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RESEARCH ARTICLE

Tracking rain events impact on soil and plant leaf water content over time

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Abstract
Background and aims In semi-arid Mediterranean ecosystems, limited water availability impacts plant performance. This study explores water movement from rainfall through soil to plants, hypothesizing that (i) vegetation buffers water stress by allowing more (and smaller) rain events to percolate deeper, and (ii) plant species' physiognomy conditions their dependence on soil moisture, with larger or deep-rooted species having their leaf water content less coupled with the temporal variation in soil moisture.
Methods We contextualize abiotic stress by analyzing 66 years of rainfall data, track rain events and vegetation influence on soil moisture with soil data loggers and a field-based pluviometer over a year, and assessed soil-leaf water coupling by measuring foliar water content of 177 individuals of nine plant species over one growing season.
Results The mean annual rainfall is ~ 366 mm, with dry years occurring more frequently (every 4.3 ± 0.9 years) than wet ones (every 7.4 ± 0.9 years). Summers have the smallest (8.7 ± 0.7 mm) and shortest (1.5 ± 0.05 days) rain events, with the largest lags with no rain 15.3 ± 0.9 days (maximum 112 days). Only rainfall ≥ 4 mm increased shallow soil moisture, and ≥ 6 mm increased deep soil moisture, and last 5–6 days to desiccate. Vegetation allows more (and smaller) rain events to percolate into deeper soil, maintaining higher moisture between events, especially in deep soil. Finally, foliar measurements showed that leaf water content across time is more correlated with deep than shallow soil moisture, with larger species (or with more developed root systems, e.g. *Stipa tennacissima,Teucrium libanitis*), being less coupled with temporal soil moisture.
Conclusion This study deepens our understanding of water movement in semi-arid Mediterranean systems connecting rainfall patterns to soil moisture and plant responses over time. This understanding will allow more accurate predictions of how rainfall variability may impact plant communities and ecosystem functioning in semi-arid ecosystems.

Keywords Abiotic stress · Rainfall events · Plant response · Semi-arid ecosystems · Soil water dynamics · Water availability

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Introduction

Temporal variation in water availability plays a central role in influencing the structure and function of semi-arid ecosystems (Noy-Meir 1973; Collins et al. 2008; Gherardi and Sala 2015; Dou et al. 2025). Water is the primary limiting resource in semi-arid ecosystems, with rainfall delivered through rain events triggering a succession of biotic responses (Collins et al. 2014; Huxman et al. 2004; Nielsen and Ball 2015; Potts et al. 2006, Ferandes et al. 2022), and restricting plant growth and development (McDowell et al. 2011). Rainfall variability has significant implications for plant communities, exerting a strong influence over a range of factors such as: productivity (Gherardi and Sala 2015; Knapp et al. 2002; Miranda et al. 2011; Luo et al. 2025); water use efficiency (Han et al. 2021; Tarin et al. 2020); species composition (Cleland et al. 2013; Qi et al. 2025); seedling growth and survival (Padilla et al. 2007), and phenology (Cleverly et al. 2016; Van Dyke and Kraft 2025). Despite these recognized impacts, detailed studies on water flow from rainfall to soil moisture and into plants are less common (but see examples such as Allison and Hughes 1983; Krüger et al. 2024). The importance of considering not only total rainfall amount, but also the temporal distribution of rainfall has been widely recognized, given that ecosystem responses are largely conditioned by the timing and magnitude of rain events (Austin et al. 2004; Luo et al. 2022; Nielsen and Ball 2015; Post and Knapp 2020; Reed et al. 2012; Schwinning and Sala 2004). Past studies on rainfall variability have utilized various approaches such as modeling frameworks to simulate rainfall scenarios (Guan et al. 2018; Hou et al. 2021; Xu et al. 2015), the analysis of long-term climate data sets (Rastetter et al. 2003) and rainfall manipulation experiments (Bates et al. 2006; Zhang et al. 2018).

The impacts of rain events on ecosystem processes have been considered on various time scales, from inter-annual variability to the timing and magnitude of seasonal rain events (Chen et al. 2009; Reichmann et al. 2013; Zeppel et al. 2014). Assessing inter-annual patterns in rainfall over time can inform how plants react to rainfall in the current year. This phenomenon, known as "precipitation legacy", is defined as the negative effect of a dry year or positive effect of a wet year on current-year net primary production (Sala et al. 2012). Additionally, the seasonal timing of rain events plays a critical role in ecosystem responses such as phenology (Prevéy and Seastedt 2014; Post and Knapp 2020), plant interactions (Potts et al. 2006) and community composition (Clary 2008; Gremer et al. 2018). Rain event size (i.e., the total amount of rain that falls during a rain event) has also been found to be an important factor in understanding how rainfall influences plant communities, as biotic responses can exhibit sensitivity to rain event size (i.e., larger events can trigger a greater quantity or magnitude of ecological processes) (Heisler-White et al. 2008; Peng et al. 2013; Post and Knapp 2020; Schwinning and Sala 2004). Soil moisture, conditioned by the timing of rainfall and legacy effects, directly influences the water stress that plants can be exposed to. Given that plants in dryland environments respond primarily to soil moisture rather than rainfall (e.g. Noy-Meir 1973; Hoover et al. 2021), it is critical to consider the spatio-temporal heterogeneity of soil moisture when assessing temporal water availability. However, in previous studies on how water availability affects semi-arid plants, there have been few attempts to merge information from long-term rainfall data and field-based ecological measurements on different spatial and temporal scales.

The same amount of water may not be distributed evenly throughout the system due to dynamic environmental factors, both biotic and abiotic, leading to spatial heterogeneity in soil moisture. Plants modify the movement of water in the environment in a multitude of ways: they can affect percolation depth, by stemflow of intercepted rainfall (Bhark et al. 2003, He et al. 2025) or soil decompaction through root growth (Verdú and García-Fayos 1996), runoff patterns (Lange et al. 2003; Liu et al. 2017, Cerdà et. al. 2021); and influence water movement via hydraulic redistribution and plant absorption of soil water (Bréda et al. 1995; Kizito et al. 2006; McCulley et al. 2004; Neumann & Cardon 2012). Abiotic factors such as soil moisture and seasonality exert a strong influence on how plants impact ecohydrological cycling (Ferrante et al. 2014; Hoover et al. 2021). Additionally, plant-controlled effects on water availability condition soil moisture and how rainfall is utilized and distributed in the system, driving a series of feedback processes (Bennett and Kilronomos 2019; Wang et al. 2017). Therefore, to enhance our understanding of how soil moisture impacts plant water status, it is crucial to consider the impact of vegetation on how water moves through the system over time.

Plants in semi-arid ecosystems are exposed to high degrees of water stress but can have strategies to moderate stress related to water scarcity. Plants can mediate their water use and loss by continually trading off between water loss and carbon gain through control of their stomatal conductance (Brodribb et al. 2009; Farquhar and Sharkey 1982). Species with deep-reaching roots can access soil water which is less susceptible to fluctuations driven by rainfall and evaporation (Kizito et al. 2006; Pierret et al. 2016).Other semi-arid plants also have dimorphic root systems which allow them to alternate between water uptake from the shallow and deep-water sources (Schenk and Jackson 2002; Wang et al. 2017). Additionally, plants can also adjust biomass allocation between above or below ground in response to soil moisture content (Gao et al. 2011). Despite the known adaptations of semi-arid plants to face temporal water variability, it remains less clear how coupled plant and soil water content is over time in this environment.

