

Water Resources Research

RESEARCH ARTICLE

10.1029/2020WR027419

Key Points:

- Isotopic, physiologic, and hydrologic observations were combined to identify oak water sources
- Rock and deep soil moisture rather than groundwater sustain transpiration in summer dry season
- Deep unsaturated zone moisture sources and oak water were isotopically depleted

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Citation:

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, e2020WR027419. <https://doi.org/10.1029/2020WR027419>

Received 27 FEB 2020

Accepted 16 OCT 2020

Accepted article online 24 OCT 2020

Oak Transpiration Drawn From the Weathered Bedrock Vadose Zone in the Summer Dry Season

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Abstract The spatiotemporal dynamics of plant water sources are hidden and poorly understood. We document water source use of *Quercus garryana* growing in Northern California on a profile of approximately 50 cm of soil underlain by 2–4 m of weathered bedrock (sheared shale mélange) that completely saturates in winter, when the oaks lack leaves, and progressively dries over the summer. We determined oak water sources by combining observations of water stable isotope composition, vadose zone moisture and groundwater dynamics, and metrics of tree water status (potential) and use (sapflow). During the spring, oak xylem water is isotopically similar to the seasonal groundwater and shallow, evaporatively enriched soil moisture pools. However, as soils dry and the water table recedes to the permanently saturated, anoxic, low-conductivity fresh bedrock boundary, *Q. garryana* shifts to using a water source with a depleted isotopic composition that matches residual moisture in the deep soil and underlying weathered bedrock vadose zone. Sapflow rates remain high as late-summer predawn water potentials drop below -2.5 MPa. Neutron probe surveys reveal late-summer rock moisture declines under the oaks in contrast to constant rock moisture levels under grass-dominated areas. We therefore conclude that the oaks temporarily use seasonal groundwater when it occupies the weathered profile but otherwise use deep unsaturated zone moisture after seasonal groundwater recedes. The ample moisture, connected porosity, and oxygenated conditions of the weathered bedrock vadose zone make it a key tree water resource during the long summer dry season of the local Mediterranean climate.

Plain Language Summary What are the water sources that allow oaks to transpire through extended dry periods? Oaks in California are thought to tap into groundwater to meet dry season water demand. Here, we show that oaks growing in a savanna woodland instead use tightly held moisture within deep soil and weathered bedrock above the saturated zone. We determined this by matching stable isotopes in the trees' water to these moisture pools. Deep soil and rock moisture were isotopically lighter than shallow soil moisture, which was affected by evaporative enrichment, and the groundwater, which looked more like average wet season rainfall. Monitored moisture declines within the weathered bedrock corroborate the isotopic interpretation that rock moisture sustained oak transpiration. Although the saturated zone was only a few meters below the ground surface in late summer, the trees did not use it due to its low oxygen content and residence in low permeability fresh bedrock. Our findings matter to forest management because of the need to determine when and where trees use groundwater, which regulates ecologically critical baseflow. Moisture extraction from the weathered bedrock unsaturated zone is likely important globally, as forests are widespread on hillslopes with thin soils overlying weathered bedrock.

1. Introduction

Transpiration is a dominant flux in the hydrologic cycle (Schlesinger & Jasechko, 2014), impacting Earth's near-surface temperature (Bonan, 2008), ecosystem productivity (Jones, 1998), and streamflow generation (Vose et al., 2016). Describing how water is distributed belowground and taken up by plants is therefore fundamental to our understanding of Earth system functioning and is an important feature of land surface and dynamic vegetation models (e.g., Fan et al., 2019; Ruiz et al., 2010; Verhoef & Egea, 2014). However,



Figure 1. Many woody plant communities, including those with Oregon white oak depicted here, inhabit landscapes underlain by weathered bedrock with a thin to nonexistent soil layer. Photos taken throughout the natural range of Oregon white oak by the authors, Keir Mose, Kevin Newell, Tom Armstrong, and Gary Ansell, sourced from CalPhotos, E-Flora BC Photo Gallery, and the Royal Ontario Museum.

our knowledge of plant water uptake from the subsurface and attendant water storage patterns remains incomplete for many ecosystems, plant functional types, and landscapes (Allen et al., 2010).

Water uptake patterns are difficult to ascertain because root water uptake is hidden belowground. In general, water can reside in the subsurface within (i) the soil, that is, the surface mantle that lacks parent material structure (e.g., Amundson et al., 2015; Dawson et al., 2020). Soil has been a primary focus in studies of plant water uptake, because roots tend to be concentrated in the near surface (Schenk & Jackson, 2002) and because of soil's relative accessibility in field investigations. However, plant-available water can also reside within (ii) the fractures and matrix of in situ weathered bedrock, which is found below the soil (e.g., Carrière et al., 2020; Klos et al., 2018; Rempe & Dietrich, 2018; Rose et al., 2003). If present, it can be useful to distinguish saprolite (a soil-like material that retains relict bedrock structure) as the uppermost part of the weathered bedrock column because of its different water holding properties (Jones & Graham, 1993). Water can also be found within (iii) the pore spaces of fresh bedrock, where in general, minimal mineral weathering has occurred; porosity and hydraulic conductivity are low; there is negligible meteoric water influx; and fractures, if present, tend to be disconnected from the near surface or cemented (e.g., Brantley & White, 2009).

The thickness of eroding soil is commonly less than 1 m, and in uplands where many forests are found it is generally less than half a meter (Amundson et al., 2015). In such places, woody plants are observed to root into weathered bedrock, which is commonly exposed at the surface or lies just beneath thin soils (Figure 1; e.g., Canadell et al., 1996; Dietrich & Dunne, 1978; Hasenmueller et al., 2017; Hellmers et al., 1955; Jackson et al., 1999; Nie et al., 2011; Querejeta et al., 2007; Scholl, 1976; Sternberg et al., 1996; Witty et al., 2003). During periods without precipitation, soils can dry out due to the combined action of drainage and evapotranspiration. Further plant water uptake is then sustained by water sources below the soil (e.g., Dawson et al., 2020). The weathered bedrock zone contains both unsaturated and saturated zones, is typically many meters thick, and is a potentially large plant-accessible water storage reservoir (e.g., Graham et al., 2010; Hahm, 2019; Rempe & Dietrich, 2018; Schwinning, 2010). In Mediterranean climates—where plants rely on subsurface water storage that is infrequently recharged during the prolonged summer dry season—weathered bedrock has been identified as a key water source for plant transpiration (Anderson et al., 1995; Arkley, 1981; Baldocchi et al., 2004; Bales et al., 2011; Eliades et al., 2018; Dralle et al., 2020; Hahm, Rempe, et al., 2019; Hubbert et al., 2001; Lewis & Burg, 1964; Miller et al., 2010; Rempe & Dietrich, 2018; Rose et al., 2003; Salve et al., 2012; Zunzunegui et al., 2018; Zwieniecki & Newton, 1996).

The aforementioned studies indicate that water extraction from below the soil is likely the norm rather than the exception across upland landscapes in water-limited environments. In general, however, root water uptake from below the soil is not incorporated into land surface or dynamic global vegetation models (e.g., Smith et al., 2001), in part due to lack of information about the deeper subsurface. Furthermore, it remains challenging to differentiate plant water use between saturated and unsaturated sources below the soil. For the purposes of this paper, we describe moisture (unsaturated water content) held in the soil as soil moisture and, analogously, moisture held in weathered, fractured bedrock as rock moisture (in the sense of Rempe & Dietrich, 2018; Salve et al., 2012). We emphasize that rock moisture refers to the moisture in this weathered zone, not to the moisture in or on stones or rock fragments located in the soil. The soil moisture and rock moisture zones typically lie above groundwater, which completely fills pore spaces regardless of the material it occupies (soil, weathered bedrock, or fresh bedrock). In many areas, the fresh bedrock zone is permanently saturated, whereas the soil and weathered bedrock zones may be seasonally saturated by rising and receding groundwater. Because predicted ecosystem feedbacks with hydrology and climate depend on accurate representations of where different plant groups source water (e.g., Verhoef & Egea, 2014), it is important to distinguish between these zones. For example, if plants use water primarily from the saturated zone, then lateral groundwater flow that recharges the root zone should affect the amount of water that can be returned to the atmosphere (e.g., Chang et al., 2018; Love et al., 2019; Schaller & Fan, 2009). If, instead, plants rely primarily on tension-held, unsaturated moisture, it is important to understand how water is accessed throughout structurally complex vadose zone profiles (Schwinning, 2010). This is because the hydraulic properties that govern flow and water retention may differ significantly between dilated and physically mobile soil, where texture may matter the most, and physically intact underlying weathered bedrock, where fracture distribution and aperture may be more important (e.g., Rouxel et al., 2012; Tokunaga & Wan, 1997).

Previous studies that have sought to differentiate plant water sources between these zones have largely relied on stable isotope tracking in source waters and xylem water but arrived at different conclusions. For example, Barbeta and Peñuelas (2017) proposed, based on a literature review of water stable isotope data sets, that groundwater supplies half of all transpiration in locations with a pronounced dry season. In contrast, Brooks et al. (2010) proposed that summer water use by conifers in the Oregon Cascades was derived from tightly held soil moisture (with a distinct isotopic signature) and not groundwater. Such isotope-based methods require complete isotopic characterization of the entire depth of the critical zone (Oshun et al., 2016) and may be subject to uncertainty given the emerging understanding that subsurface fractionation may occur (e.g., Gaj et al., 2017; Kurz-Besson et al., 2006). Furthermore, different pools of water may have distinct isotopic signatures depending on the sampling methodology (e.g., Sprenger et al., 2018). Studies based on stable isotopes in water of plant water uptake are seldom coupled with observations of transpiration rates and subsurface water losses, which could help discriminate between groundwater and unsaturated zone water use. This highlights the ongoing need for studies based on multiple lines of field and isotopic evidence at intensively monitored sites with well-understood hydrologic contexts and subsurface weathering profiles to better understand subsurface water sourcing dynamics.

Here, we report the results of an intensive multiyear field study to identify the contributions of groundwater, rock moisture, and soil moisture to dry season transpiration in Oregon white oak (also known as Garry oak; *Quercus garryana* var. *garryana* Douglas ex Hook.). *Q. garryana* has the largest latitudinal range of any oak in western North America (Stein, 1990) and forms the backbone of a high biodiversity terrestrial ecosystem (Erickson, 1996; Fuchs, 2001; Zack et al., 2005) but has experienced severe habitat loss following post-Euro-American settlement fire exclusion and land use (Agee, 1996; Blazina, 2016; Devine & Harrington, 2006; Lea, 2006; MacDougall et al., 2004; Thompson, 2007). Oaks in general constitute an important component of plant communities: The *Quercus* genus has the most species and biomass of any woody plant group in the United States and Mexico (Cavender-Bares, 2016; Hipp et al., 2018). The ecosystem at our study site—an oak savanna woodland in Mendocino County, California—is typified in the dry season by rolling golden-colored hills mantled with green trees—a now common phenological state across much of California following the widespread takeover of predominantly European annual herbaceous ground cover that senesces in early summer (Schnabel et al., 2013).

