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Plant nurse effects rely on combined hydrological and ecological components in a semiarid ecosystem

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Abstract. Plant establishment in semiarid ecosystems is affected by the limited spatial and temporal availability of resources and adequate microsites provided by nurse plants. There has been little research on plant establishment in these ecosystems that consider both the ecological roles of different plant types and the abiotic properties of their microsites. Such studies could provide important insights about the functioning of semiarid ecosystems. Here, we investigated the links between the patterns of plant establishment and the hydrological and microsite properties of shrubs and grasses in a semiarid ecosystem northeastern Spain. For ecological experiments, we measured the spatial patterns of the establishment of shrubs and grasses in eight $6 \times 6 \text{ m}^2$ quadrats over 2 years; we also sowed seeds of *Salsola vermiculata* (a dominant shrub) and *Lygeum spartum* (the dominant perennial grass) under adult shrubs (*S. vermiculata*) and grasses (*L. spartum*) and in bare soil and then examined seedling germination, survival, and growth over 4 years. For hydrological experiments, we analyzed soil water content under the two codominant shrubs (*S. vermiculata* and *Artemisia herba-alba*), the dominant perennial grass (*L. spartum*), and in bare soil over 18 months; we also measured water infiltration and solar radiation at the same four microsites to identify the hydrological processes responsible for the observed ecohydrological patterns. The three potential nurse plants greatly improved the hydrological and microsite conditions. They increased soil water content after rainfall relative to bare soil. Moreover, *S. vermiculata* and *L. spartum* slowed the drying process. However, only *S. vermiculata* acted as a nurse plant. It improved plant density, diversity, performance, and survival during the whole study period. *L. spartum* facilitated plant establishment during early stages, but interfered with seedling performance and survival during later stages, probably because of the increasing competition for water with seedlings. *A. herba-alba* did not facilitate plant establishment at any stage, most likely because of water scarcity during prolonged dry periods and its allelopathic effects. We conclude that the ecological role of a plant cannot be directly inferred from its hydrological or microsite properties. Long-term ecohydrological studies are required to understand the role of nurse plants on seedling establishment.

Key words: ecohydrology; facilitation; infiltration; interference; plant establishment; shrub–grass interactions; soil water content.

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INTRODUCTION

Plant establishment (i.e., seedling emergence and survival) is a critical stage for the maintenance of plant diversity and productivity in arid and semiarid ecosystems, and it is mostly conditioned by water availability (Noy-Meir 1973). Most recruitment occurs during exceptionally wet years, and most seedling mortality occurs during drought periods (Beatley 1974). Water availability in these ecosystems has significant spatial variability, because of the redistribution of rainfall through surface runoff and subsurface water flows, and because infiltration varies at different locations (Ludwig et al. 2005). The significant spatial and temporal heterogeneity of water availability in these semiarid ecosystems has led to their classification as “source-sink” systems (Cerdà 1997, Imeson and Prinsen 2004). These ecosystems typically have patches of vegetation within a bare soil matrix, with substantial water runoff from bare soil and water infiltration beneath established plant canopies. Thus, most new seedlings are established near plant canopies. The ecological and hydrological dynamics

of semiarid ecosystems are well known (Ludwig et al. 2005, Bautista et al. 2007, Pueyo et al. 2013). However, few studies have simultaneously examined the spatial dynamics of hydrology and patterns of plant establishment within these plant communities (Drezner 2007). Such studies are clearly necessary because they can provide important information for conservation by identifying environmental factors that determine successful plant establishment in semiarid ecosystems (Gomez-Aparicio et al. 2005).

Soil water content, or soil water storage (*sensu* Reynolds et al. 2004), is the most important hydrological component for plant dynamics. It accounts for spatial and temporal variability due to water gains (by infiltration after rainfall and run-on) and losses (by evaporation, uptake, and transpiration by plants, leakage, and runoff; Fig. 1). Thus, this hydrological component best characterizes the spatiotemporal availability of water for plant establishment and dynamics (Reynolds et al. 2004, Jenerette et al. 2012). However, resources such as nutrients and availability of light can also affect plant establishment, as can non-resource factors related to the

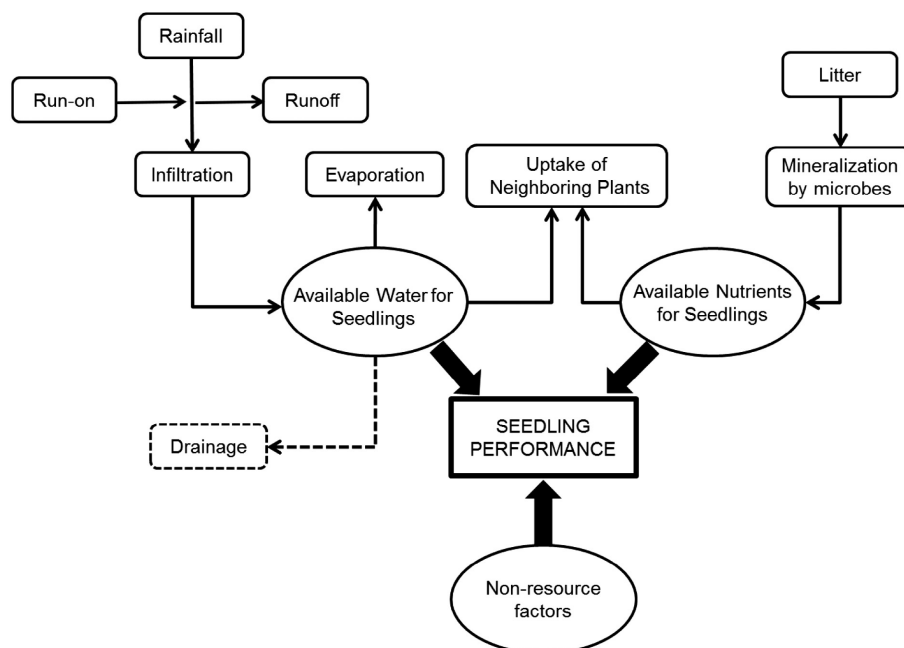


Fig. 1. The most relevant factors related to seedling performance in a semiarid “source-sink” ecosystem. Dotted arrow: Water losses by drainage are negligible in ecosystems where infiltration is low and evaporation is high.

microsite environment (Fig. 1), such as maximum temperatures during the warm season and minimum temperatures during the cold season (Callaway 2007).

Nurse plants can improve the resource and non-resource factors that are important for plant establishment in semiarid environments (Flores and Jurado 2003). While it is clear that non-resource microsite environmental conditions for plant establishment are generally improved by a wide array of nurse plant types, nurse plants can either facilitate or interfere with seedlings for resources (i.e., competing for water) (Michalet 2007, Maestre et al. 2009b). The net outcome of the interaction between a nurse plant and a seedling depends on the morpho-functional traits of both the benefactor and beneficiary species (Gómez-Aparicio 2009, Maestre et al. 2009b). In semiarid plant communities, coexisting shrubs and perennial grasses account for most of the perennial biomass. In these ecosystems, shrubs usually act as nurse plants that improve plant establishment (Gómez Aparicio et al. 2004, Maestre et al. 2009a, Poulos et al. 2014), because they can ameliorate harsh abiotic conditions providing shade and increasing the availability of water and nutrients without exerting strong competition for water (Callaway 2007). This is because they usually have deep roots that do not compete directly for water with established plants in the upper layers of soil (Soriano and Sala 1983). Previous research in experimental plantations indicated that perennial grasses facilitate establishment by providing more favorable abiotic conditions than bare soil. However, in natural ecosystems, there is long-term competition of the roots of grasses with those of annuals and seedlings of woody plants (Aguilera and Lauenroth 1993, Jurena and Archer 2003), because, in contrast to shrubs, their root systems are mostly in the upper layers of soil (Soriano and Sala 1983, Armas and Pugnaire 2011). Thus, the depletion of water from the upper layers of soil (Aguiar et al. 1996) prevents the establishment of shallow-rooted plants (Armas and Pugnaire 2011), such as seedlings and annuals (Jurena and Archer 2003). Still, grass–shrub interactions at establishment stage are not yet well understood (Browning et al. 2014), because there may be species-specific effects (Alados et al. 2006),

and the outcome of the interactions may vary among different environmental conditions (Maestre et al. 2009b). Moreover, previous studies have examined interference and facilitative interactions among shrubs and grasses from an ecological perspective. However, given that water is the main limiting resource in semiarid environments, simultaneous examination of the ecological and hydrological properties of each plant type (together with other microsite properties under plant canopies) could provide important insights into the role of each plant type in community dynamics (Archer et al. 2012) and in the maintenance of plant diversity and productivity.

