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LETTER

Subsurface storage capacity controls on tree ring sensitivity to precipitation

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Abstract

Tree growth sensitivity to precipitation varies dramatically across Mediterranean climate regions, but the mechanisms controlling this variation remain poorly understood. We investigated how subsurface water storage capacity mediates the relationship between winter wet season precipitation and annual tree ring width across seasonally dry ecosystems of the western United States. We analyzed tree ring chronologies from the International Tree-Ring Data Bank combined with climate databases and a root zone water storage capacity dataset encompassing both soil and bedrock storage.

We categorized seasonal water storage at tree-ring sites into precipitation-limited, intermediate, and storage-capacity-limited groups based on the ratio of net winter precipitation to root zone storage capacity. Our central hypothesis was that sites where winter precipitation consistently exceeds storage capacity would show weaker precipitation-growth coupling than sites where precipitation inconsistently fills available storage. Using Spearman rank correlations between ring width and winter precipitation, we found that storage-capacity-limited sites indeed showed significantly weaker precipitation-growth coupling compared to precipitation-limited sites.

This pattern suggests that when subsurface storage is consistently filled, trees have access to similar amounts of water each year regardless of precipitation variability, buffering growth against climate fluctuations. Conversely, where storage is inconsistently filled, tree growth remains sensitive to precipitation variation. These findings have important implications for understanding drought resilience in Mediterranean ecosystems and for paleoclimate reconstruction using tree rings. In storage-capacity-limited environments, tree rings may not reliably record precipitation variability, potentially limiting their utility for drought reconstruction. Our results emphasize the critical role of subsurface storage dynamics in mediating plant responses to climate variability.

1. Introduction

Meteorological droughts pose significant challenges to water resources and ecosystem resilience in Mediterranean climates, which are characterized by pronounced seasonality. Climate change has exacerbated these challenges (Lionello and Scarascia 2018, Swain *et al* 2018, Tramblay *et al* 2020, Cos *et al* 2022). These droughts profoundly impact groundwater recharge, streamflow initiation, and baseflow, affecting municipal water supplies (Apurv and Cai 2020) and ecosystems (Bond *et al* 2008).

Among the most visible impacts of drought are mass tree mortality events. For instance, during the 2012-2015 drought in California, millions of trees died primarily due to water stress (Carnicer *et al* 2011, Asner *et al* 2016). While insects and historical land use practices such as fire exclusion contribute to these events, the ultimate cause of drought-induced mortality results from the interplay between subsurface water availability and atmospheric water demand (Allen *et al* 2010, Breshears *et al* 2013, Park Williams *et al* 2013, Choat *et al* 2018).

Predicting drought-induced tree mortality at regional scales remains challenging due to gaps in our understanding of Earth's near-surface weathering profile (Rempe and Dietrich 2014, Dralle *et al* 2023), which influences plant-available water storage capacity and its response to rainfall and snowmelt.

In upland landscapes, the size of the detectable subsurface root-zone water storage capacity (S_R)—comprising both soil water storage capacity and bedrock water storage capacity— represents primarily vadose zone storage in the unsaturated zone rather than groundwater storage in the saturated zone (Hahm *et al* 2020, McCormick *et al* 2021). This storage includes water in soil pores and bedrock fractures accessible to plant roots, and plays a pivotal role in determining water availability to vegetation and controlling plant productivity (Hahm *et al* 2019b, McCormick *et al* 2021, Hahm *et al* 2022, Ehlert *et al* 2024). Total porosity, defined as the total void space within subsurface materials such as soil or bedrock, represents the upper limit of water storage capacity. This includes all pore spaces that could potentially hold water, but not all of it is accessible to plants, as only a fraction of the water within these spaces is available due to factors like pore size distribution and water retention characteristics (Klos *et al* 2018). Woody plants, particularly in Mediterranean climates, heavily rely on water stored in the bedrock during dry seasons (Rempe and Dietrich 2014, McCormick *et al* 2021, Miguez-Macho and Fan 2021, Ehlert *et al* 2024). This highlights the importance of subsurface storage in shaping plant-water interactions and ecosystem function (Ichii *et al* 2009, Kelly and Goulden 2016).

The relative size of subsurface storage capacity compared to precipitation significantly influences water retention and plant water availability. In winter-wet, summer-dry climates, water storage dynamics can fall into two end-member categories based on the subsurface storage capacity relative to precipitation: (1) precipitation-limited, where mean annual precipitation is less than the root zone storage capacity, and (2) storage-capacity-limited, where mean annual precipitation exceeds the root zone storage capacity (Hahm *et al* 2019a, 2022). At storage-capacity-limited Mediterranean sites, seasonal water storage is constrained by the storage capacity itself rather than precipitation, resulting in stable annual storage dynamics despite fluctuations in annual precipitation. This has been shown to confer resilience to meteorological drought (Hahm *et al* 2019a, Dralle *et al* 2023). Similarly, Carey *et al* (2010) found that catchments where precipitation exceeds storage capacity exhibit high 'resilience,' defined as the ability to sustain expected precipitation-discharge relations in response to changing inputs. In areas with large water storage capacity relative to precipitation, deficits may persist during the wet season due to reduced precipitation, leading to inadequate replenishment of plant-available water storage and potentially decreased plant productivity (Klos *et al* 2018, Hahm *et al* 2022) or even mass tree mortality (Goulden and Bales 2019). Additionally, during high precipitation periods, plants may experience an increased water supply from larger storage, producing additional biomass that may not be sustainable in subsequent dry periods, a phenomenon known as structural overshoot (Jump *et al* 2017).