The *Q. garryana* are water limitation tolerant relative to their common sympatric competitor, Douglas fir (*Pseudotsuga menziesii*), and maintain high sapflow at low water potentials throughout the dry season

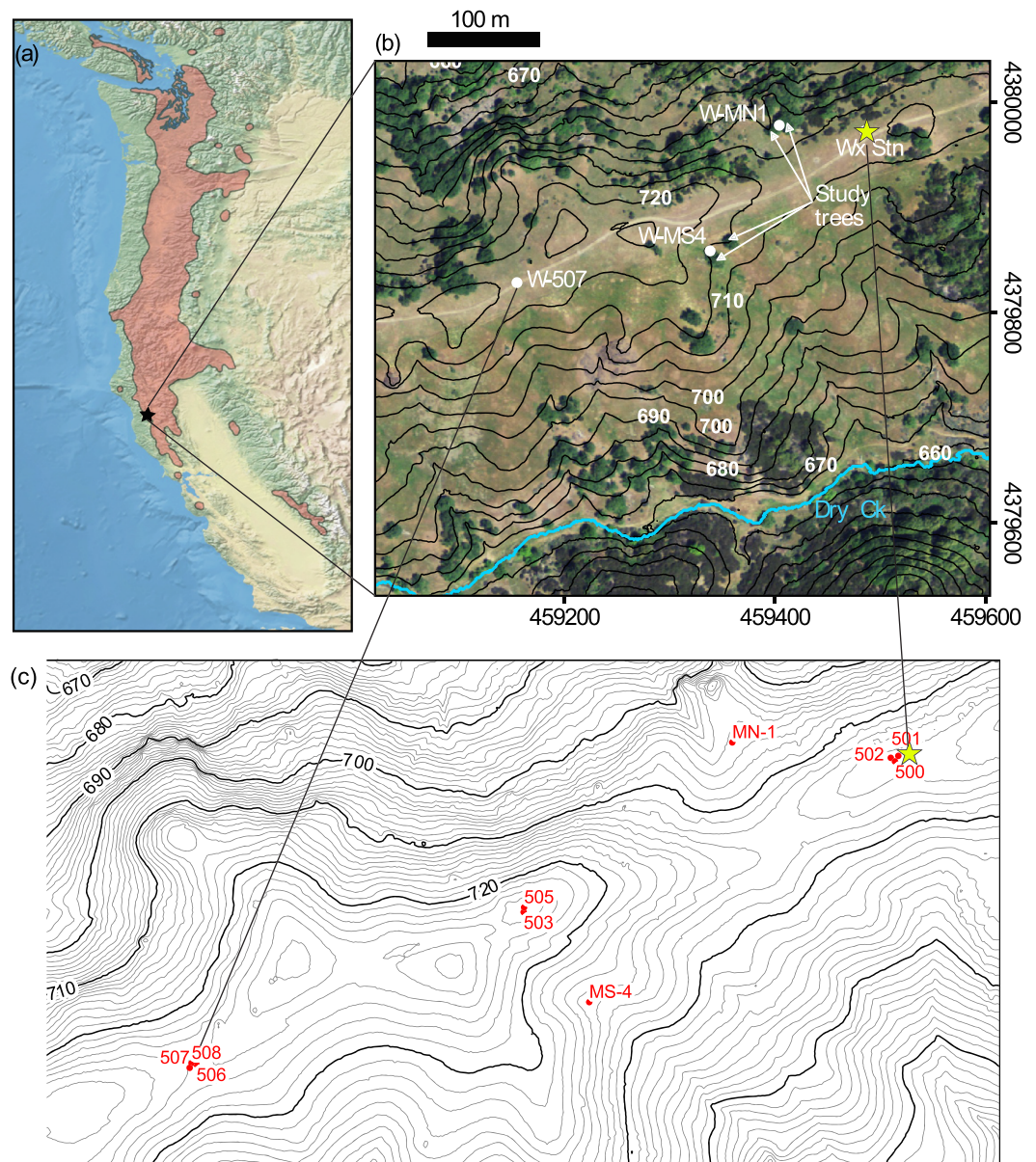


Figure 2. (a) Location of study area (star) and approximate natural range of *Q. garryana* along the west coast of North America (red shaded area; from Little, 1971). Background map is Natural Earth II shaded relief of topography. (b) Location of groups of study trees (indicated with white arrows), isotope groundwater monitoring wells (prefix “W”), and weather station (“Wx Stn”). Study trees are located on gently sloped north and south facing hillsides, along a WSW-ENE trending topographic divide. The divide is generally demarcated by the beige dirt road visible on the underlying USDA NAIP aerial orthoimagery (29 May 2012). National Center for Airborne Laser Mapping-Lidar derived contour interval is 5 m; numbers refer to elevation in m above sea level; map projection and grid are NAD 83/UTM Zone 10 N. (c) 1 m elevation contour Lidar blow-up map of study area, showing the location of monitoring wells, reprinted from Hahm, Rempe, et al. (2019).

(Hahm et al., 2018). In the vicinity of the study trees, *Q. garryana* is the only plant with significant functional leaf area in the summer (Hahm et al., 2017). Along with negligible summer precipitation, fog input, or runoff at the site (Dralle et al., 2018; Lovill et al., 2018), this results in a simplified ecohydrologic context to discern the relative importance of different subsurface water reservoirs. *Q. garryana* is winter deciduous, relying on carbon acquisition during the mostly rainless summer for growth. Other similar oaks in California have been reported to obtain water for summertime transpiration primarily from groundwater (e.g., Miller et al., 2010). In this study, we ask what subsurface water sources sustain *Q. garryana* transpiration through the summer dry season. We tested the hypothesis that these oaks rely on groundwater. Our

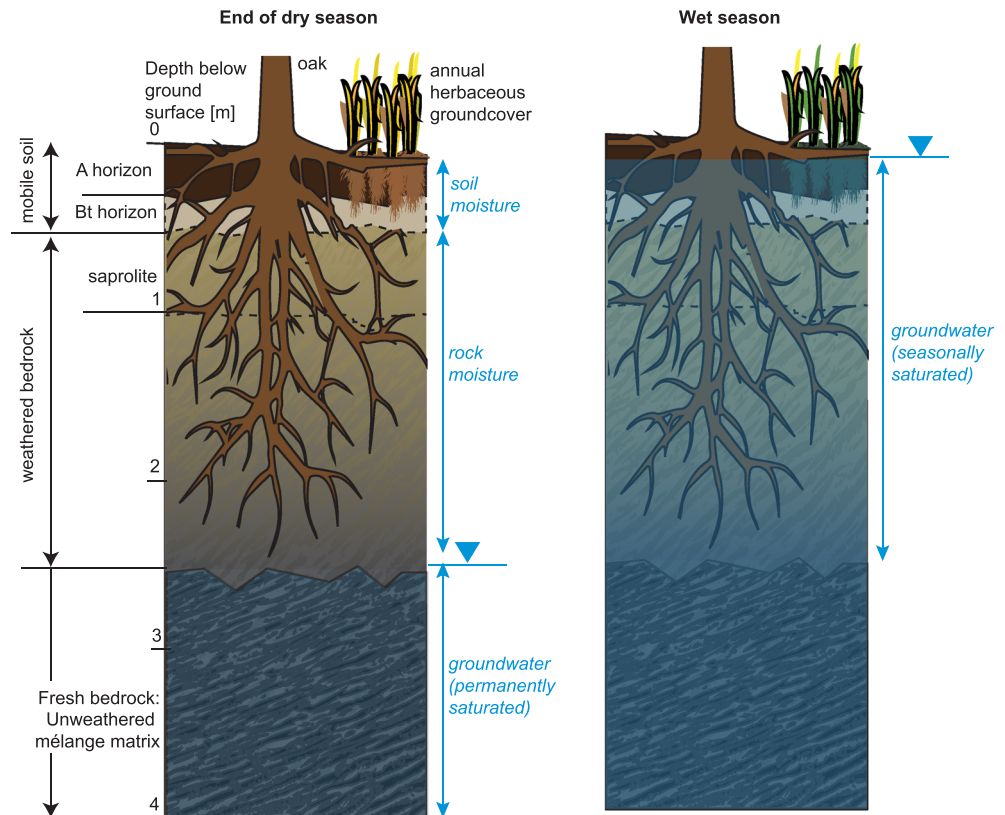


Figure 3. Conceptual diagram of the subsurface critical zone in the Central Belt mélangé of the Franciscan complex. Water table dynamics are highlighted on the right side of each panel (water table depicted with inverted triangle); subsurface delineations of the critical zone at left. In the dry season (left panel), we distinguish between soil moisture, which resides in the unsaturated soil, and rock moisture, which resides in the unsaturated weathered bedrock (including saprolite). We also distinguish the seasonal groundwater, which saturates the upper portion of the critical zone (weathered bedrock and soil) in the wet season (right panel), from permanent groundwater, which resides in fresh bedrock that remains perennially saturated.

combined observations of stable isotopes in water, sapflow, tree water potential, and groundwater and vadose zone storage dynamics led us to reject this hypothesis and instead infer that these oaks primarily use water from the deep unsaturated zone that forms after the seasonal groundwater recedes at the start of the dry season. Even though the depth to the saturated zone in summer at our site is relatively shallow (2–4 m), it is unavailable to the roots because that groundwater system resides in permanently saturated, anoxic, and low-conductivity fresh bedrock.

2. Site Description

The Sagehorn Ranch study site is located within the mainstem Eel River watershed on a private cattle ranch in the Northern California Coast Ranges of Mendocino County, California, USA (Figure 2). The ranch is part of the Eel River Critical Zone Observatory. Pre-Euro-American contact inhabitants of the area include the Coast Yuki, the California Dene (Athabaskan), and Pomo, who managed the land with fire for acorns and improvement of hunting grounds (Baumhoff, 1958; Foster, 1944; Johnson, 1979; Stewart, 1943).

