# Evidence for widespread woody plant use of water stored in bedrock

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## 1 Summary paragraph

Woody plant transpiration is a major control on Earth's climate system, streamflow, and human water supply. Soils are widely considered to be the primary reservoir of water for woody plants, however, plants also access water stored in the fractures and pores of bedrock, either as rock moisture (water stored in the unsaturated zone) (Schwinning, 2010) or bedrock groundwater (below the water table) (Miller et al., 2010). Bedrock as a water source for plants has not been evaluated over large scales, and consequently, its importance to terrestrial water and carbon cycling is poorly known (Fan et al., 2019). Here, we show that woody plants routinely access significant quantities of water stored in bedrock —commonly as rock moisture —for transpiration across diverse climates and biomes. For example, in California, the volume of bedrock water transpired by woody vegetation annually exceeds that stored in man-made reservoirs, and woody vegetation that withdraws bedrock water accounts for over 50% of the aboveground carbon stocks in the state. Our findings show that bedrock water storage dynamics are a critical element of terrestrial water cycling and therefore necessary to capture the effect of shifting climate on woody ecosystems, above- and belowground carbon storage, and water resources.

#### 2 Introduction

Plants return water stored in the subsurface to the atmosphere through the process of transpiration. The amount of plant accessible subsurface water storage, and its variability in space and time, is a critical determinant of water and energy exchange at Earth's surface. Appropriate characterization of root-zone water storage is thus key to accurate prediction of environmental response to change, particularly the face of widespread drought-induced die off (Madakumbura et al., 2020; McDowell et al., 2019), massive wildfires (McEvoy et al., 2020), and woody encroachment (Hauwert and Sharp, 2014).

Soils, which can be defined as physically mobile, disaggregated material, are thought to host the majority of root-zone water storage. Because soils are relatively accessible for sampling, their hydraulic properties are estimated at large scales (Soil Survey Staff, 2019), and they are mechanistically represented in the modeling frameworks used to predict Earth system processes such as landsliding, contaminant remediation, and global nutrient cycling. However, the root-zone commonly extends beyond soils



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into bedrock, where hydraulic (Nimmo et al., 2017) and biological (Leshem, 1970) processes can differ significantly from soils. This bedrock retains relict primary rock structures such as bedding or joint planes, and in some cases, can be so weathered as to be called a C-horizon or saprolite. While woody plants can access water and nutrients from bedrock (Brantley et al., 2017), bedrock is not broadly considered a significant water reservoir, largely because root-zone water storage in bedrock is unmeasured at large scales (Fan et al., 2019).

Here, we quantify dynamic root-zone water storage in bedrock by estimating transpiration of bedrock water by woody vegetation across the continental United States (CONUS). Using publicly available datasets and a compilation of data from published field studies, we document the spatial extent of bedrock rooting and quantify the magnitude and frequency of woody plant access to bedrock water stores.

#### 3 Results and Discussion

#### 3.1 Plant-accessible water storage in bedrock sustains evapotranspiration

The majority (55%) of wooded land area in the continental U.S. (CONUS) is characterized by shallow (< 1.5 m deep) soils underlain by bedrock (see S1). In these areas, which are distributed across a broad range of environments (Figure 1), the root zones of woody plants are likely to include bedrock. Field studies reporting rooting into bedrock (shown as points on Figure 1) confirm that, indeed, roots penetrate bedrock across a broad range of plant species, climates, and rock types (see S2).

To quantify where bedrock water is routinely accessed by woody vegetation, we report a conservative estimate of the volume of bedrock water accessed by plants in a given year ( $D_{bedrock,Y}$ , see Methods) for areas where woody vegetation overlies shallow bedrock. Figure 1 and 2 report the spatial distribution of  $D_{bedrock,Y}$ , defined as the annual bedrock water storage deficit (see Methods). In locations shown in black in Figures 1,  $D_{bedrock,Y}$  is 0 in all years, and therefore soil water storage capacity is sufficient to explain observed ET (see Methods). However, in many areas across CONUS, soil water storage capacity is insufficient to explain ET (that is,  $D_{bedrock,Y}$  is commonly greater than 0; pink and green in Figure 1), and therefore bedrock must supply water for transpiration. Green areas, where  $D_{bedrock,Y}$  is greater than zero across all study years, indicate routine use of bedrock water for transpiration. These locations host substantial aboveground biomass. For example, woody vegetation that withdraws bedrock water for ET on an annual basis (green in Figure 1) accounts for over 50% of California's aboveground carbon stocks (587 Tg of carbon) (see S6, Spawn et al. (2020); Spawn and Gibbs (2020).

