

Vascular Plants and Biocrusts Modulate How Abiotic Factors Affect Wetting and Drying Events in Drylands

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ABSTRACT

Understanding how organisms control soil water dynamics is a major research goal in dryland ecology. Although previous studies have mostly focused on the role of vascular plants on the hydrological cycle of drylands, recent studies highlight the importance of biological soil crusts formed by lichens, mosses, and cyanobacteria (biocrusts) as a major player in this cycle. We used data from a 6.5-year study to evaluate how multiple abiotic (rainfall characteristics, temperature, and initial soil moisture) and biotic (vascular plants and biocrusts) factors interact to determine wetting and drying processes in a semi-arid grassland from Central Spain. We found that the shrub *Retama sphaerocarpa* and biocrusts with medium cover (25–75%) enhanced water gain and slowed drying compared with bare ground areas (BSCI). Well-developed biocrusts (>75% cover) gained more water, but lost it faster than BSCI microsites. The grass *Stipa tenacissima* reduced water gain due to rainfall interception, but increased soil moisture

retention compared to BSCI microsites. Biotic modulation of water dynamics was the result of different mechanisms acting in tandem and often in opposite directions. For instance, biocrusts promoted an exponential behavior during the first stage of the drying curve, but reduced the importance of soil characteristics that accentuate drying rates. Biocrust-dominated microsites gained a similar amount of water than vascular plants, although they lost it faster than vascular plants during dry periods. Our results emphasize the importance of biocrusts for water dynamics in drylands, and illustrate the potential mechanisms behind their effects. They will help to further advance theoretical and modeling efforts on the hydrology of drylands and their response to ongoing climate change.

Key words: water dynamics; infiltration; *Retama sphaerocarpa*; *Stipa tenacissima*; pulse reserve; semi-arid; soil water.

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INTRODUCTION

Water is the main resource constraining the activity of organisms, and thus of the rate of ecosystem processes depending on them, in arid, semi-arid, and dry-subhumid ecosystems (drylands hereafter; Whitford 2002). The pulsed nature of rainfall events in drylands (Noy-Meir 1973; Reynolds and

others Reynolds and others 2004) determines soil water content, and hence those ecosystem functions that are constrained by it, such as plant productivity (Whitford 2002), nutrient cycling (Austin and others Austin and others 2004), or soil respiration (Huxman and others 2004). Rainfall regimes are likely to change with ongoing climatic change, with scarcer but more intense precipitation events forecast for future climatic scenarios in drylands worldwide (IPCC 2007). Expected changes in rainfall patterns will alter soil moisture dynamics, affecting multiple ecosystem processes in drylands (Laio and others 2001). Thus, understanding the spatio-temporal variability of soil water content is crucial to understand how drylands function, and how they will respond to ongoing global environmental change (Maestre and others 2012).

Drylands are fundamentally heterogeneous ecosystems, and their vegetation is typically arranged in a two-phase mosaic composed by plant-covered patches interspersed in a matrix of open areas devoid of perennial vascular vegetation (see Tongway and others 2001 and references therein). Vegetated and open areas have contrasted hydrological behaviors, with infiltration rates being typically higher beneath plant patches, which also have lower water losses via run-off and evaporation (Yepez and others 2005; Bhark and Small 2003). Plants, however, are not the only organisms modulating the water cycle in drylands. Communities dominated by mosses, lichens, fungi, and cyanobacteria living in the soil surface (biocrusts hereafter) are also known to play key hydrological roles in water-limited environments worldwide (Belnap 2006; Maestre and others 2011). Biocrusts largely affect processes such as infiltration and runoff, although the results obtained so far are contradictory. Although some studies indicate that biocrusts increase infiltration and, consequently, decrease runoff (for example, Greene and Tongway 1989; Eldridge 1993), others have reported the opposite (for example, Eldridge and others 2000) or that biocrusts have no effect on either of them (for example, Eldridge and others 1997). Results are also contradictory regarding whether biocrusts enhance (for example, Belnap and others 2005; Chamizo and others 2013b) or diminish (for example, Fischer and others 2010) evapotranspiration. As a result, some studies have reported higher soil moisture values in biocrust-dominated microsites (Cantón and others 2004; Castillo-Monroy and others 2010), but others have found the opposite (Harper and Marble 1988; Castillo-Monroy and others 2011). The mechanisms

underlying these contrasting results are poorly understood, and the divergences found so far could be promoted by the multiple factors that are simultaneously affected by biocrusts (Chamizo and others 2012b). For example, the differential effects of biocrusts on temperature and soil moisture have been suggested to be opposite mechanisms enhancing and diminishing, respectively, soil evaporation in biocrust-dominated soils (Belnap and others 2005; Chamizo and others 2013a).

Despite being two key biotic components of dryland ecosystems worldwide, few studies so far have evaluated the joint effects of biocrusts and vascular plants on soil moisture dynamics (Castillo-Monroy and others 2010, 2011; Cantón and others 2004; Li and others 2004; Kidron 2009). Moreover, previous studies on this topic have focused either on the examination of total water content (for example, Maestre and others 2003; Castillo-Monroy and others 2011), or on particular processes such as infiltration (for example, Eldridge and others 2010), evaporation (Yepez and others 2005; Domingo and others 2001), or run-off (Puigdefábregas and others 1999; but see Cantón and others 2004; Chamizo and others 2012a), without comprehensively assessing how abiotic and biotic factors simultaneously affect them. Although these studies provide substantial insights regarding water dynamics in drylands, they are often performed across short periods (<2 years, but see Belnap 2002; Li and others 2004; Kidron and Yair 1997; Kidron 2009). Long-term studies including a wide range of natural conditions, such as extremely dry events or unusual rainfall intensities for example, are necessary to advance our understanding of how both plants and biocrusts determine soil water dynamics in drylands, and hence to improve current predictions on their responses to ongoing climate change.

In this paper, we evaluate how multiple abiotic (rainfall intensity and amount, temperature, and initial soil moisture) and biotic (vascular plants and contrasting biocrusts' covers) factors interact to affect soil wetting and drying processes. To do this, we measured soil moisture continuously during 6.5 years at different biocrust microsites with contrasting cover levels and plant-dominated microsites from a semi-arid grassland located in Central Spain. Specifically, we aimed to: (1) assess how biotic and abiotic factors interact to determine drying and wetting events, and (2) evaluate how vascular plants and biocrusts modulate the effects of abiotic factors on soil moisture dynamics.