In this study we provide a long-term context of the rainfall patterns that plants growing in a Mediterranean semi-arid ecosystem experience and assess how water moves through the soil after a rain event, conditioning leaf water status. We hypothesize that (i) the presence of vegetation, by altering the soil through root growth, can buffer water stress by permitting more (and smaller) rain events to percolate into deeper soil and (ii) plant species physiognomy will condition the temporal coupling between plant and soil water content over time, such that species with a greater ability to regulate water content (i.e., larger species or those with more developed root systems) will be less coupled with temporal soil moisture. We combine long-term rainfall data with field-based measurements to track temporal water movement and to assess how coupled leaf water content is with soil moisture. This multi-scale approach can elucidate specific characteristics of rain events necessary to impact soil moisture and, consequently, water availability for plants. Additionally, it can identify which soil layers are more relevant for leaf water uptake and whether species differ in spatial water use patterns, conditioned by differences in plant physiognomy (i.e., plant size, root architecture). The aims of this work are to: (1) understand long-term rainfall patterns and their effect on soil water dynamics in a Mediterranean semi-arid ecosystem, (2) evaluate how vegetation and plant physiognomy influence water percolation and plant-soil water interactions, and (3) identify rain events characteristics and species-specific water uptake patterns related to plant physiognomy.

Materials and methods

Study site

The study was conducted in a gypsum outcrop located in the semi-arid southeast of the Iberian Peninsula (Petrer, Alicante, Spain; 38°29′N, 0°44′E) at an elevation of 568 m. The soil is dominated by gypsum ($CaSO_4·2H_2O$), which imposes strong chemical and physical constraints on plant growth due to its low water retention capacity, high calcium and sulfate content, and poor nutrient availability, particularly nitrogen (N) and phosphorus (P) (Montesinos-Navarro 2023). The plant community consists primarily of chamaephytes and small shrubs, some of them specialists of gypsum soils, such as *Helianthemum squamatum, Teucrium libanitis, Helianthemum syriacum, Thymus vulgaris,* and *Fumana ericoides* (Delalandre and Montesinos-Navarro 2018). These species exhibit similar vegetative stem sizes, ranging from 11.8 ± 0.9 cm in *H. squamatum* to 17.4 ± 0.9 cm in *H. syriacum*, and share comparable growth strategies and life spans (Moreno-Colom and Montesinos-Navarro 2024). Adaptation to gypsum stress varies among species, with some relying on deep water uptake and high transpiration rates to tolerate excess calcium and sulfates, while others optimize water-use efficiency and foliar nutrient accumulation (Sánchez-Martín et al. 2021).

Long-term rainfall patterns

A period of 66 years (1955–2020) of daily rainfall data was obtained from meteorological stations located in Petrer (Alicante), Spain (Fig. 1). These data were compiled by the Agencia Estatal de Meteorología (AEMET) using the homogenization tool Climatol (Guijarro 2018).

In order to characterize more precisely the general rainfall trends across years, only the years whose mean annual rainfall fell within the 95th percentile (62 years out of the 66-year dataset) were

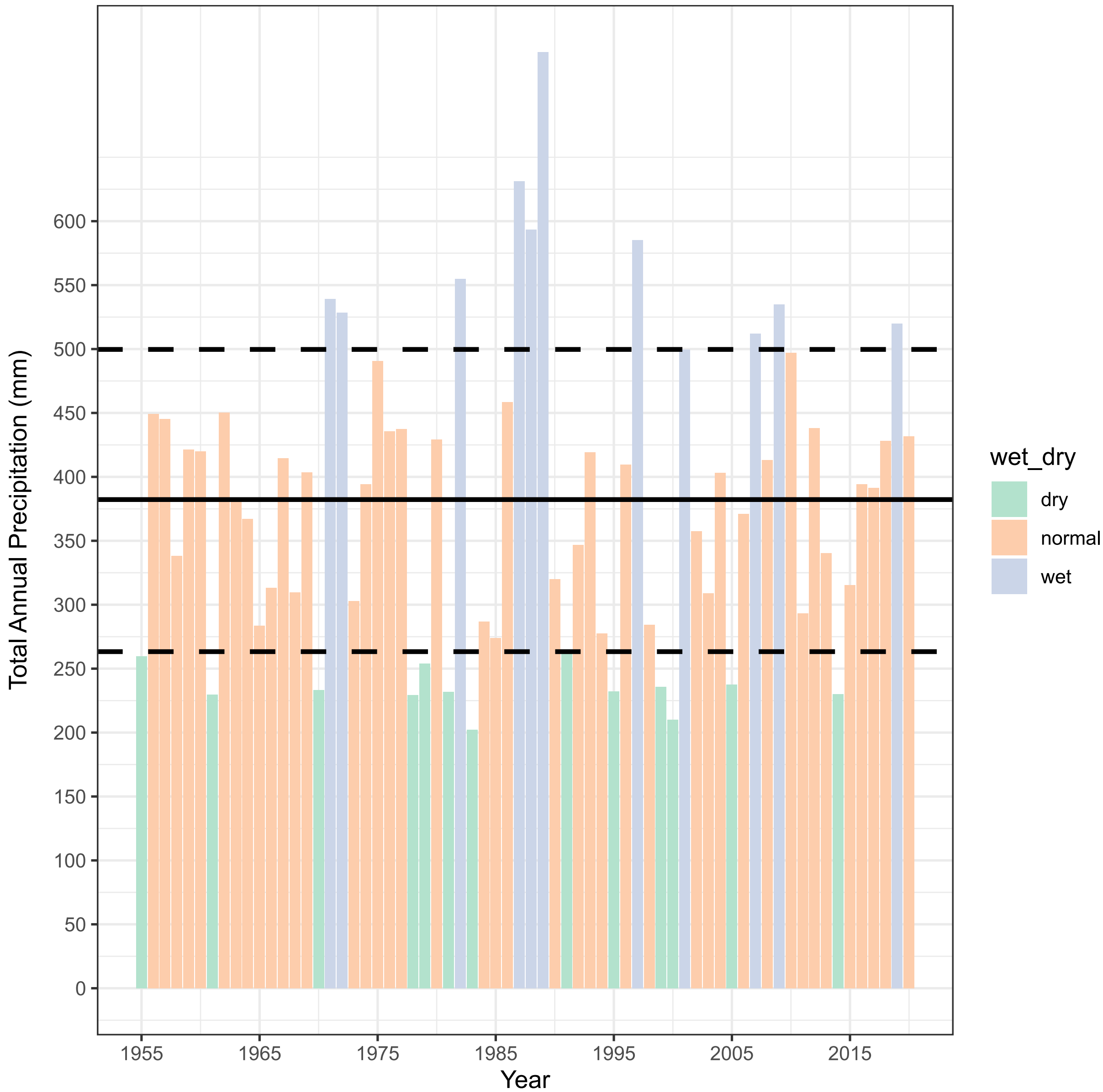

Fig. 1 A bar plot illustrating the total annual rainfall (mm) across all 66 years (1955–2020). Extreme years shown as green for dry years and blue for wet years. The continuous horizontal line represents the average total annual rainfall for all years combined (382.2 mm). The discontinuous horizontal lines represent the upper and lower (i.e., a z-score of ± 1) thresholds defining wet (≥ 499.7 mm) and dry years (≤ 263.3 mm)

considered. Long-term rainfall trends were calculated at different temporal scales: inter-annual, intra-annual (seasonal), and intra-seasonal (rain events). On the inter-annual scale, wet (or dry) years were defined as those with z-scores greater (or lower) than 1 standard deviation from the average annual rainfall across years (hereafter "wet" and "dry"). For seasons, using this same method, the frequency of a dry (or wet) summer, fall, winter, and spring, across years were characterized. For rain events, consecutive rainfall events were grouped together and considered a single rain event. Finally, the size of each rain event (mm), the lag between rain events (days), and the number of total events per season were registered.