Figure 2A reports the magnitude and spatial distribution of  $D_{bedrock,Y}$  across California and Texas, where at least 28-30% and 5-10% of the total land areas respectively withdraw bedrock water for transpiration in a given year (Figure 2A). ( $D_{bedrock,Y}$  for CONUS is reported in S3.) In some areas,  $D_{bedrock,Y}$  can exceed 500 mm and can constitute a significant fraction of the mean annual precipitation (see S4), despite being a highly conservative estimate of the magnitude of water withdrawn by vegetation from bedrock (see Methods). This indicates that bedrock is a critical storage reservoir for plant-accessible water.  $D_{bedrock,Y}$  will more closely reflect actual bedrock water storage withdrawal when and where energy and precipitation delivery are out of phase (such as the seasonally dry west coast), and will be a significant underestimate where energy and precipitation delivery are in phase (such as the humid eastern U.S.).

We calculate a bedrock root-zone water storage capacity,  $S_{bedrock}$ , which is defined as the largest storage used by woody vegetation over a multi-year time window (2004-2017) that cannot be accounted for by soil water storage capacity (see Methods, see S5). Figure 3 reports  $S_{bedrock}$  as a fraction of total root-zone storage capacity and shows that  $S_{bedrock}$  often constitutes the majority of total storage capacity in the root-zone (Figure 3).

In some locations, the magnitude of  $D_{bedrock,Y}$  is relatively consistent across different years, and consequently similar to  $S_{bedrock}$ , indicating that plants withdraw similar amounts of bedrock water each year. However, in other locations, such as the southern Sierra Nevada in California and the Edwards Plateau in Texas,  $S_{bedrock}$  can be significantly larger than  $D_{bedrock,Y}$  (see S4, S5), indicating that the storage capacity of plant accessible water in bedrock is much greater than the storage that is withdrawn in a given year. In these locations bedrock water must be progressively drawn down over multiple years to explain the observed ET and multi-year drought may control plant access to bedrock water storage (Twidwell et al., 2014; Goulden and Bales, 2019).

Bedrock water serves as a reservoir for transpiration across a range of biomes and Köppen climate types (Figure 4). Arid, semi-arid and Mediterranean climate types are associated with the largest  $S_{bedrock}$ , however, significant bedrock water withdrawal also occurs in humid climate types (Figure 4).  $S_{bedrock}$  tends to be higher for evergreen forests, savannas, and shrubland, relative to deciduous and mixed forests. Overall, combined analysis of  $S_{bedrock}$  for both biome and climate type reveal that the largest median  $S_{bedrock}$  occurs in semi-arid shrubland, Mediterranean savannas, and Mediterranean needleleaf forests (Figure 4, see Table S1). Locations where  $S_{bedrock}$  is positive tend to be associated with areas at high elevation and significant above-ground biomass (see S5).

## 3.2 Rock moisture as a common water source for transpiration

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Locations with field evidence for use of unsaturated bedrock water storage (i.e.,rock moisture) documented in our literature compilation coincide with areas in which we calculate positive median  $D_{bedrock,Y}$ .  $D_{bedrock,Y}$  for each study location shown in Figure 2B. Comparisons between volumes of rock moisture used and our  $D_{bedrock,Y}$  confirm that, as expected,  $D_{bedrock,Y}$  is a conservative estimate of bedrock water used. For example, in a 1993 study, Sternberg et al. (1996) found over 300 mm of rock moisture used by chaparral where we calculate a  $D_{bedrock,2004-2017}$  of 88-253 mm, and between 2013-2017, Rempe and Dietrich report an average of 280  $\pm$  80 mm of rock moisture used by a mixed hardwood and conifer forest where we calculate a  $D_{bedrock,2004-2017}$  of 113-283 mm.

