Plants as sensors: vegetation response to rainfall predicts root-zone water storage capacity in Mediterranean-type climates

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Abstract

In Mediterranean-type climates, asynchronicity between energy and water availability means that ecosystems rely heavily on the water-storing capacity of the subsurface to sustain plant water use over the summer dry season. The root-zone water storage capacity \( S_{\text{max}} \) defines the maximum volume of water that can be stored in plant accessible locations in the subsurface, but is poorly characterized and difficult to measure at large scales. Here, we develop an ecohydrological modeling framework to describe how \( S_{\text{max}} \) mediates root zone water storage \( (\bar{S}) \), and thus dry season plant water use. The model reveals that for \( S_{\text{max}} \) high relative to mean annual rainfall, \( S \) is not fully replenished in all years, and root-zone water storage and therefore plant water use are sensitive to annual rainfall. Conversely, where \( S_{\text{max}} \) is low, \( S \) is replenished in most years but can be depleted rapidly between storm events, increasing plant sensitivity to rainfall patterns at the end of the wet season. In contrast to both the high and low \( S_{\text{max}} \) cases, landscapes with intermediate \( S_{\text{max}} \) values are predicted to minimize variability in dry season evapotranspiration. These diverse plant behaviors enable a mapping between time variations in precipitation, evapotranspiration and \( S_{\text{max}} \), which makes it possible to estimate \( S_{\text{max}} \) using remotely sensed vegetation data — that is, using plants as sensors. We test the model using observations of \( S_{\text{max}} \) in soils and weathered bedrock at two sites in the Northern California Coast Ranges. Accurate model performance at these sites, which exhibit strongly contrasting weathering profiles, demonstrates the method is robust across diverse plant communities, and modes of storage and runoff generation.

1. Introduction

Measuring and predicting spatial variations in critical zone (the CZ, Earth’s ‘dynamic skin’ (Granth and Dietrich 2017), extending from the vegetation canopy down to fresh bedrock) architecture is a challenging earth science research frontier (Riebe et al 2017, Pelletier et al 2016, Fan et al 2019). One CZ property central to understanding the ecohydrological function of landscapes is the capacity for the subsurface to store water that can be used by ecosystems. This property can be quantified as the root-zone water storage capacity, \( S_{\text{max}} \) [L] (de Boer-Euser et al 2016, Dawson et al 2020), defined as the volume of subsurface void space available to store water that can be accessed by vegetation, per unit ground area (Klos et al 2018). Physically, \( S_{\text{max}} \) is constrained by the depth and extent of weathering in the CZ, in conjunction with the depth of the active root zone (e.g. Hahn et al 2019b).

In rain-dominated seasonally dry or drought-prone regions, the only source of water available to plants during extended dry periods is that which is stored and available to root systems in the subsurface. The capacity of the subsurface to store this water therefore (i) regulates plant water use and productivity, impacting the Earth’s near-surface energy budget and climate, and (ii) mediates water balance
partitioning, including runoff responses to rainfall during wet periods, and baseflow production during dry periods. These outcomes have been extensively explored in Mediterranean climates, where water delivery via precipitation and energy delivery through insolation are out of sync, so that dry season water use and productivity are almost completely constrained by the availability of water carried over from the wet season in soil, rock moisture, snowpack, and groundwater (Hahm et al. 2019a, Graham et al. 2010, Rempe and Dietrich 2018, Klos et al. 2018, Garcia and Tague 2015, Hahm et al. 2019b, Lewis and Burgy 1964, Zwieniecki and Newton 1996, Arkley 1981, Anderson et al. 1995, Rose et al. 2003, Smettem et al. 2013, Eiadès et al. 2018, Enzminger et al. 2019, Peel et al. 2007). Given this, appropriate representations of the root-zone water storage capacity are urgently needed for use in novel large-scale modeling frameworks (Fan et al. 2019) and in the range of existing modeling and empirical frameworks that rely on the concept of root-zone water storage capacity (Porporato et al. 2004, Seyfried et al. 2009). However, while maps of near-surface soil and its water storage properties exist (Geza and McCray 2008, Entekhabi et al. 2010), information on whole-CZ subsurface properties, including water storage capacity in deep (>2m) soils, saprolite and weathered bedrock, is generally lacking at large spatial scales. For example, soil maps that are widely used to parameterize land surface and hydrological models not only rely on interpolation between sparsely spaced soil pits (Natural Resources Conservation Service 2019), but are generally confined to shallow depths (<2m) that do not cover the entire root zone.