The general objective of this research was to examine the role of hydrological and microsite properties of different plants on the pattern of plant establishment in multispecies “source-sink” semiarid ecosystems. The specific aim of this study was to assess the different roles of dominant plants (shrubs and grasses) on the dynamics of a semiarid plant community in northeastern Spain, by investigating the effects of these dominant plants on soil moisture, microsite environment (solar radiation and soil nutrient content), and plant establishment at different life-cycle stages.

We hypothesized that (1) shrubs function as nurse plants in the establishment of plants in the studied ecosystem because of their physiognomy and water uptake patterns. Further, we hypothesize that perennial grasses do not function as nurse plants because, even though they improve some microsite conditions related to plant establishment, they compete with seedlings for access to water. (2) We also expected that the different ecological roles of these two plant types would predominantly derive from their differing effects on the spatial–temporal patterns of soil moisture (with higher water availability in the upper layers under shrubs than under perennial grasses; Appendix S1: Fig. S1) and not from differences in nutrient availability or other microsite properties. Finally, we measured cumulative water infiltration, and we related this hydrological property and the microsite environmental properties (solar radiation) to observed soil moisture dynamics, as (3) they are expected to be important driving forces for the observed ecohydrological processes.

METHODS

Study area

The study area is located in “El Planerón,” a nature reserve in the Middle Ebro Valley (NE Spain, 41°22' N 0°37' W) that has a semiarid Mediterranean climate. The average annual temperature is 15.3°C, and the average annual precipitation is 308.6 mm (Cuadrat et al. 2007), most of which occurs in spring and autumn. The soils are predominantly silty clay and have low water infiltration in the bare areas because of high compaction (Pueyo et al. 2009, Moret et al. 2011). The landscape is predominantly flat (elevation 240 m a.s.l) and is composed of a mosaic of dry cereal croplands and uncultivated lands that consist of an open plant community of small shrubs (*Salsola vermiculata* L. and *Artemisia herba-alba* Asso), perennial grasses (*Lygeum spartum* L., *Stipa parviflora* Desf., and *Dactylis glomerata* L.), and numerous forbs and ephemeral plants. The vegetation occurs in patches, and the non-vegetated areas are mostly bare with compacted clay soil and some scattered biological soil crusts (i.e., lichen species *Diploschistes diacapsis*, *Squamarina lentigera*, and *Fulgensia* sp.). Traditional land use in the area was based on a traditional agropastoral system involving extensive sheep (*Rasa aragonesa*) production. Despite the fact that grazing in the study site is restricted since 1990, past land use is still patent on plant communities that are more open and less dominated by perennial grasses than original plant communities (Pueyo 2005).

Patterns of plant establishment

We investigated the spatial pattern of perennial plants establishment (all the dominant shrubs and perennial grasses), by the study of eight 6 × 6 m² quadrats that were established in spring 2011 in a well-preserved plant community that was dominated by two shrubs (*S. vermiculata* and *A. herba-alba*) and three perennial grasses (*L. spartum*, *S. parviflora*, and *D. glomerata*). A quadrat size representative of the plant community was selected taking into account that the average size of adult plants was 0.36 ± 0.02 m² ($n = 246$; Wiegand and Moloney 2014). In each quadrat, we located the central point of the canopy, and the identity, phenology (seedling, juvenile, or adult), and status (alive or dead) of all shrubs and perennial grasses. We recorded plant

survival and new seedling establishment in autumn 2011, spring and autumn 2012, and spring 2013.

Additionally, we assessed the role of shrubs and grasses on overall plant establishment of perennials and annuals in spring 2011. To do so, we identified the number of individuals of each species that occurred under the canopy of adult individuals of *S. vermiculata*, *A. herba-alba*, and *L. spartum* in each quadrat. For these measurements, we randomly selected 15 individuals of *S. vermiculata* and *A. herba-alba* per quadrat; we selected all individuals of adult *L. spartum* in the quadrats (5 individuals in total), because adults of this species were very scarce in the plots. We measured the canopy cover of the adult plants to compute the density and the species richness per surface unit, by measuring the largest radius of the canopy (r_1), and the perpendicular radius (r_2), and estimating the area of canopy cover as: $A = \pi \times r_1 \times r_2$.

In 2007, we began a sowing experiment in the same plant community to quantify the emergence and survival of seeds of the dominant shrub (*S. vermiculata*) and perennial grass (*L. spartum*) at three different interspersed microsites: bare soil (BS), under the canopy of *S. vermiculata* (SA), and under the canopy of *L. spartum* (LY). For each microsite and plant species, 200 seeds were soaked in water for 24 h and planted (200 seeds per microsite × 3 microsites × 2 seed species = 1200 seeds in total) in February 2007. In the BS microsite, seeds were planted in a regular grid, with 20 cm between adjacent seeds. In the SA and LY microsites, seeds were planted around the border of the canopy of randomly selected adults of *S. vermiculata* and *L. spartum* (~25 individuals per species), with 10 cm between adjacent seeds. In all microsites, preexisting seedlings were removed from the vicinity of the planted seeds to prevent interactions. The location of each planted seed was marked with a nail to ensure that germinated seedlings were not confused with naturally occurring seedlings. Germination rates were determined in April 2007. Seedling survival and growth were recorded in May and September 2007, March 2008, June 2010, and June 2011. Growth was estimated by seedling height (*S. vermiculata* and *L. spartum*) and the number of leaves (*S. vermiculata*).

Hydrological and environmental properties of microsites

Concurrent to the plant establishment measurements, we investigated the spatiotemporal patterns of soil water availability for seedlings. We installed 16 soil moisture probes (EC-5 Decagon Soil Moisture Probe; Decagon Devices, Inc., Pullman, Washington, USA; accuracy $\pm 3\%$ for most soil types) in January 2012; these probes were buried obliquely, 10 cm in the soil, to register soil moisture at depths of 5–10 cm. We avoided the top 5 cm of the soil, because the volume of influence (0.3 L) would include air volume. There were four probes per microsite, in the base soil (at least 50 cm away from all perennial plants), and under the canopies of *A. herba-alba*, *S. vermiculata*, and *L. spartum* adults. Plants were randomly selected in the same area as the vegetation experimental plots. Volumetric water content (VWC) was recorded every hour from 19 January 2012 to 5 July 2013. Probability density functions (PDFs) were built with the hourly VWC records from the four microsites to assess soil water content during the study period. Later, to evaluate the mechanism underlying the VWC patterns on the PDFs, wetting and drying processes after rainfall events were studied separately. The comparison of wetting processes among the four microsites allowed the evaluation of the soil water recharge as a net balance between canopy interception of rainfall, water redistribution processes between bare soil and plants, and the infiltration capacity at each microsite. Analysis of the drying process after rainfall allowed the estimation of the width of the window of high water availability at each microsite. The differences in the drying process beneath plants relative to bare soil allowed the assessment of the relevance of water uptake (via transpiration and that required for growth) and evaporation to total soil water loss. To investigate the wetting and drying processes at the four microsites, after each rainfall event larger than 1 L/m^2 , we computed the maximum VWC, the time required to reach that maximum, the minimum VWC, and the time required to reach that minimum. Data from the first 2 months were excluded to assure stable measurements by the probes (Chamizo et al. 2013). Rainfall was obtained from a meteorological station that was about 1500 m from the experimental area.