Soil moisture measurements

To assess how much rain infiltrates and percolates into the soil layers, the rainfall amount was registered with a pluviometer and tracked its movement through the soil by recording soil moisture over time under vegetation and in the bare ground (Fig. 2). A pluviometer (AO-6465 M-HOBO Davis Rain Gauge with Aero-Cone) was placed directly in the soil in the study site (38.4985539° N, −0.7434957° E) to measure water input via rainfall with a precision of 0.2 mm between August 2020-April 2021. Rainfall registered by the pluviometer within a 6 h window was considered a single rain event. The amount of rainfall (mm), and duration (hours) was calculated for each rain event.

Soil moisture was measured using two sets of 6 sensors (TEROS 12 Soil Moisture and Electrical Conductivity (EC) and Temperature sensor (METER) embedded in the soil which record measures of volumetric soil water content (VWC) across time (every 15 min between May 2020-December 2021; Fig. 3). The two sets of sensors were located 100 m apart within the study site to capture some spatial variability in soil moisture. Within each set, the sensors were placed in pairs inserted in the soil at three microsites within the study site: beneath a vegetation patch, in the bare soil near the vegetation (1 m away), and in the bare soil at a farther distance from the vegetation (20 m; Fig. 2). Two bare soils per set of sensors were used to account for spatial variability. For each pair of sensors, one was placed at 10 cm depth and the other was buried deeper in the subsoil at 40 cm depth. One set of sensors was vandalized in November 2020 and was replaced in February 2021. As a result, data from this period is only available from the remaining set of sensors.

Characterization of rain events

To understand the characteristics of rain events that impact soil moisture, the events detected between August 2020-April 2021 (33 total) that resulted in an increase in shallow soil moisture were assessed. For this analysis, only the set of sensors that have complete data for this period were used. An increase in soil moisture was defined as the difference between the soil moisture content recorded at the nearest date-time preceding a rain event and the peak (i.e. highest) soil moisture level reached after the rain event (and before the next one). To distinguish ecologically relevant rain events from erroneous pluviometer inputs, only rain events which were at least 3 mm and create a $\geq$ 5% (VWC) increase in shallow soil moisture

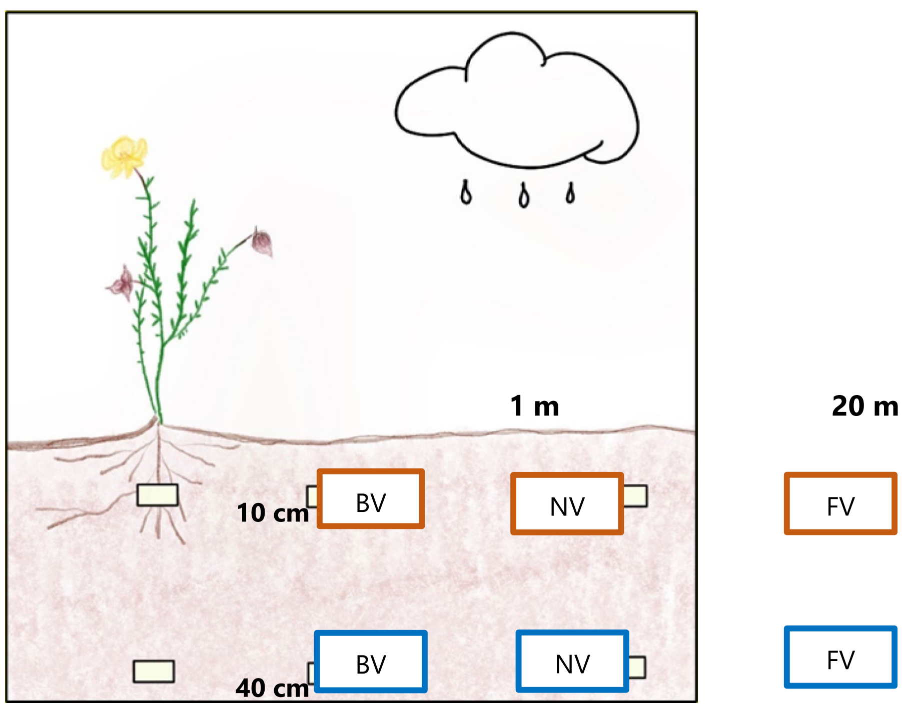

Fig. 2 Conceptual diagram illustrating the placement of the soil data loggers in both shallow (10 cm) and deep (40 cm) soil layers, beneath vegetation (BV), near vegetation (1 m; NV), and further from vegetation (20 m; FV). Shallow soil sensors are marked with red boxes and the deep soil sensors are marked with blue boxes

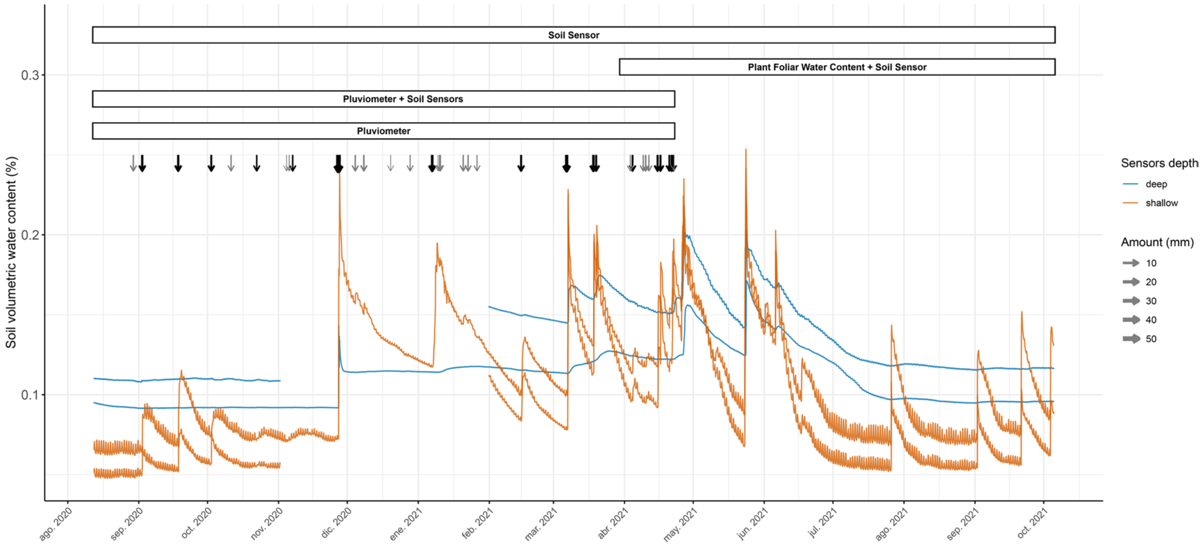

Fig. 3 Average soil water content (VWC (%)) across microsites (beneath vegetation, and near (1 m) and further apart (20 m)) in shallow and deep soil layers (brown and blue lines, respectively) across time measured in two sets of sensors. Soil volumetric water content values represent hourly average for each date shown on x-axis. The upper boxes show the time periods for which data is available for the pluviometer and the soil moisture sensors, and therefore the periods in which correlations could be established between them and with the water content in leaves. The vertical arrows indicate the rainfall events recorded by the pluviometer, with their thickness representing their magnitude (in mm). Grey arrows correspond to events of less than 3 mm

