April), the EFS NDVI was on average 0.37, while the PFS NDVI was on average 0.32. During the oak tree growing season (April—October), the PFS had higher average NDVI (0.39) than the EFS (0.28). During the 2021 water year, which coincided with our field-based measurement time period, the average NDVI values on the PFS and EFS were 0.33 and 0.28, respectively.

The remotely-sensed monthly ET was always higher on the PFS than the EFS (Figure 4b). During the winter, the average ET on the PFS was 41 mm/month, while the average ET on the EFS was 21 mm/month. During the oak tree growing season, the average ET on the PFS was 64 mm/month, while the average ET on the EFS was 29 mm/month. During the 2021 water year, the total ET on the PFS and EFS were 649 and 195 mm, respectively.

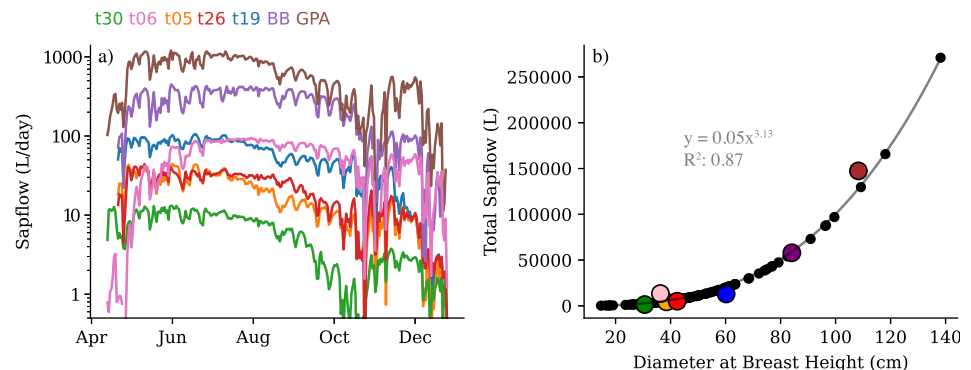


Figure 3. (a) Daily sap flow (L/day) on log-scale, (b) total sap flow (L) by diameter at breast height (cm) for each instrumented tree (colors) and surveyed trees fitted with a power-law function (black line).

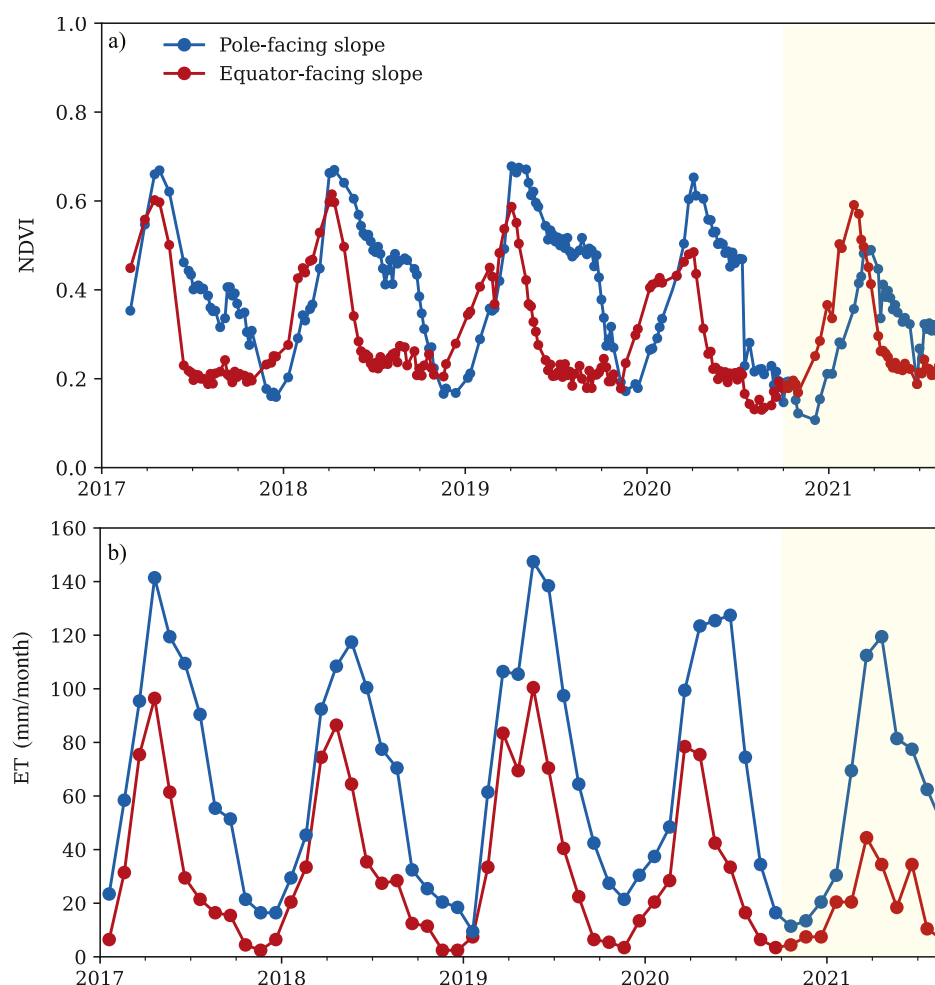


Figure 4. (a) Weekly normalized difference vegetation index on pole-facing slopes (PFS) (blue) and equator-facing slopes (EFS) (red) from January 2017 to September 2021. (b) Ensemble monthly ET on the PFS (blue) and EFS (red) for the same period. The field-based measurements timeframe is shaded in yellow (see Figures 2, 3, and 5).

3.3. Subsurface Water Storage Deficit

During the 2021 water year, the timing and magnitude of field-calculated soil water storage varied by season between hillslopes with opposing aspects (Figure 5b). There was higher subsurface water storage depletion on the EFS during the winter season, when grasses were active (January–April, Figure 2). In contrast, during the beginning of summer (April–June), the EFS had negligible soil water depletion, while there was considerable soil water storage depletion on the PFS with active oak trees (Figure 5b). At the end of the summer (September), there was a slightly lower soil water storage deficit on the EFS (94 mm) than the PFS (104 mm). In comparison, field-based ET measurements for the 2021 water year (October 2020–September 2021) were used to calculate a subsurface storage deficit of 99 mm on the EFS (i.e., total grass transpiration) and 198 mm on the PFS (i.e., total grass and oak tree transpiration).