The impact of storage capacity constraints on plant productivity and water use sensitivity to precipitation variability across landscapes has yet to be extensively investigated. Although some studies (Hahm *et al* 2019a, Zhu *et al* 2021, Hahm *et al* 2022, Dong *et al* 2023, Cui *et al* 2024) have explored the relationships between storage capacity, precipitation, and plant dynamics at the hillslope to catchment scale with both field observations and through remote sensing, to our knowledge no study has directly examined the relationship between individual tree ring width, precipitation dynamics, and a subsurface storage capacity dataset that includes both soil and bedrock water storage capacity at large spatial scales.

In previous work, Hahm *et al* (2019a) used the remotely sensed summer enhanced vegetation index (EVI) to explore storage-capacity limitation at the catchment scale. In contrast, this study examines individual tree ring datasets and, for the first time, a root zone storage capacity dataset (including both soil and bedrock storage) to investigate the relationship between plant productivity and water availability in precipitation-limited and storage-capacity limited sites in the Mediterranean climates of the western United States. Tree ring widths are an annual resolution record of radial growth, i.e., wood production.(Fritts 1966, Xu *et al* 2017). Wide rings typically form during years with favourable climatic conditions, while narrow rings develop in response to unfavourable conditions (Fritts 1976). Mediterranean climates, where water availability and demand operate asynchronously (Feng *et al* 2019), offer an ideal setting to explore the insensitivity of tree growth to inter-annual precipitation swings within storage-capacity-limited watersheds. Plants rely on water stored from previous wet seasons during the dry season, emphasizing the critical role of subsurface storage capacity (Goulden and Bales 2019). Previous studies (Lévesque *et al* 2016, Weigel *et al* 2023) on the role of subsurface storage in tree growth have typically focused solely on soil water storage capacity. However, McCormick *et al* (2021) have shown that in Mediterranean climates, soil water storage alone is insufficient, as plants often tap into water stored in the pores and fractures of bedrock. The recent availability of a subsurface water storage capacity that includes bedrock storage (Wang-Erlandsson *et al* 2016) allows for a more comprehensive assessment by combining it with soil water storage capacity, thus providing a total storage capacity accessible to many woody plants.

The central question of our study is whether root-zone storage capacity—including both soil and bedrock —mediates the sensitivity of annual tree ring growth (a proxy for plant productivity) to wet season

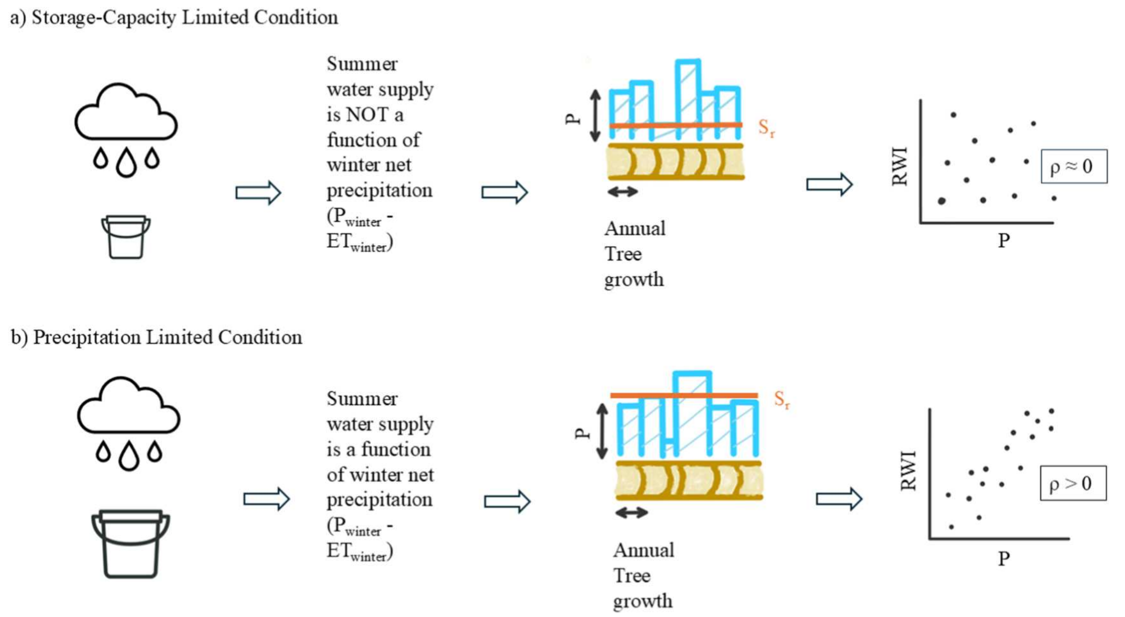

Figure 1. A conceptual diagram illustrates the relationship between tree growth and the relative sizes of net winter precipitation ($P_{net} = P_{\text{winter}} - ET_{\text{winter}}$) and subsurface root zone water storage capacity (S_R; orange line). In watersheds where P_{net} exceeds S_R (a), a consistent minimum storage value is attained, and the summer water supply is independent of winter P_{net}. Tree growth is independent of P_{net} variation, as depicted for six hypothetical years. Consequently, Spearman's rank correlation coefficient (ρ) is approximately zero, indicating decoupling between ring width index (RWI) and P. Conversely, in watersheds where P_{net} matches S_R (b), summer water supply becomes contingent on winter P_{net}. Tree growth varies with P_{net} quantity, as shown for six hypothetical years. This results in ρ exceeding zero, indicating coupling between RWI and P_{net}.