While field studies corroborate our metric of bedrock water use and suggest that bedrock water storage used by plants is commonly in the form of rock moisture,  $D_{bedrock,Y}$  and  $S_{bedrock}$  do not discriminate between rock moisture (unsaturated) and bedrock groundwater (saturated). Discriminating between saturated and unsaturated water supplies to vegetation remains challenging, even in field study, yet the distinction between them is germane to mechanistically modeling biogeochemical and hydraulic processes. Rock moisture use has been confirmed under circumstances that might commonly be attributed to groundwater use. For example, Hahm et al. (2020) show that oaks relied on rock moisture to sustain dry season transpiration at an oak savanna site where groundwater remains within 3 m of the surface throughout the year. Insensitivity of ET to extended drought is another tool used to attribute groundwater as a transpiration source, however, storage capacity in the unsaturated

zone can produce similar insensitivity of ET to drought (Hahm et al., 2019a). These circumstances suggest that mis-attribution of rock moisture as groundwater is likely, and that rock moisture use by woody plants may be common.

#### 3.3 Implications of widespread bedrock water use

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While it has long been recognized that woody plants root into bedrock (Cannon, 1911), widespread and routine transpiration of bedrock water, reported here for the first time, suggests that the dynamics of bedrock water storage may be as fundamental to understanding terrestrial water and carbon cycling as soil moisture. Across the western U.S. in particular, significant volumes of water are stored in bedrock and released back into the atmosphere on an annual basis. For example, in California, at least  $20 \text{ km}^3$  (16.2 million acre-feet) of water are extracted from bedrock by woody plants annually. This is approximately equal to the volume of water stored in all of the state's reservoirs combined (California Department of Water Resources), and about three times the state's annual domestic water use (United States Geological Society).

Investigation of biological and hydraulic processes in the bedrock rhizosphere is a frontier research area (Schwinning, 2020). New studies are needed to clarify the role of bedrock water storage under precipitation volatility, including multi-year drought and alternation between extreme wet and dry years. In the 2011-2016 California drought, for example, forest ecosystems with access to rock moisture exhibited diverse responses from insensitivity (Hahm et al., 2019a) to vulnerability (Goulden and Bales, 2019). This motivates new field-based observational studies of belowground structure and bedrock water storage dynamics across diverse lithological, climatic, and ecological settings to clarify the different ways in which bedrock water storage mediates ecohydrological processes (Ding et al., 2020; Dawson et al., 2020).

Significant plant usage of bedrock water, and specifically rock moisture, occurs in critical locations for water supply, including the Sierra Nevada, the recharge zone of the Edwards and Trinity Aquifers, and the headwaters of the Colorado River (Figure 1), which together supply water to at least one quarter of the U.S. population. Given that the dynamics of rock moisture have the potential to regulate the timing of groundwater recharge and runoff (Salve et al., 2012), bedrock water storage may be critical to water resource planning.

Woody ecosystem dependence on stored subsurface water will likely increase in the future as community ranges shift (Harsch et al., 2009), snowpack declines in high elevation and high latitude regions, and many environments undergo a transition from energy to water-limited conditions (Kapnick and Hall, 2012). Thus, the availability of bedrock water storage may be key to predicting large scale vegetation dynamics, including the stability or vulnerability of ecosystem carbon storage, under climate change.

Long-term, intensive monitoring studies are increasingly documenting mechanisms by which roots in bedrock impact ecosystem function (Hahm et al., 2019b), groundwater and stream chemistry (Tune et al., 2020), and rates of soil production and weathering (Brantley et al., 2017; Keller, 2019). While bedrock water may not be needed to explain ET in the humid eastern U.S., vegetation nevertheless roots into bedrock and water storage dynamics in bedrock driven by roots could lead to largely unmeasured drivers of carbon cycling (Hasenmueller et al., 2017). Thus, bedrock water storage dynamics are likely key to understanding the sensitivity of carbon, water, and latent heat fluxes to changes in climate.

#### 4 Methods

#### 4.1 Literature compilation of rooting in bedrock

Available published evidence of rooting into rock is included in our literature compilation (available https://www.hydroshare. org/resource/e7ad140edaf54d69ba4f1cf1ec8e7f73/), which builds upon compilations by Jackson et al. (1996); Schenk and Jackson (2002a, b); Schwinning (2010) and Fan et al. (2017). Each entry includes information about rooting, climate, soil, and bedrock properties (see S2). A subset of sites report use of rock moisture by vegetation. For these entries, where possible, we report estimates of the contribution of rock moisture to evapotranspiration, as well as any estimates of plant available soil and rock moisture capacities.

