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Low Subsurface Water Storage Capacity Relative to Annual Rainfall Decouples Mediterranean Plant Productivity and Water Use From Rainfall Variability

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Key Points:
- Where annual rainfall reliably exceeds subsurface storage capacity, plant productivity should be insensitive to rainfall variability
- Water balances reveal sites where storage is replenished in both wet and dry winters, resulting in consistent summer plant water supply
- Such storage-capacity limited sites are inherently resilient to meteorological drought

Supporting Information:
- Supporting Information S1
- Table S1
- Figure S1

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Abstract Plant water stress in response to rainfall variability is mediated by subsurface water storage, yet the controls on stored plant-available water remain poorly understood. Here we develop a probabilistic water balance model for Mediterranean climates that relates the amount of water stored over the wet season to annual rainfall statistics and subsurface storage capacity in soil and weathered bedrock. This model predicts that low storage capacity—relative to winter rainfall—results in similar year-to-year summer water availability, as both relatively wet and dry winters replenish storage. Observed water balances in seven catchments in the Northern California Coast Ranges exhibited this dynamic. We hypothesized that plants would be decoupled from precipitation variability at these storage-capacity-limited sites and observed that summer productivity and water use (inferred from the enhanced vegetation index) were independent of winter rainfall totals. These areas emerged largely unscathed from recent extreme drought, despite widespread plant mortality elsewhere.

Plain Language Summary When does a shortage of precipitation become a shortage of water supply to plants? In rain-dominated seasonally dry climates, the answer depends on how water is stored belowground. Here we propose—perhaps counterintuitively—that *low* water storage capacity in Earth's critical zone (which includes soil and weathered bedrock) relative to average rainfall can decouple plant community productivity and water use from rainfall variability, and conversely that relatively large storage capacity increases plant sensitivity to annual swings in rainfall totals. A simple model and analysis of watersheds in winter wet, summer dry climates in California reveal that where it consistently rains much more than the subsurface can store, a similar amount of water is stored belowground in both relatively wet and dry years, with excess rainfall leaving as runoff. We hypothesized that this would result in similar year-to-year summer plant water availability, in spite of highly variable winter rainfall. We found, via satellite observations, that summer plant greenness was insensitive to swings in precipitation at these “storage-capacity-limited” sites. Contrary to predictions based primarily on tree density and rainfall deficits, these sites did not experience widespread mortality in the 2011-2016 extreme drought.

1. Introduction

Recent droughts have dramatically altered plant communities throughout many of the world's arid and mesic biomes (Hartmann et al., 2018), and climate models predict further increases in the frequency of extreme precipitation events (Swain et al., 2018). Analyses of the drivers of plant response to drought, including die-off, have largely focused on physiological and pest responses to climatic proxies for plant water stress (Adams et al., 2017; Choat et al., 2018). However, in rain-dominated Mediterranean climates —home to many of the world's most biodiverse and threatened plant communities (Cowling et al., 1996) —plants generally rely on subsurface water storage to sustain transpiration during the dry season (e.g., Klos et al., 2018). Storage dynamics should therefore be central in regulating plant response to climatic variability. Water storage dynamics have been shown to impact plant greenness, with numerous satellite-based studies showing that the spectral signatures of leaves correlate with water storage in the upper few centimeter of soil measured with microwaves (e.g., Geruo et al., 2017) or with storage in the entire hydrosphere measured from gravity (e.g., Yang et al., 2014). A major knowledge gap remains, however, in our knowledge of both the structure of Earth's near-surface weathering profile, which sets the plant-available water storage capacity in the critical zone (CZ; Figure S1)—extending from the top of the vegetation canopy through the soil and down to fresh bedrock (Grant & Dietrich, 2017; Riebe et al., 2017)—and how this structure's interaction with rainfall dynamics determines how much water is stored for plants through wet and dry periods. Improving our understanding of the nature of deeper hillslope plant-available water storage has been identified as a pressing research frontier and will improve the accuracy of Earth system models (Fan et al., 2019).