precipitation. We hypothesize that subsurface storage capacity mediates tree growth sensitivity to precipitation because when storage capacity is consistently replenished annually, excess precipitation is not stored for plants and generates streamflow instead. This buffers trees against inter-annual precipitation variability. We predict that this buffering effect will result in diminished correlation between tree ring width and precipitation as mean annual precipitation increases relative to storage capacity, indicating a decoupling of plant water availability from annual precipitation totals. Conversely, we predict positive coupling between plant productivity and precipitation in precipitation-limited sites where storage is not consistently replenished. Our study thus takes a mechanistic approach by focusing specifically on winter (wet-season) precipitation—the dominant water input in Mediterranean climates—to test whether subsurface storage capacity buffers the relationship between precipitation and tree growth. While previous studies have applied exploratory information-theoretic approaches (e.g. with climwin, a package designed to detect a time period over which a response variable is sensitive to the environment (Bailey and Van De Pol 2016)) to identify optimal climate windows and quantify the explanatory power of different seasonal predictors, such as prior winter precipitation, for Mediterranean tree and shrub growth (Camarero and Rubio-Cuadrado 2020), our research addresses a narrower process-based question: whether the storage capacity itself modulates the precipitation-growth relationship. We assess this by exploring whether the correlation between plant productivity and precipitation remains consistent across different levels of mean annual precipitation relative to root zone water storage capacity.

2. Methods and data

2.1. Conceptual framework: storage-capacity-limited versus precipitation-limited sites

In the conceptual figure 1(a), we illustrate the storage-capacity-limited condition, wherein the net winter precipitation ($P_{net} = P_{\text{winter}} - ET_{\text{winter}}$) always surpasses the subsurface root zone water storage capacity (S_R). This leads to an annual replenishment of S_R and runoff (streamflow generation) of excess precipitation. Consequently, trees consistently access the same amount of water each growing season (roughly equal to the size of the bucket), resulting in tree-ring width index that is uncorrelated with the preceding wet season's precipitation magnitude. Under this condition, tree growth becomes independent of inter-annual precipitation variability. This relationship is evaluated using the non-parametric Spearman correlation coefficient, ρ, which measures the correlation between the annual precipitation and ring width index (RWI) by comparing their rank orders. We predict that ρ will tend toward zero in this scenario.

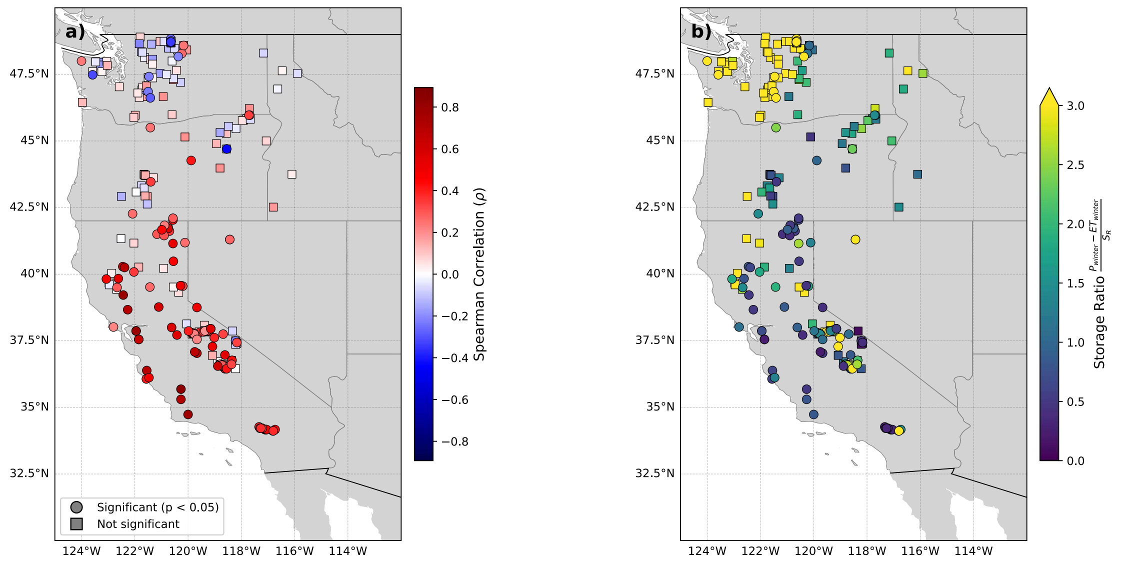

Figure 2. (a) The strength of the coupling between annual ring width index (RWI) and winter (wet season) precipitation, expressed via the Spearman rank correlation (ρ). (b) The ratio of net winter precipitation ($P_{\mathrm{winter}} - \mathrm{ET}_{\mathrm{winter}}$) to root-zone water storage capacity (S_R), which classifies the hydrological regime. In both panels, circles denote sites with statistically significant rank correlations ($p < 0.05$), while squares denote non-significant relationships.

In figure 1(b), we depict the precipitation-limited condition, where winter P_{net} may commonly fall below S_R. Here, the availability of water to plants hinges on the replenishment of S_R by P_{net}. Consequently, annual tree growth (tree-ring width index) becomes dependent upon precipitation variability. We anticipate that ρ will exhibit a positive trend in this scenario.