2.1. Geology, Soils, and Critical Zone Structure

The site is underlain by the Central Belt mélangé of the Franciscan complex, which consists of a chaotically sheared, argillaceous (i.e., primarily clay-sized particle) matrix encompassing mm- to km-scale coherent blocks of diverse lithologies (Blake et al., 1985; Cloos, 1982; Hahm, Rempe, et al., 2019). In this study, we focus on trees underlain by mélangé matrix bedrock. The mélangé matrix bedrock is colloquially known as “blue goo” due to its ductile, paste-like texture in the near surface and reduced hue. Approximately 40 soil pits (dug to approximately 1 m) and augered holes (typically to 1.5 m) indicate that soils are humic

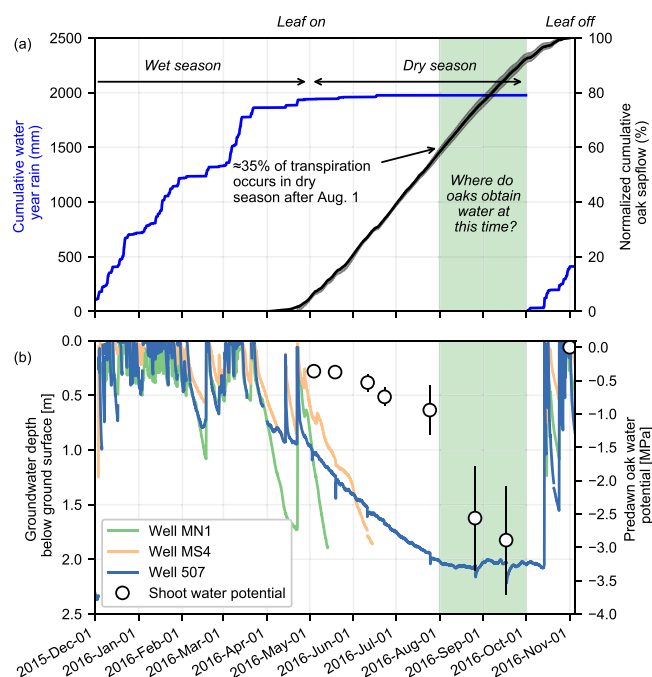


Figure 4. (a) Time series dynamics of precipitation (blue) and sapflow (black), and (b) groundwater tables and predawn water potentials (b). The precipitation is strongly seasonal under the local Mediterranean climate, with rains falling in the winter wet season (a) that saturate the subsurface, driving groundwater tables to the surface (b). A 6 month phase lag separates water delivery (as rain) from tree water use (a), highlighting the role of the subsurface in storing water. Groundwater tables respond to most storm events, rapidly rising and then slowly receding. Sapflow (mean denoted with solid line, shading denoting range of maximum and minimum across sensors) ramps up in the early part of the summer dry season; when soils are wet, the seasonal groundwater table is high, and water potentials are fairly relaxed (> -1 MPa). Sapflow continues at a relatively constant rate even in the latter portion of the summer dry season (region highlighted in green) when soils are dry, the groundwater table has receded, and predawn water potentials fall below -2 MPa. Dry season groundwater table data gaps reflect water table recession below the depth of the boreholes (approximately 2 m below ground surface) in MN1 and MS4. Small abrupt drops in dry season ground water level are due to sampling.

acrisols (World Reference Base for Soil Resources system) or mollisols (U.S. Department of Agriculture soil taxonomy system) in the savanna woodland areas of the site, consistent with the county-level soil survey description (Rittiman & Thorson, 2001). Soils have an approximately 30 cm thick dark, organic rich A horizon that overlies a 10–20 cm thick clay-rich yellow Bt horizon (Figure 3). Collectively, these horizons constitute the physically mobile soil, which is bioturbated by small burrowing mammals and roots. These soils move downslope along convex hilltops to depositional hollows and local gullies that feed into the larger streams. The hillslope length from ridge to valley bottom is typically between 10 and 30 m (supplementary Figure 6 in Hahm, Rempe, et al., 2019, shows lidar-hillshade and topographic cross sections in the study area). Below the soil, a saprolite with yellow-red weathering rinds on bedrock fragments grades with depth into darker-hued but still physically and chemically altered weathered bedrock. The unweathered *mélange* matrix is typically encountered at 2–4 m depth and remains saturated year-round, due to its exceptionally low hydraulic conductivity (Dralle et al., 2018; Hahm, Rempe, et al., 2019; Lovill et al., 2018).

The average geochemical composition of four unweathered bedrock samples recovered from deep boreholes and reported by Hahm, Rempe, et al. (2019) is nearly indistinguishable from a composite of North American metamorphosed shales described by Gromet et al. (1984). XRD diffraction patterns showed that illite, albite, quartz, chlorite, muscovite, and regularly interstratified chlorite/smectite each constitute more than 10% of the fresh material (Hahm, Rempe, et al., 2019). Calcite, kaolinite, gypsum, and microcline are present in lesser abundance. Small amounts of smectite, not detected in the fresh material at depth, are found in the soil, but we have not observed any desiccation cracks at the ground surface in summer.

2.2. Climate and Hydrologic Setting

The climate is Mediterranean and strongly seasonal, with wet, cool winters and hot, dry summers. In the summer, daytime temperatures and vapor pressure deficits routinely exceed 30°C and 4 kPa, respectively (Hahm et al., 2018), and there is negligible precipitation. Between the years 1981 and 2010, the average annual precipitation was 1,811 mm, and the temperature was 13.3°C (version M2; PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>).

Dralle et al. (2018) and Hahm, Rempe, et al. (2019) documented that 50–150 mm of cumulative rainfall at the start of the wet season is sufficient to cause an abrupt rise in groundwater level within the *mélange* matrix. In subsequent wet season storms, small additional amounts of rainfall (generally <100 mm) cause the water table to rise to the surface and transiently saturate the entire soil and weathered bedrock profile, causing widespread saturation overland flow (Hahm, Rempe, et al., 2019). Near the studied trees, the water table remained within 1 m of the ground surface for nearly the entire wet season of 2016. During major storms, the water table rose to the surface for periods of approximately 24 h (Figure 4). Similar groundwater dynamics occurred in the ridgetop monitoring wells distributed across the site that were drilled into *mélange* matrix. The wet season typically ends in April or May, at which point groundwater recession begins. By mid-June, groundwater recedes below 2 m. Because the relatively (compared to annual precipitation) small subsurface water storage deficit is replenished even in dry years, the plant community's greenness in summer does not correlate with the preceding winter's total rainfall (Hahm, Dralle, et al., 2019).

Runoff to Dry Creek, south of the study hillslope, is primarily supplied by overland flow and macropore flow and is flashy. During large storms the wetted channel network extends throughout the geomorphic channel network, including the channels immediately adjacent to the study trees (Lovill et al., 2018). Dry Creek is seasonally ephemeral and by May typically has disconnected flow (i.e., reaches without surface water). There

is no sustained flow along the mainstem or at the catchment outlet throughout most of the summer dry season. Lack of flow in the channel network indicates that summer groundwater drainage from the mélange matrix critical zone is negligible. More details about the weather, groundwater, and stream dynamics can be found in Hahm, Rempe, et al. (2019), Hahm et al. (2018), Lovill et al. (2018), and Dralle et al. (2018).

2.3. Plant Community Composition

The plant community on mélange matrix at the site is primarily *Q. garryana* woodlands with interconnected canopies (on north facing slopes) and savanna with widely spaced trees (on south facing slopes). *Q. garryana* is interspersed with occasional Black oak (*Quercus kelloggii*), California buckeye (*Aeschylus californica*), and manzanita (*Arctostaphylos* sp.). *Q. garryana* leaf-out occurs in April to early May. Drought deciduous behavior was not observed in 5 years of monitoring (2014–2018); instead, leaf abscission occurs in November, typically after the first wet season rains. The ground cover consists primarily of herbaceous annuals, which begin to green up with the first rains of the wet season (typically October), peak in greenness in early May, and senesce rapidly at the end of June. A tree survey of the study area (Hahm et al., 2017) indicates that current stand species compositions are maintained at the site (i.e., little conversion of existing oak savanna and oak woodland to conifer habitat is occurring).

3. Materials and Methods

3.1. Oak Water Relations

Predawn water potential is commonly interpreted as a metric of rhizosphere water potential (and water availability) under the assumption that sapflow is negligible after stomata have closed at the end of the night, such that minimal water potential gradients exist within the tree and shoots come into equilibrium with the roots (e.g., Boyer, 1995). Coincident with most of our stable isotope collection campaigns, we measured the *Q. garryana* predawn water potential across multiple shoots from seven individual trees with a Scholander-type pressure chamber (PMS Instruments Model 1000, Albany, OR; Scholander et al., 1965). The balancing pressure for all shoots originally reported in Hahm et al. (2018) were averaged for each tree and then across all trees.

The ascent of water in xylem along stems (sapflow) reflects total tree water use and therefore tree transpiration. We installed probes (ICT International) into the main trunks of mature *Q. garryana* that use the heat ratio method (Marshall, 1958) to measure vertical sapflow velocity every half hour. Because we lack information on radial sapflow patterns and sapwood area, we did not convert sapflow into volumetric fluxes. Instead, using the data originally reported in Hahm et al. (2018), we normalized sapflow to the maximum recorded, averaged across two trees with nonmalfunctioning sensors and then plotted cumulative water use between 1 April and 1 November. This reveals the relative timing of transpiration throughout the leaf-on growing period. Here we present 2016 data, which overlaps with the highest frequency water isotope campaign. More information on water relations in relationship to climatic variables including temperature, precipitation, and vapor pressure deficit (VPD) can be found in Hahm et al. (2018), where the growth, leaf pressure-volume relations, and leaf hydraulic conductance for these trees are also reported.

3.2. Vadose Zone Moisture Content

We surveyed volumetric moisture content in the vadose zone via neutron probe (Model 503DR Hydroprobe, Instrotek, Concord, CA) across the 10 wells shown in Figure 2, and show data for the 2016 water year dry season. The wells are grouped into three categories. One group contains wells adjacent to the monitored oak trees, which are underlain by mélange matrix (MS-4, MN-1), another group contains wells located in herbaceous ground cover areas also underlain by mélange matrix (500, 501, 502, 506, 507, 508), and a third group contains wells adjacent to a mixture of mature bay and live oaks, in a deeply weathered monolithologic sandstone block (503 and 505). In neutron logging surveys, hydrogen in the borehole casing is assumed to remain constant between survey dates, such that changes in the count of returning slow neutrons are uniquely attributable to changes in water content in the surrounding material (Long & French, 1967). We surveyed for 25 s at depth increments of 30.5 cm with the same cable each time, from the ground surface to the bottom of the borehole or just above the water table at the time of survey, following the methods outlined in Salve et al. (2012) and Rempe and Dietrich (2018). We converted neutron counts to volumetric water content based on borehole diameters and probe-specific laboratory-based calibrations determined with barrels filled with combinations of sand, air, and water; these equations are provided in Rempe and Dietrich (2018),

and the calibration procedure is described in detail in Rempe (2016). To calculate rock moisture declines (ΔS_{RM}) over the dry season for the entire measurement profile, we first took the difference between the volumetric water content at a date of interest and the latest dry season (driest) volumetric water content. We then multiplied this difference in water content by the vertical measurement interval (305 mm), and summed across the vertical profile, to arrive at a volume of water per unit surface area. We report the rock moisture zone storage change, which we define as the unsaturated zone moisture change at depths greater than the local soil depth. We report changes across measurement dates that bracket essentially all of the dry season (2 May to 17 September 2016) and for just the middle-to-late dry season (25 July to 17 September 2016); the annual herbaceous ground cover is mostly dead across the site by late July, and there is no streamflow in August and September, such that rock moisture losses during this time are largely due to tree transpiration. These values should represent minimum (conservative) estimates of change because (i) the end-of-summer dry season survey date is likely not perfectly aligned with the absolute driest state, as wet season rains did not return until some time after the last survey, and (ii) because the unsaturated zone extends below the bottom of the borehole in some wells (including those near the monitored oaks, MS-4 and MN-1). At the start and end of each survey, we took five standard count readings on bare ground with the probe on top of its shielding case, to monitor the probe for long-term bias due to possible sensor drift, which we did not observe. The mean coefficient of variation (CV) of these standard counts was 0.74% over the course of the study. We also took repeat measurements at a specific depth (1.5 m on the cable length) during every survey in an individual well. After converting to volumetric water content, the instrument's measurement precision is 0.31%, which is the representative standard deviation of these repeat measurements. We report the uncertainty in the change in unsaturated zone storage as the standard error of the mean, determined by multiplying the instrument measurement precision uncertainty by the overall depth interval and then dividing by the square root of the number of depth intervals in each borehole.