were considered. From this subset of rain events, extreme rain events were defined as those that created an increment in soil moisture with z-scores ≥ 1 SD and the average amount of rainfall (mm) delivered by these extreme events was calculated. Finally, the rain events that increased VWC at both shallow (10 cm) and deeper (40 cm) depths were assessed.

To explore how quickly soil moisture responds to rainfall, the average time that takes two key phases (the “rehydration phase” and the “desiccation phase”) was calculated. Rehydration phase refers to the time it takes for soil to reach its maximum moisture level after a rain event starts and was calculated by measuring the time from the beginning of a rain event (captured by a pluviometer) to when the soil moisture peaks (before the next rain event). Desiccation phase refers to the time it takes for the soil to dry out after reaching its peak moisture level after a rain event and was measured as the time from the peak soil moisture after a rain event to the lowest soil moisture level before the next rain event. In order to avoid potential misleading estimates due to legacy effects between consecutive rain events, only the pairs of rain events that were at least 12 h apart were considered. Finally, to determine how much water was at shallow soil depths (10 cm) between rain events, the average soil moisture between the start of one rain event and the start of the next was calculated, and compared this soil moisture beneath vegetation and in bare soil.

Leaf water content

The temporal changes of foliar water content were characterized in 177 individuals of 9 plant species growing in the field by sampling foliar tissue weekly, between 10:00 and 14:00 h, from April 2021-December 2021, resulting in 25 samples per individual. The study species were *Brachypodium retusum, Matthiola fruticosa, Fumana ericoides, Fumana thymifolia, Helianthemum squamatum, Helianthemum syriacum, Stipa tennacissima, Teucrium libanitis,* and *Thymus moroderi*. For each sample (comprised of ~ 3 leaves per plant), the proportion of water per fresh leaf mass, weighing fresh leaves and dry leaves after 42 h at 60 °C were quantified. The amount of water in the plant (expressed as percent water (%)) was calculated by dividing the water content value by the weight of the fresh foliar tissue. Finally, to compare the range of water content across plant species, the minimum and maximum water content recorded across individuals over time were averaged to calculate the species' range.

Statistical analyses

For all rain events recorded by the field-based pluviometer, two separate linear regression models were used to test for a significant relationship between soil moisture increase for both shallow and deep soil depths (response variable) and rainfall amount and duration (each as a fixed factor). To determine how the presence of vegetation can influence soil moisture dynamics, the measurements of soil data loggers, in shallow and deep soil, at the different microsites (beneath vegetation and bare soil) were used. For each soil depth, the average soil moisture between rain events, and the duration of the rehydration and desiccation phases across microsites were compared through three separate one-way ANOVA analyses, with soil moisture measurements as a response variable and the microsite where the soil data logger were located (i.e. beneath vegetation and bare soil) as a fixed factor.

To explore the degree to which plant and soil water content is correlated over the growing season, the soil moisture content recorded by the two sets of sensors at 12:00 pm on the same day as each foliar sampling was consider. To explore the correlation with the amount of water in shallow and deep soil over time, the Pearson correlation coefficient for each individual at each soil depth in each set of sensors was calculated. As the soil water content (VWC (%)) across microsites (beneath vegetation, and near (1 m) and further apart (20 m)) within each soil depth was highly correlated (R^2 range from 0.80 to 0.96 between sensors buried at 10 cm, and R^2 range from 0.92 to 0.97 for sensors buried at 40 cm), the averages of the three sensors in shallow and deep soil layers respectively were used. Then, the percentage of individuals per species that show a significant correlation was calculated. Finally, differences between species in the strength of their correlations were estimated by using a two-way ANOVA for each soil depth. In these analyses, the correlation coefficient of individuals with a significant correlation ($p < 0.05$) was the response variable and species, the sensor set, or their interaction the independent variables.

Post-hoc contrasts between groups were assessed with 'emmeans' package (Lenth 2023). All statistical analyses were performed using R software version 1.4.1717 (R Development Core Team, 2010).

Results

Long-term rainfall patterns

To contextualize the water availability for plants in the studied system, long-term rainfall data were analyzed to characterize patterns of annual rainfall, seasonal variability, and the characteristics of rain events. While the mean annual rainfall was ~ 366 mm, during dry years, the study site received 36% less rainfall (234.5 ± 4.80 mm) than an average year, and these dry years occurred more frequently (every 4.3 years ± 0.9 SE) than wet years (every 7.4 years ± 0.9 SE) (Table 1).

On a seasonal scale, the system showed a high degree of seasonality. Annual rainfall was mostly concentrated in the spring and fall, representing ~ 31% and ~ 34% of the total annual rainfall, respectively (Table 2). However, the frequency of dry springs was high compared to other seasons (16% of total years; Table 2). Summer was the driest season (47.6 ± 5.01 mm), with less than half of the rainfall compared to spring and fall, making up ~ 13% of the total rainfall for the year, but highly variable across years (CV = 80%; Table 2). Dry summers were infrequent (7% of total years, n = 4), but the reduction in rainfall was severe, with 92% less rainfall compared to an average summer (Table 2).

Finally, regarding the average amount (mm), duration (hours) and lags (days) between single rain

Table 1 Long-term (1952–2020) rainfall trends analyzed on an inter-annual scale based on natural years. Wet (dry) years were defined as those with z-scores greater (lower) than 1 standard deviation from the average annual rainfall across years

Mean Total rainfall ± S.E. (mm)	Total rainfall driest year (mm)	Total rainfall wettest year (mm)	% Wet years	% Dry years	Mean duration of lags between wet years ± S.E. (years)	Mean duration of lags between dry years ± S.E. (years)
365.9 ± 12.41	202.1	555.0	14.5	21.0	7.4 ± 2.2	4.3 ± 0.9

Table 2 Long-term (1952–2020) rainfall trends analyzed on a seasonal scale based on natural years. Rain event characteristics assessed on a seasonal scale: the average total rainfall, record lowest total rainfall observed, record highest total rainfall observed, coefficient of variation for rainfall within each season, proportion of wet seasons across years, proportion of dry seasons across years, the average lag between wet years for each season, and the average lag between dry years for each season