2.2. Site selection

The study sites in the western contiguous United States (figure 2) were chosen to investigate the correlation between tree growth and precipitation while taking into account subsurface storage dynamics. Two primary factors informed site selection:

- Hydrological seasonality: The selected sites demonstrate a distinctive energy and precipitation distribution pattern, with a notable Mediterranean-type winter-wet/summer-dry seasonality (Beck *et al* 2018). We identify these areas using an asynchronicity index (ASI) exceeding 0.50 (Feng *et al* 2019), indicating a significant lag in timing between energy input and precipitation delivery. The ASI quantifies the seasonal mismatch between precipitation (water supply) and potential evapotranspiration (water demand) using the Jensen-Shannon distance, a statistical measure of divergence between two probability distributions (Feng *et al* 2019). By comparing the distributions of these hydroclimatic variables, the ASI captures both timing and magnitude differences, offering a globally applicable metric for assessing climate asynchronicity. For an open-access map of the asynchronicity index across the United States please see figure S1. of Ehlert *et al* (2024).
- Data availability: The selected sites are constrained by the availability of tree-ring width data, distributed water flux data, and root zone water storage capacity.

2.3. Tree-ring data

We obtained tree-ring chronology files (.crn) from the International Tree-Ring Data Bank (ITRDB) covering sites across the United States available as of June 5, 2025. The complete dataset was downloaded from the NOAA National Centers for Environmental Information repository (https://www.ncei.noaa.gov/pub/data/paleo/treering/chronologies/) as a compressed archive file (itrdb-v713-usa-crn.zip).

We applied several quality control filters to ensure data consistency and reliability. First, we filtered the dataset to include only standard chronologies, excluding residual chronologies, ARSTAN chronologies, and other specialized chronology types that undergo additional statistical processing beyond basic standardization. Standard chronologies were selected because they represent ring-width index (RWI) values that have been standardized using conservative detrending methods to remove biological age-related growth trends while preserving high-frequency climate signals that are the focus of our analysis. Second, we retained only sites with metadata records including geographic coordinates.

We used the dplR R library (Bunn 2008) to read the Tucson format files (.crn). The Tucson format stores chronology data in a standardized decadal structure where each line contains a site identifier, decade, and ten annual RWI values with associated sample depth information. Site metadata were extracted from the chronology file headers to obtain coordinates (latitude/longitude in decimal degrees). Data processing and subsequent analyses were conducted in Python using pandas for data manipulation (McKinney *et al* 2010).

To assess the potential impact of temporal autocorrelation on our correlation analyses, we explored whether the inherent year-to-year persistence in tree-ring chronologies would bias our climate-growth relationships. Tree-ring series typically exhibit positive autocorrelation due to biological carryover effects, where previous year's growing conditions influence current year growth through stored carbohydrates and other physiological processes. We applied a first-order autoregressive pre-whitening procedure to remove lag-1 autocorrelation while preserving the variance structure and climate sensitivity of the original time series. For each chronology, we modeled the temporal autocorrelation using a first-order autoregressive process and defined the pre-whitened series as the residuals of this model. For each chronology, we calculated the lag-1 autocorrelation coefficient (α) and generated pre-whitened series by subtracting the product of this coefficient and the previous year's value from each annual measurement.

Comparative analyses using both original standard chronologies and pre-whitened chronologies yielded qualitatively identical results in terms of correlation magnitudes, spatial patterns, and statistical significance levels; given this negligible impact of temporal autocorrelation on our primary findings, we present results based on the original standard chronologies throughout the manuscript. However, results from the pre-whitened analyses are documented in our computational notebook and available in the supplementary data repository.

2.4. Environmental variables

For each tree-ring site, we extracted multiple environmental variables using Google Earth Engine's `reduceRegions` function to sample gridded datasets at point locations. Sites were filtered using the Asynchronicity Index (ASI) to include only those with ASI > 0.5, focusing our analysis on Mediterranean environments where seasonal precipitation-potential evapotranspiration mismatches are pronounced (Feng *et al* 2019).

Precipitation data were obtained from the AN81m PRISM monthly precipitation dataset at 4 km resolution (Daly *et al* 2008), with winter wet-season precipitation summed on a water year basis from October-April spanning 1895-2021.

Winter evapotranspiration was calculated by summing monthly evapotranspiration components (canopy transpiration [Ec], soil evaporation [Es], and canopy interception [Ei]) from the PML (Penman-Monteith-Leuning) dataset at 500 m spatial resolution and 8-day temporal resolution, averaged over the 2003-2020 period (Zhang *et al* 2019). We utilized the 2003–2020 mean winter evapotranspiration as a static climatological constant to characterize each site's typical evaporative demand. We relied on this period because winter ET in energy-limited Mediterranean regions is inter-annually stable relative to the high variability of precipitation, making the mean a robust metric for regime classification. Furthermore, we selected the PML ET dataset to ensure methodological consistency with the inputs originally used to derive the root-zone water storage capacity

Root-zone water storage capacity (S_R, mm) was obtained from a 1 km resolution dataset representing the maximum plant-accessible water storage in the subsurface, derived using flux-tracking methods that track cumulative water deficits to estimate storage capacity (Dralle *et al* 2021). See figure S5 in Ehlert *et al* (2024) for a map.