3.3. Stable Isotope Composition of Water

We report the stable isotope composition of samples collected between 2015 and 2018 from seven different pools of water: (1) precipitation, (2) groundwater from wells, (3) stream runoff, and water cryogenically extracted from (4) soil, (5) saprolite/weathered bedrock, (6) fresh bedrock, and (7) tree tissue. For Pools 4 and 5 (soil and saprolite/weathered bedrock), we also distinguish if the sample was from above or below the groundwater table (saturated or unsaturated) at the time of sampling. The fresh bedrock samples were always taken from below the groundwater table.

3.3.1. Collection

When sufficient precipitation had fallen, it was collected each morning (daily sampling frequency) 1.3 km west of the weather station in an open field at an elevation of 645 m a.s.l. (above sea level), approximately 50 m lower than the groundwater wells and instrumented trees. Precipitation was funneled into 1 L high-density polyethylene (HDPE) bottles (Nalgene) and then subsampled and stored in 30 ml HDPE bottles that were kept in a cool, dark location until analysis. Rainfall totals from the weather station rain gauge between each sample collection were used to weight the isotopic value of each storm to define the local meteoric water line (LMWL), using a standard major axis linear fit. The first storms in the 2016 water year occurred before the initiation of the precipitation collection program (which began on 10 December 2015), resulting in a missing data window. However, at Sagehorn's Eel River Critical Zone Observatory sister site at the nearby Angelo Coast Range Reserve ("Angelo," 23 km northeast), samples were collected for the first storms (sampling program is described in Oshun et al., 2016, and samples were analyzed at the same lab and via the same methods as the data reported here).

Groundwater was sampled approximately monthly from the top 1 m of the water column in wells continuously slotted along their entire lengths, typically with HDPE bailers. In this study, we present groundwater isotope data from the two monitoring wells (named MN-1 and MS-4) adjacent to the study trees (each approximately 2 m deep) and a 7.3 m deep well drilled on the ridge (named 507) approximately 250 m east (Figure 2). Groundwater samples were placed in 4 ml vials, sealed with parafilm, and kept in a dark container until analysis.

We collected tree tissue samples approximately monthly from mature *Q. garryana* during the daytime from suberized stems that lacked external green tissue (typical stem diameters 6–10 mm) and supported mature, healthy, sun-exposed leaves. Bark was left on the stem. The study trees ($n = 7$) are 20 to 65 cm diameter at breast height and are distributed in two groups immediately north and south of the northern divide of the

Dry creek watershed (Figure 2; Hahm et al., 2018, show exact tree locations and diameters). On average, 14 individual stem samples were collected and analyzed per tree over the course of the study. No samples were taken when the trees lacked leaves. Samples were collected at various times throughout the day between 7:30 and 19:30 local time. Vials were capped and sealed with parafilm and kept in a dark container at ambient temperature for up to 24 h before freezing (to prevent decomposition) until extraction.

We collected bulk soil and saprolite/weathered bedrock samples approximately monthly at roughly 20 cm depth intervals to 2.15 m depth with a trowel or hand auger at each the south and north group of study trees. We stored samples in a manner similar to the tree stems until extraction. We identified the transition from soil to saprolite in the field during augering where we encountered continuous *mélange* matrix or large rock clasts of argillite/sandstone that were recovered in the auger that appeared to be in place and not colluvial cobbles. In September 2015, we also deployed a drill rig to install deep monitoring wells along the ridge. As part of this effort, we recovered and measured samples when the drilling method did not introduce fluids or overheat the samples. This precluded measurement of samples recovered via diamond core bit and air rotary drilling but allowed for recovery of samples collected with a standard penetration test bit or flight auger. We also present water isotope data from streamwater samples collected near the mouth of Dry Creek (sampling location = 39°34'22.57"N, 123°27'46.76"W; 3.5 km² drainage area) on a campaign basis that began in fall 2015.

3.3.2. Extraction and Analysis

All samples were analyzed at the UC Berkeley Center for Stable Isotope Biogeochemistry. Water from tree and bulk subsurface samples was extracted via cryogenic vacuum distillation for 70–80 min, following the procedures outlined in West et al. (2006). The extraction line was pumped to a pressure of less than 10 mTorr. In this process, glass chambers enclosing the sample and its storage vial were immersed in liquid nitrogen to freeze all water, and ambient air was evacuated from the sample and collection chambers. After a vacuum was achieved, sample chambers were immersed in boiling water (100°C), and an adjacent collection chamber was immersed in liquid nitrogen to recover the vapor driven off the sample. Experiments performed by Oshun et al. (2016) with this laboratory setup and sample size indicated that extraction times beyond 1 h did not significantly change the isotopic composition of recovered water, even for samples very rich in clay (with similar composition to those measured here). We weighed bulk subsurface sampling vials before and after sample collection and after extraction to determine gravimetric moisture content, defined as the mass of water in the sample divided by the dry mass of the sample. After cryogenic extraction, we pipetted water into glass analysis vials for separate δD and $\delta^{18}O$ analysis (100 μ l of water into each vial). We displaced the headspace air in the glass vial for $\delta^{18}O$ analysis with a mixture of N₂ and 0.2% CO₂ gas and let the water equilibrate for 48 h prior to analysis via isotope ratio mass spectroscopy (IRMS) on a Thermo Delta PLUS XL instrument. Hydrogen isotopic ratios were also measured via the same IRMS, after isolation via a Cr catalyst reactor. Data are expressed in per mil delta notation (‰) relative to Vienna Standard Mean Ocean Water (VSMOW): δD or $\delta^{18}O$ ‰ = $\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) 1,000$, where R is the ratio between the heavy and light isotope (i.e., D to H or ¹⁸O to ¹⁶O). Measurements made using the gas phase isotope ratio mass spectrometer are corrected for drift by calibration to a known standard interspersed with samples. The long-term precision is ± 0.12 ‰ $\delta^{18}O$ and ± 0.60 ‰ δD (<https://nature.berkeley.edu/stableisotopelab/analyses/water-analysis/>).

3.3.3. End-Member Mixing Analysis

We performed a three-end-member isotope linear mixing model (Rothfuss & Javaux, 2017; von Freyberg et al., 2020) to assess the relative fraction of oak transpiration sourced from (i) unsaturated soil (i.e., soil moisture), (ii) unsaturated saprolite/weathered bedrock (rock moisture), and (iii) groundwater. The analysis was restricted to the 2016 summer dry season over the time period for which samples of all three end-members were collected (mid-June to mid-September). At each sampling date, all samples in each end-member group as well as the oak stems were averaged, and linear interpolation was used to fill end-member compositions between sampling dates. Each day we determined a best fit solution to a system of three equations (linear mixing of δD and $\delta^{18}O$ from each end-member and the constraint that the fractions sum to unity) using a nonnegative least squares solver to determine the three unknowns (the fractions of each end-member contributing to the oak transpiration), according to Equations 1–3:

$$\delta D_T = \delta D_G f_G + \delta D_{SM} f_{SM} + \delta D_{RM} f_{RM} \quad (1)$$

$$\delta^{18}O_T = \delta^{18}O_G f_G + \delta^{18}O_{SM} f_{SM} + \delta^{18}O_{RM} f_{RM} \quad (2)$$

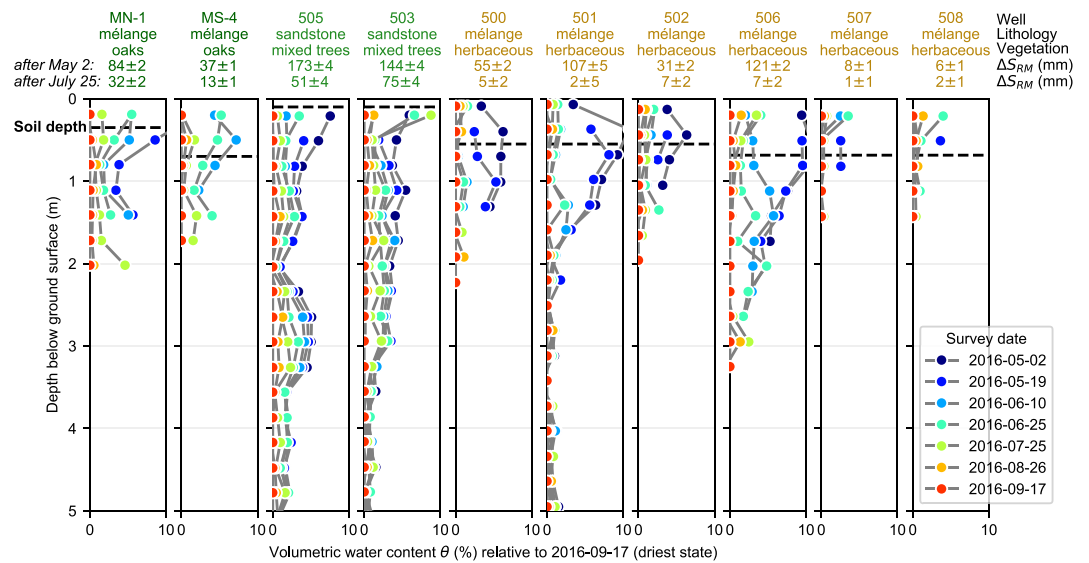


Figure 5. Dry season decline in neutron probe-inferred unsaturated zone moisture content. The x axis ranges from 0% to 10%, and instead of the actual volumetric water content, the figure shows the magnitude of the difference in volumetric water content at the time of survey relative to the last survey of the dry season. A value of 0% therefore does not indicate that the subsurface has no moisture at a particular depth; rather, it means the moisture content at the time of survey was no different from the 17 September survey. Moisture decreases below the soil (dashed lines) through the end of August around monitoring boreholes under oak canopies (first and second panels on the left) in the *mélange* and under a mixed canopy in a sandstone block, which differs from boreholes under annual herbaceous ground cover (fifth to tenth panels). Numbers at top represent total dry season (2 May to 17 September) and middle-to-late dry season (25 July to 17 September) depth-integrated rock moisture declines in mm (ΔS_{RM}) ± 1 s.e.m. (standard error of the mean) propagated instrument measurement uncertainty. Storage change is determined by the sum of the change in water content between dates at each measurement location multiplied by the depth interval between measurement locations. The depth to fresh bedrock is below the deepest extent of the water table in each well and therefore below the deepest neutron probe measurements.

$$f_G + f_{SM} + f_{RM} = 1, \quad (3)$$

where δD_X and $\delta^{18}O_X$ refer to the compositions on a particular date of end-member X denoted by the subscript (X is either T = oak tree, G = groundwater, SM = soil moisture, or RM = rock moisture), and f_X describes the fraction of oak tree water derived from end-member X ($f_X \geq 0$). This analysis assumes that the oak xylem water is sourced from a mixture of the average composition of all samples from each zone in the subsurface (i.e., groundwater, soil moisture, and rock moisture).

We partitioned these fractions into the relative daily oak sapflow and also rescaled the cumulative sapflow from 0 to 1 during this time period and multiplied by the fraction of each end-member to assess the relative running total fluxes sourced from each subsurface pool.