Some methods exist to infer root-zone water storage capacity based on plant optimality principles (e.g. plants 'set' \(S_{\text{max}}\) so as to maximize productivity (Speich et al. 2018, Yang et al. 2016, Cabon et al. 2018)), or variations in subsurface water storage inferred either through mass balance or remote sensing of terrestrial water storage. Storage-deficit approaches (Gao et al. 2014, Wang-Erlandsson et al. 2016) isolate accumulated evapotranspiration during dry periods to place lower bounds on \(S_{\text{max}}\), although these methods typically assume vegetation themselves determine \(S_{\text{max}}\) at a value sufficient to overcome droughts with a specific, user-defined return interval. Other forms of storage-tracking approaches require data from stream gauging stations (Hahm et al. 2019a), which are often too sparsely distributed to allow findings to be reliably interpolated. Microwave-based satellite observations of soil moisture storage dynamics are extensive but coarsely resolved and limited to shallow near-surface soils (Entekhabi et al. 2010). Space-based gravity observations (Swenson et al. 2003) and ground-based surface deformation (Argus et al. 2014, Enzminger et al. 2019) are sensitive to changes in water storage, but only over extremely large spatial scales. These methods may also measure changes in water storage within deep aquifers which do not relate to changes within the root zone.

An alternative method to infer \(S_{\text{max}}\) from observations is to use the plants themselves as sensors of water availability, and therefore as windows into root-zone water storage dynamics (Thompson et al. 2011, Thompson and Katul 2011). These ‘inverse methods’ (Wang-Erlandsson et al. 2016) rely on the fact that plant productivity and water use are sensitive to both water and energy availability (Holdridge 1947, Stephenson 1990). Thus, if \(S_{\text{max}}\) determines how much water is stored and available to vegetation, \(S_{\text{max}}\) could potentially be inferred by inverting models of the rainfall-CZ-vegetation interactions using remotely sensed measures of vegetation activity and precipitation (Ichii et al. 2009, Campos et al. 2016, Kieold 2004). In a more recent study, Hahm et al. (2019a) demonstrated, via remote-sensing of plant greenness and water-balance tracking, that water storage properties of the CZ could decouple dry season water availability, and thus plant productivity, from year-to-year rainfall variability, suggesting that simplified statistical measures of evapotranspiration, such as its coefficient of variation, might also be diagnostic of root-zone water storage capacity.

Here, we expand on this collection of approaches by developing a simple stochastic model for root-zone water storage. The model introduces a simplified representation of ecohydrological seasonality within existing stochastic modeling frameworks (Zanardo et al. 2012, Drale and Thompson 2016, Feng et al. 2015) to explicitly examine the dependence of \(S\) on intra-seasonal features of rainfall and \(S_{\text{max}}\). We demonstrate that the model can be used as an inversion tool to infer \(S_{\text{max}}\), given the basic premise that year-to-year variability in dry season plant water use should reflect year-to-year variability in root-zone water storage, manifested through the control of \(S_{\text{max}}\) on rainfall storage in the subsurface.

Using a remotely sensed ET dataset and empirical rainfall statistics, we find that the inversion accurately predicts \(S_{\text{max}}\) at two Eel River Critical Zone Observatory (ERCZO) field sites in the Northern California Coast Ranges where independent hillslope- and catchment-scale measurements of \(S_{\text{max}}\) have previously been made.

2. Methods

To understand how \(S_{\text{max}}\) mediates dry season water availability from year to year, we rely on a stochastic framework to predict the end-of-wet season root-zone water storage (\(S_0 \in [0, S_{\text{max}}]\)), the key variable which links wet season root-zone water storage dynamics to dry season water availability (figure 1(b)). We follow the formulations in Porporato et al. (2004) and simulate wet season root-zone water storage (\(S(t) [L]\)) using a 1-D, vertically integrated model
Table 1. Definition of terms used.

| Term       | Dimensions | Definition |
|------------|------------|------------|
| S          | L          | root-zone water storage |
| S$_{\text{max}}$ | L          | root-zone water storage capacity |
| t          | T          | time |
| P          | L[T]$^{-1}$ | rainfall that enters the root zone |
| $\lambda$ | T$^{-1}$   | rainfall event frequency |
| $\alpha$  | L          | mean depth of rainfall in an event |
| ET         | L[T]$^{-1}$ | evapotranspiration losses from the root zone |
| ET$_{\text{dry}}$ | L          | evapotranspiration loss from the root zone in dry season |
| PET        | L[T]$^{-1}$ | wet season average potential evapotranspiration |
| ET$_{\text{max}}$ | L[T]$^{-1}$ | maximum allowable evapotranspiration rate from the root zone |
| D          | L[T]$^{-1}$ | drainage from root zone |
| n          | -          | porosity |
| Z$_r$      | L          | root-zone depth |
| $\theta$  | -          | volumetric water content |
| $s$        | -          | relative water content |
| $s_{wp}$   | -          | relative water content at wilting point |
| $s_f$      | -          | relative water content at field capacity |
| $T_{\text{wet}}$ | T         | duration of wet season |
| $T_{\text{dry}}$ | T         | duration of dry season |
| $C_{2.5}$, $C_{97.5}$ | T         | days on which 2.5 and 97.5 percent, respectively, of cumulative annual rain falls in an average composite year |