## 4.2 Woody vegetation on shallow bedrock area calculations

To determine where depth of bedrock is less than 1.5 m and therefore likely to intersect with the root-zone of a woody plant, we use USDA's Gridded National Soil Survey Geographic Database (gNATSGO) product. We determine where the depth of soil restrictive layer for the classifications of lithic, densic, and paralithic bedrock occurs at depths less than 1.5 m (Soil Survey Staff, 2019; Staff) and mask out all other locations. gNATSGO data are generated using raw soil data from field surveys and subsequent laboratory analysis, and are ultimately reported by soil 'unit', which are mapped at around a 10m scale and resampled to 90 m resolution for analysis here. These surveys are occasionally repeated and the newest data is validated against historical surveys before replacing it in the official nationwide database (Staff). To determine woody landcover, we used the shrubland and forest landcover classes reported by the NLCD: USGS National Land Cover Database (Yang et al., 2018). NLCD forest classes include evergreen, deciduous, and mixed forest, while the shrubland designation includes the 'shrub/scrub' class only.

#### 4.3 Soil water storage capacity

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The gNATSGO product, from which the depth to soil restrictive layer and soil available water storage parameters are taken, supplies the 10m resolution SSURGO dataset, the highest resolution soil product available, and fills in missing areas with STATSGO (100-200km resolution) and the Raster Soil Survey to provide the most complete possible set of soil parameters across the U.S.(Soil Survey Staff, 2019). Soil data were down sampled to 90 m resolution through weighted mean averaging prior to analysis.

We define the soil water storage capacity ( $S_{soil}$ ) as the 'soil available water storage (AWS)' reported by the gNATSGO database (Soil Survey Staff (2019), see S5). This AWS product is calculated as the storage volume, in units of depth, between field capacity (1/10 or 1/3 bar) and wilting point (15 bars) and is measured for each soil layer or horizon until a restrictive layer (e.g. bedrock) or the maximum measurement depth (2 meters) is reached. This value is also adjusted for rock fragments and salinity. AWS for each soil unit is then calculated as the weighted average over the thickness of each layer. Each layer includes a high, low, and likely value of reported AWS.

# 4.4 Root-zone water storage capacity, $S_R$ , and maximum annual root-zone storage deficit, $D_{max}$

Here, we use a statistically interpolated precipitation (Oregon State's PRISM daily precipitation, Daly et al. (2008, 2015)) and a remotely-sensed evapotranspiration (Penman-Monteith-Leuning Evapotranspiration V2, Zhang et al. (2019); Gan et al. (2018)) data product to estimate the minimum magnitude of root-zone water storage capacity ( $S_R$ ) following the method developed by Dralle et al. (2020), which adapts the original method of  $S_R$  estimation from Wang-Erlandsson et al. (2016) to account for the presence of snow.

The method takes a mass balance approach and is therefore broadly applicable, not requiring place-based soil or plant-community parameterization. Specifically, the technique tracks a root-zone storage deficit (D) as a running, integrated difference between water fluxes exiting or entering the root zone, here taken to be evapotranspiration and precipitation where  $F_{out} = ET$  and  $F_{in} = P$ . This is accomplished by first computing the accumulated difference between  $F_{out}$  and  $F_{in}$  over a given time interval  $t_n$  to  $t_{n+1}$ :

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$$A_{t_n \to t_n + 1} = \begin{cases} 0 & \text{if } C \ge C_0 \\ \int_{t_n}^{t_{n+1}} F_{out} - F_{in} dt & \text{if } C < C_0 \end{cases}$$

where  $C_0$  is the threshold of snow cover which is deemed non-negligible, here chosen as 10%. This avoids attributing evapotranspiration from snowmelt recharge into the rooting-zone to unreplenished water storage depletion. Snow data is acquired from the Normalized Difference Snow Index (NDSI) snow cover band from the 500m MODIS/Terra data product (Hall et al., 2016).

170 With this, the root-zone storage deficit at any given time is defined iteratively as:

$$D(t_{n+1}) = \max\left(0, D(t_n) + A_{t_n \to t_{n+1}}\right) \tag{1}$$

Following these equations, D at any given time represents a lower bound on the volume of water that plants have used which must have been withdrawn from root zone storage without replenishment by precipitation. The deficit is effectively 'reset' to zero during wet periods, because the updated  $D(t_{n+1})$  is taken only as the maximum of 0 and the previous deficit plus the current difference between outgoing and incoming fluxes (Equation 4.4). Over the course of a year or many subsequent seasonal cycles, the maximum value of D represents the largest amount of water storage that must have been sourced from the subsurface.