A common but often implicit hypothesis is that ample belowground water storage capacity buffers plants from interannual variations in precipitation. Here we explore instead whether *low* subsurface plant-available water storage capacity—relative to precipitation—can decouple plant water supply (and, consequently, plant productivity) from precipitation anomalies, including droughts. We exploit the strong seasonality of Mediterranean climates to test this hypothesis. We propose that where subsurface storage capacity is low relative to typical winter precipitation totals, winter precipitation will be sufficient to replenish storage in wet and dry years alike, resulting in similar year-to-year summer water availability. We call this condition "storage-capacity limitation" because the amount of stored water is limited by storage capacity rather than precipitation. Winter precipitation at storage-capacity limited sites that exceeds this capacity contributes to winter runoff rather than greater storage at the start of the dry season. Established plants adapted to a summer water supply capped by the storage capacity therefore may not experience diminished water availability and increased stress in anomalously dry years. Elements of this mechanism have emerged in ecohydrologic models and field studies (Fellows & Goulden, 2016; Hahm et al., 2019; Link et al., 2014; Milly, 1994; Porporato et al., 2004; Rempe & Dietrich, 2018; Sayama et al., 2011; Smith et al., 2011; Stephenson, 1990; Zanardo et al., 2012), yet to our knowledge the role of storage-capacity limitation in mediating plant productivity and water use sensitivity to precipitation variability at landscape scales remains unexplored.

Here we formulate a probabilistic hydrologic model for Mediterranean catchments to investigate whether dynamic storage capacity ($S_{\max}$) can decouple accumulated winter water storage (S) from winter precipitation (P) variability. We then use data from 26 rain-dominated catchments across California to test the hypothesis that where S is independent of P—diagnostic of storage-capacity limitation—summer plant productivity and water use, as measured by the enhanced vegetation index (EVI), are also uncorrelated with P. We apply a simple catchment water balance technique for estimating S (Dralle et al., 2018; Sayama et al., 2011), which is not limited to specifying storage capacity using mapped soil databases alone. These databases typically contain storage-capacity information only for shallow soils, while plants in Mediterranean climates are known to extract water in summer from both unsaturated and saturated weathered rock below the soil throughout the CZ (Figure S1 in the supporting information) to depths of tens of meters (Arkley, 1981; Jones & Graham, 1993; Rempe & Dietrich, 2018; Witty et al., 2003). Both the modeling framework and empirical analysis support the notion that low storage capacity relative to winter precipitation can decouple summer plant productivity and water use from precipitation variability. Our method provides a simple approach for identifying subsurface controls on terrestrial ecosystem function. It also highlights a novel mechanism by which subsurface storage dynamics can shield plant communities from the potential ecohydrological risk associated with possible increased volatility of annual precipitation in Mediterranean climates globally.

2. Model Development and Catchment Water Balance Methodology

2.1. Stochastic Hydrological Model

The hydrological model assumes that (i) a consistent minimum storage value is reached at the end of the dry season each year, that is, negligible interannual carryover of water occurs; (ii) cumulative winter evapotranspiration (ET) is constant from year to year, includes interception losses, and is always less than P in the energy-limited winter; and (iii) runoff (Q; stream discharge normalized by catchment area) is generated

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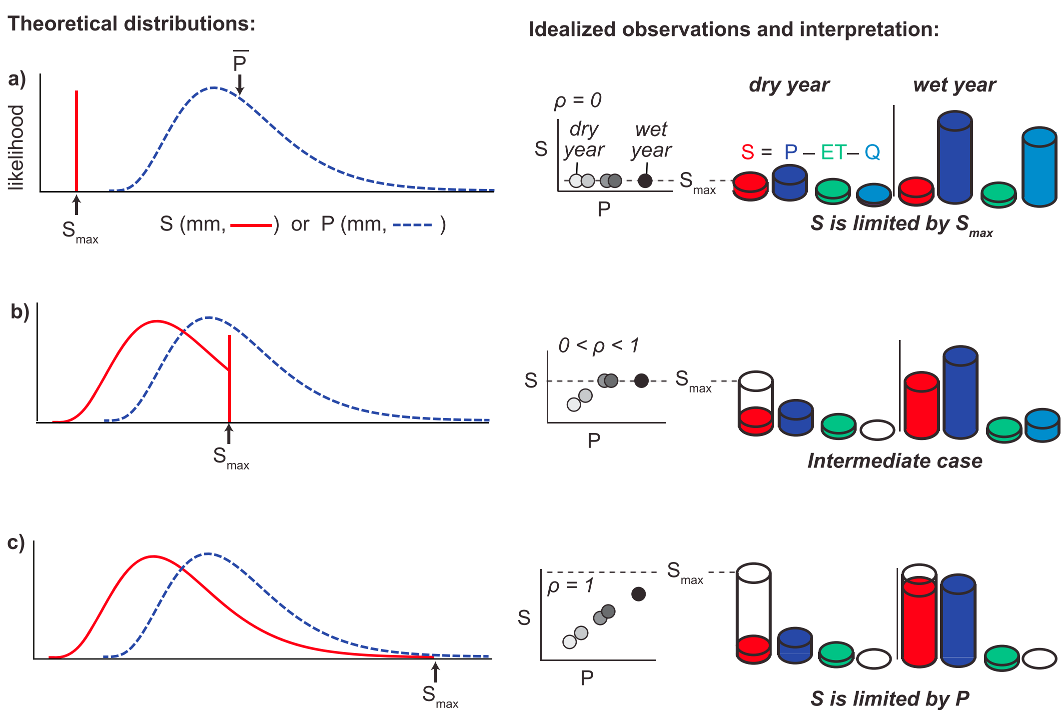