(illustrated in figure 1), where the governing mass balance can be expressed as:

$$\frac{dS}{dt} = P(t) - ET[S(t)] - D[S(t), P(t)]. \quad (1)$$

P [L/T] is rainfall entering the root zone, ET [L/T] represents evapotranspiration losses from the root zone, and D [L/T] represents drainage from the root zone. S is defined as the volume of water (expressed as a depth of liquid water) stored in the root zone that is accessible to vegetation, which ranges from 0, representing a wilting point, to $S_{\text{max}}$, the previously defined root-zone water storage capacity. Evapotranspiration increases linearly from zero at $S = 0$ to a maximum allowable evapotranspiration (ET$_{\text{max}}$, which we approximate with potential evapotranspiration, PET) at $S = S_{\text{max}}$. PET is assumed to be constant and equal to its average value during the rainy season. On daily timescales, rainfall volumes entering the root zone that would increase storage above $S_{\text{max}}$ are instantaneously removed by drainage (D), so that $S$ is always less than or equal to $S_{\text{max}}$. We note that S and $S_{\text{max}}$ can be expressed in terms of typical parameters in simple soil moisture models (e.g. Porporato et al 2004): a relative soil moisture ($s$) equal to volumetric water content ($\theta$) divided by porosity ($n$), a root-zone depth ($Z_r$), a field capacity $s_f$, and a wilting point $s_{wp}$, such that $S_{\text{max}} = nZ_r(s_f - s_{wp})$ and $S = nZ_r(s - s_{wp})$. Although mathematically equivalent to the model presented by Porporato et al (2004), the formulation here is expressed in terms of $S$ (as opposed to a relative soil moisture, $s$) to highlight the fact that plant accessible water need not be restricted to soils; $S$ may include storage within unsaturated saprolite and weathered bedrock. Vegetation access to water in the saturated zone is not considered within this framework.

2.0.1. Seasonal rainfall as a stochastic process
Wet season rainfall is modeled as a stochastic Poisson process (Milly 1993, Porporato et al 2004, Good et al 2017), assuming rainfall events occur at random with frequency $\lambda [T^{-1}]$. Due to the properties of Poisson processes, the inter-arrival times between rainfall events can be described with an exponential probability density function with mean $1/\lambda [T]$. Upon the occurrence of a rainfall event, the event depth (volume of fallen rain per unit area) is also described using an exponential distribution with mean $1/\alpha [L]$. The average seasonal rainfall is therefore equal to the product of $\alpha$, $\lambda$, and the length of the wet season, $T_{\text{wet}}$. Rainfall seasonality is assumed to be binary, with no rainfall during the dry season, and stationary hydroclimatic features (constant $\alpha$, $\lambda$, and ET$_{\text{max}}$) during the wet season.

2.0.2. Seasonality and running the model
Porporato et al (2004) found a steady-state solution for equation (1) under stationary climate conditions, and showed that the root-zone water storage follows a truncated gamma probability distribution (such that $S$ is greater than zero and less than or equal to $S_{\text{max}}$). However, to our knowledge, unsteady, stochastic formulations of equation (1), such as the model formulated here, cannot be solved in closed form. Other
authors have found approximate solutions for certain types of seasonality (Feng et al 2015), but to avoid error potentially associated with such approximations, we opt to solve the governing equation using Monte Carlo simulations (for implementation details, see code availability statement).

2.1. Role of dry season evapotranspiration (ET$_{dry}$) for predicting S$_{max}$

We wish to infer root-zone water storage capacity, S$_{max}$, as a function of hydroclimate and vegetation water use. The model takes values of S$_{max}$ to map wet season hydroclimate to S$_0$, which is not easily measured or observed. We therefore exploit the fact that in winter-wet summer-dry climates, the more readily observable magnitude of ET$_{dry}$ typically will scale linearly with S$_0$ (Feng et al 2017). That is, dry season water use will increase proportionally with the storage condition at the end of the wet season. While we do not explicitly model ET$_{dry}$, it will equal $S_0 - S_0 \exp(-S/S_{max} \cdot ET_{max} \cdot T_{dry}) = S_0 (1 - \exp(-S/S_{max} \cdot ET_{max} \cdot T_{dry}))$, where T$_{dry}$ is the duration of the dry season (365 - T$_{wet}$). The final equality shows that the volume of water evaporated during the dry season is proportional to dry season initial storage (S$_0$), which in turn is set by the stochastic realization of that year’s wet season rainfall. This relationship between observable plant water use and root-zone storage dynamics is a key linkage that we leverage in the following section to infer subsurface CZ storage properties.

As a simplifying assumption, the model uses a zero root-zone storage condition ($S = 0$) at the start of the wet season. This is reasonable if dry season rainfall is negligible, and if root-zone water storage declines exponentially over the dry season as described above, such that end of summer S is small relative to S$_0$.