Across the 2017–2021 water years, the remotely-sensed root-zone storage deficits between the PFS and EFS showed contrasting behavior. Despite variability in precipitation magnitude, the root-zone storage deficit on the EFS (average 110 mm; standard deviation = 84 mm) was replenished each year (i.e., returned to zero; Figure 6). In contrast, on the PFS, the root-zone storage deficit was not annually replenished and increased from 534 mm at the end of water year 2017 to 1,608 mm at the end of water year 2021.

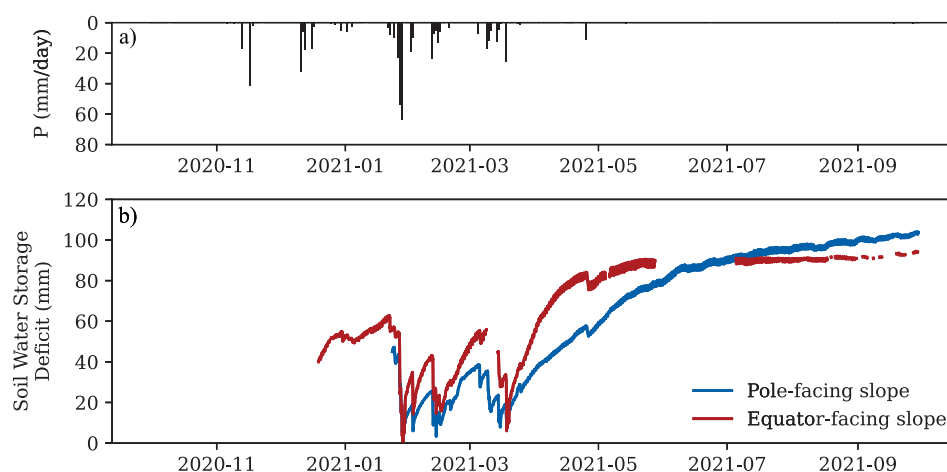


Figure 5. (a) Daily precipitation from October 2020 to September 2021, (b) Field observations of slope-averaged soil water storage deficit within the top 50 cm from January to September 2021 on the pole-facing slopes (blue) and equator-facing slopes (red).

4. Discussion

4.1. Ecohydrologic Implications for Higher ET on PFS

Within Arbor Creek Experimental Catchment, we found that the woody-vegetation (i.e., oak trees) transpired more than herbaceous vegetation (i.e., grasses). Therefore, oak tree transpiration contributed a larger portion to overall catchment ET than grasses, which aligns with other studies in California savannas (Baldocchi et al., 2021; Ma et al., 2020). During the water year 2021 (1 October—30 September), the estimated average ET within Arbor Creek Experimental Catchment ranged between 149 mm (field-based measurements) and 422 mm (remotely-sensed measurements). We interpret this observed range to represent a possible lower and upper bound on the true ET magnitude (see Section 4.3), which encompasses other reported ET values in California oak savannas (Baldocchi et al., 2010, 2021; Lewis et al., 2000; Ma et al., 2020).

The magnitude and timing of ET exerts a strong control on subsurface water storage and movement (Li et al., 2018; Sadayappan et al., 2023). In both the field-based estimates and remotely-sensed estimates of subsurface storage deficits, we observed higher subsurface water storage deficits on PFS compared to EFS. It is likely that oak tree water uptake from rock moisture (i.e., water stored within weathered bedrock) may limit water

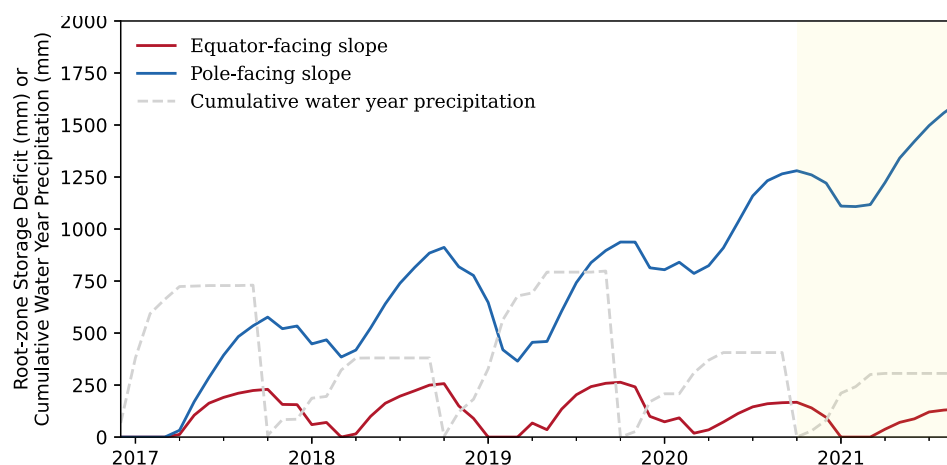


Figure 6. Monthly root-zone storage deficit for pole-facing slopes (blue) and equator-facing slopes (red) and cumulative water year precipitation (dashed gray; Parameter-elevation Regressions on Independent Slopes Model Climate Group, Oregon State University, <http://prism.oregonstate.edu>). The period of field-based ET and soil moisture measurements are shaded in yellow.

available for groundwater recharge and streamflow generation on PFS (Dralle et al., 2023). Under these conditions, we hypothesize that groundwater recharge and streamflow contributions may be higher on EFS, which is contrary to existing conceptual models of water partitioning between hillslopes with opposing aspects (Pelletier et al., 2018; Regmi et al., 2019; Webb et al., 2023). Future field work utilizing deeper measurement tools, such as a neutron probe or other geophysical tools, will be used to validate the derived estimates of subsurface water storage and test this hypothesis.