Figure 1. Conceptual diagram illustrating how the start-of-summer dynamic water storage (S), depends on winter precipitation (P) and subsurface critical zone water storage capacity (S_{max}). Evapotranspiration (ET) is winter evapotranspiration (assumed constant here) and Q is the winter runoff. The three rows (a–c) show, for an increase in S_{max}: (left column) the probability distribution of annual precipitation (P) relative to S_{max}, and the resultant S distribution, shifted left due to ET; (middle column) corresponding scatter plots of S versus P for five hypothetical years, along with the Spearman rank correlation coefficient (ρ) expressing the dependence of S on P; (right column) relative water volumes, stylized as columns, of S, P, ET, and Q for an exemplary dry (left) and wet (right) year. In cases when $P < S_{max}$ - ET, the volume of S (colored red) is less than S_{max} (the column's wire frame).

only when dynamic storage reaches S_{max}. The model does not distinguish between unsaturated and saturated storage. S for any given year is therefore piecewise defined:

$$S = P - ET \qquad \text{if } P - ET < S_{max}; \qquad Q = 0 \tag{1a}$$

$$S = S_{max} \qquad \text{if } P - ET > S_{max}; \qquad Q = P - ET - S_{max} \tag{1b}$$

Equation (1a) represents a "precipitation-limited" condition, where S is limited by P. The inequality in equation (1b) signifies a "storage-capacity-limited" condition, in that S_{max} limits S. Thus, summer plant water availability, to the extent that it scales with S, is limited by either precipitation (equation (1a)) or storage capacity (equation (1b)). Although this model omits some elements of the winter climate and hydrology, it provides a minimal description of the seasonal dependence of S on P and S_{max}. Assumptions (ii) and (iii) above are only present in the model; actual fluxes are tracked in the empirical catchment water balances described below, and the same variable names are used for consistency. We discuss the role of interannual carryover (assumption (i)) in Text S1 in the supporting information.

As input to the water-balance–storage relationships, we assume that annual P is a gamma distributed random variable (e.g., Abramowitz & Stegun, 1965; Ison et al., 1971), with a probability distribution function $f_P(p)$ that is defined by its mean ($\overline{P}$) and coefficient of variation (CV). CV captures the spread of the annual precipitation distribution, which may yield wet years and drought years. The theoretical distributions in the left column of Figure 1 conceptually show how equation (1) maps values of P to values of S, for different values of S_{max} (increasing downward from (a) to (c)). In case (a), S consistently reaches the relatively low S_{max}, in spite of variable year-to-year winter precipitation. In case (c), S rarely reaches the relatively high S_{max}, and the resulting variability in annual storage reflects variability in annual precipitation.

Across many years, P may take a range of values as determined by $f_P(p)$. The resulting strength of the relationship between P and S will determine the extent to which a watershed is precipitation-limited or storage-capacity-limited. This can be quantified by the nonparametric Spearman correlation coefficient, ρ, which is the Pearson correlation of the rank orders of P and S (Fieller et al., 1957). As equation (1) indicates, the correlation between P and S should be zero at a completely storage-capacity-limited site, as S is a constant $S_{\max}$ from year to year, and therefore statistically independent of P. Conversely, ρ will be equal to 1 at a completely precipitation-limited site.

Idealized plots of S versus P and the corresponding value of ρ are shown in the center column of Figure 1 for five hypothetical water years. The right-hand side of Figure 1 illustrates the winter catchment water balance in wet and dry years corresponding to the precipitation and storage conditions illustrated in the first column. This shows how $S_{\max}$ controls the partitioning of P between S, Q, and ET. Note that P and ET are the same in each column, and when S is less than $S_{\max}$ there is no predicted runoff.