2.2. Model inversion for estimating S$_{max}$

Given the four hydroclimate parameters ($T_{wet}$, $\alpha$, ET$_{max}$, $\lambda$), Monte Carlo simulations can be used to obtain wet season root-zone storage dynamics, including a distribution for S$_0$, for a range of values of S$_{max}$. This yields a function which maps the range of S$_{max}$ to variability in S$_0$:

$$CV[S_0] = f(S_{max}).$$

Using the proportionality between ET$_{dry}$ and S$_0$ described in the previous section (ET$_{dry} \propto S_0$), we can use simple statistical properties to link remotely observable evapotranspiration to model predictions of S$_0$ for a given S$_{max}$ and hydroclimate. Specifically, linear proportionality between two random variables implies that their coefficients of variation are equal:

$$CV[ET_{dry}] = CV[S_0],$$

This yields a function which maps the range of S$_{max}$ to variability in S$_0$:

$$CV[S_0] = CV[ET_{dry}] = f(S_{max}).$$

This method for estimating storage is more widely applicable than the flux-tracking methodology presented in Hahm et al (2019a), because it does not rely on closure of the water budget, and thus can be applied even where stream gauging is unavailable or stream hydrology is modified.
2.3. Case studies: model application and inversion at well-characterized field sites

To parameterize the stochastic model, we rely on hydroclimatic records from two study watersheds within the Eel River Critical Zone Observatory: Elder Creek (16.9 km$^2$) and Dry Creek (3.5 km$^2$). Intensive hillslope monitoring of hillslope hydrology, plant dynamics, and stream runoff has been ongoing at Elder Creek for roughly a decade (Salve et al. 2012, Link et al. 2014, Oshun et al. 2016, Kim et al. 2014, Hahm et al. 2019b, Lovill et al. 2018, Rempe and Dietrich 2018), and at Dry Creek since 2015 (Hahm et al. 2018, Dralle et al. 2018, Lovill et al. 2018). The regional Mediterranean climate here has a warm summer dry season, followed by cool winter wet season (Peel et al. 2007). Elder Creek receives approximately 2000 mm of annual precipitation, and Dry Creek approximately 1800 mm (PRISM Climate Group 2004), almost all of which falls as rain, primarily between November and April. Although it rains more at Elder Creek, the greater canopy cover (see below) results in more interception, and the amount of throughfall at both sites is similar (Hahm et al. 2019b).

Both sites lie within the Franciscan Formation, an exhumed subduction complex that is locally comprised of three coast-parallel (roughly north-south) belts (Blake Jr and Jones 1974). The Elder Creek watershed is located in the westernmost Coastal Belt, which is comprised mostly of shale (argillite), with lesser components of sandstone and conglomerate (Jayko et al. 1989, Salve et al. 2012, Lovill et al. 2018). The Dry Creek watershed is about 20 km to the southeast and is underlain by the Central Belt, which consists of mélangé with an intensely sheared, primarily argillaceous matrix with coherent blocks of various lithologies, dominated by sandstone (Blake Jr and Jones 1974, Lovill et al. 2018).

Despite the proximity and similar climates of the sites, their contrasting lithologies lead to dramatic differences in the depth of weathering and structure of the critical zone, and corresponding large differences in storage dynamics (Hahm et al. 2019b). Hahm et al. (2018b) demonstrate that lithologically-controlled differences in subsurface water storage explain the contrasting vegetation communities between the two sites: the limited depth of weathering at Dry Creek results in low root-zone water storage capacity, and correspondingly an oak savanna plant community typically associated with much lower rainfall climates, while the thick subsurface CZ at Elder Creek seasonally stores enough water to support dense evergreen forest. Dralle et al. (2018) develop a mass-balance based approach to estimate volumes of seasonally dynamic water storage in the subsurface that do not generate pressure gradients that drive streamflow generation, and suggest that these water volumes may be representative of root-zone water storage. Rempe and Dietrich (2018) measure unsaturated, root-zone water storage in weathered, fractured rock and saprolite at the Elder Creek site, demonstrating that this rock moisture supplies the vast majority (up to 300 mm) of transpiration water during the protracted dry season. Collectively, these studies provide multiple independent estimates of $S_{\text{max}}$ (100-200 mm at Dry Creek, and 300-400 mm at Elder Creek; mostly within weathered bedrock below soils) that can be used to evaluate the results of the stochastic modeling framework.