All environmental variables were extracted by sampling the respective gridded datasets at tree-ring site coordinates using Earth Engine's point-based sampling functionality.

2.4.1. Data considerations

PRISM requires a minimum of 85% non-missing daily values for a monthly value to be considered valid, and uses cross-validation procedures to identify and remove stations with insufficient data quality or spatial consistency (Daly *et al* 2008). For stations with limited temporal coverage, PRISM employs localized precipitation-DEM elevation relationships and continuously adjusts its frame of reference to accommodate regional changes in orographic regime, ensuring robust interpolation even when station density varies across the domain (Daly *et al* 1994).

Mediterranean climates are characterized by pronounced seasonality with wet winters and dry summers, where precipitation falls predominantly from October to April (Beck *et al* 2018). In mixed evergreen forests, productivity is highest in the summer (Hahm *et al* 2019a), and in Mediterranean savannas and woodlands dominated by deciduous species such as blue oaks (Hahm *et al* 2022), growth occurs primarily during the growing season when leaves are present, not during winter when trees are leafless. This seasonal separation between precipitation input (winter) and tree growth (spring-summer) makes our approach of comparing winter precipitation to summer water availability appropriate for Mediterranean climate regions.

The root-zone water storage capacity (S_R), representing primarily vadose zone storage including both soil and bedrock storage capacity for each specific site was obtained from the dataset documented by Dralle *et al* (2021), which adapts the original S_R estimation method from Wang-Erlandsson *et al* (2016). This storage capacity encompasses water storage in both saturated and unsaturated conditions within the root-accessible zone, though validation from diverse field settings indicates that it is primarily unsaturated zone storage (McCormick *et al* 2021). This approach estimates S_R using a broadly applicable mass-balance method that does not require site-specific soil or plant community parameters. It tracks the root-zone storage deficit (D) as the cumulative difference between water fluxes exiting (F_{out}) and entering (F_{in}) the root zone, where F_{out} is evapotranspiration (ET) and F_{in} is precipitation (P). By integrating these differences over time, the method determines the maximum moisture deficit, providing an estimate of the root zone storage capacity over the desired period of record. We use the notation F_{in} and F_{out} rather than simply precipitation and evapotranspiration because F_{in} represents liquid water flux entering the root zone, which may include delayed inputs from snowmelt in addition to direct precipitation, particularly important in snow-dominated regions (Dralle *et al* 2021). Following conservative estimation approaches, drainage fluxes are assumed negligible to provide lower-bound estimates of storage capacity.

The mass-balance approach underlying the storage capacity dataset specifically avoids the need to quantify or measure bedrock porosity, soil water retention heterogeneity, and pore size distribution—parameters that are notoriously difficult to characterize at large spatial scales and are often unknowable across regional extents. As Wang-Erlandsson *et al* (2016) demonstrated, the fundamental advantage of this mass balance method is that it bypasses the requirement for detailed subsurface property measurements by instead inferring storage capacity from observable water balance dynamics. Because the method determines root zone storage capacity as the maximum observed deficit between evaporation and precipitation, it serves as a direct estimate of functional storage capacity. While uncertainties certainly exist in evaporation and precipitation products, these are more readily quantifiable and addressable than the spatially heterogeneous subsurface properties that would be required for direct approaches. The underlying precipitation and evapotranspiration datasets used to calculate root zone storage capacity have been validated through water balance closure at streamflow gauges, with PRISM precipitation and PML evapotranspiration data achieving Nash-Sutcliffe efficiency of 0.93 across our study region (Ehlert *et al* 2024). Additionally, deficit-based water storage estimates calculated using similar mass-balance approaches show general agreement with field measurements of plant bedrock water use across diverse geological and climatic settings (McCormick *et al* 2021).

2.5. Analysis

We analyzed the relationship between tree growth and wet-season precipitation sensitivity across different water storage regimes. For each tree-ring site, we matched annual ring-width index (RWI) values with corresponding winter precipitation totals by water year. We computed Spearman rank correlation coefficients (ρ) between the RWI and winter precipitation time series for each site, providing a measure of growth-climate coupling strength. Sites with fewer than 10 overlapping years of data were excluded from correlation analysis to ensure statistical robustness.

We then examined how growth-climate coupling varies with water storage capacity by plotting site-level Spearman correlations against the dimensionless water storage capacity ratio: $(P_{\text{winter}} - \text{ET}_{\text{winter}})/S_R$, where P_{winter} is mean winter precipitation, $\text{ET}_{\text{winter}}$ is mean winter evapotranspiration, and S_R is root-zone water storage capacity. This ratio represents the balance between winter (wet-season) water supply and subsurface storage capacity.

To test for systematic differences in growth-climate coupling across water limitation regimes, we grouped sites into three categories based on their water storage capacity ratio: precipitation-limited ($(P_{\text{winter}} - \text{ET}_{\text{winter}})/S_R < 0.75$), intermediate ($0.75 \leqslant (P_{\text{winter}} - \text{ET}_{\text{winter}})/S_R < 1.25$), and capacity-limited ($(P_{\text{winter}} - \text{ET}_{\text{winter}})/S_R \geqslant 1.25$). We used Kruskal-Wallis tests to assess statistical differences in correlation coefficients among the three water limitation regimes, followed by pairwise comparisons to identify specific group differences.