Figure S2 plots contours of the Spearman coefficient, ρ, as a function of the CV of P and a dimensionless combination of the average winter precipitation ($\overline{P}$), $S_{\max}$, and ET, according to equation (1) for gamma-distributed P (derivation in the supporting information). The storage-capacity-limited condition is approached (i.e., ρ approaches 0) for increasing $\overline{P}/(ET + S_{\max})$. Under these conditions, summer ET may be limited by neither energy nor annual precipitation (in the sense of Budyko, 1974), but by the storage capacity (e.g., Milly, 1994). As CV increases along the horizontal axis in Figure S2, occasional dry years will not replenish the subsurface storage, resulting in a higher correlation between P and S. The analytical formulation of the model is found in Text S2.

2.2. Selection of Catchments and Analysis of Winter Water Balance and Summer Plant Sensitivity

We tested whether rain-dominated Mediterranean sites in the U.S. exhibited storage-capacity-limited or precipitation-limited behavior by quantifying basin-wide storage dynamics. To calculate $S = P - ET - Q$, we rely on gridded precipitation (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu), a process-based ET model driven by remotely sensed data (Baldocchi et al., 2019; Ryu et al., 2011), and U.S. Geological Survey (USGS) runoff records. We queried the entire stream gauge network reported by the USGS to find suitable catchments that were winter wet, summer dry, unimpaired, rain-dominated, and relatively undisturbed (see Table S1 in the supporting information for complete criteria). Only 25 USGS-gauged catchments—all found within the state of California—met this selection criteria (see Table S2; we also include a non-USGS station at the Eel River Critical Zone Observatory [ERCZO], Dry Creek, which we classify as storage-capacity-limited based on intraseasonal storage dynamics; Dralle et al., 2018; Hahm et al., 2019). The 26 sites span a large gradient in precipitation and biome, from mixed-coniferous-broadleaf evergreen forests to deciduous oak savanna (see Table S2 for more detail), as well as underlying bedrock (marine sedimentary sequences to the granitic Sierra Nevada). A broader application of this empirical framework would likely register snow-dominated catchments as precipitation-limited, because higher precipitation typically results in higher storage as snowpack (see Text S3 for further discussion).

To test whether the subsurface storage dynamic governs plant community response to precipitation variability, we examined the correlation between catchment-wide mean summer EVI (derived from satellite observations [MOD13A1; Didan, 2015] between April and September) and winter precipitation. EVI is used here as a proxy for plant productivity and water use (Mu et al., 2007; Sims et al., 2006) and has been widely used as a metric of plant sensitivity to changes in measured subsurface water availability (e.g., Bai et al., 2019; Geruo et al., 2017). In our presentation of results, the annual summer EVI provided by the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite program and obtained from the Google Earth Engine for each site is normalized by the site-specific mean across all study years. This allows for easy visual intercomparison between sites without affecting the rank correlation (ρ) between summer EVI and winter P. Nonnormalized data for each site are provided in Figure S3. Uncertainties in the EVI and water balance data are discussed in Text S1. In order to explore the role of summertime meteorological conditions on plant response, we also compared the sensitivity of summer EVI to summer PET (calculated via the Hargreaves method (Hargreaves & Samani, 1982) with temperatures determined from PRISM).

We restricted the analysis to the 2002-2013 water years because (i) this marks the start of MODIS products that the ET data set relies on, (ii) we wanted to limit the total number of years studied to minimize trends in EVI associated with long-term plant community growth or succession that were distinct from the seasonal