Season	Mean Rainfall ± S.E. (mm)	Record min (mm)	Record Max (mm)	CV (%)	% Wet seasons	% Dry years	Average Lag Wet-Wet ± S.E. (years)	Average Lag Dry-Dry ± S.E. (years)
Spring	113.9 ± 7.16	18.4	253.0	50	21.0	16.1	4.5 ± 1.2	5.1 ± 1.2
Summer	47.6 ± 5.02	2.7	144.8	80	16.1	6.5	7.1 ± 1.5	10.2 ± 5.9
Fall	124.6 ± 9.02	14.7	321.8	60	14.5	9.7	6.5 ± 1.7	9.8 ± 2.4
Winter	79.7 ± 5.74	17.4	226.5	60	14.5	14.5	6.1 ± 1.4	6.5 ± 1.7

events, in spring, rain events were 11.4 ± 0.7 mm and they lasted 2 ± 0.05 days occurring about once every week (7.2 ± 0.3 days) (Table 3). Summer rain events were the smallest of all the seasons with respect to total rainfall per event (8.7 ± 0.7 mm), last the shortest (1.5 ± 0.05 days), and had the longest lags between events, with an average of two weeks with no rain (15.3 ± 0.9 days). However, the longest lag on record was up to 112 days without rain. Fall had the largest rain events (13.4 ± 0.9 mm) which lasted 2 ± 0.05 days and events are 8 ± 0.3 days apart. Finally, winter rain events (9.1 ± 0.7 mm) were slightly larger than summer events (by about 1 mm) and typically lasted 2 ± 0.06 days. The intervals between rain events are 9 ± 0.4 days.

Soil Moisture

Characterization of rain events that impact soil moisture

During the year studied, 36 rain events were recorded, with the majority (21) having very low rainfall amounts (below 3 mm). On average, rain events of 12 mm (11.5 ± 3.2), and lasting around 10 h (10.2 ± 3.5) increased shallow soil moisture by 52% (52.0 ± 15.5%), while these events only increased deep soil moisture by 5% (5.1 ± 14.9%) (Table 4).

Only rain events of at least 4 mm or 6 mm were needed to increase shallow and deep soil moisture respectively, with increases between 5–25% in shallow soil moisture, and 25–75% in deep soil moisture (Table 4). However, to enhance shallow soil moisture more than 75% beneath vegetation, smaller rain events (8 mm) were sufficient, whereas bare soil microsites (both near and far from vegetation) required rain events of at least 23 mm to achieve a similar increase in soil water content. Of the rain events that increased shallow soil moisture (15 total), only three increased deep soil moisture ≥ 5%, and only in the microsites beneath or near (1 m) vegetation. Deep soil moisture content in the bare soil near the vegetation was more sensitive to smaller rain events (6 mm) compared to deep soil moisture beneath vegetation, which required a rain event of at least 23 mm to create the same increase in soil moisture (Table 4).

Table 3 Long-term (1952–2020) rainfall trends analyzed on an intra-seasonal scale (rain events) based on natural years

Season	Mean rainfall per rain event ± S.E	Max rainfall per rain event (mm)	Average duration of rain event (days) ± S.E	Max duration of rain event (days)	Average lag between rain events ± S.E. (days)	Average number of rain events ± S.E
Spring	11.4 ± 0.7	198.0	1.9 ± 0.05	9	7.2 ± 0.3	10.2 ± 0.4
Summer	8.7 ± 0.7	91.6	1.5 ± 0.05	6	15.3 ± 0.9	5.5 ± 0.3
Fall	13.4 ± 0.9	203.0	1.9 ± 0.05	13	7.8 ± 0.3	9.4 ± 0.3
Winter	9.1 ± 0.7	116.0	1.8 ± 0.06	11	8.5 ± 0.4	8.9 ± 0.4

Table 4 Rain event characteristics associated with increased shallow and deep soil moisture. Rain event size (mm) associated with the magnitude of soil moisture increase based on three thresholds of soil moisture increase: 5–25%; 25–75%; and increments greater than 75%. For each range of soil moisture increase, it is shown the minimum and maximum rain event amount (mm) needed to create this increase and the average rain event amount and duration (± SD) to create these increments in soil moisture. Cells with "- -" mean that that were no cases of a rain event increasing soil moisture within the specified ranges in that soil microsite

	Soil microsite	5-25% increase in soil moisture			25-75% increase in soil moisture			≥ 75% increase in soil moisture		
		Min rain event (mm)	Max rain event (mm)	Average rainfall amount (mm) [duration (hours)]	Min rain event (mm)	Max rain event (mm)	Average rainfall amount (mm) [duration (hours)]	Mini rain event (mm)	Max rain event (mm)	Average rainfall amount (mm) [duration (hours)]
Shallow (10 cm)	Beneath vegetation	3.8	8.2	5.6±0.6 [3.7±1.8] (n=6)	5.8	13.6	9.0±1.6 [16.3±9.4] (n=5)	8.6	53.8	23.6±10.6 [12.4±4.9] (n=4)
	Bare soil close to vegetation (1 m)	3.8	8.6	5.7±0.6 [1.7±0.7] (n=7)	6.2	13.6	9.4±1.2 [16.6±7.4] (n=6)	23.2	53.8	38.5±15.2 [20.4±0.6] (n=2)
	Bare soil further from vegetation (20 m)	3.8	8.2	5.8±0.6 [3.8±1.7] (n=6)	6.2	13.6	9.4±1.2 [14.7±7.9] (n=6)	23.2	53.8	38.5±15.2 [20.4±0.6] (n=2)
Deep (40 cm)	Beneath vegetation	23.2	23.2	23.2 [21.1] (n=1)	--	--	--	53.8	53.8	53.8 [19.8] (n=1)
	Bare soil close to vegetation (1 m)	6.2	53.8	27.7±13.9 [15.6±4.8] (n=3)	--	--	--	--	--	--
	Bare soil further from vegetation (20 m)	--	--	--	--	--	--	--	--	--

Rainfall amount (mm) was positively correlated with increases in both shallow and deep soil moisture, showing a stronger correlation with shallow soil moisture ($R^2 = 0.76$, $F_{1,43} = 135.4$, $p < 0.001$ and $R^2 = 0.32$, $F_{1,43} = 20.4$, $p < 0.001$, respectively). The duration (hours) of a rain event was positively correlated with increases in shallow soil moisture ($R^2 = 0.27$, $F_{1,43} = 16.2$, $p < 0.001$) but not with deep soil moisture increases ($R^2 = 0.02$, $F_{1,43} = 0.70$, $p = 0.41$).

Soil rehydration and desiccation phases

Beneath vegetation, shallow average soil water content between rain events was significantly higher compared to the bare soil ($F_{2,42} = 11.5$, $p < 0.001$), but the presence of vegetation (versus bare soil) did not have a significant effect on the duration of the shallow soil rehydration (1–2 days) or desiccation (5–6 days) phases ($F_{2,42} = 1.7$, $p = 0.20$; $F_{2,42} = 0.18$, $p = 0.84$, respectively) (Table 5). In the deep soil, soil water content between rain events was significantly lower in the bare soil further from vegetation ($F_{2,23} = 36.9$, $p < 0.001$) compared to beneath the vegetation and the bare soil nearby, which were more similar ($p = 0.90$). The duration of deep soil rehydration (3–4 days) and desiccation phases (2–4 days) were not significantly different across microsites ($F_{2,42} = 0.18$, $p = 0.84$ and $F_{2,42} = 0.24$, $p = 0.79$, respectively) (Table 5).