MATERIALS AND METHODS

Site Description

The study was conducted in the Aranjuez Experimental Station, located in central Spain (40°02'N–3°37'W; 590 m.a.s.l; Figure S1 in the Supplementary Material). The climate is semiarid, with average annual temperature and rainfall of 14.7°C and 349 mm, respectively (1983–1988 and 1997–2012 periods; data from the nearby Aranjuez weather station and an onsite weather station; see also Figure S2 for climatic data during the study period). There is a pronounced dry period from June until September. Soils are derived from gypsum, have pH values of approximately 7, and are classified as Gypsic Leptosols (IUSS Working Group WRB 2006). Soils have carbon and nitrogen contents ranging between 1–3.2% and 0.2–0.4%, respectively (see Castillo-Monroy and others 2010 for details). The vascular vegetation is dominated by *Stipa tenacissima* tussocks (~18% of total cover) with scattered individuals of the shrubs *Retama sphaerocarpa* and *Helianthemum squamatum* (~6% of total cover). The space between vascular plants holds a well-developed biocrust community (~34% of total cover) dominated by lichens such as *Diploschistes diacapsis*, *Squamarina lentigera*, *Fulgensia subbacteata*, *Toninia sedifolia*, and *Psora decipiens* (see Maestre and others 2013 for a full species checklist).

Data Collection

We selected the five most common microsites at the study site (Figure S3): *Stipa* tussocks (*Stipa*), *Retama* shrubs (*Retama*), and open areas devoid of

perennial vegetation with very low (<5%, BScI), medium (25–75%, BScM) and high (>75%, BScH) cover of biocrust-forming lichens. *Stipa* microsites were placed at the north-face of *S. tenacissima* tussocks, within 10 cm of the base of the plant, and are characterized by shaded conditions and a biocrust community dominated by mosses (mainly *Pleurochaete squarrosa* and *Tortula revolvens*). *Retama* microsites occur beneath the canopy of *R. sphaerocarpa* shrubs, and are characterized by moderate shade and litter accumulation. All microsites were selected in flat areas, to reduce runoff influence, and were separated at least 2 m from one another (see Table 1 for further information on their soil characteristics).

We monitored soil moisture at each microsite every 6 h using sensors (EC-5, Decagon Devices Inc., Pullman, USA; error ±3%). Three replicated sensors per microsite (total $n = 15$) were installed according to a stratified random design in November 2006 (Figure S4). Measurements of volumetric water content (VWC) were continuously gathered (every 6 h) from November 2006 to March 2013 (Figure S5). The sensors were introduced vertically in the soil, so that the probe registered soil moisture from 0 to 5 cm depth. The study area also had a meteorological station (Onset, Pocasset, MA, USA) that collects continuous data (every 10 min) on temperature, precipitation, and relative air humidity (error of ±0.2°C; ±0.2 mm and ±3.5%, respectively).

Data Arrangement

We focused our analyses on the wetting and drying events measured during the approximately

Table 1. Main Characteristics of the Different Microsites Sampled (Measured in Autumn 2008)

	BScI	BScM	BScH	St	Rs
pH	7.2 ± 0.06	7.2 ± 0.03	7.4 ± 0.07	7.7 ± 0.05	7.4 ± 0.04
OC (mg g ⁻¹ soil)	9.0 ± 1.1 ^a	12.0 ± 1.3 ^a	14.0 ± 1.1 ^a	15.0 ± 2.1 ^a	32.0 ± 0.9 ^b
TN (mg g ⁻¹ soil)	0.8 ± 0.08 ^a	1.4 ± 0.12 ^b	1.4 ± 0.2 ^b	1.8 ± 0.32 ^a	4.0 ± 0.17 ^b
Silt (%)	38.0 ± 1.1	32.0 ± 2.3	30.0 ± 2.7	29.2 ± 1.0	28.4 ± 0.7
Clay (%)	6.3 ± 0.0	6.3 ± 0.0	6.3 ± 0.0	6.7 ± 0.5	7.9 ± 0.4
Sand (%)	55.7 ± 1.1	61.7 ± 2.3	63.7 ± 2.7	64.1 ± 0.8	63.7 ± 0.6
Slope (°)	1.17 ± 0.44	1.73 ± 0.15	1.33 ± 0.73	1.96 ± 0.57	1.83 ± 0.89
Azimuth (°)	199 ± 24	198 ± 14	202 ± 17	188 ± 11	174 ± 21
RMC (%)	17.1	17.2	14.1	65.6	70.3
RLC (%)	82.9	82.8	85.9	34.4	29.7

Data represents mean ± SE ($n = 5$). Different letters indicate significant differences between microsites after one-way ANOVA (Stuart-Newman-Keuls post hoc test, $P < 0.05$). OC = organic carbon (0–4 cm depth); TN = total nitrogen (0–4 cm depth); RMC (relative cover of mosses); RLC (Relative cover of lichens); *Stipa* = *Stipa tenacissima*; *Retama* = *Retama sphaerocarpa*; BScI = open areas devoid of perennial vegetation with very low (<5%) cover of biocrust-forming lichens; BScM = open areas with medium (25–75%) cover of biocrust-forming lichens; BScH = open areas with high (>75%) cover of biocrust-forming lichens.