The Kruskal-Wallis test is a non-parametric alternative to one-way ANOVA that does not assume normal distribution of residuals or homogeneity of variances. This test was appropriate for our data because: (1) the Spearman correlation coefficients (ρ) were not normally distributed across categories, and (2) the variances differed among the three water limitation groups. Following a significant omnibus test, we performed Dunn's post-hoc test for pairwise comparisons to identify which specific categories differed from one another. To control for multiple comparisons, we applied Bonferroni correction to the significance threshold.

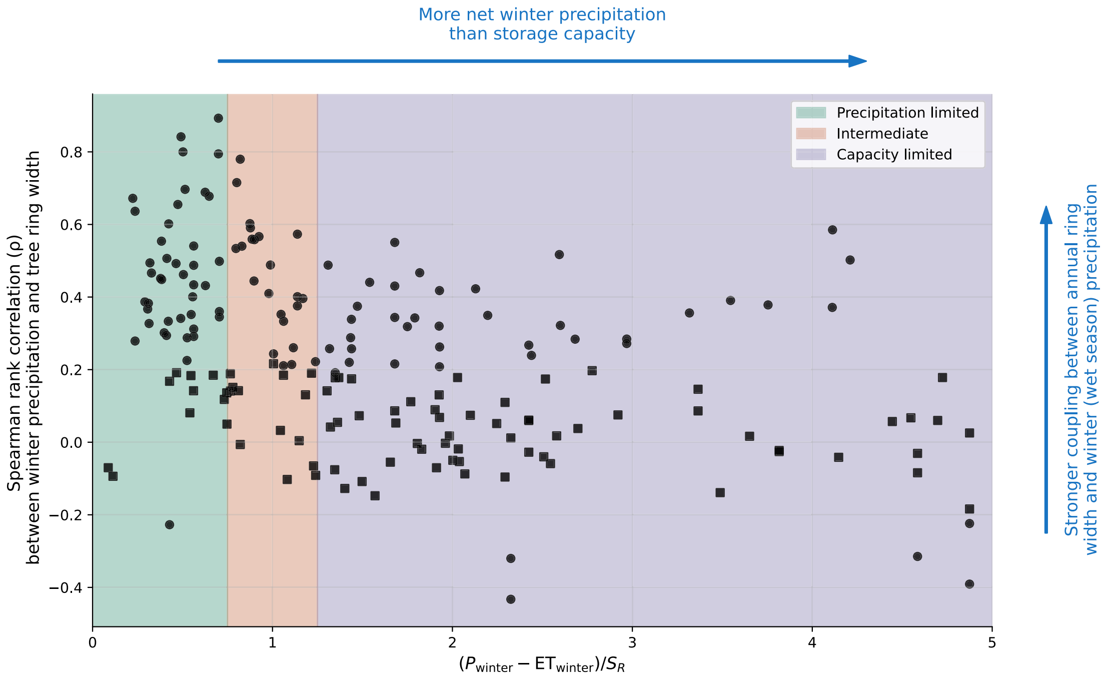

Figure 3. The relationship between the strength of the coupling between annual ring width (RW) and winter (wet season) precipitation, expressed via the Spearman Rank Correlation (ρ) and the ratio of P_{winter} - ET_{winter} to subsurface root zone water storage capacity (S_R). Break points at 0.75 and 1.25 demarcate the three classifications: precipitation limited, intermediate, and capacity limited. Each point denotes an individual site, with squares denoting non-significant ($p > 0.05$) correlations.

3. Results

We found that the strength of the coupling between the annual ring width and winter (wet-season) precipitation (expressed via the Spearman rank correlation, ρ) decreased as the relative size of net winter precipitation increased compared to the subsurface root zone water storage capacity (S_R).

3.1. Ring width index (RWI) sensitivity to winter precipitation

The categorization of sites based on the relative sizes of net winter precipitation ($P_{net} = P_{\text{winter}}$ - ET_{winter}) and subsurface root zone water storage capacity (S_R) into three groups—precipitation-limited, intermediate, and storage capacity-limited—revealed variations in ρ values across these distributions (figures 3 and 4). We focus on this ratio rather than absolute values of S_R because storage capacity alone can be influenced by multiple factors including geology, plant community composition, and climate (Hahm *et al* 2024), whereas our hypothesis specifically concerns the interaction between storage capacity and precipitation in mediating tree growth sensitivity. The spatial distribution of correlation strengths (figure 2) reveals distinct geographic patterns, with consistently positive correlations ($\rho > 0.4$) concentrated in the southern portions of the study area, particularly in Southern California, around the Central Valley, and in the eastern Sierra Nevada. In contrast, sites in the Cascade Range show predominantly weak or non-significant correlations. The ratio $(P_{\text{winter}} - \text{ET}_{\text{winter}})/S_R$ scales with Pwinter, and so (all else equal) we would expect wetter sites to have stronger capacity-limitation, and thus weaker correlations.

A positive ρ value signifies increasing RWI with increasing precipitation, zero indicates decoupling and a negative value means RWI decreases with increasing precipitation. Most storage capacity-limited sites showed decoupling or weak negative/positive coupling (figure 4). Conversely, precipitation-limited sites predominantly exhibited positive precipitation-RWI coupling.