2.3.1. Data

Daily rainfall volumes are measured with tipping bucket rain gauges at the ERCZO weather stations, and are corrected for wind-induced undercatch and interception (see Dralle et al. 2018 for details). Although the Poisson rainfall model assumes that rainfall event occurrences are independent in time, rainfall events are often temporally autocorrelated along the California coast (Müller et al. 2014). Therefore, we define a rainfall event as any consecutive period of days with non-zero rainfall, with a total event depth equal to the sum of rainfall over the consecutive period, and an occurrence date marked halfway through the event. Rainfall frequency $\lambda$ is calculated as the total number of events divided by the length of the wet season ($T_{\text{wet}}$, calculated as described below), and $\alpha$ is calculated as the average of all event depths. $ET_{\text{max}}$ is set equal to average daily potential evapotranspiration (PET) over the wet season. We compute daily PET (the same at both sites) using Eel River CZO weather station data and the Hargreaves equation (Hargreaves and Samani 1985):

$$ET_{\text{max}} = PET = 0.0023 \cdot (T_{\text{mean}} + 17.8) \cdot (T_{\text{max}} - T_{\text{min}})^{0.5} \cdot 0.408 \cdot R_{\text{ext}},$$

where $T_{\text{max}}$, $T_{\text{min}}$, and $T_{\text{mean}}$ are the daily max, min, and mean air temperatures, and $R_{\text{ext}}$ is extraterrestrial solar radiation computed from latitude and day of year following (Allen et al. 1998). We choose this particular model for PET due to its simplicity and its previous successful application at the two study sites (Dralle et al. 2018).

We implement a new method to determine the length ($T_{\text{wet}}$) and boundaries of the wet season. First, we add the rain on each day of the year across all years (2001 to 2017) to collapse the rainfall record into a single composite representative year. Beginning in the heart of the dry season (August 1), we define the start of the wet season ($C_{2.5}$) as the day on which 2.5 percent of the cumulative rain has fallen in the composite representative year, and the end of the wet season ($C_{97.5}$) as the day on which 97.5 percent of the cumulative rain has fallen. The number of days between these dates ($|C_{97.5} - C_{2.5}|$) defines $T_{\text{wet}}$. The selected cutoff values are subjective, and other definitions and methods for estimating wet season length yield similar results (e.g. Müller et al. 2014, Dralle and Thompson 2016). The proposed method,
however, is advantageous for three reasons: 1) The slope of the cumulative rainfall distribution between the thresholds that emerges based on this definition is approximately linear (see acknowledgements for repository with supporting plots), consistent with the model requirement of stationary rainfall statistics, 2) This method allows the wet season length to vary on a site-by-site basis depending on local climatology, and 3) The algorithm is simple and readily applicable across large spatial scales. The four model parameters ($\lambda$, $\alpha$, $T_{wet}$, and $ET_{max}$) are reported in Table 2.

During the dry season months of June, July, and August, negligible rain falls, and therefore variability in ET is likely attributable to variations in storage conditions. Estimates of actual evapotranspiration during these months are therefore used to compute $CV[ET_{dry}]$ to predict $S_{max}$. $ET_{dry}$ estimates are obtained from a biophysical evapotranspiration model (Breathing Earth System Simulator, BESS) that has been evaluated across California and FLUXNET sites globally (Ryu et al 2011, Baldocchi et al 2019, Jiang and Ryu 2016). The ET dataset used here is available from 2001 to 2017. Similar results were obtained using other ET datasets that are available at larger scales, such as the NASA/EOS MODIS global evapotranspiration product (Mu et al 2013). All 17 years of the Baldocchi et al (2019) ET dataset used in this study are freely available, and provided with the code required to replicate results at https://github.com/daviddralle/storage_cvs/.

2.3.2. Simulation exercises

We perform two simulation exercises; one to illustrate model output for a fixed climate and different $S_{max}$, and a second to infer $S_{max}$ from $CV[ET_{dry}]$ and explore the potential effects of changing rainfall statistics at the two case study sites.

2.3.2.1. Simulation exercise 1

In the first simulation exercise we use the model to illustrate seasonal patterns of wetting for three different values of $S_{max}$ holding wet season length and climate statistics constant. Thirty years are simulated for each case to illustrate controls on $S_{max}$ and its interannual variability. This reveals how $S_{0}$ and its relative variability ($CV[S_{0}]$) depend on $S_{max}$ and the specific occurrence and depth of rainfall events.

2.3.2.2. Simulation exercise 2

The second simulation first computes $CV[S_{0}]$ across a range of values of $S_{max}$ for the hydroclimatic parameters in Table 2. We use the resulting relationship between $CV[S_{0}]$ and $S_{max}$ ($CV[S_{0}] = f(S_{max})$) outlined in section 2.2, along with estimates of dry season evapotranspiration variability, to predict $S_{max}$ at the two study sites. This procedure is equivalent to finding the mathematical inverse of the function $f$. We then compare these predictions to independently determined field-based estimates of $S_{max}$. We additionally illustrate how changes in rainfall frequency ($\lambda$) and intensity ($\alpha$) might alter the relationship between $S_{max}$ and $CV[S_{0}]$.