We defined a rainfall event as the sum of rainfall pulses with interpulses no longer than 12 h; after 12 h without rainfall, the next rainfall event was considered separate. Based on these criteria, we registered 56 rainfall events (and thus, wetting periods) during the study period. In the study of drying processes, we only considered periods of 10 consecutive days in which there was no rainfall as a drying period. There were 18 drying periods during the study period.

To better understand the potential drivers of changes in soil water content, we experimentally measured infiltration rates and solar radiation at the four microsites. With the infiltration measurements, we compared the water cumulative infiltration, I (mm), at different times at each microsite without considering the magnitude of the input water. Thus, this measurement excluded factors such as canopy interception and lateral water redistribution. Infiltration was experimentally measured in the field with a tension infiltrometer. A total of 11, 9, 7, and 8 infiltration measurements were performed at random sites on bare soil and adult individuals of *S. vermiculata*, *A. herba-alba*, and *L. spartum*, respectively. The cumulative infiltration curves on *S. vermiculata*, *A. herba-alba*, and bare soil were measured with a hat infiltrometer (HI) (Moret Fernandez et al. 2015), a modification of the tension infiltrometer that allows measurement of the transient infiltration curve on the soil surface with undisturbed plants. The high porosity between the surface stems of *L. spartum* prevented the formation of the vacuum in the HI hat, making these measurements impossible; thus, on this microsite, a conventional disk infiltrometer (Perroux and White 1988) with a base radius of 50 mm was employed. Measurements with these different tension infiltrometers are similar (Moret Fernandez et al. 2015). To set up the disk infiltrometer, the *L. spartum* stalks were cut at ground level and a circular thin layer of commercial sand (80–160 μm diameter), with the same radius as the disk base, was layered on the soil surface. Only infiltration measurements at soil saturation conditions (which last up to 15 min) were conducted. Flow readings were automatically recorded every 5 s based on the decline of water level in the water supply reservoir. Water infiltration values were measured at 0.5, 1, 5, and 10 min.

Solar radiation was assumed to be directly correlated to potential water evaporation (Ritchie 1972, Franco and Nobel 1989, Valiente-Banuet and Ezcurra 1991), and thus, in order to estimate the relevance of potential water evaporation at the four microsites, solar radiation was measured on the bare soil, and under the canopies of adults of *A. herba-alba*, *S. vermiculata*, and *L. spartum*. Photosynthetic photon flux (PPF, solar radiation from 400 to 700 nm) was measured 10 times in bare areas and under the canopies of adults of *A. herba-alba*, *S. vermiculata*, and *L. spartum* adult plants, on a cloudy day (25 April 2012) and a sunny day (25 May 2012) using a portable Apogee MQ-200 quantum meter.

Soil temperature was monitored at the four microsites as a complementary measurement to better understand the potential drivers of changes in soil water content (see Appendix S1 for details on complementary analyses).

Finally, soil chemical analyses were performed to control for the effects of differences in soil nutrient content among the microsites. We collected 16 soil samples from the upper 15 cm of soil from the four microsites in October 2013 (four samples per microsite; samples collected in the north aspect of the canopy). Soil samples were dried in the laboratory and passed through a 2-mm sieve. The soil pH in water following a dilution of 1:2.5, electrical conductivity of the saturated soil paste extract, organic matter content (Heanes 1984), and total carbon and nitrogen (Vario MAX CN elemental analyzer) were measured for all samples.

Statistical analysis

The spatial patterns of adults, juveniles, and seedlings of *S. vermiculata*, *A. herba-alba*, and perennial grasses were investigated with univariate and bivariate pair-correlation functions (Stoyan and Stoyan 1994, Wiegand and Moloney 2014). The different species of perennial grasses (*L. spartum*, *S. parviflora*, and *D. glomerata*) were analyzed together because the small number of individuals did not allow analysis of individual species. The pair-correlation function is a second-order analysis similar to Ripley's K, but is a non-cumulative statistic; in other words, the pair-correlation function does not integrate smaller-scale effects into larger scales (Wiegand and Moloney 2004). We followed the procedure

of Wiegand and Moloney (2004) for computation of pair-correlation functions correcting for edge effects. A significant departure of an observed pattern from the null random model was tested by comparison with the 5th largest and smallest simulation envelopes using 99 Monte Carlo simulations. The significance of the aggregation or segregation in a univariate patterns (i.e., univariate spatial patterns of adults, juveniles, and seedlings of each plant type) was assessed with a heterogeneous Poisson null model with a kernel width of 20 cm (Wiegand and Moloney 2004). The spatial association between adults, juveniles, and seedlings (i.e., bivariate patterns between adults of each plant type and juveniles and seedlings of each plant type: nine adult vs. juvenile patterns and nine adult vs. seedling patterns) was tested for independence with a toroidal shift null model (Wiegand and Moloney 2004). To facilitate interpretation and increase test power, the pair-correlation functions of the eight quadrats were combined into average functions as described by Wiegand and Moloney (2014).

Differences in the density of species and individuals underneath the three nurse species (*A. herba-alba*, *S. vermiculata*, and *L. spartum*) were analyzed with the Kruskal–Wallis test (ANOVA was not used due to the large difference in sample size between microsites). The Wilcoxon test with Holm correction was used for pairwise post hoc comparisons between the three microsites.

For the sowing experiment, differences in seedling emergence at the microsites were tested in April 2007 with a chi-square test. Differences in seedling survival between microsites were tested after 1 month (May 2007), 5 months (September 2007), 11 months (March 2008), 38 months (June 2010), and 50 months (June 2011) with chi-square tests. Fisher's exact test was used when there were fewer than five seedlings at a microsite. The Marascuilo procedure (Marascuilo 1966) was employed to simultaneously compare seedling emergence and survival at all pairs of microsites (SA vs. LY, SA vs. BS, and LY vs. BS microsites) on each census date. To investigate seedling growth at the three microsites, we performed a generalized linear mixed model (GLMM) for longitudinal data with repeated measures: height and number of leaves of *S. vermiculata* seedlings (Height_Salsola and Leaves_Salsola) and height of *L. spartum* seedlings (Height_Lygeum) were

the response variables. The explanatory variables in the three models were the sowing microsite and the number of months after seedling emergence. The identity of each individual seedling measured over time was included in the model as a random factor. The best final model for each response variable was selected by comparing Akaike's information criterion (AIC) values with ANOVA, following the procedure described by Zuur et al. (2009).

Soil wetting and drying processes after rainfall events were analyzed with GLMMs. Responses variables in the wetting-process analysis were (1) the difference between the VWC before a rainfall event and the maximum VWC after rainfall (Increment_VWC) and (2) the rate of the wetting process (Wetting_slope). This was calculated by dividing Increment_VWC by the time required to reach maximum VWC. The main explanatory variable in the wetting-process analysis was the microsite (nurse species vs. bare soil, four levels). The covariables were the total amount of rainfall in the event (Amount_rainfall) and the soil water content before the rainfall event (VWC_before). We also included the effect of the interaction between the microsite and the covariables. The response variable in the drying process was the VWC value after 10 d without rainfall (VWC_10days). The main explanatory variable in the drying-process analysis was the microsite (four levels). We also included the mean temperature during the 10 d of drying (Mean_temp, obtained from the meteorological station) and the initial VWC after rainfall (Initial_VWC) as covariables, and the interactions between microsites and covariables. We included a random factor in all of the models: each set of four probes (one per microsite) connected to the same data logger (Box) that was closer between them than with the rest of the probes. Temporal autocorrelation was controlled by incorporating initial soil water content and temperature as covariables (Berdugo et al. 2014). To obtain the most suitable and parsimonious models for the wetting and the drying processes, we followed the procedure described by Zuur et al. (2009).