4. Results

4.1. Oak Water Use and Potential

Figure 4 shows consistently high rates of oak transpiration for the 5 months in the heart of the summer growing season (May–September). Predawn water potentials remain high (above -1.0 MPa) at the start of the dry season and through July (Figure 4), but then drop below -2.0 MPa on average in August and September. With the return of the first major rains of the wet season and saturation of the subsurface, the predawn potentials are indistinguishable from 0 MPa.

4.2. Dry Season Vadose Zone Moisture Dynamics

Monthly neutron probe surveys reveal declines in water content throughout the deep vadose zone through the end of August (Figure 5) in boreholes located under the *Q. garryana* canopies in the *mélange*. Declines were minimal between the late-August and mid-September surveys. Rock moisture losses during the dry season were 84 and 37 mm (volume per unit surface area) in MN-1 and MS-4 (the two boreholes near the

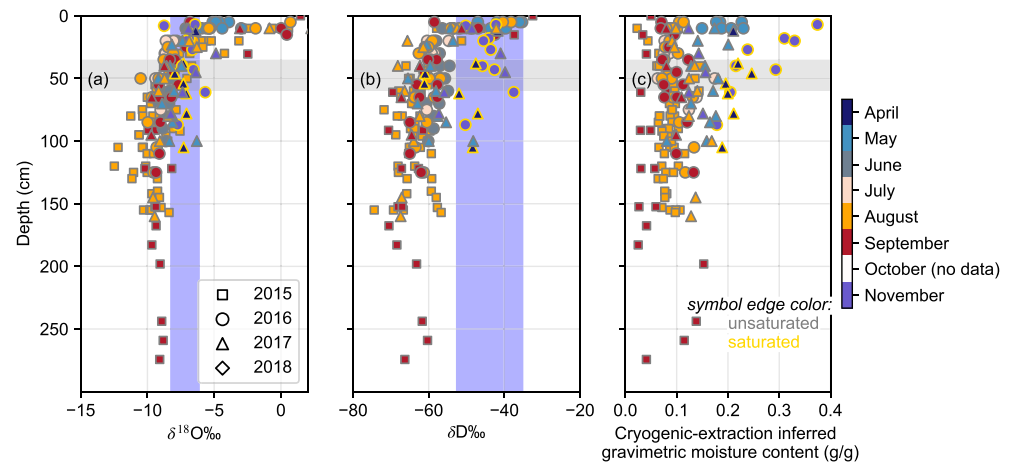


Figure 6. Depth profiles of stable isotope composition of extracted subsurface waters (a, b) and gravimetric water content (c). Extracted waters tend to indicate evaporative enrichment (heavier or more positive isotope composition) from the ground surface downward through the soil to 30 cm depth; deeper unsaturated samples tend to be depleted relative to groundwater, whose mean ± 1 s.d. (standard deviation) range over the study period is indicated by the vertical light blue band. Horizontal light gray bands denote the typical depth of soil-saprolite transition. Symbol shape refers to the sample year, face color to the collection month, and edge color to the saturation state at time of sampling (gray, unsaturated; gold, saturated). Gravimetric moisture is not available for all isotope samples.

Q. garryana), respectively, with an average of 23 mm across both wells after 25 July, when the herbaceous ground cover had largely senesced. The rock moisture dynamic in deeply weathered sandstone block boreholes adjacent to live oak and bay trees (Boreholes 503 and 505) was even deeper and greater, with average overall dry season losses of 150 mm, one third to one half of which occurred after 25 July. In contrast, sites underlain by *mélange* within low-lying annual herbaceous ground cover far from any woody shrubs or trees (Boreholes 500, 501, 502, 506, 507, and 508) were characterized by negligible declines in water content in the vadose zone beneath the soil after 25 July (Figure 5). Early in the dry season (before 25 July), however, large declines in rock moisture did occur around Boreholes 501 and 506 within the herbaceous ground cover areas.

The gravimetric water contents of the soil and saprolite from samples collected below the canopy of the studied trees at the end of the wet season in April, when the ground was still near or at saturation, were typically >0.15 g/g (Figure 6c), whereas dry season samples (May to September) were typically between 0.03 and 0.15 g/g. The largest gravimetric water contents (approaching 0.4 g/g) were saturated samples near the ground surface (saturated symbols denoted with gold outlines in Figure 6). The gravimetric moisture content differences between relatively wet and dry sampling times are generally consistent with the patterns revealed in the neutron probe data, showing moisture declines in the unsaturated soil and upper weathered bedrock (saprolite) through the dry season. It is not possible to determine the deepest extent of this moisture change from the gravimetric data alone as samples below 1 m were not collected during wet times.

4.3. Stable Isotope Dynamics

4.3.1. Precipitation

The dual-isotope compositions of precipitation for the latter portion of the 2016 water year and all of the 2017 and 2018 water years are shown in Figure 7. These samples have a large variance relative to stream and groundwater samples. The local meteoric water line (LMWL) fit to these precipitation samples, weighted by rainfall amount, is $\delta D = 8.25\delta^{18}O + 17.3$ (‰).

Rainfall collected from 1 October to 4 December 2015 at Angelo (before the Sagehorn collection program began) had a rainfall-weighted average of -47.3 ‰ δD and -8.17 ‰ $\delta^{18}O$, close to the overall weighted average collected at Sagehorn across all years (pink star in Figure 7 shows Sagehorn average). Analysis of subsequent periods revealed that the two sites did not receive systematically different isotopic inputs at the individual storm time scale during overlapping sampling times. These late 2015 samples were collected for 213 mm of total rainfall at Angelo, spread fairly evenly over the course of just over a month. These storms were sufficient to nearly completely saturate the *mélange* matrix areas at Sagehorn.

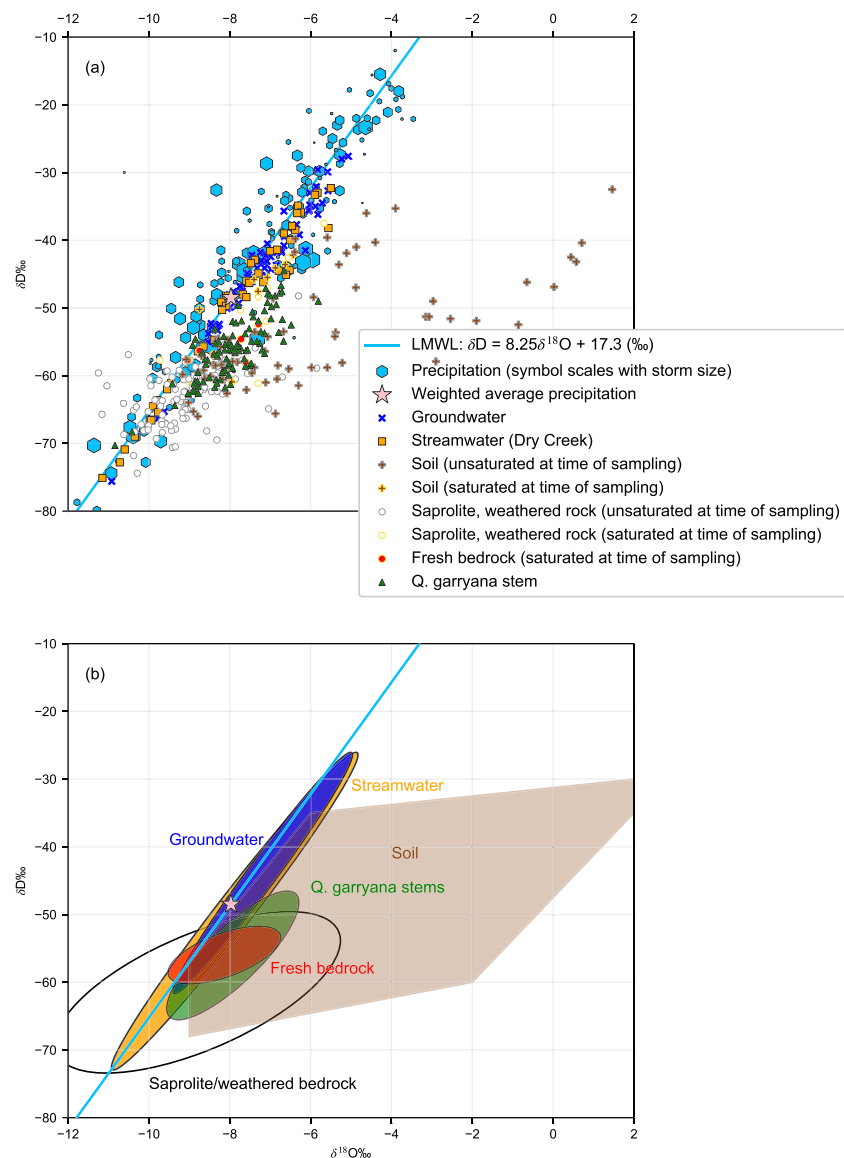


Figure 7. Dual-isotope plot for individual samples (a) of precipitation, groundwater, stream, and bulk water extracted from *Q. garryana* stems and bulk subsurface materials (divided between soil (brown fill), saprolite/weathered bedrock (white fill), and fresh bedrock (red fill)), collected between 2015 and 2018. Gold outline denotes water extracted from saturated material at time of sampling; gray outline denotes water extracted from unsaturated material. Regions of water composition by sample type (b, based on data from a) with 2σ (standard deviation) ellipses centered on means (except for soil, whose region is outlined with a hand-drawn polygon).

4.3.2. Stream and Groundwater Samples

Stream water from Dry Creek and groundwater sampled from the monitoring wells closely overlap in dual-isotope space (Figure 7). The stream and groundwater samples generally cluster around the LMWL but vary less relative to the precipitation input. This damping of variability is also evident in the time series of Figure 8, where scattered precipitation inputs tend to bound stream and groundwater samples.

The last streamwater samples prior to the cessation of flow in Dry Creek at the start of the summer dry season in 2016 were collected on 3 and 19 May and had isotopic values of -40 ‰ to -41.4 ‰ δD (Figure 8). These values are similar to the ridgetop groundwater samples collected in May and throughout the rest of the summer dry season (Figure 8).