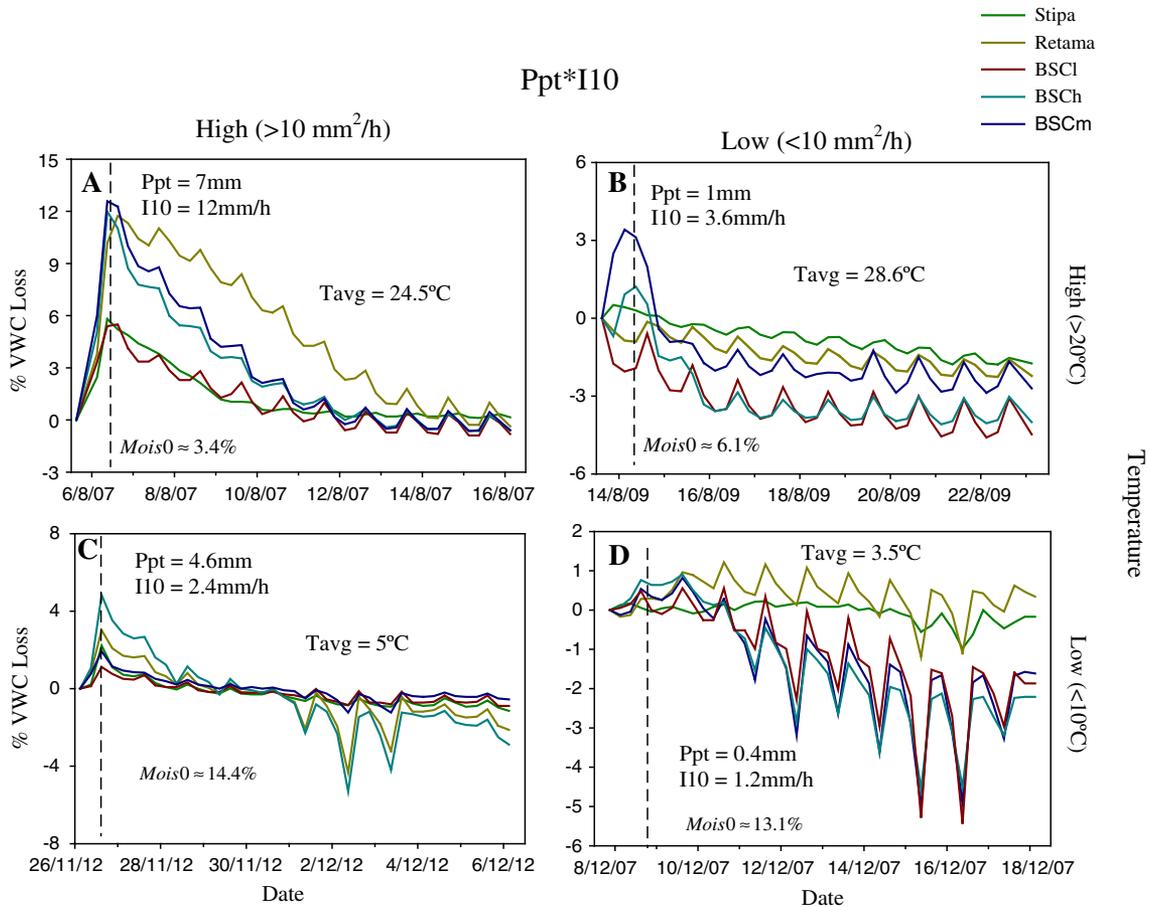


Figure 1. Example curves illustrating soil moisture behavior in the different microsites studied. Curves are relativized to the initial soil moisture content preceding the rainfall. *Dashed line* separates wetting and drying events. Wetting and drying events must be interpreted separately because they are different processes and are influenced by a different set of environmental variables. Events with high (*left panels*) and low (*right panels*) precipitation characteristics, and for high (*upper panels*) and low (*bottom panels*) temperature during the drying events are shown. Precipitation characteristics are represented by the interaction between precipitation amount (Ppt) and intensity (I10). The examples correspond to similar initial soil moistures within each panel, low in the upper panels and high in the bottom panels. Temperature during the drying event (Tavg); precipitation amount and intensity; as well as the average initial moisture of the series (Mois0) are displayed in each panel. Stipa = *Stipa tenacissima*; Retama = *Retama sphaerocarpa*; BScI = open areas devoid of perennial vegetation with very low (<5%) cover of biocrust-forming lichens; BScM = open areas with medium (25–75%) cover of biocrust-forming lichens; BSCh = open areas with high (>75%) cover of biocrust-forming lichens.

6.5 year study period. We organized our data into blocks of 6 h instead of full days to better evaluate the rapid water dynamics that follow small rainfalls, which constitute the bulk of rainfall events in drylands (Laio and others 2001). We selected 6-h periods because they provided the maximum accuracy we could gather with our sensors. This temporal window also allowed us to consider small dry periods that could confound our soil moisture measurements if longer periods were taken. Drying events were defined as periods after a rain pulse, where no further rainfall was registered for at least ten consecutive days (similar

definitions in Cantón and others 2004; Chamizo and others 2013a). Wetting events were defined as any set of consecutive rainy 6 h-periods. We considered events separated by at least 6 h without rain to be different. According to these criteria, we identified 55 and 379 drying and wetting events, respectively, throughout the study period (see Figure 1 for some illustrative examples). It must be noted that our results were qualitatively the same and did not change any of our conclusions when our data were analyzed using longer periods (12 h) between rain events (Figures S6 and S7).

We calculated several covariates for every event considered of paramount importance to determine soil water content. We selected as covariates of drying events the following variables: average temperature during the drying event (a surrogate of energy budget), and soil moisture when the drying event started. For the wetting events, we considered precipitation amount, intensity, and their interaction, and initial soil moisture before the rain pulse (see Appendix S1 for additional information and rationale on the different covariates used and Table S1 for a full description of their role in the analyses). We selected intensity of rainfall as a covariate for the wetting events, together with precipitation amount and their interaction (intensity \times amount). We did so because both are important features of rainfall events that are likely to have opposite effects on soil water (rainfall amount increases water gain while rainfall intensity decreases it). Furthermore, the effect of rainfall intensity and amount on soil moisture may vary according to the microsite considered (Bergkamp 1998; Mayor and others 2009), and addressing it is especially relevant to the objectives of this study. Run-off was not measured, but it is indirectly considered when measuring water gain after rainfall events. We selected the initial water content before the rainfall pulse as covariate for wetting events, and water content after the rain pulse as initial moisture covariate of drying events.

We selected as response variables for our analyses the slope (the b parameter) and shape (unified in a single metric [aR^2], see below) of the drying curve (decrease in soil moisture vs. time), and the increase in soil moisture after a rainfall (hereafter water gain) for drying and wetting events, respectively. The slope of the drying event corresponded to the “ b ” parameter of the linear regressions between time and the decrease in soil moisture after a water pulse ($N = 40$, one sample every 6 h during 10 days of drying process). The shape of the drying curve was formed by two different parameters: the “ a ” parameter given by a quadratic regression between soil moisture and time. We used quadratic regressions for these analyses because they allow us to characterize linear ($a = 0$), exponential ($a > 0$), and inversed exponential ($a < 0$) decays (Figure 2). Because some drying events were poorly fitted, we multiplied the parameter a by the coefficient of determination from the same regression (aR^2 hereafter), and this was our response variable regarding the shape of the drying event for subsequent analyses. This transformation approximated the curvature of “no fitting” cases to 0 and by doing so we defined their behavior as linear. We

did this because the curvature in the poorly-fitting cases is an artifact of the statistical method, and has no biological meaning. We identified four types of general drying curves regardless of the microsite according to aR^2 (Figure 2, see also Figure 1 for particular examples in the water dynamics of microsites): positive in exponential-like behaviors (Figure 2C; BSCm or BSCh in Figure 1A), negative in inversed exponential-like behaviors (Figure 2B; Retama in Figure 1A), close to 0 in those cases of linear behavior (Figure 2A; Stipa in Figure 1B), and forced to close to 0 in the case of poor fitting (Figure 2D, E or F; Retama in Figure 1D). For wetting events, we calculated the differences between the volumetric water content (VWC) before and after the precipitation event as a surrogate of water gain.

Statistical Analyses

We first evaluated how our three response variables (slope [b] and shape [aR^2] of the drying curve, and water gain) varied among the microsites studied. To do this, we conducted an ANOVA using the marginal means of the response variables over microsites. Marginal means are corrected average values of the response variables obtained after controlling by continuous covariates that affect them (Searle and others 1980). For obtaining marginal means, we performed a generalized linear model (GLM) for each response variable using microsite as the main factor (five levels: Stipa, Retama, BSCl, BSCm and BSCh) and different climatic variables as covariates. The covariates were average temperature during the drying event and initial soil moisture (drying events) or precipitation amount, intensity and amount \times intensity and initial soil moisture before the rain pulse (wetting events). We analyzed 165 (three replicates of 55 events) and 1,137 (three replicates of 379 events) drying and wetting events, respectively. It must be noted that for BSCm, 961 instead of 1,137 replicates were used because of sensor malfunction of one of the replicates during part of the study period. By including a large number of wetting/drying events and considering the initial moisture within each wetting/drying event, we effectively removed temporal autocorrelation among the different rainfall events, as suggested by the Durbin–Watson tests performed (Table S2). Thus, wetting/drying events were considered to be independent from each other and are analyzed and interpreted separately throughout this manuscript.