To detect differences among microsites in water infiltration at different times, photosynthetic photon flux, and soil chemical properties, a one-way ANOVA was employed, with a logarithmic or arcsine transform when necessary to assure

normality. Holm post hoc tests were employed to detect differences between pairs of microsites.

Point pattern analysis was performed with Programita software (Wiegand and Moloney 2004, 2014). All other statistical analysis was performed with R (R Core Team 2014); for GLMM, we employed the nlme R-package (Pinheiro et al. 2014).

A summary of the research questions and the different methodological approaches employed is provided as Appendix S1: Table S1.

RESULTS

Patterns of plant establishment

Univariate point pattern analysis showed that *Artemisia herba-alba* adults and juveniles had segregated patterns, and seedlings of this species had small-scale aggregation. *Salsola vermiculata* adults had a segregated pattern at a small scale (<5 m), but juveniles and seedlings were aggregated at a small scale (Table 1; Appendix S1: Fig. S2). Perennial grass adults and juveniles were segregated, but the pattern for seedlings appeared random (Table 1; Appendix S1: Fig. S2). Thus, there was a tendency for aggregation in early life stages and for segregation at adult stages for all studied plants, although *A. herba-alba* and perennial grasses had segregation already at the juvenile stages. Bivariate point pattern analysis showed that *S. vermiculata* juveniles and seedlings and *A. herba-alba* juveniles were spatially segregated from *A. herba-alba* adults, but that perennial grass adults, juveniles, and seedlings (marginally) were spatially associated with *A. herba-alba* adults. Perennial grass adults, juveniles, and seedlings, and *S. vermiculata* juveniles were spatially associated with *S. vermiculata* adults. Only *A. herba-alba* juveniles were negatively associated with *S. vermiculata* adults (Table 1; Appendix S1: Fig. S2). *S. vermiculata* adults, *A. herba-alba* adults, and perennial grass juveniles were spatially associated with perennial grass adults, but *S. vermiculata* juveniles were spatially segregated from them (Table 1; Appendix S1: Fig. S2). Consideration of all juveniles and seedlings together indicated negative associations with *A. herba-alba* adults and positive associations with *S. vermiculata* adults (Table 1, columns Juveniles ALL, Seedlings ALL, and Juveniles and Seedlings ALL; Appendix S1: Fig. S2).

Table 1. Univariate and bivariate spatial patterns between adults, juveniles, and seedlings of *Artemisia herba-alba* (A), *Salsola vermiculata* (S), and perennial grasses (PG) based on the pair-correlation function.

	Adults A	Adults S	Adults PG	Juv. A	Juv. S	Juv. PG	Juv. All	
Adults A	–	0	+	–	–	+	–	
Adults S		–	+	–	+	+	+	
Adults PG			–	0(+)	–	+	0	
Juv. A				–				
Juv. S					+			
Juv. PG						–		
Seedl. A								
Seedl. S								
Seedl. PG								
Juv. and Seedl. A								
Juv. and Seedl. S								
Juv. and Seedl. PG								
	Seedl. A	Seedl. S	Seedl. PG	Seedl. All	Juv. and Seedl. A	Juv. and Seedl. S	Juv. and Seedl. PG	Juv. and Seedl. All
Adults A	–	0	0 (+)	0(–)	–	–	+	–
Adults S	0	0	+	+	0(–)	+	+	+
Adults PG	0(+)	0	0(–)	0	+	0(–)	0(–)	0
Juv. A								
Juv. S								
Juv. PG								
Seedl. A	+							
Seedl. S		+						
Seedl. PG			0					
Juv. and Seedl. A				0				
Juv. and Seedl. S						+		
Juv. and Seedl. PG						0		

Notes: –, Significant small-scale segregation (<1 m); +, significant small-scale aggregation; 0, random small-scale pattern; 0(–) and 0(+), marginally significant small-scale segregation and aggregation. The univariate patterns were compared with a heterogeneous Poisson null model (intensity function estimated with a kernel width of 20 cm). The bivariate patterns were tested for independence with a toroidal shift null model. Appendix S1: Fig. S2 shows the plots for each analysis. Empty cells indicate associations that were not evaluated. Average number of points per quadrat was 625 ± 90 ($n = 8$).

The nurse plants had significant differences in the density of plant species beneath their canopies (Kruskal–Wallis $\chi^2 = 143.36$, $P < 0.001$). A post hoc test showed that *S. vermiculata* had significantly more species per m^2 than *A. herba-alba* and *L. spartum*. *A. herba-alba* also had significantly more species per m^2 than *L. spartum*. The density of individual plants was significantly dependent upon the nurse plant (Kruskal–Wallis $\chi^2 = 127.948$, $P < 0.001$). A post hoc test showed that *S. vermiculata* had significantly more plants per m^2 than *A. herba-alba* and *L. spartum*.

The results of the sowing experiment indicated no significant differences between microsites in *S. vermiculata* seedling emergence in April 2007 ($\chi^2 = 4.73$, $P = 0.094$; Fig. 2a), but significant differences in *L. spartum* seedling emergence ($\chi^2 = 20.95$, $P < 0.001$). The Marascuilo

procedure showed that *L. spartum* seedling emergence was significantly greater at the BS microsite than at the SA and LY microsites (Fig. 2b). Analysis of seedling survival indicated no significant differences in *S. vermiculata* in May 2007 ($\chi^2 = 1.91$, $P = 0.369$), September 2007 ($\chi^2 = 4.54$, $P = 0.103$), March 2008 ($\chi^2 = 0.15$, $P = 0.925$), and June 2010 ($\chi^2 = 1.78$, $P = 0.411$), although there were significant differences in June 2011 (Fisher's exact test, $P = 0.004$), presumably due to new germination at SA microsite (Fig. 2a). There were marginally significant differences in *L. spartum* seedling survival in May 2007 ($\chi^2 = 5.70$, $P = 0.058$) and significant differences in September 2007 ($\chi^2 = 23.761$, $P < 0.001$), March 2008 ($\chi^2 = 16.2$, $P < 0.001$), June 2010 ($\chi^2 = 63.402$, $P < 0.001$), and June 2011 ($\chi^2 = 40.495$, $P < 0.001$; Fig. 2b). The Marascuilo