Groundwater from the shallow wells at MN-1 and MS-4 has slightly less deuterium relative to the deeper wells along the ridge line (e.g., W-507 in Figure 8) in the wet season but overlaps in the dry season. These

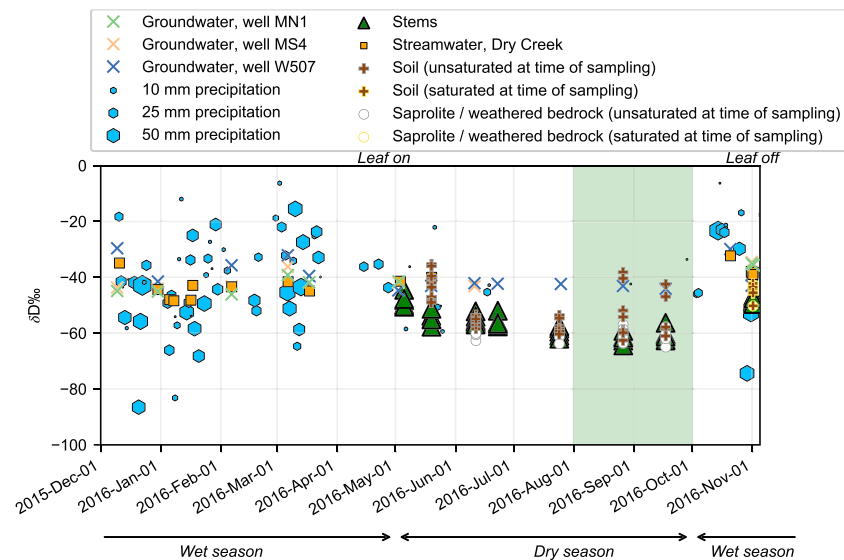


Figure 8. Time series dynamics of deuterium. Precipitation symbol size scales with total storm rainfall amount. Green shaded region matches time period highlighted in Figure 4. Gold symbol outlines denote water extracted from subsurface material that was saturated at time of sampling; gray symbol outlines denote water extracted from unsaturated subsurface material. A version of this figure with oxygen isotopes is available in the data repository.

shallow wells eventually became dry as the summer progressed. Given the isotopic similarity with the deeper groundwater sampled nearby, especially early in the dry season, we assume that the deeper well isotopic record represents the isotopic characteristic of the deeper groundwater at the tree locations.

4.3.3. Bulk Subsurface Samples

Collectively, water obtained from cryogenic extraction of bulk subsurface samples span a large range in dual-isotope space (Figure 7). Shallow unsaturated samples of soil collected in the summer dry season (May–September) tend to fall to the right of the LMWL (Figure 7a). Isotope composition versus depth plots (Figure 6) show that unsaturated samples from within 30 cm of the ground surface were typically more enriched than deeper samples in the dry season.

Water extracted from samples taken from deeper unsaturated soil and the unsaturated saprolite/weathered bedrock (rock moisture) zone are generally lighter than the weighted average precipitation input in dual-isotope space (Figure 7a) and tend to be depleted relative to the groundwater sampled through the summer dry season (Figure 9). This is also evident in the depth profiles shown in Figures 6a and 6b, where typical groundwater samples from wells are plotted as light vertical blue bands.

Water extracted from saturated bulk samples taken from the subsurface in the permanently saturated zone (below the fresh bedrock boundary) obtained during deep drilling in late September 2015 generally had less deuterium than both the overall average rainfall and groundwater (Figure 7; all fresh bedrock samples shown in the figure [red symbols] are from this September 2015 campaign). Waters extracted from saturated bulk samples of deep soil and saprolite/weathered bedrock within the seasonally saturated zone (within ≈ 2 m of the surface) tend to plot higher up the LMWL, nearly overlapping with freely sampled groundwater from wells (Figures 8 and 9). The weathered bedrock vadose zone beneath the studied oaks where rock moisture declines were observed in the late dry season is at least 1.5 m thick, or about six times thicker than the lower portion of the soil that does not indicate evaporative enrichment (Figures 5 and 6).

4.3.4. *Q. garryana* Isotope Dynamics

Figures 8 and 9 show the temporal shifts in isotope composition of *Q. garryana*. In May, groundwater levels begin to decline (Figure 4) and *Q. garryana* stem isotopic composition is slightly depleted in deuterium relative to the groundwater and shallow unsaturated soil (Figure 8). As the dry season progresses, *Q. garryana* xylem water isotope compositions tend to become more depleted, shifting toward lighter isotopic compositions roughly parallel to the LMWL (Figure 9). In 2016, *Q. garryana* average stem water compositions shifted from -48.5‰ δD and -6.99‰ $\delta^{18}\text{O}$ ($n = 7$) in early May to -60.8‰ δD and -8.66‰ $\delta^{18}\text{O}$ ($n = 7$) by mid-September. The middle- to late-summer dry season isotopic values of the *Q. garryana* stems generally

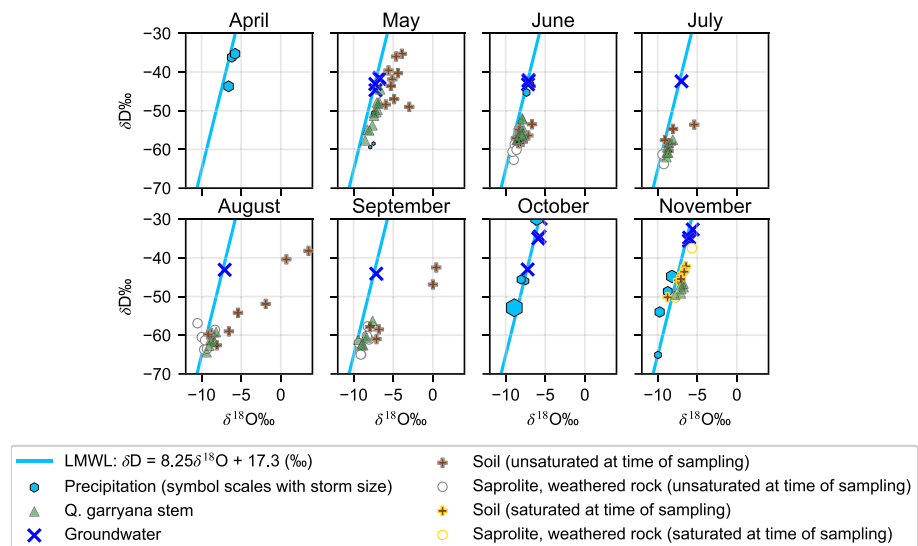


Figure 9. Dual-isotope snapshots for each month of oak and subsurface water dynamics in 2016. Oak xylem water samples shift down the LMWL through the dry season, away from the groundwater toward a region defined by moisture held in the deep soil, saprolite, and weathered bedrock. Shallow soil samples exhibit evaporative enrichment in midsummer, which is not reflected in the oak samples. With the return of the wet season in November, oaks and subsurface solid samples shift up the LMWL toward the groundwater.

fall within the dual-isotope space region defined by waters extracted from deep soils, saprolite, and weathered bedrock in the vadose zone but not groundwater (Figures 8 and 9). The progression toward isotopically lighter values during the summer dry season coincides with declining subsurface water availability. As the seasonal groundwater receded and predawn water potential progressively decreased from approximately -0.5 to -1 MPa between May and July 2016; for example, *Q. garryana* stem δD became progressively lighter (Figure 10). At water potentials below -1 MPa, *Q. garryana* stem δD remains roughly the same at the most depleted values that correspond to the composition of unsaturated deep soil, saprolite, and weathered bedrock.

With the arrival of the first rains of the wet season in October and November 2016, the water table rose, saturating the entire subsurface profile (Figure 4). At this time the predawn water potential values were indistinguishable from 0 MPa, consistent with complete subsurface saturation. *Q. garryana* stem isotopic composition trended toward more enriched values at the start of the wet season, overlapping with water

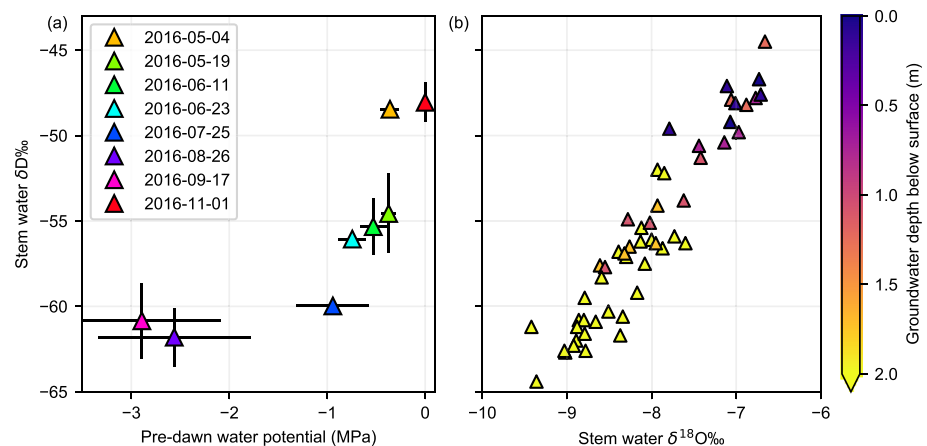


Figure 10. Stem water (xylem) isotopic composition in relation to water availability in 2016. As the tree water potential declines (from right to left in a) and the groundwater table drops (blue to yellow in b), stem water isotopic composition becomes depleted (lighter or more negative).

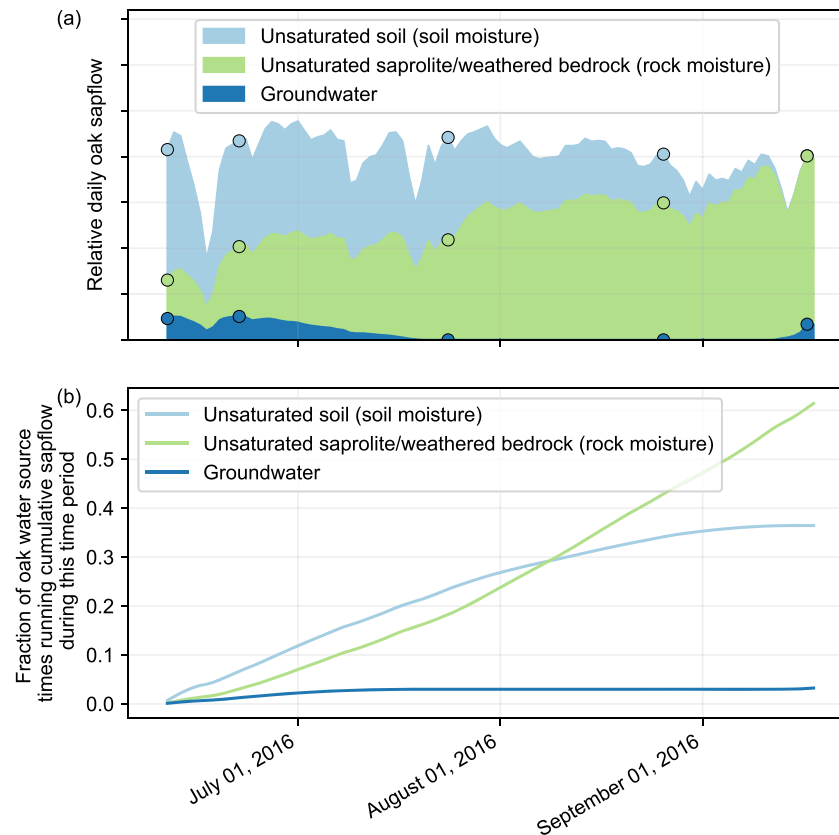


Figure 11. Three-end-member isotopic linear mixing analysis of oak water source, partitioned into the daily sapflow time series (a), for which the y axis is relative, and weighted by the running cumulative sapflow flux (b). The trends are interpolated between sampling dates highlighted in (a) with points.

extracted from saturated soils and weathered bedrock (shown as gold outlined symbols in Figures 8 and 9) but remaining slightly lighter than contemporaneously sampled groundwater from the top of the wells.