We used structural equation modeling (SEM) to evaluate how plants and biocrusts affect the rela-

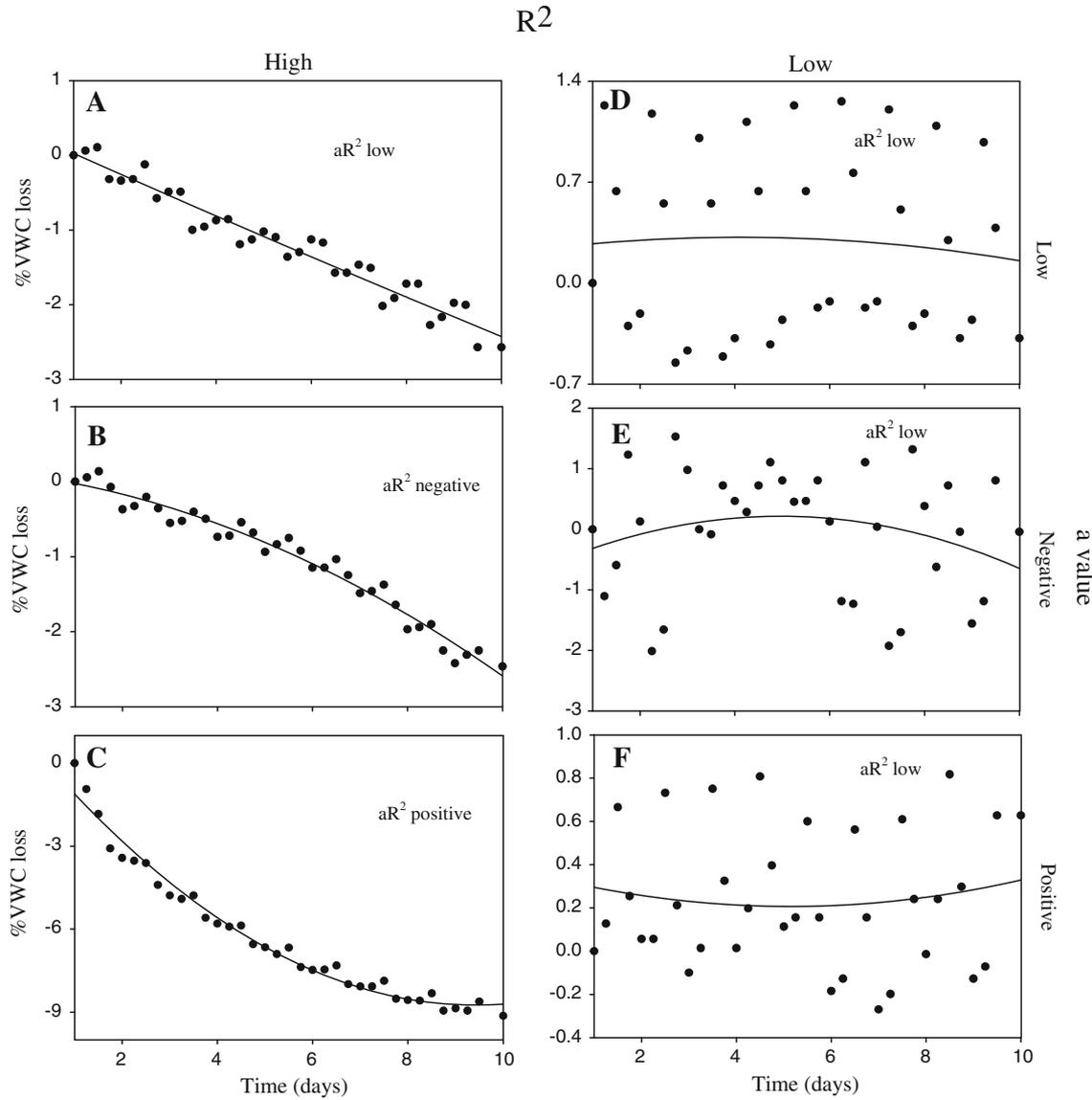


Figure 2. Examples of the different behaviors found when analyzing drying curves. Soil water loss represents the differences between the soil moisture registered at each day and the soil moisture at the beginning of the drying event. **A**, **B** and **C** show examples of linear (low a), inverse-exponential (negative a) and exponential (positive a) behaviors respectively; panels **D** to **F** show different cases of no-fitting behaviors (low R^2 with either positive, low or negative a).

tionships between abiotic factors and our response variables (b and aR^2 in the drying events, and water gain in the wetting events). This analytical approach helps to improve causal inference from observational data without formal experimental manipulation (Grace 2006). SEM assesses multivariate causal relationships by comparing the (co)variance structure of the data with an a priori model that identifies plausible causal relationships among the variables introduced based upon previous knowledge. SEM tests whether the data are satisfactorily fitted to this model, assigning a stan-

dardized weight, or coefficient, to each causal relationship or path (Grace 2006). The path coefficient is directly analogous to a partial correlation coefficient, and is interpreted as the size of an effect that one variable exerts upon another. These are also contrasted analytically by testing the hypothesis that these path coefficients are equal to 0.

We used different SEMs for drying and wetting events (see a priori models in Figure 3), and contain the same covariates considered in the GLMs (see Appendix S1 for rationale). These models were analyzed using Multi-Group SEM, which allows

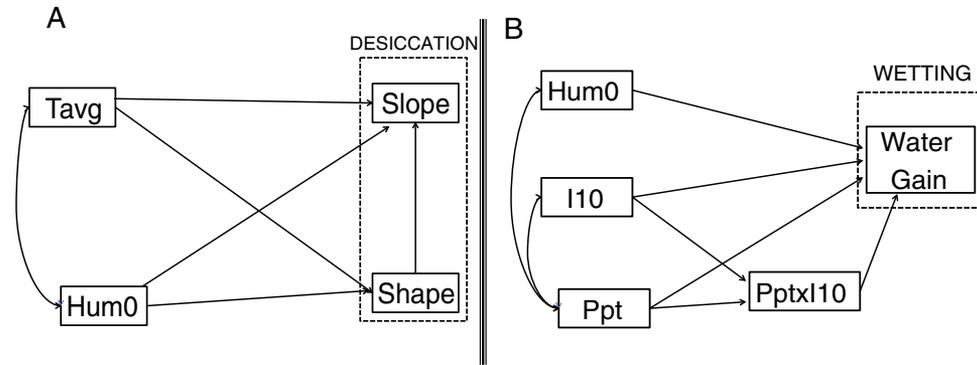


Figure 3. The a priori SEM models employed for drying (**A**) and wetting (**B**) events. The response variables are drawn within a dashed line frame. Hum0 = initial soil moisture (before rainfall for wetting events and after rainfall for drying events); Tavg = average temperature of drying event; Ppt = precipitation amount; I10 = intensity of rainfall; PptxI10 = interaction of precipitation amount and intensity (see Appendix S1 for further explanation about the rationale of these models). SEM model paths and *P* values are displayed in Table S5.