The Kruskal-Wallis analysis (non-parametric statistical test) revealed a statistically significant difference among the three distributions (capacity limited, intermediate, and precipitation limited; figure 4) with a test statistic of 90.41 and a p-value < 0.001. The analysis revealed clear differences in precipitation-RWI correlations among limitation categories. Precipitation-limited sites showed the strongest correlations (median $= 0.38$), followed by intermediate sites (median $= 0.26$), and capacity-limited sites showed the weakest correlations (median $= 0.05$). The distribution shapes in figure 4 are particularly revealing: precipitation-limited sites show a right-skewed distribution with most sites exhibiting positive correlations, while capacity-limited sites show a more symmetric distribution centered near zero, with roughly equal proportions of sites showing weak positive and weak negative correlations. This symmetry around zero for capacity-limited sites

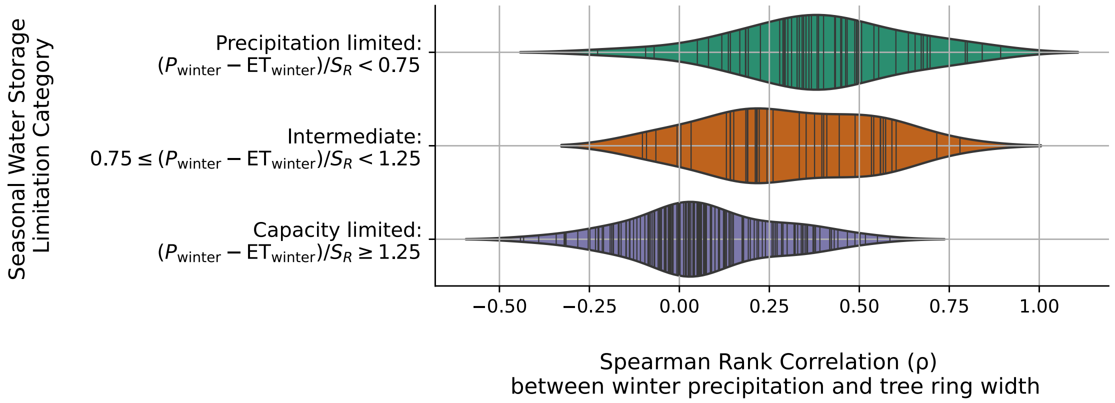

Figure 4. The distribution of Spearman rank correlation (ρ) values within three categories: precipitation-limited, intermediate, and capacity-limited. Thicker sections within each category signify a higher frequency of correlation values. Lower ρ values signify ring width index (RWI) and precipitation decoupling, indicating that increased precipitation does not correspond to increased tree growth. Conversely, higher ρ values indicate RW and precipitation coupling, suggesting increased precipitation enhances tree growth.

strongly supports our hypothesis that storage capacity buffers these sites from precipitation variability, effectively randomizing the relationship between annual precipitation and growth. Dunn's test confirmed significant differences between capacity-limited sites and both other categories ($p < 0.001$ for both comparisons), but no significant difference between precipitation-limited and intermediate sites ($p = 0.22$). This suggests that capacity-limited sites respond fundamentally differently to precipitation-RWI relationships compared to sites with any degree of precipitation limitation.

The consistency of near-zero correlations across capacity-limited sites is remarkable given the diversity of species, elevations, and local climates represented in the dataset. This suggests that storage capacity limitation is a dominant control on tree-water relations that can override species-specific physiological differences and local climatic variations.

4. Discussion

The scatter in correlation values within each category (figure 4) reveals important nuances in the precipitation-growth relationship. Even among precipitation-limited sites, correlation strengths range from near zero to above 0.8, indicating that factors beyond storage capacity influence growth sensitivity. The transition from positive to near-zero correlations occurs around $P_{net}/S_R \approx 1.0$, suggesting a critical threshold where storage capacity begins to buffer trees from precipitation variability. This underscores that hydrological buffering is not a function of the absolute volume of storage or precipitation, but rather the relative balance between supply and capacity—specifically, whether the subsurface 'bucket' effectively fills.

The relationship between tree ring chronologies and climate has been extensively studied, with numerous dendroecological studies (Cook and Jacoby 1977, Vose and Swank 1994, Orwig and Abrams 1997, Peterson and Peterson 2001, Nakawatase and Peterson 2006, Martín-Benito *et al* 2009, Williams *et al* 2010) focusing on the impact of climate factors, primarily precipitation and temperature, on the radial growth of various tree species. We recognize that tree-ring collections in the ITRDB often reflect a sampling strategy biased toward sites with high sensitivity to specific climate variables (Klesse *et al* 2018). Rather than claiming this bias has no effect, we argue that our findings are significant in light of this context. Our primary goal is to demonstrate a mechanism: that storage capacity can fundamentally decouple growth from precipitation. Finding clear evidence of this process operating within a dataset designed to maximize climate sensitivity only serves to highlight the robust and pervasive nature of this ecohydrological control. While many studies highlight the influence of climate on tree growth, only a few have considered the role of subsurface storage. Recently, research has begun to include soil water storage as a factor in tree growth studies (Lévesque *et al* 2016, Chakraborty *et al* 2021, Stolz *et al* 2021, Weigel *et al* 2023). These studies have demonstrated that soil water storage significantly impacts tree ring growth, depending on the rooting depths of the trees (Lévesque *et al* 2016, Gadermaier *et al* 2024). However, much of this research often overlooks water stored in unsaturated weathered bedrock, also known as rock moisture, which can be a crucial water source for woody plants during dry periods (Witty *et al* 2003, Rempe and Dietrich 2018, McCormick *et al* 2021, Hahm *et al* 2022, Ehlert *et al* 2024). For example, McCormick *et al* (2021) found that the withdrawal of bedrock water is widespread and is essential to account for the observed evapotranspiration (ET) in many regions, including the seasonally dry areas of the continental United States. Their deficit-based water balance analysis indicates that in California alone, woody plants can extract 20 km^3 (16.2 million acre-feet) of water from bedrock annually. Root zone water storage capacity (S_R) accounts for storage beyond the soil in bedrock, thereby considering the total storage capacity accessible to many woody plants.