In water-limited and rain-dominated landscapes, variability in root-zone storage deficit is a strong control on the spatial distribution of ecosystem resilience to disturbances, such as drought (Callahan et al., 2022). Our results suggest that multiple consecutive years of low precipitation inputs may exacerbate root-zone water storage deficits on PFS. During multi-year droughts, consistently high root-zone storage deficits on PFS may cause oak trees to be more susceptible to mortality (Ackerly et al., 2020; Brown et al., 2018; Kueppers et al., 2005). To test this hypothesis, more research is needed to understand the evolution of oak drought tolerance traits (e.g., leaf size, water use efficiency, hydraulic safety margin) to mediate the effects of warmer and drier conditions due to a changing climate (Skelton et al., 2021).

In comparison, even in relatively low precipitation years, our results indicate that subsurface water storage is replenished on the EFS. This finding highlights an important question: why aren't there oaks on the EFS with a lower subsurface water storage deficit? We hypothesize that the absence of oak trees on EFS may be driven by higher air temperature, higher vapor pressure deficits, lower shallow soil moisture, and/or greater competition with grasses that may limit oak seedling survival, despite potentially higher water availability below the soil (Nudurupati et al., 2023; Swiecki & Bernhardt, 1998). These findings highlight the importance of adequately representing plant functional group distributions and water uptake patterns through time to accurately refine water balances within aspect-regulated landscapes (Fan et al., 2019; Istanbuloglu & Bras, 2005; Nudurupati et al., 2023; Zhou et al., 2013).

4.2. Stability and Resiliency of Semi-Arid Savanna Ecosystems in a Changing Climate

Within dry savannas (<650 mm mean annual precipitation), Walter's two layer model, which suggests a spatial hydrologic niche partitioning between shallow-rooted grasses and deep-rooted trees, is commonly shown to hold true (Walter, 1939; Ward et al., 2013). We similarly observed evidence for spatially distinct water sources between grasses and trees within Arbor Creek Experimental Catchment. For example, total grass transpiration was equivalent to the total soil water storage deficit, and the grasses went dormant in early June corresponding to when the soils dried (Figure 2). This suggests that the grasses were reliant on water storage within the shallow soil layer (<50 cm). By comparison, the deciduous oak trees became active in April and had peak transpiration from June to August when the upper soil layers were likely close to wilting point, which suggests oak trees were accessing deeper water (>50 cm deep). While this supports Walter's spatially distributed two layer model, the distinct phenology between oak trees and grasses also emphasizes the importance of temporal hydrological niche partitioning (Matos et al., 2022; Ward et al., 2013). Importantly, more research is needed to identify whether hydrologic competition and/or facilitation occurs through the hydraulic redistribution of deeper water to shallower depths by oak tree roots from April to June, when both the oak trees and grasses are active (Barron-Gafford et al., 2017; Ishikawa & Bledsoe, 2000; Scott et al., 2008). Moreover, future work investigating the controls on oak tree spring budburst is required to constrain how climate changes will influence the extent of overlapping grass and oak tree activity (Gómez-Giráldez et al., 2020; Liu et al., 2017).

Seasonally dry savannas have pronounced interannual variability in rainfall (timing, intensity and magnitude) which have important implications for plant-available water storage and vegetation water use (Vico et al., 2015). Within Arbor Creek Experimental Catchment, grass transpiration was highly responsive to relatively small and frequent rainfall pulses during the winter season (<20 mm, Figure 2). By comparison, oak tree water use (largely limited to the dry summer) was temporally decoupled from the direct effects of event-scale rainfall (Figure 3a). Instead, oak water use was likely more sensitive to the total magnitude of previous winter rainfall that was partitioned into the deep subsurface (Hahm et al., 2019), which may indirectly be influenced by event-scale rainfall dynamics (e.g., intensity may influence infiltration totals). Despite differences in rainfall seasonality, these vegetation water use strategies are consistent with research at the Santa Rita Experimental Range (SRER) located near Tucson, Arizona where precipitation dynamics are defined by the North American monsoon during the summers (Adams & Comrie, 1997; Scott et al., 2009). SRER is characterized as a savanna dominated by

evergreen mesquite trees and a mixed herbaceous understory (Scott & Biederman, 2019). Previous studies within this landscape have demonstrated that small, frequent, rainfall pulses are hydrologically important for the herbaceous understory, while the proportion of large rain events that adequately recharge the deeper subsurface are critical for woody-vegetation (Liang et al., 2021; Szutu & Papuga, 2019). As future rainfall intensities and drought conditions are expected to become more severe across the American west, it is essential for future research to investigate the role of rainfall variability on vegetation water uptake across seasonally dry savannas (Fust & Schlecht, 2022; Zhang et al., 2021).

Limited research has investigated the interplay between ET and subsurface storage dynamics below the top meter of soil despite widespread evidence of deeply rooted vegetation and drainage within savannas (Seyfried et al., 2005). A notable exception includes work by Hahm et al. (2022) within a California blue oak savanna which showed that oak water use during the dry growing season was sustained by water stored in weathered bedrock below the soil and above the water table. However, while the authors describe the landscape as “aspect-regulated with negligible woody-vegetation on EFS,” the authors do not include information about the differences in oak tree and grass water uptake. While previous studies in California have suggested that groundwater may sustain oak transpiration when soil water is depleted (Miller et al., 2010), within Arbor Creek Experimental Catchment the winter transient water table at ~5 m is absent during the summer growing season (Donaldson et al., 2023) and the permanent water table is tens of meters below the land surface (Callahan et al., 2024). Given the lack of groundwater present, this suggests that oak transpiration is likely reliant on unsaturated water storage within weathered bedrock (Hahm et al., 2020, 2022). Our research contributes to a growing body of literature that demonstrates the ecohydrologic importance of water stored in weathered bedrock for oak trees and the need to expand hydrologic measurements below the soil in savanna ecosystems.