assessing whether or not averages and error of the variables introduced, or the paths among them, differ across groups (the five different microsites considered in our case). The following steps are performed in a Multi-Group SEM (Grace 2006): (1) apply the same model structure separately to the five different microsites studied; (2) obtain the paths of these five models through standard SEM analyses; (3) compare analytically whether the equivalent paths of these models differ among microsites and hence, assess whether the importance of these paths changes depending on the microsite considered. Overall, the models for the wetting events showed a relatively poor but acceptable goodness-of-fit according to RMSEA criteria, excepting the Retama microsite's model (see Table S3 for other metrics). Having a common model structure to all groups is a sine qua non condition for multi-group analysis, and we were more interested in comparing the size of path coefficients among the different groups than testing the overall fitness of a particular model. Thus, we continued with this structure in spite of this relatively poor fitting. For the drying events, the overall fitness of the models could not be tested because they were saturated (that is, all the possible causal relationships were considered in the models). Even when no test of overall fitness is possible, the strength and significance of each path, and the presence of significant differences among groups for a given path, can still be estimated and tested (Grace 2006).

We transformed some variables to meet the assumptions of the statistical analyses conducted. Precipitation amount and intensity were double-squared root-transformed. Linear and quadratic regressions were performed using the polyfit

function in MATLAB version 7.0 (The MathWorks Inc., Natick, Massachusetts). GLMs were performed using STATISTICA v.8 (StatSoft Inc, Tulsa, OK, USA). Multi-group SEMs were performed with AMOS v.18 (SPSS, AMOS Development Corporation, Crawfordville, FL, USA). The data used in our analyses are available from figshare (Berdugo and others 2014).

RESULTS

Soil moisture was higher in Retama and BSCm than in BSCL microsites throughout the study period (see Figures S5B and C). Soil moisture after rainfall events was usually higher in Retama and Stipa than in BSCL microsites (Figures 1B and S5A). BSCm and BSCh microsites had different soil moisture content during the study period, with higher moisture levels registered in BSCm than in BSCL or BSCh microsites (see Figures 1D and S5C).

Biotic Modulation of Soil Moisture Dynamics

We found significant differences among microsites in both the slope ($F = 12.61$, $P < 0.001$) and shape ($F = 17.62$, $P < 0.001$; Table S4) of the drying curve. For both variables [b and aR^2 , respectively], BSCL microsites had the steepest slope and BSCh the highest aR^2 value (Figure 4A, B), which indicates that these microsites were the fastest in losing water. The slope and shape of the drying curve were less steep and more linear in Retama, Stipa, and BSCm microsites than in the BSCL microsites. We also found significant differences among microsites in water gain ($F = 25.54$, $P < 0.001$, Table

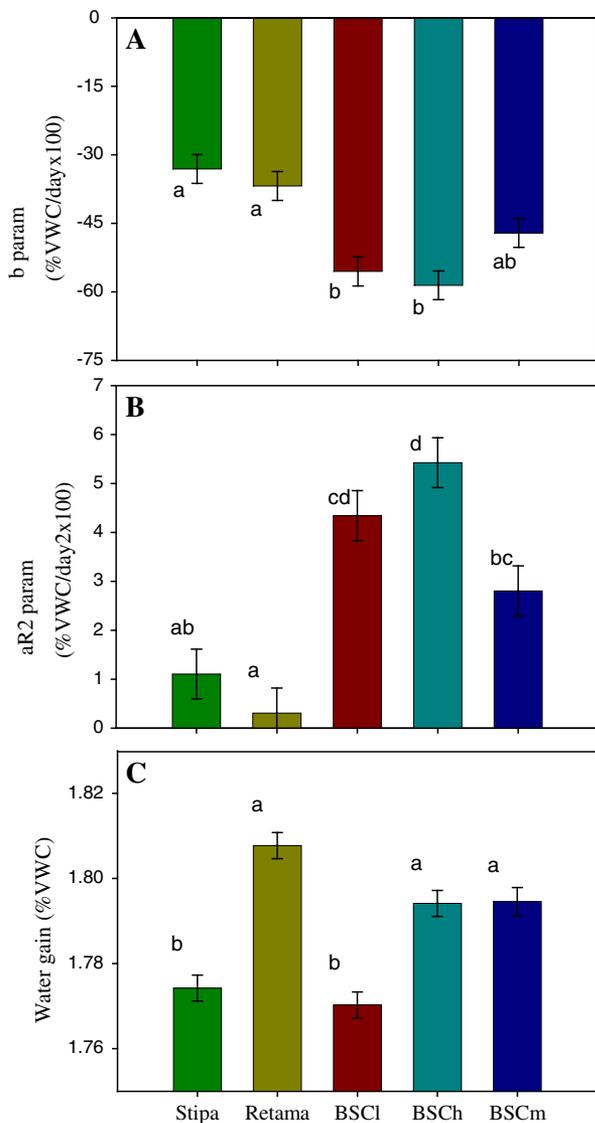


Figure 4. Least squared means (mean \pm SE) of the slope (A) and shape (B) of drying curves, and water gain (C) in the different microsites studied after the general linear models performed. Different letters indicate a significant difference in marginal means at $P < 0.05$ (Scheffé post hoc). Rest of legend as in Figure 1.

S4). This variable was higher in Retama and both BSCm and BSCh than in Stipa or BSCI microsites (Figure 4C).

Biotic and Abiotic Effects on Drying Processes

High temperatures and initial soil moisture values promoted steeper slopes and exponential behaviors (that is, faster water loss) of the drying curve (Figure 5A). The relationship between shape and slope was negative, so that more exponential-like

behaviors (for example, high aR^2) promoted steeper slopes. The influence of soil moisture on the slope of the drying curve was higher in BSCI than in the other microsites. This also promoted linear behaviors in the drying curves of Stipa and Retama microsites versus exponential ones in the curves from the rest of microsites (Figure 5A). Overall, these results indicate a more rapid soil drying in BSCI or BSC-dominated sites than under vascular plants. The path between shape and slope qualitatively changed across microsites; it was not significant under the canopy of vascular plants and in bare ground (BSCI) areas (Table 1), but was significant in both BSCm and BSCh microsites. Contrary to BSCm sites, environmental conditions (temperature and initial moisture) were more important as drivers of the shape of the drying curve in BSCh microsites than in BSCI microsites (Figure 5A).