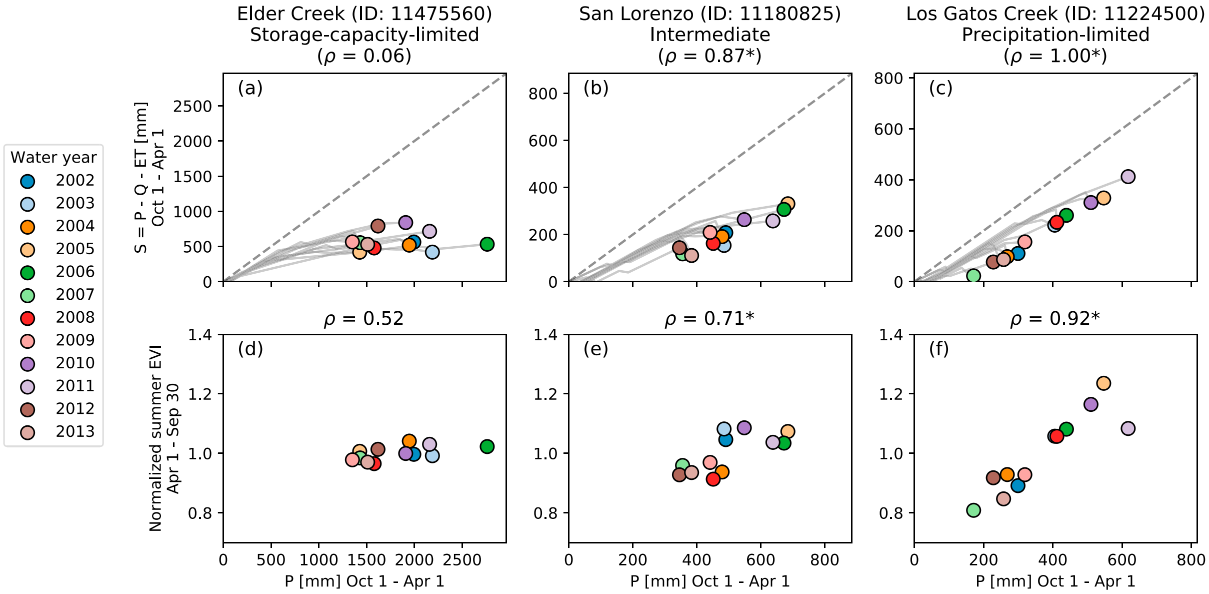

Figure 2. Winter storage (*S*) and the summer enhanced vegetation index as a function of winter precipitation (*P*). Plots (a–c) track the running catchment-wide *S* water balance (grey line traces) for each water year as a function of cumulative winter precipitation (up to 1 April). The dashed 1:1 lines reflect a reference case of no runoff (*Q*) or evapotranspiration. Plots (d–f) plot mean-normalized summer enhanced vegetation index between 1 April and 30 September, also as a function of total winter precipitation (*P*). ρ denotes the Spearman rank correlation for each scatter plot; asterisks denote significance at $p<0.05$.

storage-climate signal we sought to isolate, (iii) there was large variation in *P* across the sites during this time period, and (iv) many trees across the state began to die at the end of this time period (USFS, 2016), which results in a step-change in the EVI signal, precluding our ability to detect the sensitivity of summer EVI to interannual variability in *P*.

3. Winter Water Balance and Summer Plant Sensitivity to Variable Precipitation

The first row of Figure 2 illustrates annual storage dynamics from three sites spanning a gradient from storage-capacity-limited to precipitation-limited. The grey lines show the seasonal progression of *S* through multiple winters; the end-of-winter *S* value is shown with a colored point (evaluated from mass-balance between 1 October and 1 April). In each site, the same 12 years (water years 2002-2013) were selected. At Elder Creek, early winter rains steadily increase *S*. Storage eventually plateaus, however, and further precipitation instead results in runoff. Thus, across multiple years, end of winter *S* and *P* are largely uncorrelated, and ρ is not significantly different from zero (Figure 2a). The catchment is classified as storage-capacity-limited. At Los Gatos Creek, *S* increases with additional precipitation throughout the winter, consistent with precipitation limitation. Unlike Elder Creek, the seasonal storage traces do not plateau, and winter runoff is typically small (Figure S3). *S* and *P* are strongly correlated: ρ=1.0 and is significant at $p < 0.05$. A strong positive correlation is guaranteed in this case, as small runoff results in the storage term being dominated by *P*; this arises because precipitation is generally smaller than the storage capacity. San Lorenzo Creek is an intermediate case, where *S* increases with *P* during relatively dry years, but begins to plateau in wetter years.

The second row of Figure 2 illustrates the sensitivity of summer plant growth to the previous winter's rainfall. At Elder Creek, there is no significant correlation between *P* and EVI, consistent with our hypothesis that storage-capacity limitation results in insensitivity of plant summer productivity and water use to year-to-year variability in total precipitation. In contrast, at Los Gatos Creek, EVI is strongly correlated with winter precipitation. In this precipitation-limited catchment, the EVI signal suggests that plants are more productive and return more water to the atmosphere in summers that follow wet winters.