Here, we report two deficit-related quantities: the observed maximum root zone storage deficit in water year Y ( $D_{max,Y}$ ) and the maximum root zone storage deficit over the period of record (2003 to 2017), taken as a lower bound on the actual root-zone storage capacity,  $S_R$ .  $D_{max,Y}$  is calculated for a given water year Y (that is, from October 1 in year Y-1 to September 30 in year Y) first by assuming the root zone storage deficit on October 1 is zero, then tracking that deficit through to the end of the water year.  $D_{max,Y}$  is the maximum value of the deficit time series over that water year. The procedure for computing

 $S_R$  is similar, but the deficit time series is computed over the period of record. That is, D is taken to be zero on October 1, 2003 and is tracked continuously until September 30, 2018.  $S_R$  is then taken to be the maximum value of the multi-year deficit time series.

Importantly,  $S_R$  and  $D_{max}$  are conservative lower estimates of water storage capacity and do not account for all possible withdrawal. This is true so long as no irrigation or lateral subsidies (e.g. groundwater or surface water) to the root zone occur.

# 4.5 Bedrock root zone water storage capacity and annual bedrock root zone water storage

To quantify the root zone storage capacity that cannot be accounted for by soil water storage capacity,  $S_{bedrock}$ , we subtract the soil water storage capacity from  $S_R$ , making sure to bound  $S_{bedrock}$  at zero:

$$S_{bedrock} = \begin{cases} 0 & \text{if } S_{soil} \ge S_R \\ S_R - S_{soil} & \text{if } S_{soil} < S_R \end{cases}$$

We perform a similar calculation to quantify the annual bedrock root zone water storage,  $D_{bedrock,Y}$ , which is the maximum annual root-zone storage deficit that cannot be accounted for by soil water storage capacity:

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$$D_{bedrock,Y} = \begin{cases} 0 & \text{if } S_{soil} \ge D_{max,Y} \\ D_{max,Y} - S_{soil} & \text{if } S_{soil} < D_{max,Y} \end{cases}$$

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Note that we use the highest AWS value reported. Therefore,  $S_{bedrock}$  and  $D_{bedrock,Y}$  are intended to represent conservative lower bounds, as we use the upper bound on  $S_{soil}$  and the lower bound on  $S_R$  and  $D_{max,Y}$ , respectively.

We restrict our calculation of  $S_{bedrock}$  and  $D_{bedrock,Y}$  to conditions where three criteria are met: (1) woody vegetation, (2) bedrock is encountered within the upper 1.5 m of the surface, and (3) where total ET is less than total P from 2003 to 2017. The first two criteria define locations where bedrock water storage could be important to woody plants (see S1), and the third criterion removes locations where either the mass balance is not physical (outputs cannot exceed inputs over long time spans), or there exist significant unmeasured fluxes entering the rooting zone, such as irrigation or lateral groundwater flow, that are a significant source for ET (Wang-Erlandsson et al., 2016). This approach leads to underestimates of the spatial extent of bedrock water use, because there are some locations, such as some of the study sites listed in Figure 2, which do not meet these criteria but nonetheless use bedrock water storage for transpiration. As remotely-sensed ET and P datasets continue to rapidly improve, these datasets could be incorporated into the workflow we present to arrive at better estimates of bedrock water use.

We propose that root zone storage deficits that exceed soil water storage indicate bedrock water use, however, alternative explanations could include fog, lateral inputs of water to soils across analyzed pixels, or uncertainty in calculations of  $D_{bedrock,Y}$  and  $S_{bedrock}$ . Our comparison of  $D_{bedrock,Y}$  to field studies demonstrates that these alternative explanations are not needed to account for root-zone storage deficits in excess of soil water storage capacity.