4.3.5. End-Member Mixing Analysis

The isotopic end-member mixing analysis (Figure 11) indicates that by the start of July, groundwater contributed minimally (<10%) to the oak water supply. The bulk of the oak water supply was sourced approximately evenly between the unsaturated saprolite/weathered bedrock (rock moisture) zone and the unsaturated soil (soil moisture) zone. For the rest of the dry season, the relative fraction of the oak sapflow sourced from rock moisture grew steadily, to nearly 100% in early September. By weighting the end-member mixing fractions by the cumulative running sapflow, we infer that from mid-June to mid-September the oak sourced about 3% of its water from groundwater, 36% from soil moisture, and 61% from rock moisture (final values (right-hand side) of the cumulative flux plot of Figure 11).

5. Discussion

5.1. Spatiotemporal Dynamics of *Q. garryana* Subsurface Water Extraction in the Franciscan Mélange

When oak transpiration ramps up in April and May, predawn water potentials and the groundwater table are relatively high (Figure 4). At this time, xylem water stable isotope compositions are only slightly depleted relative to the seasonal groundwater and unsaturated soil (Figure 8 and 9). As the seasonal groundwater recedes, shallow soil moisture content declines by a factor of approximately two (Figure 6). Although significant deep soil and rock moisture declines are observed under herbaceous areas early in the dry season (Figure 5) as well, these declines effectively cease by the end of July, following senescence and the cessation of flow in Dry Creek. In contrast, further declines in rock moisture are observed under the studied oaks until late August. By June, oak stem water stable isotopic composition had shifted toward lighter values that match the moisture extracted from deep vadose zone samples in the lowest portion of the soil and throughout the

weathered bedrock (Figures 8 and 9). In contrast, the unsaturated samples from the uppermost portion of the soil are relatively heavy, consistent with evaporative enrichment (Figures 6 and 9). The lighter isotopic composition of the oaks persists through September. Sapflow remains relatively high through the dry season as predawn tree water potential declines (Figure 4). With the return of rains at the start of the wet season and subsurface saturation, the oaks return to high predawn water potentials, and saturated samples throughout soil and weathered rock shift isotopically toward well samples of seasonal groundwater (Figure 4). The oaks track this change, also shifting isotopically up the LMWL toward the seasonal groundwater samples (Figures 8 and 9). Together, the isotopic data, groundwater levels, neutron probe surveys, gravimetric analyses and physiological observations indicate that the oaks use water from the saturated zone only at the end and start of the wet season. Throughout most of the dry season, when sapflow is highest, our observations indicate that deep unsaturated zone moisture, from the lowest portion of the soil and from throughout the weathered bedrock (i.e., rock moisture) is the primary source of the oak water supply.

5.2. *Quercus* Water Sources in Mediterranean Climates

Many studies have used a variety of methods to investigate oak water sources in Mediterranean environments—including sources used by the deciduous white oak group of California, to which *Q. garryana* belongs. These studies generally suggest that groundwater constitutes a significant fraction of transpiration, particularly in the summer dry season (e.g., Balugani et al., 2017; Cannon, 1971; Cooper, 1926; Lewis & Burg, 1964; Lubczynski & Gurwin, 2005). For example, Miller et al. (2010) proposed that *Q. douglasii* in the western foothills of the Sierra Nevada, CA, obtains 80% of its water from groundwater in June, July, and August based on hydrometric data. This is consistent with reported rooting patterns: Mediterranean oaks are noted for their dimorphic root structure (David et al., 2013; Koteen et al., 2015), in which a dense shallow root system is underlain by vertically oriented sinker or taproots that can extend to great depth (Canadell & Zedler, 1995; Canadell et al., 1996; Matsuda & McBride, 1986). These taproots are particularly common where the oaks inhabit easily penetrated substrates with accessible water like fine alluvium (e.g., Mendes et al., 2016). Previous studies of *Q. garryana* rooting and water acquisition have shown that seedlings rapidly develop taproots (Hibbs & Yoder, 1993), like other Mediterranean oaks (David et al., 2007).

Krygier (1971), working at a midslope position on a small hillside in a plantation in Oregon, found *Q. garryana* that root density declined with depth, from a maximum of $\approx 5,000$ roots per square meter near the surface to fewer than 250 per square meter at 1.2 m below the surface. Despite lower root density at depth, Krygier (1971)'s neutron probe surveys revealed that in late summer almost no change in water content occurred from 0–0.6 m, whereas significant depletion occurred from 0.6–2.4 m below the ground surface, which coincided with a zone described as crumbly shale. Similarly, Bréda et al. (1995), working at a gently sloping forested hillslope in France with soils classified as luvisols developed on a deep loam, found that *Q. petraea* and *Q. robur* root density declined approximately exponentially with depth, yet they also observed via neutron probe measurements that the shallow soil dried by midsummer and that the deeper unsaturated zone (to 2 m depth) likely provided water to the oaks during the dry period; they did not report any information on the transition to bedrock. These patterns are consistent with our observations of an unsaturated moisture pool below the shallow soil that sustains transpiration in the summer dry season.

Q. garryana is also noted to occur along alluvial lowlands (Stein, 1990), in contrast to the upslope hillslope positions of our study trees. This observation, and its similarity to the closely related *Q. douglasii* suggests that *Q. garryana*, like *Q. douglasii*, in some locations may rely on groundwater in the summer dry season. Our isotopic observations indicate instead that the *Q. garryana* on hillslopes within the Franciscan mélange shift through the summer from exploiting the seasonal groundwater pool to relying on the unsaturated lowest portion of the soil and rock moisture pools that develop in the wake of the receding groundwater as the summer progresses. This occurs in spite of a saturated zone being present at between 2 and 4 m below the ground surface in late summer.

5.3. Soil Moisture, Rock Moisture, and Variably Available Groundwater

Several observations in the Central Belt mélange may explain why the water in the saturated zone in the middle- to late-summer dry season—despite being relatively near the surface—is not used by the *Q. garryana*. The trees studied here inhabit a relatively thin subsurface critical zone. Even in upslope positions near the topographic divide, the depth to fresh, unweathered parent material that remains permanently saturated is only 2 to 4 m below the ground surface (Dralle et al., 2018; Hahm, Rempe, et al., 2019). However, this permanent groundwater system is anoxic, based on the blueish hue of the mélange and negligible summer

groundwater oxygen in the boreholes across the site (Hahm, Rempe, et al., 2019). The hydraulic conductivity of the parent material is also extremely low ($<10^{-10}$ cm/s), as shown by permeameter measurements (Dralle et al., 2018), persistent meter-scale head differences in water table levels in adjacent monitoring wells in late summer (Hahm, Rempe, et al., 2019), scanning electron microscopy imagery of fresh *mélange* matrix revealing negligible interconnected porosity (Hahm, Rempe, et al., 2019), the lack of streamflow in the adjacent channel network for most of the summer, in spite of a relatively large topographic head gradient from the channel to ridge (Lovill et al., 2018), and, finally, very slow rising water levels in wells in the permanently saturated zone after initial drilling. We suggest that the combination of lack of oxygen and low-conductivity substrate render the permanent groundwater that resides within the fresh parent material unsuitable for trees.

In the early summer and early fall (and even in winter, when the oaks lack leaves but parasitic evergreen mistletoe draws up water through the oak's hydraulic pathways for their transpiration needs (Hahm et al., 2018)), the oaks apparently do use seasonally ephemeral groundwater that intrudes into the weathered bedrock and soil. This follows the proposal of Thomas (2014) that for many phreatophytes “the fraction of the water demand that is covered by uptake of groundwater seems to be determined by environmental conditions rather than by inherent traits of the plants.”

Both the accessibility of a rock moisture pool and the inaccessibility of the permanent groundwater present challenges for tree water uptake patterns as currently prescribed in dynamic global vegetation and Earth system models. The vast majority of Earth system models either prescribe a uniform soil thickness (e.g., Smith et al., 2001) or exploit existing spatially distributed databases of soil characteristics (e.g., Ke et al., 2012). These models would predict that exhaustion of plant-available water held within a relatively thin soil layer leads to a decline in transpiration through the dry season. In contrast, the oaks studied here maintain high rates of transpiration throughout the summer due, in part, to the presence of moisture from the unsaturated weathered bedrock zone that underlies the soil. For models that are informed by genus- or species-level rooting patterns and locally determined water table depths (e.g., Li et al., 2017), the deep tap-rooting tendency in Mediterranean oaks and the observation of a shallow saturated zone within the *mélange* would inaccurately suggest that the trees source a significant portion of transpiration from groundwater in the summer dry season. Alternatively, models that are informed by topographic position (e.g., Fan et al., 2017) would inaccurately predict a well-drained, relatively deep vadose zone near the topographic divide where our study trees are located. Accurate parameterization of water uptake patterns requires detailed description of plant-accessible subsurface water pools, as determined by local subsurface critical zone structure and the hydrologic properties of the underlying fresh bedrock.

Our observations also contradict proposed metrics for the identification of groundwater dependent ecosystems. Eamus et al. (2006), for example, proposed that if (i) a portion of the vegetation continues to fix carbon during extended dry periods or (ii) some plant communities retain a similar leaf area index while others exhibit seasonal reductions, then that ecosystem could be classified as groundwater dependent. The sustained dry season transpiration and leaf area index of the *Q. garryana* in juxtaposition to the herbaceous ground cover die back at our site would therefore be strong indicators of groundwater dependence, which is in contrast to our findings.

5.4. Summer Isotope Dynamics in the Deep Vadose Zone and Mechanisms for Isotopic Depletion of Deep Soil and Rock Moisture

In the summer dry season, the bulk water extracted from the unsaturated lowest portion of the soil and unsaturated weathered bedrock zone was isotopically depleted (Figures 6, 8, and 9), and lighter than both the first, last, and average rain of the wet season, as well as the seasonal groundwater sampled in wells across the site (Figures 8 and 9). Our observation of isotopically light water from the unsaturated zone below evaporatively enriched shallow soils is not unique. Nearby, at the sister Eel River CZO site, Oshun et al. (2016) obtained solid material (saprolite, weathered, and fresh bedrock) via dry drilling into fractured, weathered shale to depths of up to 32 m and found that the extracted water was significantly lighter (on average $\approx 20\text{‰}$ δD difference) than typical groundwater and average precipitation. Kurz-Besson et al. (2006), working on a gently sloping (5°) experimental plot in Portugal, found that bulk water extracted from the unsaturated soil zone extending from about 0.3 to 1.0 m below the surface was isotopically depleted relative to local rainfall and the overlying evaporatively enriched shallow soil. The xylem water of the *Quercus suber* trees they studied matched the isotopically light lower soil moisture pool in the summer dry season. A rock moisture pool

was also likely present there but was not measured: the ≈ 1 m thick soil layer lies above 12 m of unsaturated fractured and altered unsaturated aplite and gneiss. del Castillo et al. (2016) similarly found a Mediterranean oak species (*Quercus ilex*) to shift toward a deep, isotopically depleted soil moisture source in the summer dry season on a former agricultural terrace in the Monstant range in the northeastern Iberian Peninsula. McCutcheon et al. (2017), working at a steep site with shallow soils overlying weathered granodiorite in the Idaho Batholith, also observed that soils from 70–100 cm depth, below the zone of evaporative enrichment, tended to have a lighter isotopic signature than average rainfall and were shifted roughly parallel to and down the LMWL.