Figure 3 summarizes the rank correlations between *S*, EVI, and *P* for all catchments. Six of the sites exhibited storage-capacity limitation, that is, insignificant correlation between *S* and *P*. At these sites (open symbols in

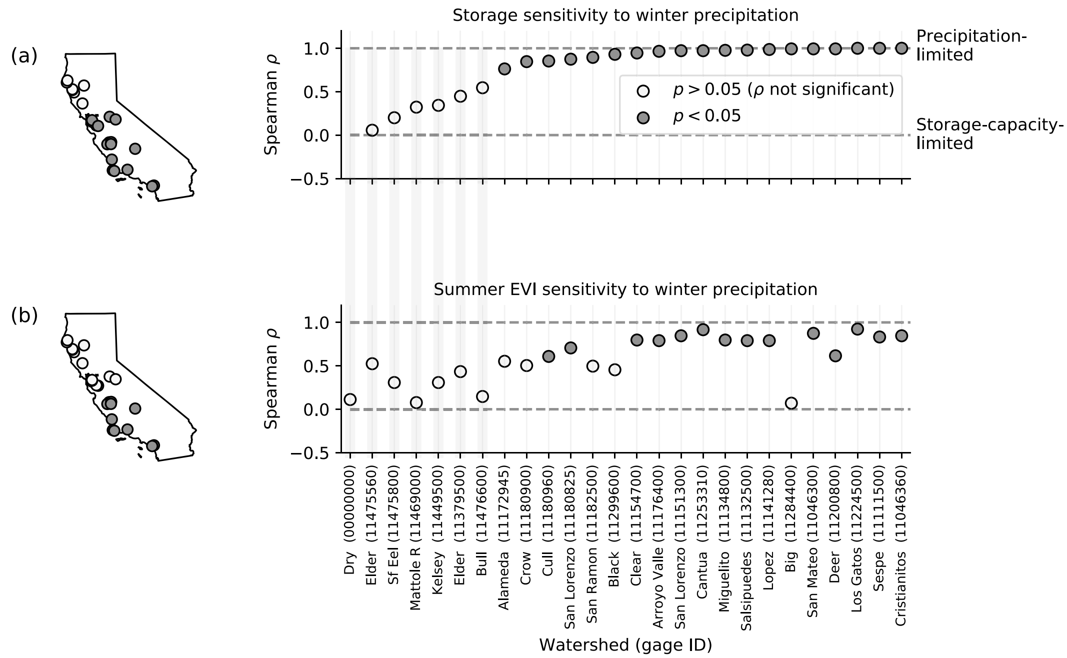

Figure 3. Winter storage and summer enhanced vegetation index (EVI) sensitivity to winter *P*. Spearman rank correlations between (a) *S* and winter precipitation and (b) summer EVI and winter precipitation. The filled symbols denote significance at $p<0.05$. The grey-shaded vertical bars connect storage-capacity-limited sites between (a) and (b). Detailed information for each site is available in Table S2. Dry Creek lacks complete runoff record but is inferred to be storage-capacity-limited based on intensive hillslope-scale monitoring.

Figure 3a) summer EVI was similarly insensitive to winter precipitation totals (open symbols in Figure 3b), as hypothesized. The storage-capacity-limited sites are found throughout the Northern California Coast Ranges (maps in Figure 3), indicating that storage-capacity limitation may be a widespread ecohydrologic phenomenon across an area with diverse plant communities, which have a large range in canopy cover (between ~20 and ~90%; Table S2 and Figure S4) and absolute mean summer EVI (~0.32 to ~0.50; Figure S3). Sayama et al. (2011) also analyzed runoff from 17 small catchments, not monitored by the USGS, in Northern California Coast Range catchments and found behavior that we interpret as storage-capacity-limited (seasonal S traces plateau relatively early within the winter). This area also tends to have higher average annual rainfall (Figure S5); as the modeling framework predicts (Figure S2), locations with higher rainfall are more likely to be storage-capacity limited. At precipitation-limited sites, variations in *P* explain variations in *S* (filled symbols in Figure 3a), and summer EVI at most sites scales with winter precipitation (filled symbols in Figure 3b).

Figure S6 shows that in general the summer EVI signal has a weak negative correlation with summer PET across the state; however, at most sites the correlation is insignificant. We interpret this to indicate that if more energy is available for plant water use, vegetation is not necessarily able to use that energy to transpire more (i.e., the sites are water-limited in the summer). Furthermore, there is no apparent difference in the sensitivity of summer EVI to summer PET between storage-capacity-limited and precipitation-limited sites.