Table 5 Rainfall impact on soil moisture at different microsites across time. For each soil microsite, it is shown the average (± SD) increase in soil water content (VWC%) created by rain events, the average soil moisture content between rain events (VWC%), the average number of days it takes for a rain event to create a peak in soil moisture ("rehydration phase") and the average number of days it takes for this peak soil moisture to diminish ("desiccation phase", days)

Soil Microsite		Average increase (%) in VWC created by rain events	Average VWC between rain events	Average time between the start of a rain event and the peak VWC ('rehydration phase', days)	Average time between peak VWC after a rain event and the next lowest soil moisture ('desiccation phase', days)
Shallow (10 cm)	Beneath vegetation	61.6±15.7	0.20±0.01	0.71±0.15	6.3±1.6
	Bare soil close to vegetation (1 m)	44.3±11.80	0.12±0.007	1.4±0.38	5.4±1.57
	Bare soil further from vegetation (20 m)	49.5±19.05	0.12±0.007	1.1±0.28	5.9±1.60
Deep (40 cm)	Beneath vegetation	12.7 ± 22.78	0.13±0.01	3.1±2.13	3.8±3.11
	Bare soil close to vegetation (1 m)	1.9±2.02	0.13±0.005	3.2±2.77	2.9±3.00
	Bare soil further from vegetation (20 m)	0.63±0.57	0.09±0.005	4.0±2.77	2.5±2.77

Leaf water content

Leaf water status and how it is conditioned by temporal variation in soil moisture was analyzed by repeatedly measuring the foliar water content of the same individuals and soil moisture across time. Then the correlation between these parameters for all the species were calculated (Fig. 4). The percentage of

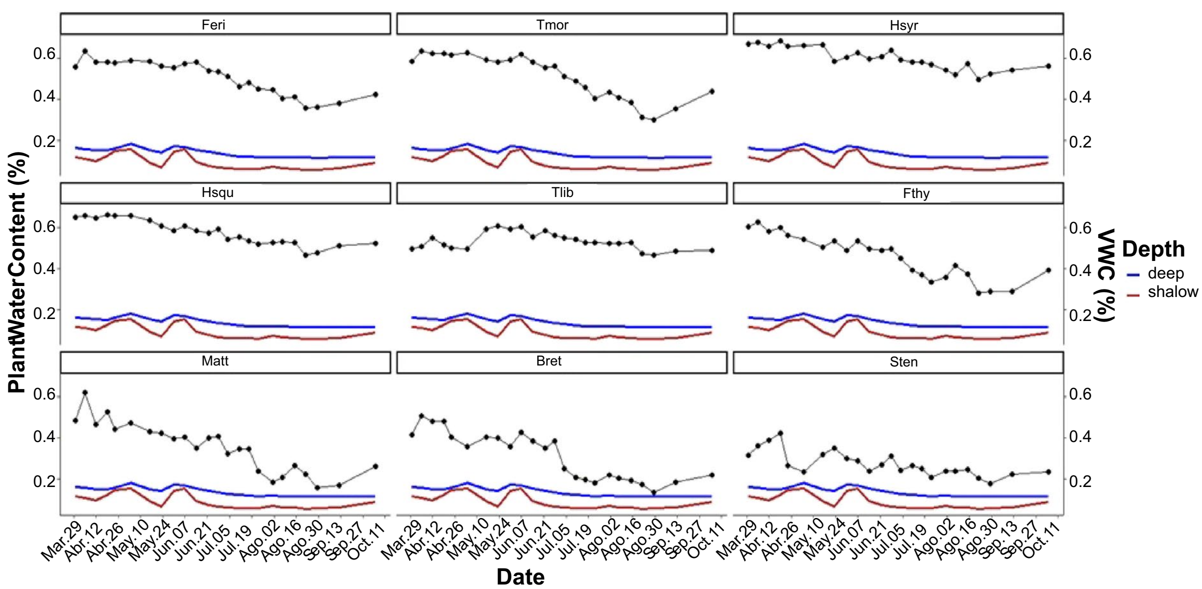

Fig. 4 Temporal trends in plant leaf and soil water content over time. The left y-axis represents leaf water content (%), illustrated by the black points and line. Each point represents the average plant water content of all individuals of each species measured on a given day. Each facet of the plot represents each of the plant species we monitored. The right y-axis represents soil water content (VWC (%)) for shallow (red line) and deep (blue line) soil layers. The soil moisture values are based on soil moisture values at 12:00:00 each for each date the plant foliar samples were taken. Time is shown on the x-axis, in two-week intervals, though note that sampling was done on a weekly basis. Feri: *Fumana ericoides*, Tmor: *Thymus moroderi*. Hsyr: *Helianthemum syriacum*, Hsqu: *Helianthemum squamatum*; Tlib: *Teucrium libanitis*, Fthy: *Fumana thymifolia*, Matt: *Matthiola fruticosa*, Bret: *Brachypodium retusum*, Sten: *Stipa tennacissima*

individuals that showed a correlation between their foliar water content and soil water content was very high and this was consistent across the two sets of sensors used (Table 6). Specifically, the percentage of individuals across species with a significant correlation in the shallow soil was 75% for both set 1 and set 2, while in the deep soil, it was 83% for both set 1 and set 2. Only two species, *T.libanitis* and *S. tenicissima*, showed a percentage below 70% of individuals with a significant correlation (Table 6). Regarding the magnitude of the correlation, there was not a significant effect of the set of sensors in shallow soil: $F_{1,258} = 0.06$, $p = 0.79$ and it was marginally significant in deep soil: $F_{1,290} = 4.12$, $p = 0.04$, but there was not a significant interaction with species in any of them (shallow soil: $F_{8,258} = 0.22$, $p = 0.99$; deep soil: $F_{8,290} = 0.75$, $p = 0.64$). However, there were significant differences among species (shallow soil: $F_{8,258} = 12.93$, $p < 0.001$; deep soil: $F_{8,290} = 29.70$, $p < 0.001$; Fig. 5A-B).

Leaf water content was more correlated with deep than shallow soil moisture (Table 6). For shallow soil moisture, *T.moroderi* and *H.squamatum* showed the highest correlation with soil moisture while *T.libanitis* and *S. tenicissima,* showed the lowest correlation (Fig. 5A; Table 6). In the deep soil, *T.moroderi, F.ericoides* and *H.squamatum* showed a higher correlation with soil moisture compared to *H.syriacum, T.libanitis* and *S. tenicissima,* (Fig. 5B; Table 6).