Biotic and Abiotic Effects on Wetting Events

The amount of rainfall, and amount \times intensity interaction increased water gain, and this effect was more important in Retama, BSCh, and BSCm microsites than in Stipa or BSCI microsites (Figure 5B, Table S6). This suggests higher infiltration in Retama, BSCh, and BSCm microsites than in the rest. Rainfall intensity, however, had a negative, although weak effect on water gain (Figure 5B). The indirect positive influence of rainfall intensity through the interaction term on water gain (Figure 5B) was highest in the Retama microsite, being also significant in Stipa and BSCm microsites. Initial moisture was less influential for water gain under the canopy of vascular plants than in BSCI microsites. The importance of initial soil moisture was highest in biocrust-dominated (BSCh and BSCm) microsites, and the influence of the rainfall amount \times intensity interaction term and the precipitation amount over water gain were also incremented compared to BSCI microsites.

DISCUSSION

Vascular Plants as Drivers of Hydrological Processes

Numerous authors have found vascular vegetation to enhance soil water content in drylands (for example, Cortina and Maestre 2005; D'Odorico and others 2007; Maestre and others 2003). Our results agree with these studies, and support the notion that water retention, rather than an increased

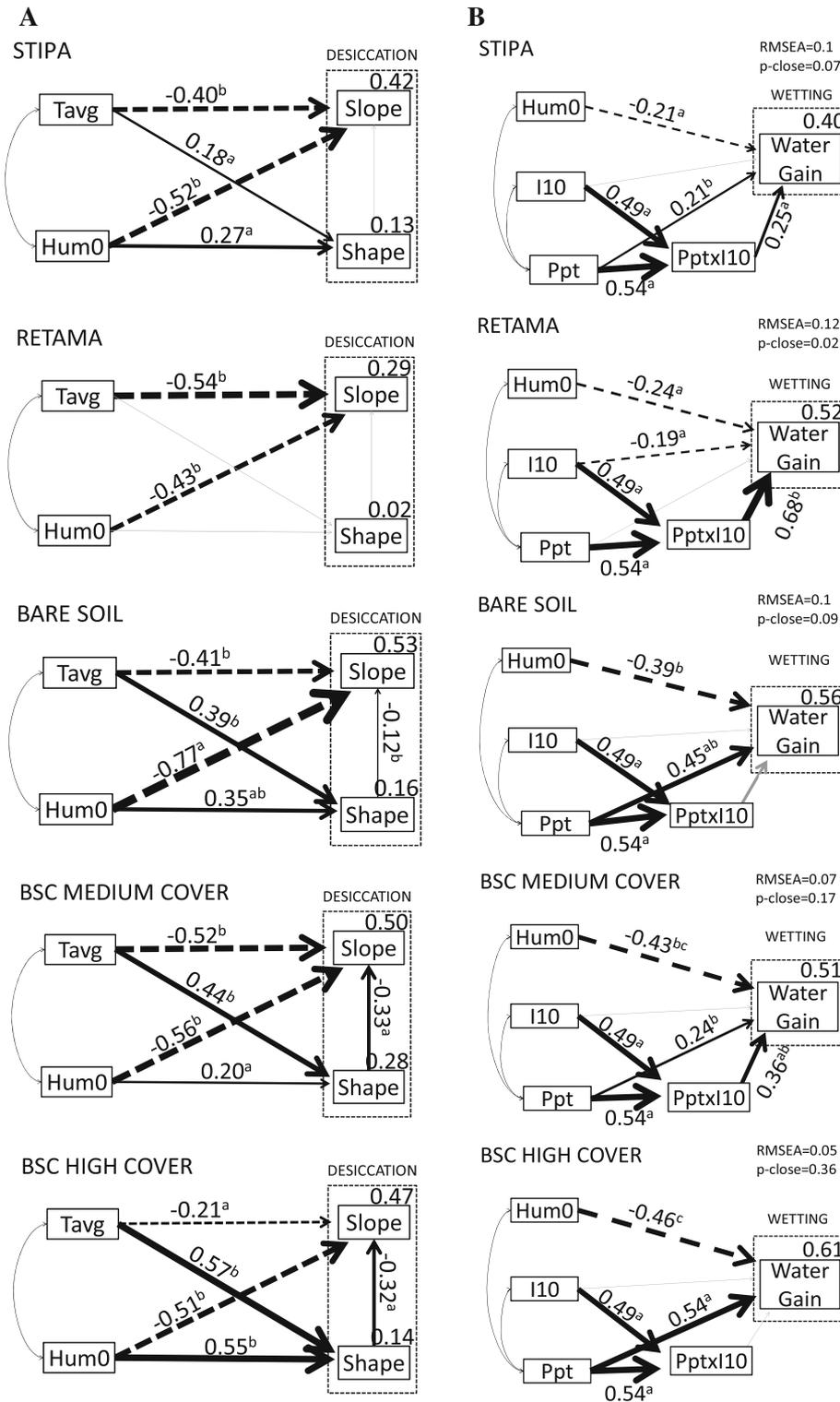


Figure 5. Multi-group SEM results for the soil drying curves (**A**) and wetting events (**B**) in the five microsites studied. Standardized path coefficients are displayed, with the width of each arrow equivalent to the strength of the path. *Dashed lines* indicate negative paths. The total amount of variance (R^2) explained for each endogenous variable (that is, those with *arrows* pointing to them) is given on top right of the variable. *Different letters* for equivalent paths indicate that they differ among the microsites evaluated. For the wetting events Root Mean Square Error of Approximation (RMSEA) and p-close are displayed as goodness-of-fit metrics; these were not calculated for the drying model because the model was saturated. Abbreviations as in Figure 3.

water gain, is the main contributor of the higher soil water contents commonly found under *S. tenacissima* tussocks than in BSCI microsites (see for instance Figures 1B and 4). The improved water status beneath *R. sphaerocarpa* shrubs, however,

was caused by both enhanced water gain and slow drying (Pugnaire and others 1996; Domingo and others 2001; Figure 1A). Both plant species ameliorated organic carbon content regarding bare ground areas (Table 1). This soil amelioration is

likely to increase the ability of soils to retain water, therefore, reducing the negative effect of initial soil moisture on water gain. The dissimilarity in water gain found between *S. tenacissima* and *R. sphaerocarpa* could be caused by differences in the interception of water by their canopies (Thurrow and others 1987; Domingo and others 1998, see Figure 1A). The stronger positive effect of precipitation amount and amount \times intensity on water gain in Retama than in Stipa microsites suggests that more water coming from rainfall water was reaching the soil (Table S6). Stipa and Retama microsites enhanced the role of the interaction between precipitation amount and intensity on water gain, suggesting that they incorporate water from intense rainfall events more effectively than other microsites (Mayor and others 2009; Figure 5B).