3. Results

3.1. Simulation exercise 1

Figure 2 depicts Monte Carlo simulation of wet season root-zone water storage for different values of $S_{max}$ using the parameters in Table 2. Note that in all three panels an equivalent absolute moisture loss from the root zone results in different relative declines in $S$ because $S_{max}$ varies in each case.

In Figure 2(a), because the root-zone storage capacity is small relative to the mean annual rainfall, $S$ reaches $S_{max}$ early in the season (grey line traces of individual yearly simulations reach the top of the plot). However, for the same reason, wet season evapotranspiration between rain events rapidly draws down the limited storage, causing $S$ to deviate from and return to $S_{max}$ many times throughout the wet season. These deviations, relative to the mean value of $S_{0}$, are large in this first case. The value of $S_{0}$ in any given year is most sensitive to the timing and magnitude of late wet season rainfall events, as demonstrated by the red and blue traces, where a late pulse of rainfall accounts for elevated $S_{0}$ in the blue trace relative to the red trace.

In contrast, in Figure 2(c), $S_{max}$ is large relative to the mean annual rainfall. Moreover, $S$ does not reach $S_{max}$ in many simulated years, resulting in highly variable $S_{0}$. However, because evapotranspiration depletes the large storage reservoir more slowly than in Figure 2(a) (smaller inter-event declines in $S$), $S_{0}$ variability is controlled by total wet season rainfall rather than the pattern and properties of rainfall events at the end of the wet season.

Figure 2(b) reveals an intermediate case, in which $S_{max}$ is small enough relative to rainfall so that $S_{max}$ is reached in almost all years, but large enough that $S$ is not significantly reduced (in a relative sense) during rainless periods. This leads to a low value for $CV[S_{0}]$, and the annual value of $S_{0}$ being relatively insensitive to both the total amount of wet season rainfall and the timing and magnitude of rain events toward the end of the wet season.

### Table 2. Empirical model parameters calculated for the study sites. The same parameters are used at both Dry Creek and Elder Creek (see Site Descriptions).

| Parameter | Value |
|-----------|-------|
| $T_{wet}$ [days] | 224 (Oct 4 to May 15) |
| $ET_{max}$, wet season [mm/day] | 1.88 |
| $\lambda$, wet season [1/day] | 0.11 |
| $\alpha$, wet season [mm] | 71.0 |
3.2. Simulation exercise 2

In the second exercise, we run Monte Carlo simulations of the model with ERCZO hydroclimatic parameters (table 2) to obtain theoretical estimates of \( CV[S_0] \) (that is, the CV of the end of wet season root-zone storage in the simulations in figure 2) for values of \( S_{\text{max}} \) ranging from 0 to 1000 mm (figure 3(a)). Note that the CV values differ slightly between figures 2 and 3(a) for values of \( S_{\text{max}} \) equal to 100, 500, and 1000 mm. This is because the number of simulated years in figure 2 is limited to 30 for illustrative purposes, and so the estimated value of \( CV \) has not converged to the theoretical, limiting value presented in figure 3(a). As described in Methods (see section 2.2), figure 3(a) also graphically depicts the inversion procedure used to estimate \( S_{\text{max}} \), with predicted values of 184 mm at Dry Creek, and 303 mm at Elder Creek. Inferred volumes of root-zone water storage capacity compare well with direct, independent estimates from the two sites. Using downhole neutron probes and soil time domain reflectometry, Rempe and Dietrich (2018) estimate that the seasonal change in vadose zone water content (which we interpret as \( S_{\text{max}} \)) at Elder Creek is between 300 and 400 mm. Dralle et al (2018) used wells to estimate \( S_{\text{max}} \) at Dry Creek between 120 and 200 mm.

Whereas figure 3(a) plots \( CV[S_0] \) for single, constant values of \( \alpha \) and \( \lambda \) representative of the ERCZO, figure 3(b) illustrates how the relationship between \( S_{\text{max}} \) and \( CV[S_0] \) would change for shifts in the frequency and magnitude of rainfall events. Increases or decreases in \( \alpha \) and \( \lambda \) have different effects on this relationship. A 50% decrease in storm frequency (\( \lambda - 50\% \)) or intensity (\( \alpha - 50\% \)) leads to a universal increase in
CV\[S_0]\). The magnitude of increase is much greater for larger values of $S_{\text{max}}$, and the increase is globally more sensitive to decreases in $\lambda$ than decreases in $\alpha$. Similarly, increases in storm frequency ($\lambda + 50\%$) lead to a larger drop in $\text{CV}[S_0]$ compared to increases in intensity ($\alpha + 50\%$). As with $\alpha - 50\%$, $\lambda - 50\%$, increases in frequency or magnitude have a greater effect for larger values of $S_{\text{max}}$.