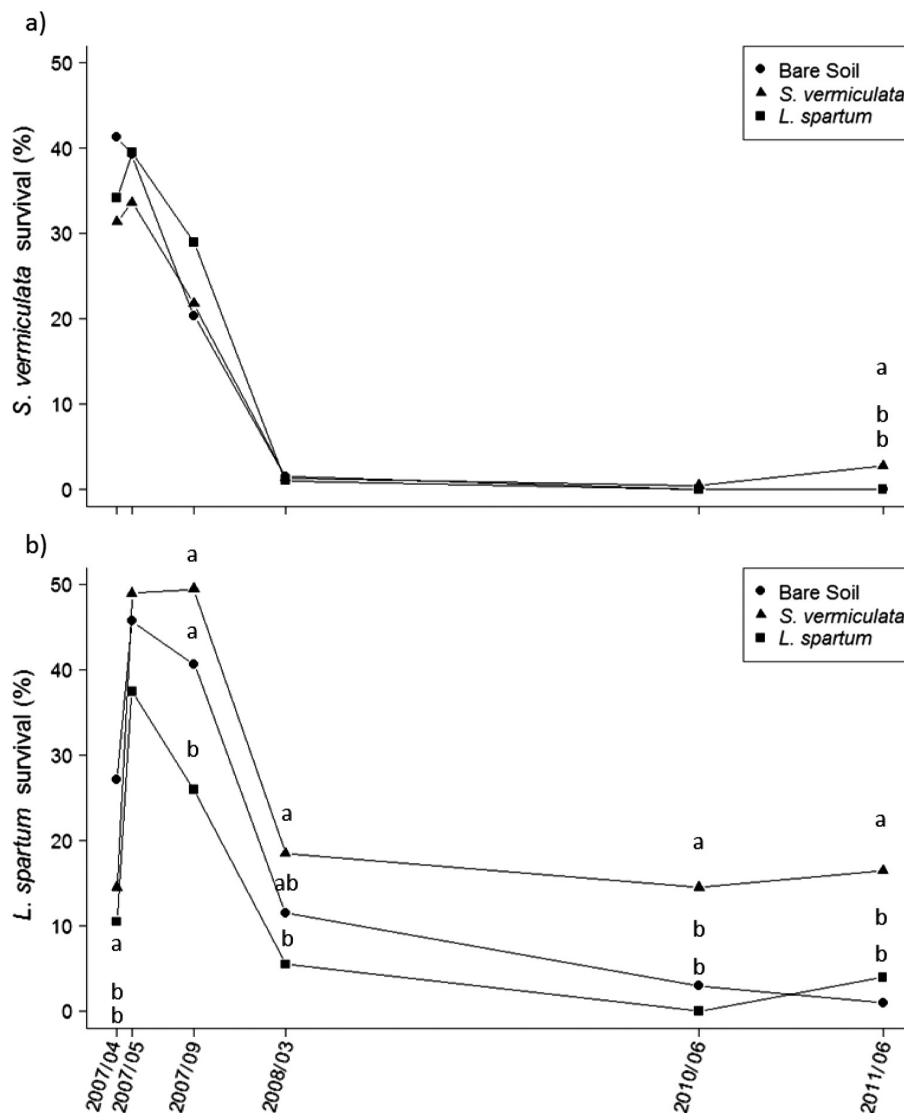


Fig. 2. Percentage germination (April 2007) and survival (May 2007 to June 2011) of (a) *Salsola vermiculata* and (b) *Lygeum spartum* on bare soil (circles), under the canopies of *S. vermiculata* (triangles), and under the canopies of *L. spartum* (squares). Different letters indicate significant differences in a post hoc test between microsites on a measurement date.

procedure showed that in September 2007, *L. spartum* seedling survival was higher at the SA and LY microsites than at the BS microsite. In March 2008, *L. spartum* seedling survival was higher at the SA microsite than at the BS microsite; after that time, survival at the SA microsite was significantly higher than at the LY and BS microsites (Fig. 2b).

Our investigation of the role of the different microsites on seedling growth only considered

data until March 2008, because seedling survival at some microsites was very low after this date. In this period, the height of *S. vermiculata* seedlings was greater at the SA and LY microsites than at the BS microsite (Table 2a). Although the LY microsite accounted for the greatest seedling growth until September 2007, the average height of *S. vermiculata* seedlings at this microsite drastically decreased to the levels at the BS microsite in March 2008; at the

Table 2. Generalized linear mixed model for repeated measures of (a) height, and (b) number of leaves of *Salsola vermiculata* seedlings, and (c) height of *Lygeum spartum* seedlings measured in May 2007, September 2007, and March 2008 relative to bare soil (reference).

(a) Response variable: Height_Salsola			AIC	BIC	logLik
Random effects: ~Microsite Individual			1809.568	1852.764	-893.784
Variable	Value	SE	df	t-value	P-value
Intercept	2.564	0.201	228	12.773	<0.001
SA_microsite	2.836	0.351	228	8.079	<0.001
LY_microsite	4.382	0.491	228	8.930	<0.001
Time	0.217	0.044	147	4.879	<0.001
(b) Response variable: Leaves_Salsola			AIC	BIC	logLik
Random effects: ~Time Individual			1496.012	1535.228	-738.006
Variable	Value	SE	df	t-value	P-value
Intercept	4.972	0.218	228	22.806	<0.001
SA_microsite	1.105	0.314	228	3.524	<0.001
LY_microsite	0.174	0.312	228	0.557	0.578
Time	0.196	0.069	145	2.824	0.005
SA_microsite:Time	-0.200	0.096	145	-2.084	0.039
LY_microsite:Time	0.045	0.095	145	0.478	0.634
(c) Response variable: Height_Lygeum			AIC	BIC	logLik
Random effects: ~Microsite Individual			2432.505	2488.791	-1203.252
Variable	Value	SE	df	t-value	P-value
Intercept	4.949	0.221	305	22.396	<0.001
SA_microsite	0.892	0.335	305	2.662	0.008
LY_microsite	1.491	0.376	305	3.964	<0.001
Time	-0.052	0.036	256	-1.464	0.1444
SA_microsite:Time	0.130	0.046	256	2.817	0.0052
LY_microsite:Time	-0.150	0.061	256	-2.466	0.0143

Notes: SA_microsite, *S. vermiculata* microsite; LY_microsite, *L. spartum* microsite. Random effects were chosen between ~1|Individual, ~Microsite|Individual, and ~Time|Individual based on the Akaike's information criterion.

SA microsite, the average growth was greatest at the end of the analyzed period (Appendix S1: Fig. S3a). *Salsola vermiculata* seedlings had significantly more leaves at the SA microsite (Table 2b). There was an interaction between SA microsite and time explained by the similar number of leaves between microsites until September 2007. At the end of the analyzed period (March 2008), the difference between the SA microsite and the other microsites became more apparent (Appendix S1: Fig. S3b). With respect to *L. spartum* seedlings, they were taller at the SA and LY microsites than at the BS microsite (Table 2c). There was also an interaction between the SA and LY microsites and time: Only at the SA microsite, taller plants were present at the end of the studied period (March 2008; Appendix S1: Fig. S3c).

Hydrological and environmental properties of microsites

The probability density functions (PDFs) showed similar trends for VWC at the four microsites, because they all had the same rainfall patterns (Fig. 3). However, the bare soil and *A. herba-alba* microsites had peak PDFs at lower VWC values than the *S. vermiculata* and *L. spartum* microsites (Fig. 3).

The increment in soil VWC (increment_VWC) after rainfall was substantially larger under the canopy of the three plant species than in bare soil (Table 3a). A Holm post hoc test indicated no differences between *A. herba-alba*, *S. vermiculata*, and *L. spartum* in the increment_VWC after rainfall ($P > 0.005$ for all pairwise comparisons). The amount of rainfall was positively related to the increment_VWC, but the antecedent VWC

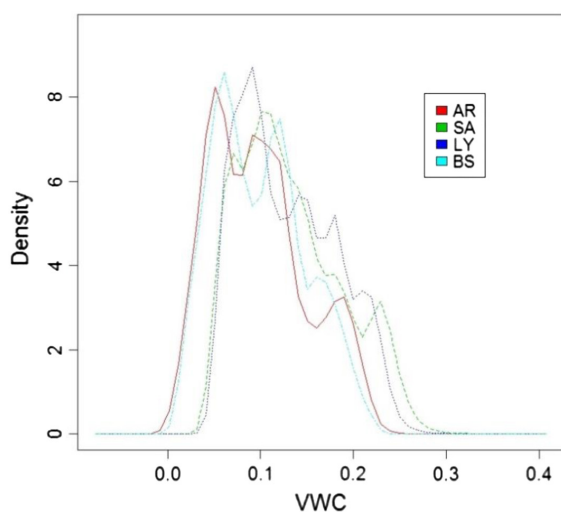


Fig. 3. Probability density function (PDF) of soil volumetric water content (VWC) measured hourly from January 2012 to July 2013 under the canopies of *Artemisia herba-alba* (AR), *Salsola vermiculata* (SA), and *Lygeum spartum* (LY), and on bare soil (BS).