Data availability. The datasets generated during and/or analysed during the current study are available in the Hydroshare repository, https://www.hydroshare.org/resource/e7ad140edaf54d69ba4f1cf1ec8e7f73/. The precipitation data are available from the PRISM Climate Group at https://prism.oregonstate.edu/. The evapotranspiration data are available from Penman-Monteith-Leuning Evapotranspiration V2 (PML\_V2) (Zhang et al., 2019) at https://github.com/gee-hydro/gee\_PML. The snow cover data are available from NASA's MODIS/Terra Snow Cover Daily at https://nsidc.org/data/MOD10A1/versions/6. The soil data are available from the USDA's gNATSGO (Soil Survey Staff, 2019) database https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/geo/?cid=nrcseprd1464625. The landcover data are available from the USGS's National Land Cover Database at https://www.usgs.gov/centers/eros/science/national-land-cover-database?qt-science\_center\_objects=0#qt-science\_center\_objects. The biome data are available from NASA's MODIS/Terra+Aqua Land Cover Type Yearly at https://lpdaac.usgs.gov/products/mcd12q1v006/. The Köppen climate data are available from Peel et al. (2007) at https://people.eng.unimelb.edu.

Code availability. Code available on Hydroshare repository https://www.hydroshare.org/resource/e7ad140edaf54d69ba4f1cf1ec8e7f73/

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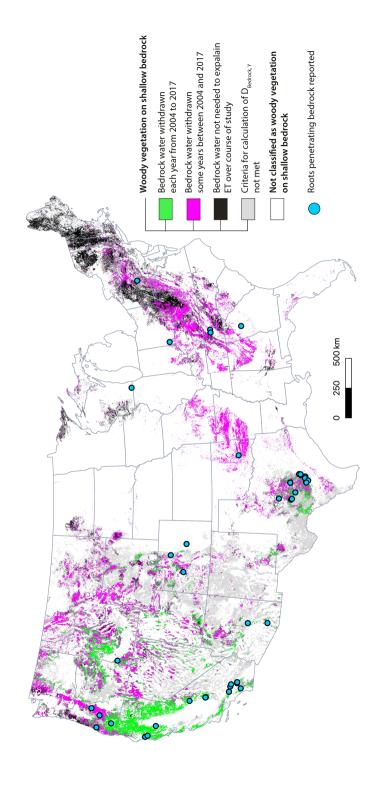
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vegetation (landcover types shrub and forest, (Yang et al., 2018)) where bedrock is encountered within the upper 1.5 meters (Soil Survey Staff, 2019) (see S1). This area is divided into four colors reflecting locations where  $D_{bedrock,Y}$  is greater than zero for each year of the study (green),  $D_{bedrock,Y}$  is greater than zero for at least one year of the study (pink),  $D_{bedrock,Y}$  is not greater than zero for any years of the study (black), and  $D_{bedrock,Y}$  is not determined because our analysis Figure 1. The spatial extent of annual bedrock water withdrawal by woody plants in the continental United States. Colored areas encompass the extent of woody criteria are not met (gray, see Methods). Where  $D_{bedrock,Y}$  is greater than zero, withdrawal of bedrock water is necessary to explain observed ET (see methods). Sites where rooting into bedrock is reported (blue circles) are listed in Supplemental File 1.