In the BSCL microsites, initial moisture was the main driver of the general slope of the drying curve, but temperature was of greater importance for its shape. These results agree with previous studies (Linacre 1973; Reynolds and others 2000) invoking potential evapotranspiration (tightly linked to temperature) as the main driver of the first stage of soil evaporation. In our case, this stage mainly concerns the shape of the drying curve, which is largely responsible for high decays in soil water content during the first days after a rainfall event if soils are close to their water holding capacity (that is, high initial moisture, Breshers and others 1998). Relative water content with respect to the water holding capacity would be the main driver of soil moisture during the second stage (less related to shape, and, hence, more related to slope in our approach) when the supply of water is limited and cannot meet evaporative demand. Accordingly, we found that plants reduce the potential evapotranspiration during the first stage of drying (Figure 5A; see also Figure 1A or B), smoothing the shape of the drying curve towards linearity and uncoupling the control of shape on slope. Plants would also reduce the influence of initial moisture on the slope of the drying curve, suggesting an improvement in the soil ability to retain moisture on the second stage of the drying process beneath their canopies (Duchafour 1995; Pugnaire and others 1996).

We also showed that vascular plants may promote inversed exponential trends in the soil drying rate (see Figure 1A), which enhanced the retention of moisture before the soil starts to dry out. A similar pattern has been previously recorded with grasses under irrigated conditions (Yepez and others 2005). This behavior could be caused by the

combination of transpiration by plants, which can increase relative air humidity, and a reduced soil temperature promoted by canopy shading (Breshers and others 1998; Maestre and others 2003; Michalet 2007). This would retard the first stage of soil drying, and even stop evaporation (Linacre 1973; Reynolds and others 2000). An alternative explanation of this delayed soil drying arises from water inputs not considered in our study, such as hydraulic lift, previously described for *R. sphaerocarpa* (Prieto and others 2010, 2011), or the adsorption of soil water vapor, already shown for *S. tenacissima* (Ramírez and others 2007).

Biocrusts as Drivers of Hydrological Processes

Higher water gains were observed in BSCm and BSCh compared to BSCL microsites (Figures 4 and S10), as have been previously observed in other fine-textured soils elsewhere (Warren 2003). Although water gain was higher in BSCh than in BSCL microsites, we observed similar soil moisture levels in both of them throughout the study period (Figure S5), probably because of the faster water loss found in BSCh compared to BSCL or BSCm microsites. Overall, the high water gain and the slow water loss in BSCm resulted in the highest soil moisture among all the microsites evaluated. These results agree with previous findings from other semiarid areas, where sites with covers of lichen-dominated biocrusts higher than 50% had the maximum values of soil moisture (Lázaro and others 2008; Cantón and others 2004). The slopes and shapes of the drying curves were similar in biocrust-dominated and BSCL microsites, but they were significantly different between BSCm and BSCh microsites (Figures 1A, B and 4). Previous studies have found that the shape of the drying curve in biocrusts follows the same exponential pattern commonly found in BSCL microsites (Cantón and others 2004; Chamizo and others 2013b; Fischer and others 2010). In sharp contrast with the behavior observed in plant microsites, the shape of the curve largely determined the drying process in biocrust-dominated microsites (see Figure 5A). Our results suggest that the first stage of the drying process (*sensu* Linacre 1973), driven by potential evapotranspiration, is more important in biocrust-dominated microsites than in bare ground areas or under the canopy of vascular plants, especially in high temperature drying events (Figure 1A or B). The increased importance of evapotranspiration for biocrust-dominated microsites could be due to their surface roughness, which

increases the area heated (Belnap and others 2005; Chamizo and others 2013b), or by the darkening of the soil surface promoted by some lichens (Harper and Marble 1988; Cantón and others 2004), which increases the heating of the soil surface and augments the evaporative demand from the atmosphere. The latter was confirmed by significantly higher temperatures (1–2°C) in BSCh than in BSCL during the study period (Figure S8). However, our results show also a reduction on the importance of the negative influence of initial moisture on the overall slope of the drying curve (Figure 5A), decreasing the steepness of drying. Other studies have found that the effects of biocrusts on soil water losses depend mainly on the initial soil moisture (Chamizo and others 2013a). Lichen-dominated biocrusts have been found to reduce soil water losses when the soil is wet, a process likely driven by the synthesis of exopolysaccharides and hydrophobic compounds by lichens during active periods (Kidron 1999; Contreras and others 2008; Fischer and others 2010), and to enhance these losses once the soil dries out (Chamizo and others 2013a). Our results on the attenuation of the path from initial moisture to the slope of the drying curve (Figure 5A) agree with this mechanism (see also Figure S9). Such a mechanism would reduce differences in evaporation rates between BSCL and biocrust-dominated microsites, despite the higher importance of the shape of the drying curve in the latter.

We found a trend toward finding more linear drying curves in BSCm than in BSCL microsites, and this trend became significant when comparing BSCh and BSCm microsites (see Figure 4 and examples in Figure 1A or B). This linearization of the drying curve was caused by a weaker effect of initial humidity and temperature on the shape of the drying curve in the BSCm microsites. Path coefficients to the shape of the drying curve were 40/60% (from initial moisture) and 15/39% (from temperature) lower in BSCm than in BSCL/BSCh microsites, respectively (Figure 5A). The significant differences observed in the drying curves of BSCm and BSCh microsites are due to the differential influence of initial moisture, which was higher in the former. According to Linacre (1973), this difference would reduce the importance of the first stage of evaporation, which only occurs when soil is close to saturation. The higher soil water content found in BSCm compared to BSCh microsites could be due to the increased abundance of cyanobacteria in the former microsite (Lázaro and others 2008), which are known to enhance soil porosity (Miralles-Mellado and others 2011). In BSCh, the lichen

component of the biocrusts would be dominant, and the synthesis of hydrophobic compounds (Contreras and others 2008) would diminish soil water content beneath them. Another plausible explanation for our results is that BSCm are likely to be more heterogeneous than BSCh microsites, mixing the rough lichen surface with bare inter-spaces, which can retain fine particles and enhance water capture (Belnap 2006; Verrechia and others 1995).

Overall, our results suggest that two opposite forces are acting in tandem to determine soil water gain in BSC microsites. On the one hand, biocrust-forming lichens strengthen the positive control that both rainfall amount and its interaction with rainfall intensity exert on the soil water gain. For example, for a given rainfall event, more water is gained in lichen-dominated microsites than in bare ground areas (Figure 5B; Table S6; examples in Figure 1A when compared to Figure 1C). This process might be driven by water channeling into the soil, as some authors have already suggested (Rodríguez-Caballero and others 2012; Eldridge and Greene 1994). Furthermore, the positive role of intensity through its interaction with precipitation amount in the BSCm microsite suggests that biocrusts are able to channel water into the soil during more intense rainfall events as vascular plants do. The fact that this control is not observed in BSCh might be explained because the effect of runoff in heavy rains is accentuated in drier soils (Mayor and others 2009), and soils in the BSCh microsite are usually drier than those in the BSCm microsite. Although both BSCh and BSCm microsites showed equal water gain (Figure 4), BSCh microsites lost water faster, which promoted the lower soil water contents observed (Figure S5). Biocrusts also reinforced the negative control of initial moisture on water gain, promoting that, for a given initial moisture, less water is gained in biocrust microsites than in other microsites (Figure 5B). This agrees with previous results obtained in our study area (Eldridge and others 2010). We think that the increased control exerted by initial moisture can be caused by hydrophobic exudates secreted by lichens when the ambient environment is wet. This has been suggested by other authors in previous studies (Contreras and others 2008; Fischer and others 2010; Kidron 1999), and agrees with the results of the analyses performed with a larger hiatus between rain events (Figures S6 and S7). In this case, the difference between BSCL and BSCm or BSCh microsites disappears after removing rainfall events over wet soils. These opposite forces controlling water gain in biocrusts (water

channeling into the soil versus water sealing of wet soils) act together, and result in the overall water gain observed under BSCm and BSCh microsites.