(ant_VWC) was negatively related to increment_VWC. This indicates that more water infiltrated into dry soils than soils that were already wet. The interaction between ant_VWC and the three plant microsites was significant and negative: The negative relationship between ant_VWC and increment_VWC was less pronounced under plants than in bare soil (Appendix S1: Fig. S4a).

The slope of the wetting process (Wetting_slope) was greater under the plant canopies (Table 3b), indicating that the water infiltration was faster under plant canopies than in bare soil. However, there were no significant differences between the three plant species in the slope of the wetting process. There was a negative relationship between the ant_VWC and the slope of the wetting process, indicating that water infiltrated into drier soils more quickly than into wet soils. Moreover, the amount of water in a rainfall event had a positive effect on the slope of the wetting process (Table 3b).

The amount of soil water after 10 days without rainfall (VWC_10days) was negatively associated with mean temperature during the drying period and positively associated with initial VWC after rainfall (Table 3c). In addition, VWC_10days was greater under *S. vermiculata* and *L. spartum* than in bare soil (Table 3c).

VWC_10days under *A. herba-alba* was not significantly different from the bare soil value, which implies faster drying under *A. herba-alba* than under the other two species. This explains the VWC pattern found for *A. herba-alba* at the PDF (Fig. 3). The interaction between initial VWC and microsite was significant. In particular, under the canopy of the three species, the relationship between initial VWC and VWC_10days had a shallower slope than on the bare soil (Table 3c; Appendix S1: Fig. S4b). This means that when sufficient water is available in the soil, water uptake by the three plant species is a relevant phenomenon.

The microsites had significant differences in cumulative water infiltration as measured with the tension infiltrometer at different times ($F_{3,31} = 5.213$, $P = 0.005$ at 0.5 min; $F_{3,31} = 9.648$, $P < 0.001$ at 1 min; $F_{3,31} = 42.953$, $P < 0.001$ at 4 min; $F_{3,31} = 20.628$, $P < 0.001$ at 10 min). The Holm post hoc test showed that cumulative water infiltration for short periods of time (< 1 min) was significantly greater under *L. spartum* and *S. vermiculata* than in the bare soil, with infiltration under *A. herba-alba* being intermediate (Fig. 4a). For longer infiltration times (> 5 min), cumulative water infiltration was much greater under *L. spartum*. *A. herba-alba* and *S. vermiculata* were not significantly different, but had significantly greater infiltration than the bare soil. For even longer infiltration times (> 10 min), cumulative water infiltration under *L. spartum* was so high that it obscured the differences in cumulative water infiltration between the shrubs and the bare soil (Fig. 4), which were only significant when removing *L. spartum* from the analysis (data not shown).

There were significant differences in the photosynthetic photon flux (PPF) between microsites both on the cloudy day ($F_{3,36} = 181.57$, $P < 0.001$) and on the sunny day ($F_{3,36} = 381.86$, $P < 0.001$). The Holm post hoc test showed that PPF was significantly greater in bare open areas than under the canopy of *A. herba-alba*, under the canopy of *S. vermiculata*, and under the canopy of *L. spartum*, on the cloudy day and the sunny day (Fig. 4b).

Maximum daily summer temperatures were substantially lower under the canopies of the three species than in the bare soil (*L. spartum*: 6.7°C lower; *S. vermiculata*: 3.2°C lower;

Table 3. Generalized linear mixed model of (a) increment in volumetric water content (Increment_VWC), (b) slope of wetting process after rainfall (Wetting_slope), and (c) VWC 10 days after rainfall (VWC_10days) for 56 wetting events (a and b) and 18 drying events (c) from 19 January 2012 to 5 July 2013 relative to bare soil (reference).

(a) Response variable: Increment_VWC			AIC	BIC	logLik
Random effects: ~Microsite box			-2373.7	-2281.9	1206.83
Explanatory variable	Value	SE	df	t-value	P-value
Intercept	0.027	0.011	723	2.411	0.016
VWC_before	-0.201	0.072	723	-2.805	0.005
Amount_rainfall	0.003	1.78×10^{-4}	723	19.421	<0.001
AR_microsite	0.053	0.014	723	3.893	<0.001
SA_microsite	0.066	0.018	723	3.608	<0.001
LY_microsite	0.061	0.018	723	3.447	0.001
VWC_before:AR_microsite	-0.357	0.105	723	-3.391	0.001
VWC_before:SA_microsite	-0.262	0.094	723	-2.801	0.005
VWC_before:LY_microsite	-0.315	0.105	723	-2.999	0.003

(b) Response variable: Wetting_slope			AIC	BIC	logLik
Random effects: ~Microsite box			-5095.5	-5017.4	2564.74
Explanatory variable	Value	SE	df	t-value	P-value
Intercept	0.005	0.001	726	5.733	<0.001
VWC_before	-0.035	0.005	726	-6.497	<0.001
Amount_rainfall	6.9×10^{-5}	0.000	726	2.475	0.014
AR_microsite	0.003	0.001	726	2.981	0.003
SA_microsite	0.005	0.002	726	3.050	0.002
LY_microsite	0.004	0.001	726	4.788	<0.001

(c) Response variable: VWC_10days			AIC	BIC	logLik
Random effects: ~Microsite box			-1065.107	-995.8304	552.553
Variable	Value	SE	df	t-value	P-value
Intercept	0.081	0.011	233	7.224	<0.001
Mean_temp	-0.004	2.5×10^{-4}	233	-14.518	<0.001
Initial_VWC	0.513	0.060	233	8.621	<0.001
AR_microsite	0.016	0.012	233	1.330	0.185
SA_microsite	0.035	0.014	233	2.526	0.012
LY_microsite	0.041	0.014	233	2.833	0.005
Initial_VWC:AR_microsite	-0.178	0.076	233	-2.352	0.020
Initial_VWC:SA_microsite	-0.175	0.070	233	-2.505	0.013
Initial_VWC:LY_microsite	-0.211	0.074	233	-2.837	0.005

Note: AR_microsite, *Artemisia herba-alba* microsite; SA_microsite, *Salsola vermiculata* microsite; LY_microsite, *Lygeum spartum* microsite.

A. herba-alba: 2.5°C lower; Appendix S1: Table S2a, Fig. S5a). The Holm post hoc test showed that the reduction in maximum daily temperatures under *L. spartum* was significantly greater than that under *A. herba-alba* ($P < 0.001$) and *S. vermiculata* ($P < 0.001$). *A. herba-alba* and *S. vermiculata* had no significant differences in maximum daily temperatures in summer ($P = 0.69$). Minimum daily winter temperatures were higher under

the canopies of the three species than in the bare soil (*L. spartum*: 2.2°C higher; *S. vermiculata*: 1.5°C higher; *A. herba-alba*: 1.0°C higher; Appendix S1: Table S2b, Fig. S5b). The Holm post hoc test showed that the minimum daily temperatures were significantly higher under *L. spartum* than under *A. herba-alba* ($P < 0.001$). The minimum temperatures in winter were not different for *S. vermiculata* and *L. spartum* ($P = 0.18$) or *A. herba-alba*

Table 4. Soil chemical analysis in bare soil, and under the canopies of *Artemisia herba-alba*, *Salsola vermiculata*, and *Lygeum spartum* (four samples per microsite).