### 3.3. Resolving the non-uniqueness in the inversion procedure

Values of $S_{\text{max}}$ computed through the inversion procedure are not unique in figure 3 because the theoretical curve $\text{CV}[S_0]$ vs. $S_{\text{max}}$ is not monotonic. Figure 2 reveals graphically why this non-monotonic behavior arises: $\text{CV}[S_0]$ is minimized at an intermediate value of $S_{\text{max}}$. The minimum is also clearly identified in figure 3 near $S_{\text{max}} \approx 600$ mm. Far left of this minimum, $S_{\text{max}}$ is small and so $\text{CV}[S_0]$ increases because late wet season ET can rapidly deplete $S_0$, which may or may not be replenished by rainfall in the final weeks of the wet season. Far right of the minimum, $\text{CV}[S_0]$ begins to increase because lower $S_{\text{max}}$ increases sensitivity of $S_0$ to variations in total wet season precipitation. This suggests that if $\text{ET}_{\text{dry}}$ is insensitive to total wet season rainfall, the inversion procedure should map to the left of the minimum on the modeled curve in figure 3. To verify the figure 3 inversions, we regress $\text{ET}_{\text{dry}}$ at both sites onto wet season precipitation (figure 4), finding statistically insignificant ($p$ values greater than 0.05) slopes of 0.002 at Dry Creek and -0.016 at Elder Creek (that is, 100 mm of additional rainfall would result in 0.2 mm and -1.6 mm change in dry season evapotranspiration at Dry Creek and Elder Creek, respectively), consistent with the findings of Hahm et al (2019a). We therefore conclude the two sites likely fall to the left of the minimum in figure 3, mapping to smaller values of $S_{\text{max}}$ that are in agreement with independent field estimates.

### 4. Discussion

A reduced complexity stochastic model for root-zone water storage dynamics in Mediterranean climates demonstrates that plant response to climatic variability can be used to estimate root-zone water storage capacity in the critical zone. At two rain-dominated sites in Northern California with strongly contrasting weathering profiles, model predictions closely match direct measurements of storage capacity in shallow soils and underlying weathered bedrock.

#### 4.1. Limitations of the modeling approach

A novel contribution of this paper is the development and validation of a relatively simple and widely applicable method in Mediterranean climates to determine root-zone water storage capacity, a key ecohydrological parameter. However, the method is only strictly valid in rain-dominated Mediterranean regions, and where fixed properties of the CZ (such as porosity profiles), rather than potentially plastic properties (such as highly variable root zone extents), determine $S_{\text{max}}$. Future work will focus on development of more general methods that can be applied to more diverse climates.

A second limitation of the method is the reliance on remotely sensed measures of vegetation water use. We used a physical evapotranspiration model (Breathing Earth System Simulator) for evapotranspiration, presented for California in Baldocchi et al (2019), which importantly does not include any specific representation of the subsurface. Other evapotranspiration models which explicitly incorporate soil water balance modeling for ET estimation should not be used for the method presented here (Martens et al 2017), because they make assumptions regarding the size of $S_{\text{max}}$, which this approach estimates. By using ET data (Baldocchi et al 2019) that relies primarily on remotely sensed spectral signatures, this method may struggle in places where plant functional group phenoology undergoes minimal change across a range of transpiration rates. This should be explored further, but we note that at the sites we studied, as is the case in much of California, there is large seasonal phenological variation (Hahm et al 2019a). One other potentially confounding factor in our analysis is the extent to which year-to-year variation in summer energy supply might impact dry season plant water use. Because plants across California are typically water-limited rather than energy-limited in the summer dry season (i.e. PET greatly exceeds ET), this is unlikely to matter, as Hahm et al (2019a) found.

Finally, the model representation of subsurface water runoff and storage dynamics is highly simplified. All rainfall is assumed to infiltrate, such that no Horton overland flow occurs, limiting the scope of the model’s applicability. We are also uncertain as to whether deeper root profiles, such as those observed in the Elder Creek watershed (from previous drilling and neutron probe campaigns (Salve et al 2012, Rempe and Dietrich 2018, Hahm et al 2019b)), can be usefully modeled within a framework that treats the entire vadose zone as a homogeneous reservoir. Within riparian areas or low-lying areas, or in areas with shallow root depths or thin subsurface critical zones, water table dynamics in the near surface may play an important role in setting $S_{\text{max}}$. Although plants do not explicitly use water from the saturated zone in the model, the Dry Creek catchment provides some evidence that where field capacity does not greatly differ from saturation (Dralle et al 2018), the model still may be useful, and likely still improves estimates of root-zone water storage capacity relative to existing soil datasets.