4.3. Multi-Tool Approaches to Quantify Oak Savanna ET

An accurate quantification of hillslope-scale ET is essential for sustainable water resource management in the face of a changing climate, but it remains one of the biggest challenges within the ecohydrologic sciences (Brooks et al., 2015; Fan et al., 2019; Marston et al., 2022). Through the advancement of field-based techniques and remote-sensing technology, the ecohydrology community is entering an exciting frontier where we can combine approaches and provide water resource managers with more accurate ET estimates (Volk et al., 2024). However, each method to quantify plant water uptake includes a suite of benefits and limitations that must be considered.

Field-based measurements using sap flow sensors can directly characterize biologically mediated plant-water uptake across diverse environmental conditions (Poyatos et al., 2021). In addition, sap flow sensors can provide high temporal resolution (e.g., minutes) data, which allows for a more robust characterization of transpiration patterns compared to remote sensing, which typically reports ET on daily to monthly time intervals (Link et al., 2014; Melton et al., 2022). However, sap flow measurements often produce a conservative estimate of ET and can be time consuming, expensive, limited in scope, and require substantial field expertise (Köstner et al., 1998). For example, re-installations early in the growing season due to probe misalignment hindered our ability to quantify transpiration in April 2021, which suggests our hillslope-scale transpiration values are underestimated. In addition, the relationship between DBH and sap flow may vary across stand structure (e.g., density, species, age) and the relationship between sapwood area and DBH may vary across the oak genus (Forrester et al., 2022; Schoppach et al., 2021, 2023). This highlights the importance of well-thought-out field-based studies to identify how stand structure influences sap flow to better constrain oak transpiration from the individual tree to hillslope-scale.

Remotely-sensed estimates of ET come with their own unique set of benefits and limitations (FAO, 2023). On the one hand, remotely-sensed ET data provides information at large spatial-scales, takes minimal time for a user to acquire, and is readily comparable between diverse landscapes and different ET models (Melton et al., 2022). On the other hand, individual ET models have known, difficult-to-resolve biases that inhibit their use within upland landscapes (Wang et al., 2022; Zhao & Li, 2015). For example, most remotely-sensed models within the OpenET ensemble do not include a correction for complex terrain (e.g., slope, aspect). The ET models' inability to correct for aspect-driven differences in solar radiation may contribute to the unexpected higher ET during the winter on the PFS despite higher field-based ET on the EFS (<https://openetdata.org/known-issues/>; last accessed 9 January 2023). Therefore, we interpreted the ensemble ET to represent an upper bound of ET and highlight the need for more remotely-sensed ET models to incorporate corrections for variable terrain indices (e.g., slope, aspect) and

vegetation phenology. Given that each approach has its limitations and produces a range of ET values, a more holistic and accurate approach to quantifying ET dynamics should include multiple methods in tandem.

5. Conclusions

A commonly used conceptual model of ET, hydrologic partitioning, and landscape evolution between hillslopes with opposing aspects is based on landscapes with similar plant functional groups (e.g., trees) (Pelletier et al., 2018; Riebe et al., 2017). This conceptual model assumes that a larger energy input on EFS will induce a higher evaporative demand, increase transpiration rates, and drive higher annual ET on EFS compared to PFS (Pelletier et al., 2018). However, these studies do not account for the potential confounding influence of distinct vegetation communities on hillslopes with opposing aspects. In the Arbor Creek Experimental Catchment, we observed that the PFS had higher annual ET due to oak tree water uptake, compared to the EFS with only grasses. Higher ET on PFS contributed to higher subsurface water storage deficits through time. The larger root-zone storage deficits on the PFS may contribute to lower groundwater recharge, lower streamflow generation, and may negatively impact oak tree health over long periods of drought. Despite lower root-zone storage deficits on the EFS, the absence of oak trees suggests that over factors such as shallow soil water limitations and increased air temperature may inhibit oak tree regeneration on the EFS. Our work reveals the importance of accurately representing vegetation types and phenology at the scale of individual hillslopes to better estimate ET and subsurface hydrologic partitioning. In a larger context, our work suggests that a spatially and temporally complex interplay between climate, hydrology, and vegetation may influence the vulnerability of ecohydrologically sensitive savanna ecosystems to future climate change.

Data Availability Statement

All data used in the publication are cited in the references and are hosted on the Consortium of Universities for the Advancement of Hydrologic Science, Inc. web-based hydrologic information system (Hydroshare). <http://www.hydroshare.org/resource/b10b7c5b64c246308524238586e2fb9b>.