Variable	Bare soil	<i>A. herba-alba</i>	<i>S. vermiculata</i>	<i>L. spartum</i>	$F_{3,12}$	P-value
pH	7.89 ± 0.01	7.75 ± 0.07	7.76 ± 0.07	7.70 ± 0.03	2.554	0.104
EC (mS/cm)	1.756 ± 0.034	1.757 ± 0.040	1.849 ± 0.050	1.855 ± 0.034	1.909	0.181
OM (%)	0.523 ± 0.047 ^a	1.762 ± 0.474 ^b	2.386 ± 0.581 ^b	1.378 ± 0.135 ^{ab}	6.708	0.007
C (%)	1.262 ± 0.038 ^a	2.399 ± 0.314 ^b	2.848 ± 0.327 ^b	2.072 ± 0.198 ^{ab}	9.371	0.002
N (%)	0.047 ± 0.002 ^a	0.130 ± 0.031 ^b	0.158 ± 0.028 ^b	0.105 ± 0.012 ^{ab}	7.183	0.005
C/N	6.39 ± 0.33 ^a	7.72 ± 0.23 ^{ab}	8.46 ± 0.69 ^b	7.654 ± 0.158 ^{ab}	4.867	0.019

Notes: Different letters indicate significant differences between microsites in a post hoc test. EC, electrical conductivity; OM, organic matter percentage; C/N, C/N ratio.

($P = 0.24$). The daily temperature ranges were smaller under the canopies of the three species than in bare soil (*L. spartum*: 5.9°C smaller; *S. vermiculata*: 3.6°C smaller; *A. herba-alba*: 2.7°C smaller; Appendix S1: Table S2c, Fig. S5c). The range of daily temperatures was significantly different for all the microsites ($P < 0.001$ for all).

Organic matter, C, and N soil contents were significantly greater under the canopies of *A. herba-alba* and *S. vermiculata* than in bare soil (Table 4); *L. spartum* had intermediate values and was not significantly different from other microsites. The C/N ratio was significantly greater in *S. vermiculata* than in the bare soil, and *A. herba-alba* and *L. spartum* had intermediate values.

DISCUSSION

We investigated the link between the ecological and the hydrological roles of shrubs and grasses in a semiarid ecosystem by quantifying their effects on plant establishment and the spatiotemporal dynamics of soil water availability beneath their canopies. Thus, this work simultaneously studied the ecological role of potential nurse plants and their hydrological and microsite characteristics and highlighted the importance of an integrative ecohydrological approach to fully understanding the functioning of semiarid ecosystems.

Overall, adult plants greatly improved the abiotic conditions for plant establishment (although there were interspecies differences) compared to the bare soil (Appendix S1: Fig. S1). This finding confirms the high spatial heterogeneity of environmental suitability for plant establishment in a semiarid ecosystem (Callaway 2007, Ward 2009). However, even though abiotic conditions beneath

the species investigated were quite similar, there were large differences in their performance as nurse plants. *S. vermiculata* had a preeminent role as a nurse plant, and it facilitated intra- and interspecific survival and growth of seedlings. *S. vermiculata* is a tall shrub, with deep roots and a large and moderately dense canopy, traits that are characteristic of benefactor species (Gómez-Aparicio 2009). Our analysis of soil water content indicated that *S. vermiculata* infiltrated water efficiently after rainfall events compared to the bare soil and that soil beneath this species took longer to dry than bare soil. Moreover, the soil beneath *S. vermiculata* had an enriched chemical composition compared to the bare soil and the soil beneath perennial grasses. All these factors together made *S. vermiculata* a good nurse plant species for plant establishment.

A. herba-alba might seem to have a similar role as *S. vermiculata*, given its similar physiognomy (both species are shrubs) and similar hydrological and chemical properties. However, our observational data showed that seedlings and juveniles seldom appeared under *A. herba-alba* canopies, and this led to low plant diversity and density beneath this species compared to *S. vermiculata*. Water scarcity during prolonged dry periods is a possible reason for the poor nurse plant function of *A. herba-alba* adults. Beneath *A. herba-alba*, wetting events were as efficient at refilling soil water content as under *S. vermiculata* and *L. spartum*. However, the dynamics of the drying process beneath *A. herba-alba* were not statistically different from those on bare soil. The deeper roots of *S. vermiculata* relative to *A. herba-alba* (Guerrero-Campo 1998) could lead to a lower water uptake in the upper soil layers under *S. vermiculata*. It could also promote a “hydraulic lift” (Callaway

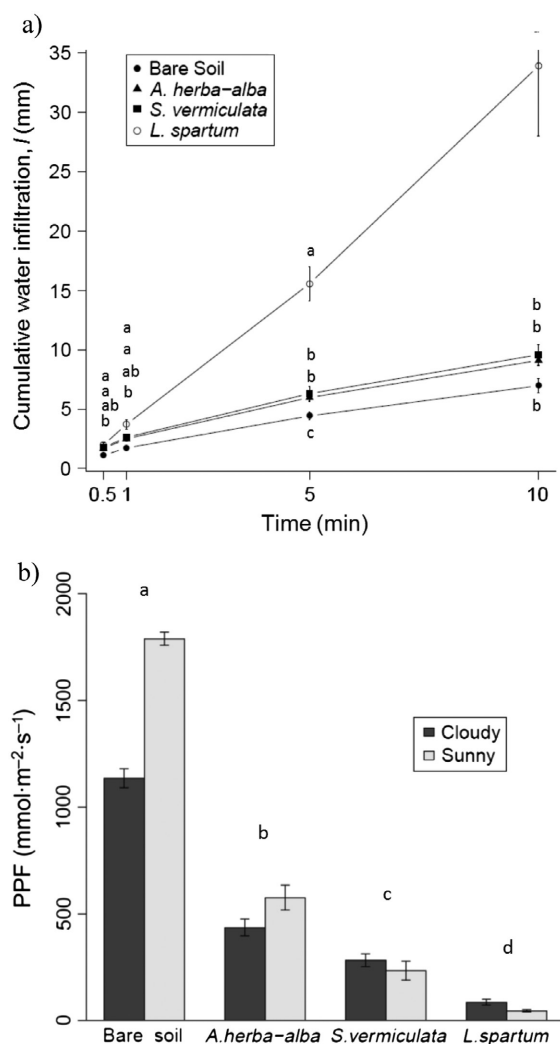


Fig. 4. (a) Means and standard errors of cumulative water infiltration (mm) from 0.5 to 10 min, in bare soil ($n = 11$, filled circles), and under the canopies of *Artemisia herba-alba* ($n = 7$, filled triangles), *Salsola vermiculata* ($n = 9$, filled squares), and *Lygeum spartum* ($n = 8$, open circles). Different letters indicate significant differences in a post hoc test between microsites on a measurement date. (b) Means and standard errors of photosynthetic photon flux (PPF, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in bare soil and under the canopies of *A. herba-alba*, *Salsola vermiculata*, and *L. spartum* on a cloudy day (25 April 2011) and a sunny day (25 May 2011). Values are from 10 measurements per microsite. Different letters indicate significant differences in a post hoc test between microsites on a measurement date. Data from sunny and cloudy days were analyzed separately, but the results were the same for a combined analysis.

1995, Caldwell et al. 1998) in which water is taken from deep soil layers and released passively into shallow soil layers, thus increasing the window of water availability under its canopy. Alternatively, it could be argued that the faster drying process beneath *A. herba-alba* could be due to its sparser canopy, which would lead to greater solar radiation (as indicated by the PPF measurements), and greater evaporation rates after rainfall. However, our soil temperature measurements indicated no differences for *A. herba-alba* and *S. vermiculata*, so this explanation should be rejected. Moreover, *A. herba-alba*, as many other species of the genus *Artemisia*, has allelopathic properties (Friedman et al. 1977, Escudero et al. 2000). Previous studies have identified several sesquiterpenes lactones, flavonoids, and essential oils in the roots and aerial parts of this species with inhibitory activity of seedling germination, growth, and survival in greenhouse experiments (Salido et al. 2004, Abou et al. 2010). Here, we showed that under natural conditions, *A. herba-alba* interferes with seedlings, both intra- and interspecifically. This allelopathic activity, together with water scarcity during prolonged dry periods, may explain its poor function as a nurse plant. Given that allelopathy is a common phenomenon in stressful environments, such as arid, semiarid, and Mediterranean ecosystems (Schenk et al. 1999, Vila and Sardans 1999), our results underline that a simple study of the hydrological or the microsite characteristics of a plant is insufficient to determine its true role as a nurse plant. In addition, other soil factors not considered in this study such as the microbiota or limiting nutrients like phosphorous may also be relevant in determining the plant species role in the plant community.