A variety of mechanisms have been proposed in the literature to explain why deeper vadose zone moisture is isotopically light. While the data we collected from our field site do not confirm any particular mechanism, they do allow us to rule some out. We sort these mechanisms into two categories: (i) biotic and/or abiotic fractionation and (ii) isolation and/or mixing of distinct isotopic inputs.

5.4.1. Biotic or Abiotic Fractionation

With the exception of certain halophytes and xerophytes (e.g., Ellsworth & Williams, 2007; Lin & Sternberg, 1993), it has long been thought that fractionation during uptake by roots in the liquid phase is negligible (Dawson et al., 2002), indicating that the water that remains in the subsurface should not be isotopically altered by plant water uptake. Although it is generally unknown to what extent fungi transport water to plants, Poca et al. (2019) recently found that xylem water in *Acacia* was more depleted when grown in the presence of arbuscular mycorrhizae. This would presumably result in an enrichment of the water left behind in the subsurface, which we did not observe. Luo and Sternberg (1992) noted that fractionation of both hydrogen and oxygen occurs during cellulose synthesis. It is conceivable that this process could result in isotopic alteration of xylem water. Zhao et al. (2016) also observed intratree fractionation of deuterium between water pools. The trunk and leaves of the oaks at our study site shrink and swell diurnally, due, presumably, to short-term water storage and release (Hahm et al., 2018), as also recently observed in oak trunks studied by Rodríguez-Robles et al. (2020). It is possible that the roots also similarly store and release water, perhaps to the surrounding materials in the subsurface; if this water is isotopically altered within the plant it could then impart a distinct isotopic signature on the soil and weathered bedrock adjacent to roots, as well as the plant transpiration stream. Water phase transitions in the subsurface could also lead to fractionation, as proposed, for example, by Kurz-Besson et al. (2006), in vapor-liquid transitions that could accompany root-mediated hydraulic redistribution. We did not measure vapor phase isotopic compositions, humidity, temperature, or sapflow belowground, so we cannot rule this out as a potential fractionation mechanism. However, vapor condensation on roots followed by uptake would presumably result in isotopic signatures in xylem water and the remaining water in the rhizosphere that shift in opposite directions, unlike the patterns we observed. We don't suspect vapor diffusion of lighter isotopes from the groundwater upward to the vadose zone to be significant, because the groundwater does not become measurably enriched as the dry season progresses.

Oshun et al. (2016), who documented a relatively light bulk water isotopic signature in the moisture of the weathered bedrock vadose zone, summarized likely mechanisms that could result in isotopic fractionation in water below the evaporative enrichment front. Surprisingly, they found that during the summer, as the near-surface weathered bedrock became drier (due to tree moisture uptake), the bulk water cryogenically extracted from this zone became systematically lighter. When rains returned, the weathered bedrock returned to heavier values. We also observed a slight isotopic depletion in the saprolite/weathered bedrock as the dry season progressed (Figure 8). Oshun et al. (2016) suggested that chemical weathering—which releases cations and results in hydration spheres that preferentially bind heavy isotopologues of water—may result in a relatively light water in adjacent pores. Oshun et al. (2016) also proposed that clay minerals could produce fractionation effects, as observed by, for example, Oerter et al. (2014). This is consistent with findings by Gaj et al. (2017) and Orlowski et al. (2016), who found via laboratory experiments that water extracted from dried and then wetted clays were systematically lighter than the water used in wetting, and earlier studies that observed significant clay water isotopic fractionation at near-surface Earth temperatures (e.g., James & Baker, 1976; Sheppard & Gilg, 1996). The mineralogy of the mélange matrix weathered bedrock at our study site contains chlorite and the weathering products of albite and muscovite (Cloos, 1983; Hahm, Rempe, et al., 2019), resulting in a clay-rich substrate where such an effect could occur. Clay content also tends to be high in the lower portion of the soil which coincides with the Bt horizon and lies below the evaporative enrichment front. We are unaware, however, of studies that have systematically documented

clay isotopic fractionation effects in field settings or performed a full mass balance accounting on the water isotope cycle of these potential isotope effects over geologic time scales. Fractionation of isotopes in water associated with calcite and organic material (both of which are present in the subsurface at our site) has also been noted (Chen et al., 2016; Meißner et al., 2014).

Barbeta et al. (2019) documented an unexplained offset in deuterium between source and plant water, and noted that other studies have made similar observations. Barbeta et al. (2020) investigated this further via pot experiments with *Fagus sylvatica*, repeating the observation and suggesting that heterogeneities at the pore and plant tissue scale could explain this phenomenon. Their findings of deuterium offset between plant and source water differ from our own in three key ways: (i) Although oak xylem water in the summer dry season is depleted in deuterium relative to the average precipitation input, it matches the proximate presumptive source (deep unsaturated zone water); (ii) our observation of depletion of subsurface moisture and xylem water relative to precipitation is pronounced for not only hydrogen but for oxygen as well, and (iii) the difference we observed between average precipitation input and subsurface moisture/xylem water increases rather than decreases as trees move from a relatively hydrated state toward the wilting point. Thus, although the mechanism suggested by Barbeta et al. (2020) may be at play at our site, our disparate observations make it difficult to confirm their hypothesis. One final consideration we consider is that it is also possible that a methodological bias associated with the cryogenic extraction process impacts the isotopic signature of water obtained from both the plant tissue and subsurface solid samples (e.g., Araguás-Araguás et al., 1995), however, this would have to impact two very different substrates (xylem and minerals) in similar ways to explain our data.

5.4.2. Isolation or Mixing of Distinct Isotopic Inputs

Brooks et al. (2010) reported that in the dry season deeper unsaturated zone material below the zone of evaporative enrichment had a lighter isotopic signature than average precipitation and streamwater. They hypothesized that the mechanism responsible for this was an isotopic rainout effect in the first large rain event of the preceding wet season, in which progressively depleted water filled small pores from the top down. They further proposed that subsequent rain throughout the wet season bypassed and did not interact with the waters sequestered in small pores in the first large storm. The following summer, bypassing water drained from large pores and fed groundwater that sustained baseflow, while isotopically light water from the end of the first major wet season rain event remained sequestered in the smaller pores at depth and was potentially available for root water uptake.

At our site, early rains were not consistently isotopically light. Furthermore, complete saturation of the subsurface occurs multiple times over the course of the wet season with groundwater that is relatively heavy compared to the summer rock moisture and deep soil moisture. In this case, even dead-end pores should equilibrate isotopically with relatively heavy water, due to diffusion-driven mixing in the saturated substrate. The diffusion coefficient D of deuterated water, HDO, in H_2O is $1.295 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$ at 5°C (Mills, 1973), a typical wintertime near-surface temperature at our site. For typical soil and rock pore sizes L on the order of 1 mm to 1 cm, the diffusion time scale τ is on the order of minutes to hours ($\tau \approx \frac{L^2}{D}$). As diffusion is slow relative to advection, this represents a conservative estimate of the time scale for isotopic homogenization, and suggests that in a seasonally saturated subsurface, isotopic heterogeneity in bulk pore water will not persist at measurable levels beyond a few days. This reasoning is generally consistent with recent experimental observations of isotope diffusion dynamics in sandy loams, in which equilibration was observed over a matter of days (Bowers et al., 2020), which is still much shorter than the months-long saturation experienced at our site in the winter. At our field site it is therefore likely that pore fluid does not preserve the signature of a single early wet season storm's rainout effect through to the following dry season. The duration of saturation and soil texture are likely important factors in determining the extent of equilibration (Bowers et al., 2020; Sprenger et al., 2019).

Exchange between mobile and bulk water requires that water molecules within a saturated pore can diffuse freely and are not adhered to mineral surfaces in a way that prevents mixing with interconnected pores or fractures. Decreased mixing may nevertheless occur if the diffusion coefficient is reduced for the adsorbed water layers, for example, between clay surfaces and adjacent pore waters. The volume of water adsorbed onto minerals in shales with similar composition to material at our site can be significant ($>5\%$) at the relatively high humidities ($>90\%$) typically encountered in the subsurface (Chenevert, 1970). Further work is needed at the mineral-surface scale to reveal the isotopic dynamics of water of wet and dry soil and rock materials commonly found in the field. In summary, although we do not know the mechanism underlying

the isotopic depletion of the lowest soil and rock moisture, it is unlikely to be due to a plant fractionation process or an isotopic rainout mechanism alone. Instead, a mineral or organic-surface-mediated and/or vapor phase transition isotopic effect is likely required to explain this observation at our site.

6. Conclusion

We observed sustained summer water uptake by a Mediterranean oak (*Q. garryana*) as surface soils dried and shallow seasonal groundwater source drained, leaving behind deep soil moisture and rock moisture in the weathered bedrock unsaturated zone. The isotopically light dry season signature of the oak water matched bulk water extracted from the deepest soil and weathered bedrock unsaturated zones. Sustained sapflow, low predawn water potentials, desiccated near-surface soils, declines in weathered bedrock vadose zone moisture, and the observed stable isotope dynamics collectively indicate that the vadose zone beneath the evaporative enrichment front—which is dominated by the rock moisture zone in terms of relative size—is the primary source of the dry season *Q. garryana* transpiration. The study trees inhabit a relatively thin subsurface critical zone that completely saturates in the wet season, and then progressively dries each summer. Although a saturated zone is present only $\approx 2\text{--}4\text{ m}$ below the surface in the late summer, it resides in fresh, permanently saturated mélange matrix parent material. This permanent groundwater is not used by the oaks, presumably due to low oxygen levels and hydraulic conductivity. These findings suggest that water uptake patterns in Mediterranean oaks—which are commonly considered to be reliant on groundwater to meet the dry season transpiration demand—are site-specific. Our findings highlight the need to better map and characterize unsaturated water within weathered bedrock—that is, rock moisture—at landscape scales, as existing spatially distributed soils databases insufficiently describe this potential plant water source. Complementary efforts to map depths to the saturated zone should also consider the nature of that water, as not all groundwater is readily plant-accessible, even if it is within reach of typical rooting depth of mature trees. Finally, our study highlights a poorly understood subsurface isotopic process, wherein bulk water extracted from deep soil and weathered bedrock is lighter than the average rainfall input and the seasonal groundwater that recedes from that critical zone at the start of the dry season.

Data Availability Statement

The data and Python notebook code used to create the data figures are hosted online (at https://github.com/jessehahm/Quercus_garryana_water_sourcing). The primary weather station data for Sagehorn is hosted online (at <http://sensor.berkeley.edu>).

Acknowledgments

We gratefully acknowledge the field access and scientific enthusiasm provided by Marilyn and Jerry Russell, and thank Renee Holleman for collecting precipitation samples. Wenbo Yang, Stefania Mambelli, Wendy Baxter, Chris Wong, Collin Bode, Sky Lovill, Logan Schmidt, Colleen Murphy, and Sami Cargill contributed to fieldwork and laboratory analyses. Funding was provided by the National Science Foundation-supported Eel River Critical Zone Observatory (EAR 1331940), the University of California Natural Reserve System Mildred E. Mathias Graduate Student Research Grant, the Carol Baird Fund for Graduate Field Science, the Institute for the Study of Ecological and Evolutionary Climate Impacts, and Simon Fraser University. Feedback from J. P. Ferrio, S. D. Carrière, and a third anonymous reviewer greatly improved the manuscript.

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