4. Discussion

Sites across California exhibit both precipitation-limited and storage-capacity limited behavior. Where the amount of water stored over the wet season is uncorrelated with rainfall, the storage capacity of the subsurface is inferred to be low relative to the winter rainfall, and correspondingly, the summer EVI is insensitive to variations in rainfall. This is consistent with our hypothesis that storage-capacity limitation can decouple plants from swings in rainfall, even when these swings are large: *P* varied more than twofold between years, and, in some cases, by more than 1,500 mm.

Similar to recent studies (e.g., Wang-Erlandsson et al., 2016), our analysis uses water flux tracking to estimate *S* independently of catchment physiographic features (e.g., soil characteristics). Considering only water storage in near-surface soils, all study sites would likely be storage-capacity-limited: the average plant-available water holding capacity in the soil is about 100 mm based on querying the Soil Survey Geographic database (Soil Survey Staff, 2018). Instead, most sites are precipitation-limited, indicating that the seasonal water storage likely extends well below the soil, consistent with large discrepancies between flux-tracked and soil survey-inferred storage capacities observed elsewhere (e.g., de Boer-Euser et al., 2016). Storage drawdowns in summer within Mediterranean climates are dominated by *ET*, not *Q*, Martens et al., 2017, and transpiration is the dominant (85-95%) component of summer *ET* at our sites. This indicates that much of the water seasonally stored below the soil is plant-available, and that plants generate the below-soil storage deficit that is replenished by wet season rains. This deeper water occurs in saprolite or weathered bedrock as rock moisture (in the sense *of* Rempe & Dietrich, 2018) or groundwater.

4.1. The Decoupling of Summer Plant Greenness From Winter Precipitation Variability

We considered additional mechanisms that could result in the decoupling of summer plant greenness from winter precipitation variability: (i) that some plant communities do not exhibit EVI variations in general and (ii) that some plant communities do not exhibit EVI variations in response to changes in water availability. We rejected these explanations because (i) there are consistent, large seasonal swings in EVI at storage-capacity-limited sites with diverse plant communities (see Figure 11 of Hahm et al., 2019), and (ii) greenness across a wide range of plant communities has been shown to be significantly correlated with water storage (Yang et al., 2014). There remain in our data set, however, five sites where precipitation limits *S* but is poorly correlated to summer EVI, contrary to our predictions. This may be due to storage capacity being met in some but not all years, significant interannual water storage carry-over, or *S* not scaling, as assumed, with plant available water, due to factors like interbasin flow that are not accounted for in our analysis.

4.2. Observations and Hydrologic Mechanisms of Storage-Capacity-Limitation

Monitoring and drilling at two storage-capacity-limited catchments—Elder Creek and Dry Creek—in the Northern California Coast Range, within the ERCZO, illustrate how diverse CZ structures impose storage-capacity limitation. The subsurface CZ at Dry Creek consists of a shallow soil (~40 cm) developed on a relatively thin saprolite and weathered bedrock zone that transitions to low porosity, low conductivity fresh parent material at only ~2-m depth (Dralle et al., 2018; Hahm et al., 2019; Lovill et al., 2018). Here early winter rains (typically between 100 to 200 mm, or less than 1/10th of the local $\overline{P}$) saturate the CZ (Dralle et al., 2018). Further precipitation generates widespread overland flow, and *S* does not increase, resulting in limited summer water availability in the summer. Despite an annual precipitation of >1,800 mm, a water-limitation tolerant oak savanna dominates (Hahm et al., 2018). This can be explained by the subsurface CZ-structure imposed cap on plant-available water storage (Hahm et al., 2019). In contrast, the subsurface CZ at the densely forested Elder Creek (USGS gage #11475560) consists of a thin soil (typically <60 cm), underlain by a weathered bedrock layer which thickens upslope away from the channel, reaching depths of up to 30 m at the ridge (Oshun et al., 2016; Rempe & Dietrich, 2014; Salve et al., 2012). The soil and weathered fractured rock progressively wet with early winter precipitation, until a field-capacity-like condition is reached in the vadose zone. Further precipitation triggers recharge to a seasonal groundwater table that develops above the fresh bedrock boundary that slopes toward the channels and drives relatively rapid runoff without completely saturating the subsurface (Rempe & Dietrich, 2018).