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References

- Acker, J., Williams, R., Chiu, L., Ardanuy, P., Miller, S., Schueler, C., et al. (2014). Remote sensing from satellites. In *Reference Module in Earth Systems and Environmental Sciences*. Retrieved from <https://cir.nii.ac.jp/crid/1360576123088102400>
- Ackerly, D. D., Kling, M. M., Clark, M. L., Papper, P., Oldfather, M. F., Flint, A. L., & Flint, L. E. (2020). Topoclimates, Refugia, and biotic responses to climate change. *Frontiers in Ecology and the Environment*, 18(5), 288–297. <https://doi.org/10.1002/fee.2204>
- Adams, D. K., & Comrie, A. C. (1997). The North American monsoon. *Bulletin of the American Meteorological Society*, 78(10), 2197–2213. [https://doi.org/10.1175/1520-0477\(1997\)078<2197:TNAM>2.0.CO;2](https://doi.org/10.1175/1520-0477(1997)078<2197:TNAM>2.0.CO;2)
- Armesto, J. J., & Martinez, J. A. (1978). Relations between vegetation structure and slope aspect in the Mediterranean region of Chile. *Journal of Ecology*, 66(3), 881–889. <https://doi.org/10.2307/2259301>
- Arnone, J. A., & Obrist, D. (2003). A large daylight geodesic dome for quantification of whole-ecosystem CO₂ and water vapour fluxes in arid Shrublands. *Journal of Arid Environments*, 55(4), 629–643. [https://doi.org/10.1016/S0140-1963\(02\)00291-4](https://doi.org/10.1016/S0140-1963(02)00291-4)
- Baldocchi, D., Chen, Q., Chen, X., Ma, S., Miller, G., Ryu, Y., et al. (2010). The dynamics of energy, water and carbon fluxes in a blue oak (*Quercus douglasii*) Savanna in California, USA. In M. J. Hill & N. P. Hanan (Eds.), *Ecosystem function in global savannas: Measurement and modeling at landscape to global scales*.
- Baldocchi, D., Ma, S., & Verfaillie, J. (2021). On the inter- and intra-annual variability of ecosystem evapotranspiration and water use efficiency of an oak savanna and annual grassland subjected to booms and busts in rainfall. *Global Change Biology*, 27(2), 359–375. <https://doi.org/10.1111/gcb.15414>
- Barron-Gafford, G. A., Sanchez-Cañete, E. P., Minor, R. L., Hendryx, S. M., Lee, E., Sutter, L. F., et al. (2017). Impacts of hydraulic redistribution on grass-tree competition vs facilitation in a semi-arid savanna. *New Phytologist*, 215(4), 1451–1461. <https://doi.org/10.1111/nph.14693>
- Bilir, T. E., Fung, I., & Dawson, T. E. (2021). Slope-aspect induced climate differences influence how water is exchanged between the land and atmosphere. *Journal of Geophysical Research: Biogeosciences*, 126(5), e2020JG006027. <https://doi.org/10.1029/2020jg006027>
- Brooks, P. D., Chorover, J., Fan, Y., Godsey, S. E., Maxwell, R. M., McNamara, J. P., & Tague, C. (2015). Hydrological partitioning in the critical zone: Recent advances and opportunities for developing transferable understanding of water cycle dynamics. *Water Resources*, 51(9), 6973–6987. <https://doi.org/10.1002/2015WR017039>
- Brown, B. J., McLaughlin, B. C., Blakey, R. V., & Morueta-Holme, N. (2018). Future vulnerability mapping based on response to extreme climate events: Dieback thresholds in an endemic California oak. *Diversity and Distributions*, 24(9), 1186–1198. <https://doi.org/10.1111/ddi.12770>
- Burgess, S. S., Adams, M. A., Turner, N. C., Beverly, C. R., Ong, C. K., Khan, A. A., & Bleby, T. M. (2001). An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiology*, 21(9), 589–598. <https://doi.org/10.1093/treephys/21.9.589>
- Burns, E. F., Rempe, D. M., Parsekian, A. D., Schmidt, L. M., Singha, K., & Barnard, H. R. (2023). Ecohydrologic dynamics of rock moisture in a Montane catchment of the Colorado front range. *Water Resources Research*, 59(6), e2022WR034117. <https://doi.org/10.1029/2022wr034117>
- Callahan, R. P., Huang, M.-H., Donaldson, A., Hudson Rasmussen, B., & Zimmer, M. (2024). Geologic and tectonic controls on deep fracturing, weathering, and water flow in the central California Coast Range. *Geophysical Research Letters*. <https://doi.org/10.1029/2024GL109129>
- Callahan, R. P., Riebe, C. S., Sklar, L. S., Pasquet, S., Ferrier, K. L., Hahm, W. J., et al. (2022). Forest vulnerability to drought controlled by bedrock composition. *Nature Geoscience*, 15(9), 714–719. <https://doi.org/10.1038/s41561-022-01012-2>