Discussion

We combine long-term rainfall patterns (66 years) with field-based monitoring of rain events, soil moisture, and leaf water content (1 year) with the objective of better understanding plant water stress by assessing how water moves through the soil following a rain event. Our findings describe the connections

Table 6 Leaf water content variation and its correlation with shallow (10 cm) and deep (40 cm) soil water content. Data are shown for each of the two sets of soil moisture sensors. *Bret: Brachypodium retusum*, *Feri: Fumana ericoides, Fthy: Fumana thymifolia, Hsqu: Helianthemum squamatum; Hsyr: Helianthemum syriacum, matt: Matthiola fruticosa; Sten: Stipa tennacissima, Tlib: Teucrium libanitis; Tmor: Thymus moroderi*

Plant species	Average minimum water content (%)	Average maximum water content (%)	Set of sensors	Average correlation (r) with shallow soil water content	Proportion of individuals with significant correlation with shallow water content	Average correlation (r) with deep soil water content	Proportion of individuals with significant correlation with deep water content
Bret	0.13 ± 0.01	0.58 ± 0.03	S1	0.55 ± 0.06	[9/10]	0.69 ± 0.03	[9/10]
			S2	0.54 ± 0.06	[9/10]	0.67 ± 0.03	[9/10]
Feri	0.32 ± 0.01	0.67 ± 0.01	S1	0.61 ± 0.02	[26/28]	0.77 ± 0.02	[28/28]
			S2	0.62 ± 0.02	[26/28]	0.77 ± 0.02	[28/28]
Fthy	0.23 ± 0.03	0.67 ± 0.03	S1	0.62 ± 0.03	[11/11]	0.73 ± 0.03	[11/11]
			S2	0.64 ± 0.03	[11/11]	0.68 ± 0.03	[11/11]
Hsqu	0.40 ± 0.02	0.70 ± 0.01	S1	0.63 ± 0.04	[28/30]	0.69 ± 0.04	[29/30]
			S2	0.63 ± 0.04	[27/30]	0.61 ± 0.04	[28/30]
Hsyr	0.40 ± 0.04	0.71 ± 0.02	S1	0.53 ± 0.02	[24/27]	0.61 ± 0.04	[24/27]
			S2	0.54 ± 0.02	[24/27]	0.54 ± 0.04	[21/27]
Matt	0.08 ± 0.03	0.65 ± 0.03	S1	0.48 ± 0.06	[7/10]	0.56 ± 0.06	[7/10]
			S2	0.49 ± 0.06	[6/10]	0.53 ± 0.06	[7/10]
Sten	0.15 ± 0.01	0.47 ± 0.03	S1	0.31 ± 0.03	[2/10]	0.41 ± 0.03	[7/10]
			S2	0.35 ± 0.03	[4/10]	0.38 ± 0.06	[6/10]
Tlib	0.42 ± 0.01	0.68 ± 0.01	S1	0.07 ± 0.04	[2/28]	0.25 ± 0.04	[7/28]
			S2	0.04 ± 0.04	[2/28]	0.38 ± 0.04	[13/28]
Tmor	0.27 ± 0.02	0.67 ± 0.01	S1	0.65 ± 0.02	[29/31]	0.78 ± 0.02	[31/31]
			S2	0.65 ± 0.02	[29/31]	0.78 ± 0.02	[31/31]

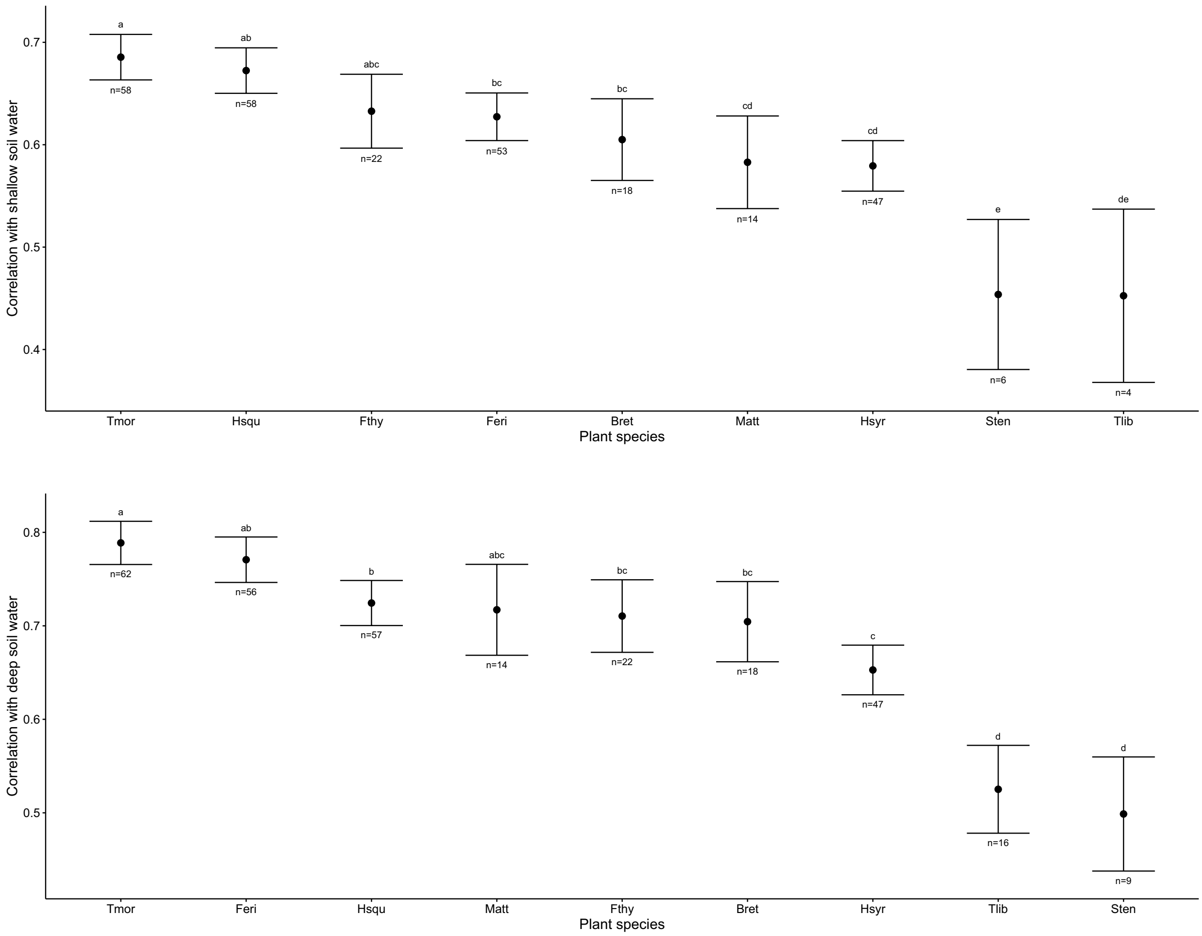

Fig. 5 Estimated marginal means ± 95% CI of the correlation between plant and shallow (top panel) and deep (bottom panel) soil water content extracted from the two-way ANOVA for each soil depth. Plant species are listed as codes along the x-axis Tmor: *Thymus moroderi*; Feri: *Fumana ericoides*, Hsqu: *Helianthemum squamatum*; Fthy: *Fumana thymifolia*; Matt: *Matthiola fruticosa*; Bret: *Brachypodium retusum*; Hsyr: *Helianthemum syriacum*; Tlib: *Teucrium libanitis*; Sten: *Stipa tennacissima*). The letters represent statistical significance based on a post-hoc test ($p < 0.05$)

within the plant-soil continuum, offer insights on rain event characteristics required to increase soil moisture, explain the role vegetation can play in soil water dynamics, and elucidate the coupling between plant and soil water content across time.