Differences in CZ structure at the two ERCZO sites correspond to different geologic units of the Franciscan Formation (Hahm et al., 2019). Other lithological settings may influence seasonal water storage through different runoff generation mechanisms. For example, at sites with low near-surface hydraulic conductivity where runoff generation is primarily via Horton overland flow or where shallow claypans promote shallow lateral subsurface flow (e.g., Swarowsky et al., 2011), greater winter precipitation (*P*) would not increase *S* but instead would increase runoff (*Q*), as suggested by Milly (1994). Our empirical approach would register this catchment behavior as storage-capacity-limited, even though such sites may have ample subsurface porosity where water could be stored if, for example, winter precipitation events were less intense but more frequent.

4.3. Storage Capacity Limitation and Drought Resilience

More than 100 million trees died across California in the 2011-2016 drought (USFS, 2016). However, we did not observe significant crown dieback or tree mortality at the two storage-capacity-limited ERCZO sites

(Elder and Dry creeks), in spite of approximately twofold precipitation declines relative to long-term averages. Indeed, at five out of six storage-capacity-limited sites, summer EVI remained uncoupled from winter *P* even when years during and after the extreme drought are considered (2014-2016; Figure S7; these years were not included in the analysis in Figure 3 in order to avoid the potential step-change in EVI signal due to dead trees at some sites; see discussion above). The site that shifted from storage-capacity limited to precipitation limited (Gage ID 11379500) likely did so because rainfall dropped low enough relative to storage capacity that it entered a precipitation-limited state in the drought, as predicted by the model and suggested by other intermediate cases (see, e.g., San Lorenzo in Figure 2). The storage-capacity limited sites are representative of much of the Northern California Coast Ranges, which avoided significant mortality compared to the Sierra and Southern California (USFS, 2016), and span a large gradient in ecosystem water-limitation tolerance, from grassland savanna to sclerophyllous shrubland to dense stands of Douglas Fir (*Pseudotsuga menziesii*). Although it rains more along the Northern California Coast Ranges compared to the rest of the state, the strong seasonal separation of water delivery to the landscape from water demand by plants results in summer water limitation in spite of annual *P* exceeding, in some years, potential *ET*.

Previous studies, in contrast to our hypothesis, concluded that these plant communities would suffer in the drought. For example, Choat et al. (2012) proposed that, in general, forests growing in relatively wet areas should be as susceptible to drought as those growing in dry environments, due to the tendency for trees to operate with narrow hydraulic safety margins within their water balance regime. Locally, relatively high canopy density and climatic water deficits resulted in model predictions of higher-than-observed mortality in the Northern California Coast Ranges in the drought (Young et al., 2017). We propose that by decoupling summer water availability from year-to-year winter precipitation variability, storage-capacity limitation is a mechanism of drought resilience in this region. Plants were not spared from the drought here because the subsurface stored large quantities of water that were mined as the drought progressed; rather, plants survived because winter rains exceeded the subsurface storage capacity and replenished storage even in relatively dry years, consistent with intensive moisture monitoring campaigns throughout the CZ (Rempe & Dietrich, 2018). At precipitation-limited sites (e.g., the Big Creek catchment included in this analysis), the patterns of mortality will depend on the severity of the meteorological drought and on plant physiological adaptations to water limitation (e.g., the varied ability of plants to avoid hydraulic failure and carbon starvation in anomalously dry years (Adams et al., 2017)).

5. Conclusions

Hydrologic analysis of 26 relatively undisturbed basins within Mediterranean-climate areas of California revealed seven basins that showed a decoupling between annual rainfall and subsurface water storage. At these sites, annual rainfall variations do not impact storage because rainfall is typically in excess of subsurface storage deficits. As hypothesized, at each of these sites summer EVI did not vary with annual rainfall, highlighting a storage-capacity limitation mechanism that decouples plants from rainfall variability, including droughts.

Models rarely incorporate estimates of storage capacity beyond the soil, primarily due to lack of accurate, spatially distributed information about the deeper subsurface. Where water flux data are available, our modeling approach provides a means to quantify the sensitivity of plants in Mediterranean climates at catchment scales to rainfall variability and water storage capacity (including rock moisture and groundwater residing in weathered bedrock) without a priori or posteriori knowledge of that water storage capacity. This reduces the reliance on estimates of soil properties alone, and the assumption that soil is the only source of water for transpiration. Our conceptual model may enable identification of plant communities with a reduced risk of mortality under drought scenarios, and if climate change forecasts predict significant reduction in precipitation or increase in its variability, the model should also identify new areas of drought vulnerability.

Acknowledgments
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