The western contiguous United States has both precipitation-limited and storage-capacity-limited sites. When the net winter precipitation surpasses the subsurface root zone water storage capacity (S_R), indicating storage-capacity-limited conditions, the relationship between annual ring width index (RWI) and annual precipitation (ρ) is either decoupled or weakly negative/positive. This finding supports our hypothesis that storage-capacity limitation can decouple plant growth from fluctuations in precipitation. Where the ratio of $P_{\text{net}} = (P_{\text{winter}} - ET_{\text{winter}})$ to the subsurface root zone water storage capacity (S_R) exceeds 1, excess water is not retained in storage. Consequently, once the storage is replenished, excess rainfall or snowmelt generates runoff or groundwater recharge, and plant productivity becomes decoupled from variable winter precipitation. Where storage capacity is not fully replenished, root-zone storage will scale with P_{net} and productivity will correlate with winter precipitation. This is apparent in figure 3, where the rank correlation shows a decreasing trend for $0 \leqslant P_{\text{net}}/S_R \leqslant 1$ and asymptotes to zero for $P_{\text{net}}/S_R > 1$.

These results align with those of Hahm *et al* (2019a), where the remotely sensed summer enhanced vegetation index (EVI) served as a proxy for plant productivity and water use at a catchment scale. In storage-capacity-limited catchments, plant summer productivity and water use were decoupled from year-to-year variability in total precipitation. Conversely, EVI exhibited a strong correlation with winter precipitation in precipitation-limited catchments. Notably, both remotely sensed EVI (in their study) and site-level tree ring data (in this study) demonstrate plant productivity and annual precipitation decoupling in storage-capacity-limited locations.

Critically, this decoupling mechanism provides an underappreciated form of drought protection for trees in storage-capacity-limited environments. During meteorological droughts when precipitation is well below average, trees at these sites effectively do not 'experience' the drought in terms of water availability—they access the same amount of stored water regardless of whether it was a wet or dry year. This buffering effect means that storage-capacity-limited sites may serve as climate refugia during droughts, maintaining relatively stable productivity while precipitation-limited sites suffer severe water stress and potential mortality. This has important implications for predicting which forests will be most vulnerable to increasing drought frequency and intensity under climate change.

It's crucial to recognize additional factors influencing plant productivity. For instance, species specific responses or the timing of precipitation and temperature can be critical (Li *et al* 2013, Wise and Dannenberg 2022), and relative humidity impacts water demand and plant stress (Jiang *et al* 2017). Nutrient availability is another vital factor (Lévesque *et al* 2016), and competition among trees for resources adds complexity to growth patterns (Blasing *et al* 1983). While this study focuses on the interplay between precipitation and root zone storage capacity, future research should explore how these additional factors interact with storage dynamics to influence plant productivity and drought resilience. Understanding these interactions will provide a more comprehensive picture of the drivers of growth variability in seasonally dry ecosystems.

Tree rings are widely used for precipitation reconstruction around the world (Fritts *et al* 1980, Touchan *et al* 2008, Liu *et al* 2009, Griffin *et al* 2013, Kostyakova *et al* 2018), including in seasonally dry climates (Blasing and Duvick 1984, Woodhouse and Meko 1997, Meko *et al* 2011, Steinschneider *et al* 2018). However, the reliability of these reconstructions depends on a strong and consistent relationship between tree growth and precipitation, a link that is not always present. Our study provides a key biophysical explanation for why this relationship can fail: in storage-capacity-limited sites, the buffering effect of subsurface water availability decouples tree growth from annual precipitation. This finding has direct implications for dendroclimatology. When this decoupling occurs, tree rings lose their sensitivity to inter-annual precipitation variability, suggesting that reconstructions from such sites may be mechanistically unsound and could fail to capture past drought signals.

The relative sizes of precipitation and root-zone storage capacity can be assessed using deficit-based water balance approaches that track whether annual storage deficits reset to zero each year (Ehlert *et al* 2024). Regions where deficits persist across multiple years indicate precipitation-limited conditions where traditional tree-ring reconstructions are viable.

5. Conclusion

The study highlights the critical role of subsurface water storage in moderating the impact of climatic variability on tree growth. Higher Spearman rank correlation values suggest a stronger coupling between annual ring width index and annual precipitation in Mediterranean climate regions of the contiguous United States, but this coupling weakens as the subsurface root zone water storage capacity S_R increases relative to net winter precipitation P_{net}. This indicates that storage-capacity-limited sites can buffer plants against inter-annual precipitation fluctuations, enhancing drought resilience but also potentially confounding paleo-climate inferences. This storage-mediated buffering represents a fundamental mechanism of drought resilience that has been largely overlooked in forest vulnerability assessments. Trees in storage-capacity-limited environments are effectively insulated from year-to-year precipitation variability, including drought years, because they consistently access the full storage capacity regardless of precipitation amount.

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Data availability statement

The data that support the findings of this study are openly available at the following (Aulakh *et al* 2025).

Competing interests

The authors declare that they have no conflict of interest.

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