The perennial grasses had only some characteristics that made them suitable as nurse plants. Our experimental study confirmed that seedling survival and growth in the first stages of development were enhanced by the presence of the perennial grass *L. spartum*. However, seedlings and juveniles were not found close to perennial grasses, and species richness and density beneath the canopy of *L. spartum* were smaller than under the two codominant shrubs. Moreover, long-term survival and growth of *S. vermiculata* and *L. spartum* seedlings were hindered in the *L. spartum* microsite in our sowing experiments. Taking

together, these findings suggest that perennial grass adults facilitated plant establishment and performance during the first year after germination, but then interfered with these same plants after the first year (Soliveres et al. 2010). Contrary to our initial hypothesis, our study of the hydrological and microsite characteristics of *L. spartum* indicated no apparent reason for this shift from positive to negative interactions with seedlings. Together with *S. vermiculata*, *L. spartum* created the largest window of water availability for seedlings after rainfall, the maximum and minimum temperatures beneath its canopy were greatly modulated, and the nutrient content was higher than in bare soil (although not as favorable as beneath *S. vermiculata*). It could be argued that the reduction in solar radiation beneath *L. spartum* could be too extreme for optimal seedling performance (Holmgren et al. 2012), but then, there would be an initial interference with seedling survival and performance, and not a shift from facilitation to interference. Strong competition for water with seedlings in the upper soil layers of perennial grasses has been reported (Köchy and Wilson 2000), but we found no signs that soil water depletion by grasses was faster than that by shrubs. We measured water content in the upper 15 cm of the soil, which may have caused evaporative processes to occur too fast to allow observation of depletion of soil water by grasses (Cavanaugh et al. 2011). Kambatuku et al. (2013) found strong competition by grasses in the upper 15 cm of soil, but reported that evaporation was not an important factor because they grew plants in containers under controlled conditions with regular watering. We argue that at shallow depths under field conditions, evaporation is more important than water uptake by neighbors (Potts et al. 2010, Cavanaugh et al. 2011). Water uptake by grasses would be relevant for seedling establishment only when seedling roots reach deeper into the soil. Moreover, non-resource microsite environmental properties could be more important for the early stages (germination and emergence) of plant establishment and resource-related interactions (mainly for water availability) for the later stages of establishment (Jankju 2013). At these later stages of development, the root systems of established plants would interfere with nurse plants. This explanation clarifies the shift of function we observed

in perennial grasses, which facilitated establishment of early-stage seedlings, but interfered with later-stage seedlings. This shift may also explain why some studies of perennial grasses in semi-arid regions reported positive effects, whereas others reported negative effects of perennial grasses on seedlings (Maestre et al. 2001, 2003, Armas and Pugnaire 2011), depending on when measurements were made (Soliveres et al. 2010). Thus, our combined ecological-hydrological results warn against making generalizations about the ecological role of plants based on consideration of the spatial pattern of seedlings at a single development stage, and oversimplifications about the ecological role of plants based on water infiltration patterns.

On the other hand, we found that belowground interference by perennial grasses was also conspecific, a phenomenon described in previous studies (Aguilera and Lauenroth 1995). This restricts recruitment of seeds near a conspecific adult (Armas and Pugnaire 2011) and confers to shrubs the role of nurses of the perennial grasses in semiarid steppes. *Salsola vermiculata* facilitated *L. spartum* and other perennial grass seedlings, but not the inverse. Thus, perennial grasses may be replacing their own nurse plants during plant succession, as previously reported in other semi-arid regions (Armas and Pugnaire 2005). This has important implications for restoration plans of these ecosystems (Pueyo et al. 2009).

We found that seed germination was independent of microsite (*S. vermiculata* seedlings) or even larger in bare soil than beneath adult plants (*L. spartum* seedlings), implying a fast response of seedlings to the rainy 2007 spring (Appendix S1: Fig. S6a) that was independent of other microsite conditions. However, summer 2007 was drier than average (Appendix S1: Fig. S6b), and subsequent survival and growth were associated with the presence of nurse plants. Later in the plant development, there was a shift from an aggregated pattern at the seedling stage to a segregated pattern when adults that was most probably caused by a self-thinning process involving density-dependent interactions (Fonteyn and Mahall 1981, Phillips and MacMahon 1987, Wiegand et al. 2005). This ontogenetic shift is a common pattern in perennial plants in deserts (Miriti 2006, Armas and Pugnaire 2009). This is attributed to an

increased interference between plants with well-developed root systems that overlap and colonize bare soil in the interpatches. This depletes soil water and increases the mortality of neighbors that are less efficient in water uptake (Armas and Pugnaire 2009).

Our field measurements allowed some assessment of the hydrological processes behind the spatial-temporal dynamics of soil water content. Thus, the extremely high infiltration capacity of *L. spartum*, which was much greater than that of the shrubs *S. vermiculata* and *A. herba-alba*, contrasted with the dynamics of soil water content after rainfall, which was more modest and had a similar magnitude than for the shrubs. As previously reported, and in agreement with our measurements, *L. spartum* has an extraordinary infiltration potential (Cerdà 1997) due to soil modification (with macropores and channels in its root zone), but this is somehow counterbalanced by high rainfall interception from the canopy (Berdugo et al. 2014), resulting in a more restricted actual infiltration.

On the other hand, although we do not have direct measurements of evapotranspiration, we can evaluate the contribution of evaporation to loss of soil water based on measurements of soil water content at the different microsites. Thus, a higher soil water content during an interpulse period under the canopy of woody plants than in the bare soil indicates that evaporation (not plant use, including transpiration) is the predominant source of water loss (Breshears et al. 1997). Moreover, both the presence of greater soil water under the canopies of woody plants than in bare soil after a rainfall event and the greater infiltration into already wet soils imply that the redistribution of water from bare areas to vegetated patches is a relevant phenomenon (Greene 1992, Pueyo et al. 2013, Berdugo et al. 2014), more important in fact than rainfall interception by plant canopies (Breshears et al. 1997). Accumulation of water in the soil beneath plants is due to surface and subsurface soil properties that affect infiltration rate and runoff, such as sediment accumulation, microtopography, the abundance of macropores, less crust development, and soil compaction (Greene 1992, Galle et al. 1999, Gomez-Aparicio et al. 2005, Michaelides et al. 2009). In bare soil, low infiltration due to soil surface sealing and the absence of barriers

cause runoff (Dunkerley and Brown 1995, Arnau Rosalén et al. 2008, Mayor et al. 2009). Notably, drainage in this particular ecosystem is negligible because of the low infiltration of clay soils (Moret et al. 2011), but this should be considered in other semiarid ecosystems with more permeable soils.

CONCLUSIONS

Our integrated ecological-hydrological study of a semiarid ecosystem showed that shrubs and grasses improved the abiotic conditions under their canopies compared to the bare soil, because they increased the availability of soil moisture and reduced solar radiation. However, our study of the three most dominant species in this plant community indicated that only the shrub *S. vermiculata* had a long-term role as a nurse plant that favored seedling establishment. The perennial grass *L. spartum* facilitated early plant establishment, and the shrub *A. herba-alba* did not facilitate establishment at any stage. Our experiments and observations suggest that competition for water and allelopathy may explain why these other two species do not serve as nurse plants, even though they improved the microsite environment. We conclude that the identification of a species as a nurse plant cannot simply be inferred by measurement of nearby abiotic conditions, but that long-term ecohydrological studies are required to fully understand the underlying mechanisms.

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