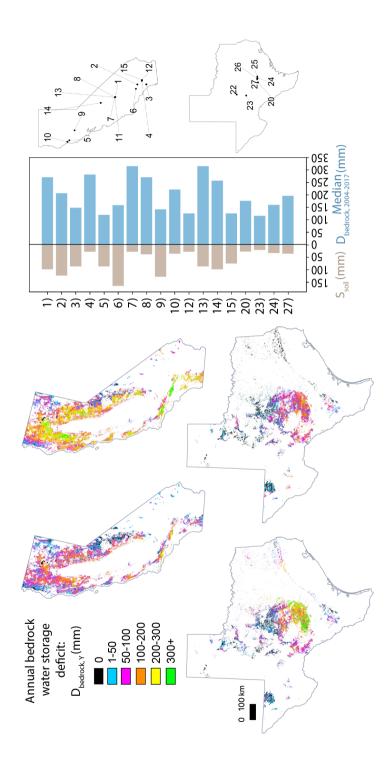


Figure 2. The distribution of  $D_{bedrock,Y}$  and sites with documented rock moisture use across Texas and California. (A) Map of  $D_{bedrock,Y}$  for 2011 and 2017.  $D_{bedrock,Y}$  for all of CONUS is shown in S3. (B) Soil water storage capacity,  $S_{soil}$ , (brown) and the median  $D_{bedrock,2004-2017}$  (blue) corresponding to locations with documented plant use of rock moisture, i.e. bedrock water storage from the unsaturated zone. Site locations are shown on maps to right and correspond to the (2010), (27) Schwinning (2008). Studies that document rock moisture use but exist in locations which did not meet our criteria for calculation of  $D_{bedrook}$ , (see following published studies: (1) Anderson et al. (1995), (2) Arkley (1981), (3) Bornyasz et al. (2005), (4) Fellows and Goulden (2017), (5) Hahm et al. (2020), (6) Hellmers et al. (1955), (7) Hubbert et al. (2001a), (8) Hubbert et al. (2001b), (9) Pedrazas et al. (in revision), (10) Rempe and Dietrich (2018), (12) Sternberg et al. (1996), (13) Witty et al. (2003), (14) O'Geen et al. (2018), (15) Graham et al. (1997), (20) McCole and Stern (2007), (23) Twidwell et al. (2014), (24) Litvak et al. Methods) are shown on the map and include (22) Bleby et al. (2010) (23) Twidwell et al. (2014), (25) Heilman et al. (2014), and (26) Tokumoto et al. (2014).

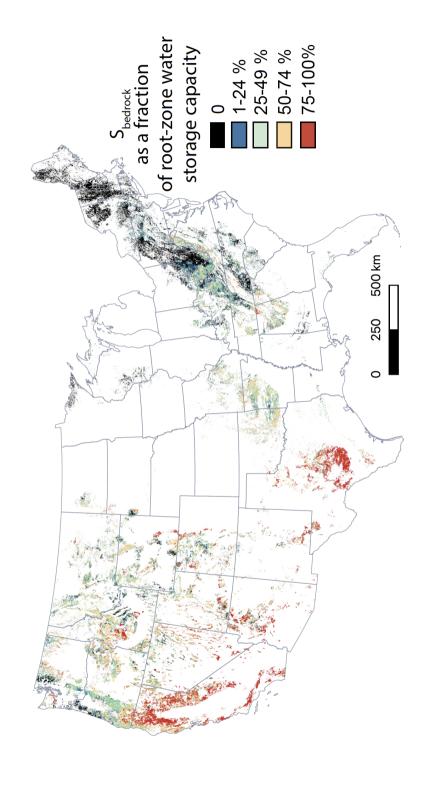


Figure 3. Sbedrock as a fraction of total root-zone storage capacity. Only locations that meet our analysis criteria (see Methods) are mapped. Figure S5 shows the magnitude of  $S_{bedrock}$ .

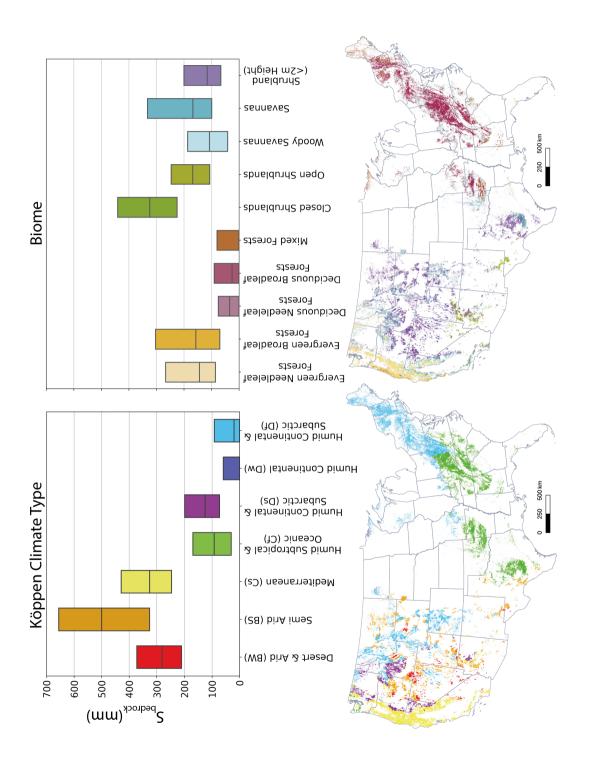


Figure 4. Boxplots shown of median and interquartile range of  $S_{bedrock}$  across Köppen climate type (Peel et al., 2007) (left) and biome (MODIS landcover classifications, Friedl and Sulla-Menashe (2015)) (right) for locations that meet analysis criteria (see Methods) shown in lower panel. The entire interquartile range is non-zero for many biomes and climates, while boxes intersecting the horizontal axis include a significant number of pixels with no bedrock water storage (i.e.  $S_{bedrock}$  is 0). Biome and climate subgroups with less than 2000  $km^2$  are excluded.