Interestingly, the overall water gain was equivalent to that found under the canopy of both vascular plants (Figure 4C). Considering that biocrusts account for a major proportion of the total soil surface in our study area, our findings indicate that they should be included in future studies that characterize and model soil water dynamics in drylands, which so far only have considered plant and bare ground microsites (Reynolds and others 2000; Breshears and Barnes 1999; Porporato and others 2002). Moreover, according to our findings, biocrusts promote higher soil moisture peaks during rainfall events, but more pronounced drying events. This promotes increased soil water values in biocrust-dominated microsites than in bare soils,

but this water remains in the soil for shorter periods of time.

CONCLUDING REMARKS

Studies addressing the influence of two major biotic components in drylands (plants and biocrusts) on their hydrological dynamics are scarce, have focused on particular processes of the water cycle and are typically conducted over relatively short periods. By using a 6.5 year-database and considering both wetting and drying events and the dominant microsites typically found in drylands, we were able to: (1) assess how biotic and abiotic factors simultaneously affect drying and wetting events, and (2) evaluate how different organisms drive the effects of abiotic factors on soil moisture dynamics. Our results help to enlighten the controversy about

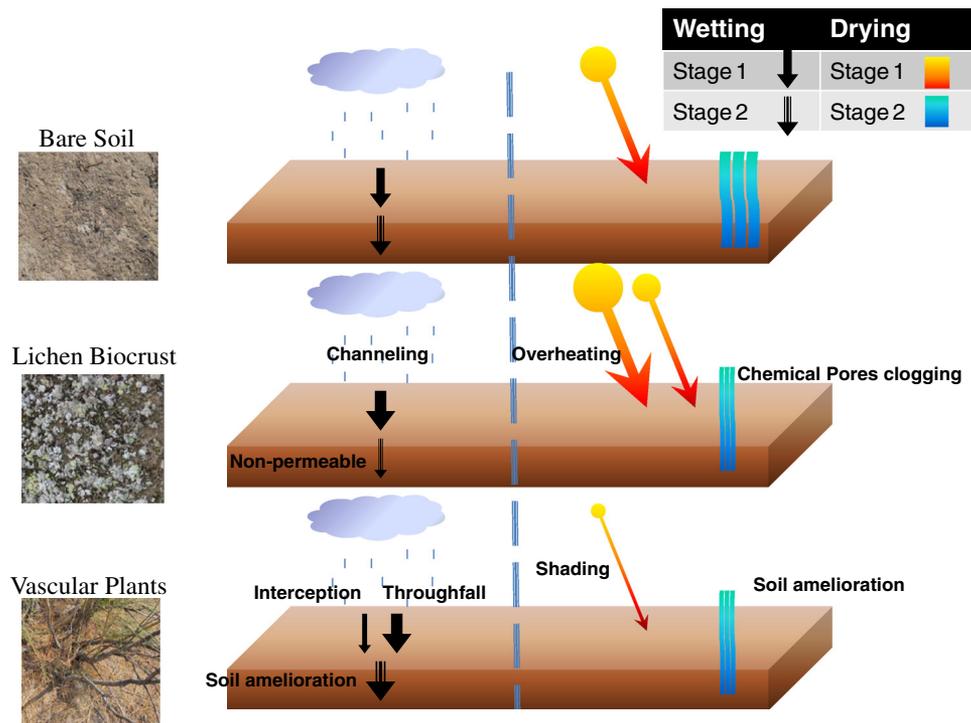


Figure 6. Schematic representation of plausible mechanisms underlying the effects of vascular plants and biocrusts on soil water dynamics. The figure is divided into wetting (*left*) and drying (*right*) events, which are divided into two stages (*Wetting* rainfall reaching the soil surface and subsequent infiltration, *Drying* initial exponential loss of soil moisture and second stage of drying). The size of the symbols in the legend relates to the magnitude of the processes they represent. During wetting events, plants can reduce or not the amount of water reaching the soil depending on their morphological features, but they always increase infiltration into the soil by improving its structure and increasing its water holding capacity. Conversely, biocrusts always enhance the channeling of water to the soil, but avoid high infiltration rates by producing impermeable exudates. During drying, the overheating that takes place in biocrust-dominated microsites contrasts with the shading provided by vascular plants, which affects the exponential behavior of drying. However, this effect is reduced when lichen-dominated biocrusts are not well developed. After the exponential stage of drying, all microsites reduce the slope of this process either by enhancing water holding capacity (plants) or reducing soil permeability to vapor through pore clogging (biocrusts).

the mechanisms driving soil moisture dynamics, especially in biocrust-dominated microsites, where multiple factors, acting jointly and in opposite directions, determine soil moisture dynamics through mechanisms different than those taking place under the canopy of vascular plants.

Overall, our results show that Retama and BSCm microsites gained more water and dried more slowly than BSCl microsites, BSCh gained more water but lost it faster than BSCl microsites, and Stipa microsites gained less water, but lost it more slowly than BSCl microsites. These contrasting hydrological behaviors were explained by the differential influence of abiotic variables (Figure 6). Initial soil moisture was more influential for drying in the BSCl than in the rest of microsites. Although the slope and shape of the drying curves were loosely related under the canopy of *S. tenacissima* and *R. sphaerocarpa*, these two variables were tightly linked in the biocrust-dominated microsites. Regarding wetting events, all microsites excepting Stipa, which showed the opposite behavior, increased the positive influence of precipitation characteristics (amount and amount \times intensity) over water gain. However, whereas plant microsites decreased the negative influence of initial soil moisture on water gain, biocrusts increased this influence.

We also showed how different processes drive both wetting and drying events toward opposite directions in the soils beneath biocrusts. For example, biocrusts decreased the soil's ability to gain water when wet but increased water gain in dry soils. These latter results help to solve the existing controversy regarding biocrusts' modulation of water dynamics by showing how mechanisms acting in opposite directions drive biocrust effects on soil moisture.

Our results also indicate that biocrust-dominated areas (specially BSCm microsites) could be more efficient in retaining water under rainfall scenarios characterized by more intense rainfall events (IPCC 2007), and that these microsites will show accelerated soil drying during dry periods (which are predicted to be warmer and longer). These findings can be used to improve predictions of the effects of future rainfall regimes on the hydrological cycle and functioning of drylands.

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