- Chorover, J., Troch, P. A., Rasmussen, C., Brooks, P. D., Pelletier, J. D., Breshears, D. D., et al. (2011). How water, carbon, and energy drive critical zone evolution: The Jemez–Santa Catalina Critical Zone Observatory. *Vadose Zone Journal: VZJ*, 10(3), 884–899. <https://doi.org/10.2136/vzj2010.0132>
- Donaldson, A. M., Zimmer, M., Huang, M.-H., Johnson, K. N., Hudson-Rasmussen, B., Finnegan, N., et al. (2023). Symmetry in hillslope steepness and saprolite thickness between hillslopes with opposing aspects. *Journal of Geophysical Research: Earth Surface*, 128(7), e2023JF007076. <https://doi.org/10.1029/2023jf007076>
- Dralle, D. N., Hahm, W. J., Chadwick, K. D., McCormick, E., & Rempe, D. M. (2021). Technical note: Accounting for snow in the estimation of root zone water storage capacity from precipitation and evapotranspiration fluxes. *Hydrology and Earth System Sciences*, 25(5), 2861–2867. <https://doi.org/10.5194/hess-25-2861-2021>
- Dralle, D. N., Hahm, W. J., & Rempe, D. M. (2023). Inferring hillslope groundwater recharge ratios from the storage-discharge relation. *Geophysical Research Letters*, 50(14), e2023GL104255. <https://doi.org/10.1029/2023gl104255>
- Fan, Y., Clark, M., Lawrence, D. M., Swenson, S. L. E. B., Brantley, S. L., Brooks, P. D., et al. (2019). Hillslope hydrology in global change research and earth system modeling. *Water Resources Research*, 55(2), 1737–1772. <https://doi.org/10.1029/2018wr023903>
- FAO. (2023). *Remote sensing determination of evapotranspiration – Algorithms, strengths, weaknesses, uncertainty and best fit-for-purpose*. Food and Agriculture Organization. <https://doi.org/10.4060/cc8150en>
- Forrester, D. I., Limousin, J.-M., & Pfautsch, S. (2022). The relationship between tree size and tree water-use: Is competition for water size-symmetric or size-asymmetric? *Tree Physiology*, 42(10), 1916–1927. <https://doi.org/10.1093/treephys/tpac018>
- Forster, M. A. (2019). The Dual Method Approach (DMA) resolves measurement range limitations of heat pulse velocity sap flow sensors. *Forests. Forests, Trees and Livelihoods*, 10(1), 46. <https://doi.org/10.3390/f10010046>
- Forster, M. A. (2020). The importance of conduction versus convection in heat pulse sap flow methods. *Tree Physiology*, 40(5), 683–694. <https://doi.org/10.1093/treephys/tpaa009>
- Fust, P., & Schlecht, E. (2022). Importance of timing: Vulnerability of semi-arid rangeland systems to increased variability in temporal distribution of rainfall events as predicted by future climate change. *Ecological Modelling*, 468, 109961. <https://doi.org/10.1016/j.ecolmodel.2022.109961>
- García-Gamero, V., Peña, A., Laguna, A. M., Giraldez, J. V., & Vanwalleghem, T. (2021). Factors controlling the asymmetry of soil moisture and vegetation dynamics in a hilly Mediterranean catchment. *Journal of Hydrology*, 598, 126207. <https://doi.org/10.1016/j.jhydrol.2021.126207>
- Gómez-Giraldez, P. J., Pérez-Palazón, M. J., Polo, M. J., & González-Dugo, M. P. (2020). Monitoring grass phenology and hydrological dynamics of an Oak–Grass savanna ecosystem using sentinel-2 and terrestrial photography. *Remote Sensing*, 12(4), 600. <https://doi.org/10.3390/rs12040600>
- Gutiérrez-Jurado, H. A., Vivoni, E. R., Cikowski, C., Harrison, J. B. J., Bras, R. L., & Istanbuluoglu, E. (2013). On the observed Ecohydrologic dynamics of a semiarid basin with aspect-delimited ecosystems. *Water Resources Research*, 49(12), 8263–8284. <https://doi.org/10.1002/2013wr014364>
- Hahm, W. J., Dralle, D. N., Rempe, D. M., Bryk, A. B., Thompson, S. E., Dawson, T. E., & Dietrich, W. E. (2019). Low subsurface water storage capacity relative to annual rainfall decouples Mediterranean plant productivity and water use from rainfall variability. *Geophysical Research Letters*, 46(12), 6544–6553. <https://doi.org/10.1029/2019gl083294>
- Hahm, W. J., Dralle, D. N., Sanders, M., Bryk, A. B., Fauria, K. E., Huang, M. H., et al. (2022). Bedrock vadose zone storage dynamics under extreme drought: Consequences for plant water availability, recharge, and runoff. *Water Resources Research*, 58(4), e2021WR031781. <https://doi.org/10.1029/2021wr031781>
- Hahm, W. J., Rempe, D. M., Dralle, D. N., Dawson, T. E., & Dietrich, W. E. (2020). Oak transpiration drawn from the weathered bedrock vadose zone in the summer dry season. *Water Resources Research*, 56(11), e2020WR027419. <https://doi.org/10.1029/2020wr027419>
- Hassler, S. K., Weiler, M., & Blume, T. (2018). Tree-stand- and site-specific controls on landscape-scale patterns of transpiration. *Hydrology and Earth System Sciences*, 22(1), 13–30. <https://doi.org/10.5194/hess-22-13-2018>
- Holst, J., Grote, R., Offermann, C., Ferrio, J. P., Gessler, A., Mayer, H., & Rennenberg, H. (2010). Water fluxes within beech stands in complex terrain. *International Journal of Biometeorology*, 54(1), 23–36. <https://doi.org/10.1007/s00484-009-0248-x>
- Huxman, T. E., Cable, J. M., Ignace, D. D., Eilts, J. A., English, N. B., Weltzin, J., & Williams, D. G. (2004). Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: The role of native versus non-native grasses and soil texture. *Oecologia*, 141(2), 295–305. <https://doi.org/10.1007/s00442-003-1389-y>
- Ishikawa, C. M., & Bledsoe, C. S. (2000). Seasonal and diurnal patterns of soil water potential in the rhizosphere of blue oaks: Evidence for hydraulic lift. *Oecologia*, 125(4), 459–465. <https://doi.org/10.1007/s004420000470>
- Istanbuluoglu, E., & Bras, R. L. (2005). Vegetation-modulated landscape evolution: Effects of vegetation on landscape processes, drainage density, and topography. *Journal of Geophysical Research*, 110(F2), F02012. <https://doi.org/10.1029/2004jf000249>
- Köstner, B., Granier, A., & Cermák, J. (1998). Sapflow measurements in forest stands: Methods and uncertainties. *Annales Des Sciences Forestières*, 55(1–2), 13–27. <https://doi.org/10.1051/forest:19980102>
- Kueppers, L. M., Snyder, M. A., Sloan, L. C., Zavaleta, E. S., & Fulfrost, B. (2005). Modeled regional climate change and California endemic oak ranges. *Proceedings of the National Academy of Sciences of the United States of America*, 102(45), 16281–16286. <https://doi.org/10.1073/pnas.0501427102>
- Kumari, N., Saco, P. M., Rodriguez, J. F., Johnstone, S. A., Srivastava, A., Chun, K. P., & Yetemen, O. (2020). The grass is not always greener on the other side: Seasonal reversal of vegetation greenness in aspect-driven semiarid ecosystems. *Geophysical Research Letters*, 47(15), e2020GL088918. <https://doi.org/10.1029/2020gl088918>
- Lewis, D., Singer, M. J., Dahlgren, R. A., & Tate, K. W. (2000). Hydrology in a California oak woodland watershed: A 17-year study. *Journal of Hydrology*, 240(1), 106–117. [https://doi.org/10.1016/S0022-1694\(00\)00337-1](https://doi.org/10.1016/S0022-1694(00)00337-1)
- Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, 49(4), 764–766. <https://doi.org/10.1016/j.jesp.2013.03.013>
- Li, H., Si, B., & Li, M. (2018). Rooting depth controls potential groundwater recharge on hillslopes. *Journal of Hydrology*, 564, 164–174. <https://doi.org/10.1016/j.jhydrol.2018.07.002>
- Liang, M., Feng, X., & Gornish, E. S. (2021). Rainfall pulses mediate long-term plant community compositional dynamics in a semi-arid rangeland. *Journal of Applied Ecology*, 58(4), 708–717. <https://doi.org/10.1111/1365-2664.13780>
- Link, P., Simonin, K., Maness, H., Oshun, J., Dawson, T., & Fung, I. (2014). Species differences in the seasonality of evergreen tree transpiration in a Mediterranean climate: Analysis of multiyear, half-hourly sap flow observations. *Water Resources*, 50(3), 1869–1894. <https://doi.org/10.1002/2013WR014023>