#### 4.2. Ecosystem sensitivity to climate

Understanding drivers of ecosystem sensitivity to climate is important for understanding the
Figure 3. A graphical demonstration of the procedure used to estimate $S_{\text{max}}$ at the study locations. In (a) $S_{\text{max}}$ is inferred from dry season ET variability ($CV[ET_{\text{dry}}]$), based on the relationship between $S_{\text{max}}$ and $CV[S_0]$. The inference is made possible by equating the more readily measurable $CV[ET_{\text{dry}}]$ with $CV[S_0]$. Measured values of $CV[ET_{\text{dry}}]$ are plotted for Elder (blue) and Dry Creek (red) on the $y$-axis. The dashed lines with arrows graphically depict the inversion procedure, whereby $S_{\text{max}}$ is estimated via intersection with the $x$-axis. Inferred values of $S_{\text{max}}$ agree well with independently measured $S_{\text{max}}$ for these sites. (b) Illustration of changes in the relationship $CV[S_0]$ and $S_{\text{max}}$ for 50% decreases or increases in storm frequency ($\lambda - 50\%$ and $\lambda + 50\%$, respectively) or storm intensity ($\alpha - 50\%$ and $\alpha + 50\%$, respectively).

Figure 4. Dry season evapotranspiration plotted against wet season precipitation on equal scale axes for the Elder Creek and Dry Creek catchments.

Impacts of climate change on global hydrologic and biogeochemical cycles. Here, we focused on how $S_{\text{max}}$ might control dry season water availability and hence productivity. We demonstrate that dependence of water use on root-zone water storage capacity is more nuanced than is traditionally assumed. Too large or too small $S_{\text{max}}$ relative to annual rainfall tends to increase the sensitivity of $ET_{\text{dry}}$ to rainfall variability, with sensitivity minimized at intermediate values of $S_{\text{max}}$. This Goldilocks-like result differs from other modeled findings, which suggest increasing $S_{\text{max}}$ monotonically increases plant water stress due to chronically low water content in the vadose zone (Porporato et al. 2004, Zanardo et al. 2012). These studies, however, did not consider the transient effects of seasonality.

Globally, rainfall patterns in many Mediterranean climate zones are predicted to change dramatically (Swain et al. 2018, Valdes-Abellan et al. 2017, Viola et al. 2016, Feng et al. 2019), though in distinct ways in different regions. In California for example, although mean annual rainfall is not predicted to change significantly, precipitation variability and event magnitudes are expected to increase (Swain et al. 2018). In contrast, mean annual rainfall totals are predicted to decrease significantly throughout the European Mediterranean climate region (Gao and Giorgi 2008). The model presented here suggests that root-zone storage capacity plays an important role in determining how vegetation might respond to these varied trends. For example, the thin grey line traces in figure 2(a) show that at locations with low $S_{\text{max}}$ relative to annual rainfall totals, late wet season rainfall patterns...
seem to control annual variations in $ET_{dry}$, and thus presumably productivity. In such watersheds, shifts in intra-seasonal rainfall patterns, such as increased event magnitudes, may significantly alter dry season water availability. In contrast, the model predicts that relatively large values of $S_{max}$ increase vegetation sensitivity to total rather than intra-seasonal dynamics of precipitation (figure 2(c)). Locations with intermediate-sized $S_{max}$ (relative to typical values of annual rainfall) may be least sensitive to increases in rainfall volatility (figure 2(b)). Figure 3(b) further illustrates these nuances, demonstrating that decreases in total rainfall (either through decreases in $\lambda$ or $\alpha$) may universally increase variability in productivity, likely due to the more frequent occurrence of years where $S$ is not constrained by $S_{max}$; that is, the effective size of $S_{max}$ relative to typical annual rainfall totals increases. This is supported by the observation that $CV[S_0]$ is more sensitive to rainfall decreases for larger values of root-zone storage capacity. Generally, vegetation in the present modeling framework is more sensitive to changes in rainfall frequency ($\lambda$) than to changes in the intensity of events ($\alpha$), especially in the case where rainfall decreases ($\lambda \approx 50\%$ or $\alpha \approx 50\%$). This finding suggests that resolving whether projected decreases in rainfall are due to changes in frequency or intensity may be particularly important for predicting plant response to climate in drying regions.

5. Conclusion

We developed an ecohydrological model for Mediterranean climates that elucidates how root-zone water storage capacity and intra-annual rainfall patterns determine the sensitivity of plant water use to rainfall variability. By assuming that dry season plant water use, measured using a biophysical evapotranspiration model forced with remote sensing data (Ryu et al 2011, Baldocchi et al 2019), scales with the amount of root-zone water storage at the end of the wet season, we predict root-zone water storage capacity, an important yet presently challenging parameter to map. We validated the predictions with independent field-based estimates of $S_{max}$ at two sites in the Northern California Coast Ranges. Our work demonstrates the potential for using remotely sensed ecohydrological datasets paired with simple, process-based ecohydrological models to infer properties about the critical zone, including deeper weathered bedrock below shallow soils. Future efforts will be most fruitful if they can be validated with hillslope-scale subsurface observations, motivating greater observatory-style exploration of the critical zone across lithologic, climatic, and tectonic gradients.

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