Long-term rainfall patterns

We found that dry years were more frequent than wet years across time. On a seasonal scale, while dry summers were the least frequent across years, they presented the most dramatic decrease in rainfall, with 92% less rainfall than average. This highlights the importance of assessing not only the frequency of extreme seasonal patterns but the degree of water deficit they impose. Mediterranean semi-arid summers present multiple abiotic factors (i.e., excessive heat and insolation, reduced water availability) that can exacerbate plant stress (Larcher 2000). Summer drought has been found to reduce photosynthetic rates (Balaguer et al. 2002), increase CO_2 ecosystem losses and reduce plant biomass due to a shorter growing season (Hoover et al. 2021; Scott et al. 2009), and enhance the accumulation of nitrate which can increase N losses through gas emissions, leaching, and run-off (Delgado-Baquerizo et al. 2014). Of all the seasons, spring experienced the highest frequency of dry years, though the decrease in water input was less severe. Nevertheless, even a slightly dry spring could be detrimental to plant functioning in this study site, since plants are more active that time of year (Montesinos-Navarro 2023). Dry spring rainfall can condition summer soil moisture even more than changes in summer rainfall due to a lag effect on soil moisture (Chelli et al. 2016). Additionally, Peng et al. (2013) found that reduced spring rainfall led to reduced summer net primary productivity, even in a summer with increased rainfall.

Regarding rain events within seasons, summer had the shortest and smallest rain events with the longest lags between events. The co-occurrence of these long dry periods along with elevated temperatures can increase the severity of abiotic stress for semi-arid plant communities.

Soil moisture

Most of the rain events did not percolate to enhance deep soil moisture. This corroborates previous studies that found large rain events were needed to enhance deep soil moisture (Heisler-White et al. 2008; Schwinning and Sala 2004). The fact that the extreme rain event reached deep soil layers more effectively under vegetation illustrates the important role of vegetation in recharging deep soil moisture. The channelization of stemflow by roots to deeper soil has been identified as a key mechanism in drylands through which vegetation promotes water percolation in the soil (Martínez-Meza and Whitford 1996; Bhark and Small 2003). The result of this process can have far-reaching ecological impacts. For example, Post and Knapp (2020) found that a single large rain event in a semi-arid ecosystem generated a season-long influence on a range of important ecosystem dynamics (i.e., soil respiration, canopy greenness, above- and below-ground productivity). Additionally, the effect of rain events on soil mediated by vegetation also occur on a species level, as Verdú and García-Fayos (1996), observed elongated soil conditions that favor seed germination beneath *Pistacia lentiscus*, an evergreen Mediterranean shrub, compared to the bare soil, mediated by processes of soil moisture and compaction. Semi-arid plants can respond rapidly to available soil water before it is lost to evaporation or competition (Ryel et al. 2008; Austin et al. 2004; Guo et al. 2016), which can diminish soil water before it can percolate to deeper layers (Jin et al. 2018; Xiang et al. 2020). Thus, the impact of plant water uptake could exert a stronger influence on reducing soil moisture after non-extreme (< 54 mm) rain events, compared to the plant root structure encouraging the downward movement of water. Interestingly, to increase deep soil moisture (+ 5–25%) beneath vegetation, a rain event of at least 23 mm was needed while in the deep bare soil near the vegetation (1 m), a lower rain event threshold (6 mm) resulted in a similar increase. This suggests that soil moisture in closer proximity to the plant root structure may benefit from water can passing more easily through macropores made by plant roots (Wu et al. 2016), while being less affected by the influence of plant water uptake reducing soil water content.

The presence of vegetation significantly enhanced shallow soil moisture between rain events. Although our results do not allow us to quantify the relative contribution of all possible mechanisms through which plants favor water percolation in the soil, we discuss some of them here. For example, the plant canopy shade preventing evaporative water-loss (Domingo et al. 2011); enhancing shallow soil water content via hydraulic lift (Horton and Hart 1998), and additionally the presence of plant organic matter can increase soil water retention and water holding capacity (Boix-Fayos et al. 2001). The positive effect of vegetation on shallow soil water content could be particularly crucial in the summer months when there is an increased threat of water-loss from shallow soil layers due to evaporation (Austin et al. 2004; Guo et al. 2016). Studies of future rainfall scenarios predict a shift towards larger but more infrequent rain events, with longer lags between occurrences (Prein et al. 2017; Papalexiou and Montanari 2019), highlighting the importance of the role of vegetation in potentially buffering water stress imposed by prolonged dry periods and high rainfall variability in semi-arid plant communities (Bayala and Prieto 2020; Prieto et al. 2011).

Leaf water content

For all plant species, foliar water content is more correlated with deep soil water content than shallow across time. While the extensive root systems of semi-arid plants have been associated with the ability of plants to access water from shallow soil layers after small rain events (Sala and Lauenroth 1982), our study supports existing evidence that plants in water-limited ecosystems strongly rely on deep water sources (Barbeta et al 2015; Ding et al 2021). Our results show that water from deeper soil layers is an important source of water for plants given the stronger correlation between plant and deep soil water content.

Different plant species vary in the degree to which their water content is coupled with soil moisture across time. We found that *Teucrium libanitis* and *Stipa tennisisima* showed the weakest correlation with soil water content across time. The flowering period of *T. libanitis* occurs significantly later than other species in the community, and it has been shown that *T. libanitis* reproduction is decoupled from peaks in soil water availability (Montesinos-Navarro 2023). Additionally, since *T. libanitis* is not reproducing earlier in the spring, its foliar content could be less variable during this time, when soil water content is higher and more variable (due to a greater frequency of water input), potentially driving this decoupling.

The canopy structure of *S. tenacissima* can retain large accumulations of dead foliage and litter, which can gather around its base, and has been shown to enhance water storage capacity compared to other plant species (Domingo et al. 1998*). S. tennacissima* can enhance its water status through the acquisition of non-rainfall water sources, such as soil water vapor or dew (Ramírez et al. 2007; Maestre et al. 2003), which could decouple *S. tennacissima* water status and requirements from fluctuations in soil water content. Additionally, *S. tennacissima* can limit water loss by reducing the ratio of exposed leaf area to less mass during dehydration periods by folding its leaves (Pugnaire et al. 1996), which could condition the lower degree of dependence on fluctuations in soil water content.

Conclusions

Our findings contribute to furthering our understanding of water-limited ecosystem functioning by studying how water moves through the system, from rainfall, through the soil, and ultimately in the plants. Although the number of rain events recorded is limited, we show that most rain events increasing shallow soil moisture do not percolate to deeper layers, even in the presence of vegetation. However, vegetation increases shallow soil moisture between rain events. Longer field studies are required to further explore and validate these trends. Plant species physiognomy conditions the temporal coupling between plant and soil water content across time with species with a greater ability to regulate water content being less coupled with temporal soil moisture. This knowledge allows us to more accurately understand how the high variability of rainfall is reflected in soil and plant water content throughout time which is vital to continue research on semi-arid plant communities and ecosystem functioning.

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Author contributions Alicia Montesinos-Navarro collected the field-based data; Sarah Collins and Alicia Montesinos-Navarro conceived the idea for the manuscript; Sarah Collins and Alicia Montesinos-Navarro analyzed the data; Sarah Collins wrote the first draft of the manuscript. All authors contributed critically to drafts of the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available as electronic supplementary material.

Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.

Conflict of interest The authors declare that they have no conflicts of interest related to this research.

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