- Liu, Y., Hill, M. J., Zhang, X., Wang, Z., Richardson, A. D., Hufkens, K., et al. (2017). Using data from Landsat, MODIS, VIIRS and PhenoCams to monitor the phenology of California oak/grass savanna and open grassland across spatial scales. *Agricultural and Forest Meteorology*, 237–238, 311–325. <https://doi.org/10.1016/j.agrformet.2017.02.026>
- Ma, S., Eichelmann, E., Wolf, S., Rey-Sanchez, C., & Baldocchi, D. D. (2020). Transpiration and evaporation in a Californian oak-grass savanna: Field measurements and partitioning model results. *Agricultural and Forest Meteorology*, 295, 108204. <https://doi.org/10.1016/j.agrformet.2020.108204>
- Marston, L. T., Abdallah, A. M., Bagstad, K. J., Dickson, K., Glynn, P., Larsen, S. G., et al. (2022). Water-use data in the United States: Challenges and future directions. *Journal of the American Water Resources Association*, 58(4), 485–495. <https://doi.org/10.1111/1752-1688.13004>
- Matos, I. S., Binks, O., Eller, C. B., Zorger, B. B., Meir, P., Dawson, T. E., & Rosado, B. H. P. (2022). Revisiting plant hydrological niches: The importance of atmospheric resources for ground-rooted plants. *Journal of Ecology*, 110(8), 1746–1756. <https://doi.org/10.1111/1365-2745.13933>
- McCormick, E. L., Dralle, D. N., Hahm, W. J., Tune, A. K., Schmidt, L. M., Chadwick, K. D., & Rempe, D. M. (2021). Widespread woody plant use of water stored in bedrock. *Nature*, 597(7875), 225–229. <https://doi.org/10.1038/s41586-021-03761-3>
- Melton, F. S., Huntington, J., Grimm, R., Herring, J., Hall, M., Rollison, D., et al. (2022). OpenET: Filling a critical data gap in water management for the Western United States. *Journal of the American Water Resources Association*, 58(6), 971–994. <https://doi.org/10.1111/1752-1688.12956>
- Miller, G. R., Chen, X., Rubin, Y., Ma, S., & Baldocchi, D. D. (2010). Groundwater uptake by woody vegetation in a semiarid oak savanna. *Water Resources Research*, 46(10), 1–14. <https://doi.org/10.1029/2009WR008902>
- Murphy, P. C., Knowles, J. F., Moore, D. J. P., Anchukaitis, K., Potts, D. L., & Barron-Gafford, G. A. (2020). Topography influences species-specific patterns of seasonal primary productivity in a semiarid montane forest. *Tree Physiology*, 40(10), 1343–1354. <https://doi.org/10.1093/treephys/tpaa083>
- Nixon, K. C. (2002). The oak (*Quercus*) biodiversity of California and adjacent regions. In *USDA forest service general technical report PSW*. Retrieved from https://www.researchgate.net/profile/William_Tietje/publication/237372538_Cavity-nesting_Bird_Use_of_Nest_Boxes_in_Vineyards_of_Central-Coast_California/links/640d142166f8522c38997b15/Cavity-nesting-Bird-Use-of-Nest-Boxes-in-Vineyards-of-Central-Coast
- Nudurupati, S. S., Istanbuloglu, E., Tucker, G. E., Gasparini, N. M., Hobley, D. E. J., Hutton, E. W. H., et al. (2023). On transient semi-arid ecosystem dynamics using Landlab: Vegetation shifts, topographic Refugia, and response to climate. *Water Resources Research*, 59(4), e2021WR031179. <https://doi.org/10.1029/2021wr031179>
- Pelletier, J. D., Barron-Gafford, G. A., Gutiérrez-Jurado, H., Hinckley, E.-L. S., Istanbuloglu, E., McGuire, L. A., et al. (2018). Which way do you lean? Using slope aspect variations to understand critical zone processes and feedbacks. *Earth Surface Processes and Landforms*, 43(5), 1133–1154. <https://doi.org/10.1002/esp.4306>
- Poyatos, R., Werner, C., Martínez-Vilalta, J., Adams, M. A., Adorján, B., Aguadé, D., et al. (2021). Global transpiration data from sap flow measurements: The SAPFLUXNET database. *Universität*, 13(6), 2607–2649. <https://doi.org/10.5194/essd-13-2607-2021>
- Quiñonez-Piñón, M. R., & Valeo, C. (2018). Assessing the transluence and color-change methods for estimating sapwood depth in three boreal species. *Forests, Trees and Livelihoods*, 9(11), 686. <https://doi.org/10.3390/f9110686>
- Regmi, N. R., McDonald, E. V., & Rasmussen, C. (2019). Hillslope response under variable microclimate. *Earth Surface Processes and Landforms*, 44(13), 2615–2627. <https://doi.org/10.1002/esp.4686>
- Riebe, C. S., Hahm, W. J., & Brantley, S. L. (2017). Controls on deep critical zone architecture: A historical review and four testable hypotheses. *Earth Surface Processes and Landforms*, 42(1), 128–156. <https://doi.org/10.1002/esp.4052>
- Sadayappan, K., Keen, R., Jarecke, K. M., Moreno, V., Nippert, J. B., Kirk, M. F., et al. (2023). Drier streams despite a wetter climate in woody-encroached grasslands. *Journal of Hydrology*, 627, 130388. <https://doi.org/10.1016/j.jhydrol.2023.130388>
- Schlesinger, W. H., & Jasechko, S. (2014). Transpiration in the global water cycle. *Agricultural and Forest Meteorology*, 189–190, 115–117. <https://doi.org/10.1016/j.agrformet.2014.01.011>
- Schoppach, R., Chun, K. P., He, Q., Fabiani, G., & Klaus, J. (2021). Species-specific control of DBH and landscape characteristics on tree-to-tree variability of sap velocity. *Agricultural and Forest Meteorology*, 307, 108533. <https://doi.org/10.1016/j.agrformet.2021.108533>
- Schoppach, R., Chun, K. P., & Klaus, J. (2023). Allometric relations between DBH and sapwood area for predicting stand transpiration: Lessons learned from the *Quercus* genus. *European Journal of Forest Research*, 142(4), 797–809. <https://doi.org/10.1007/s10342-023-01558-9>
- Scott, R. L., & Biederman, J. A. (2019). Critical zone water balance over 13 years in a semiarid savanna. *Water Resources Research*, 55(1), 574–588. <https://doi.org/10.1029/2018WR023477>
- Scott, R. L., Cable, W. L., & Hultine, K. R. (2008). The ecohydrologic significance of hydraulic redistribution in a semiarid savanna. *Water Resources Research*, 44(2), W02440. <https://doi.org/10.1029/2007wr006149>
- Scott, R. L., Jenerette, G. D., Potts, D. L., & Huxman, T. E. (2009). Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland. *Journal of Geophysical Research*, 114(G4), G04004. <https://doi.org/10.1029/2008jg000900>
- Seyfried, M. S., Schwinning, S., Walvoord, M. A., Pockman, W. T., Newman, B. D., Jackson, R. B., & Phillips, F. M. (2005). Ecohydrological control of deep drainage in arid and semiarid regions. *Ecology*, 86(2), 277–287. <https://doi.org/10.1890/03-0568>
- Skelton, R. P., Anderegg, L. D. L., Diaz, J., Kling, M. M., Papper, P., Lamarque, L. J., et al. (2021). Evolutionary relationships between drought-related traits and climate shape large hydraulic safety margins in Western North American oaks. *Proceedings of the National Academy of Sciences of the United States of America*, 118(10), e2008987118. <https://doi.org/10.1073/pnas.2008987118>
- Smith, T., & Bookhagen, B. (2021). Climatic and biotic controls on topographic asymmetry at the global scale. *Journal of Geophysical Research: Earth Surface*, 126(1), e2020JF005692. <https://doi.org/10.1029/2020jf005692>
- Swiecki, T. J., & Bernhardt, E. (1998). Understanding blue oak regeneration. *Fremontia*, 26(1), 19–26. Retrieved from https://www.researchgate.net/profile/Tedmund-Swiecki/publication/265916814_Understanding_blue_oak_regeneration/links/573f41bb08ae9f741b321bba/Understanding-blue-oak-regeneration.pdf
- Szutu, D. J., & Papuga, S. A. (2019). Year-round transpiration dynamics linked with deep soil moisture in a warm desert shrubland. *Water Resources Research*, 55(7), 5679–5695. <https://doi.org/10.1029/2018wr023990>
- United States. Forest Service. (1971). *Atlas of United States trees: (no.1146). Conifers and important hardwoods*, by E.L. Little, Jr. U.S. Government Printing Office. Retrieved from <https://play.google.com/store/books/details?id=mlovAAAAYAAJ>
- Vico, G., Thompson, S. E., Manzoni, S., Molini, A., Albertson, J. D., Almeida-Cortez, J. S., et al. (2015). Climatic, ecophysiological, and phenological controls on plant Ecohydrological strategies in seasonally dry ecosystems. *Ecohydrology*, 8(4), 660–681. <https://doi.org/10.1002/eco.1533>

- Volk, J. M., Huntington, J. L., Melton, F. S., Allen, R., Anderson, M., Fisher, J. B., et al. (2024). Assessing the accuracy of OpenET satellite-based evapotranspiration data to support water resource and land management applications. *Nature Water*, 2(2), 1–13. <https://doi.org/10.1038/s44221-023-00181-7>
- Walter, H. (1939). Savanne und Busch der arideren Teile Afrikas in ihrer ökologischen Bedingtheit. *Geographical Review*, 31(2), 345. <https://doi.org/10.2307/210222>
- Wang, L., Wu, B., Elnashar, A., Zhu, W., Yan, N., Ma, Z., et al. (2022). Incorporation of net radiation model considering complex terrain in evapotranspiration determination with sentinel-2 data. *Remote Sensing*, 14(5), 1191. <https://doi.org/10.3390/rs14051191>
- Wang-Erlandsson, L., Bastiaanssen, W. G. M., Gao, H., Jägermeyr, J., Senay, G. B., van Dijk, A. I. J. M., et al. (2016). Global root zone storage capacity from satellite-based evaporation. *Hydrology and Earth System Sciences*, 20(4), 1459–1481. <https://doi.org/10.5194/hess-20-1459-2016>
- Ward, D., Wiegand, K., & Getzin, S. (2013). Walter's two-layer hypothesis revisited: Back to the roots. *Oecologia*, 172(3), 617–630. <https://doi.org/10.1007/s00442-012-2538-y>
- Webb, R. W., Litvak, M. E., & Brooks, P. D. (2023). The role of terrain-mediated hydroclimate in vegetation recovery after wildfire. *Environmental Research Letters: ERL [Web Site]*, 18(6), 064036. <https://doi.org/10.1088/1748-9326/acd803>
- 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. <https://doi.org/10.1002/eco.1674>
- Zhang, F., Biederman, J. A., Dannenberg, M. P., Yan, D., Reed, S. C., & Smith, W. K. (2021). Five decades of observed daily precipitation reveal longer and more variable drought events across much of the Western United States. *Geophysical Research Letters*, 48(7), e2020GL092293. <https://doi.org/10.1029/2020gl092293>
- Zhao, W., & Li, A. (2015). A review on land surface processes modelling over complex terrain. *Advances in Meteorology*, 2015, 1–17. <https://doi.org/10.1155/2015/607181>
- Zhou, X., Istanbuluoglu, E., & Vivoni, E. R. (2013). Modeling the ecohydrological role of aspect-controlled radiation on tree-grass-shrub coexistence in a semiarid climate. *Water Resources Research*, 49(5), 2872–2895. <https://doi.org/10.1002/wrcr.20259>