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Short communication

Infiltration, penetration resistance and microphytic crust composition in contrasted microsites within a Mediterranean semi-arid steppe

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Abstract

In semi-arid areas with sparse vegetation cover, runoff generated in the open areas is crucial for the maintenance of vegetated patches. Microphytic crusts play a major role in this redistribution of water, thus influencing ecosystem functioning and dynamics. We investigated the effects of alpha grass (*Stipa tenacissima* L.) on the composition of the microphytic crusts, surface soil compaction, and infiltration in a semi-arid steppe of SE Spain. The microphytic crust composition differed between the upslope of *S. tenacissima* tussocks (tussock microsites) and the inter-tussock areas with sparse vascular plant cover (open microsites), with more moss cover in the tussock microsite, and more cyanobacteria and lichens in the open microsite. The surface soil compaction was higher in the open microsite. Variables related with infiltration showed a clear microsite effect, with higher infiltration rate and less time required by first drop to percolate in the tussock microsite. Partial correlation analysis showed a significant negative relationship between the cyanobacteria cover and the infiltration rate, and both the cyanobacteria cover and the percentage of bare soil showed a significant positive relationship with the time required for first drop to percolate. Our results reinforce the idea that open microsites act as sources of water for *S. tenacissima* tussocks. This study helps to understand the interactions between microphytic crusts and vascular plants in semi-arid environments.

Keywords: Infiltration; Microphytic crusts; Microsite; Surface soil compaction; Semi-arid steppe; *Stipa tenacissima*

Arid and semi-arid areas throughout the world are characterised by sparse vegetation cover in which vegetated patches are surrounded by a matrix of bare soil (Valentin et al., 1999). Under these conditions, the runoff generated in the bare areas often accumulates beneath the canopy of vascular plants, increasing the ecosystem productivity and diversity (Schlesinger et al., 1990; Boeken and Shachak, 1994). The bare areas are frequently covered by microphytic crusts composed of cyanobacteria, mosses and lichens (West, 1990). This crust plays a major role in the redistribution of water (Eldridge et al., 2000), influencing ecosystem functioning and dynamics in these areas (West, 1990). Microphytes such as cyanobacteria and soil algae also secrete gels and polysaccharides (De Philipis et al., 1993), and exude mucilaginous sheaths directly onto the soil surface. This mucilage binds the soil surface particles (Bailey et al., 1973), making them effective in preventing soil erosion by wind and water (Belnap and Gardner, 1993).

Alpha grass (*Stipa tenacissima* L.) is a common tussock grass forming open steppes that dominate the landscape of large semi-arid areas of the Mediterranean Basin (Le Houérou, 1986). In these steppes, the open areas are suppliers of water and sediments for the vegetated patches (Puigdefábregas and Sánchez, 1996), whose soils have higher infiltration capacity (Cerdà, 1997). To understand more about the interaction between the microphytic crusts and the soil surface dynamics in *S. tenacissima* steppes, we measured water infiltration, soil surface compaction, and microphytic crusts composition at vegetated and open microsites in a steppe of SE Spain. Microphytic crusts in alpha grass steppes often show complex spatial patterns that are related to the distribution of vascular plants, but there is no information on the role of these microphytic crusts on favouring surface runoff. Our main aim was to evaluate the effects of the microsite provided by *S. tenacissima* tussocks on the composition of microphytic crusts, and to explore the

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Table 1
Effect of microsite on cover of microphytic crusts and bare soil. Data represent means ± SE ($n = 9$)

	Cover (%)		ANOVA results		
	Tussock	Open	F	df	P
Cyanobacteria	6.8 ± 2.9	49.2 ± 6.0	40.55	1, 16	< 0.001
Mosses	71.4 ± 5.5	12.0 ± 4.8	50.34	1, 16	< 0.001
Lichens	0	15.56 ± 5.8	10.54	1, 16	0.005
Bare soil	5.6 ± 1.1	16.8 ± 1.8	18.67	1, 16	0.001

relationships between these effects, if any, and hydrological soil surface characteristics.

The study site is a *S. tenacissima* steppe located close to Aigües de Busot, in SE Spain (38°31′N, 0°21′W; 460 m a.s.l.; 12° slope facing SE). The soil is Lithic calciorthid (Soil Survey Staff, 1990). The soil texture (0–20 cm depth) is silty, with 20% sand, 52% silt and 28% clay for the soil under the canopy of *S. tenacissima*, and 20% sand, 55% silt and 25% clay for the soil in bare ground areas (Maestre et al., 2001). Vegetation cover is 45%, and it is dominated by two perennial sprouting grasses, *S. tenacissima* and *Brachypodium retusum* (Pers.) P. Beauv., with dispersed shrubs, such as *Globularia alypum* L., *Anthyllis cytisoides* L., and *Rhamnus lycioides* L. subsp. *lycioides*.

In December 2000, we collected samples from the upslope of a *S. tenacissima* canopy (tussock microsite) and from inter-tussock areas with sparse vegetation cover (open microsite). We randomly selected nine open and nine tussock microsites. After wetting the soil surface, one circular sample of the topsoil layer (8.4 cm diameter, 1 cm depth) was collected at each sampling point. In the immediate surroundings of each collected sample, we measured soil surface compaction as penetration resistance with a portable penetrometer for top layers (model 06.06, Eijkelkamp, The Netherlands). Due to the high spatial variability of this variable, we took five measurements at each sampled microsite, and considered the average value for subsequent analyses. We corrected these values for moisture content, as determined from one 0–3 cm depth sample taken close to the measurement points. Microphytic crusts were transferred to the laboratory and maintained in an incubator (model MLR-350, Sanyo Electric Co. Ltd, Japan) for 3 d at constant conditions (300 $\mu S\ m^{-2}\ s^{-1}$ irradiance and 20 °C temperature). We then determined the cover of microphytic crust (mosses, lichens and cyanobacteria) and the percentage of bare soil using a 25-cm^2 square (5 cm × 5 cm) centred on each sample. This square was divided into a grid of 0.5 cm × 0.5 cm sampling squares and the cover of each surface feature was evaluated by the point sampling method (100 points per sample). We evaluated infiltration capacity in each sample using the method described by Zaady (1999). We set up an experimental system in petri dishes containing the collected crust samples, previously (24 h) watered at field capacity. We drilled five holes 1 mm diameter at the bottom of each petri dish. We then added 100 ml of distilled water on the plate, and measured the time until the first drop of water percolated. We used the amount of water collected after 5 min to calculate the infiltration rate in each sample.

Differences in crust composition and infiltration between microsites were evaluated with one-way ANOVA. Differences in penetration resistance were evaluated using analysis of covariance (ANCOVA), with soil moisture as covariate. The relationships between surface features and both penetration resistance and infiltration variables were evaluated using partial correlation analysis. In each partial correlation, the effect of the other soil surface variables was removed. In the case of penetration resistance, we used the residuals of the regression between this variable and soil moisture. To meet normality, infiltration and time to first drop to percolate were log-transformed, whereas moss and lichen cover were transformed using the arcsin$\sqrt{}$cover function. All statistical analyses were performed with SPSS 9.0 for windows package (SPSS Inc., Chicago, USA).

Crust composition showed strong differences between the two microsites (Table 1). In the tussock microsites, microphytic crusts were dominated by mosses, mainly *Weissia* sp. In the open microsites, these crusts were mainly formed by cyanobacteria of the genera *Microcoleus* and *Nostoc*, with a similar percentage of mosses (*Weissia* sp.) and lichens, mainly *Psora crenata* (Th. Tayl.) Reinke. The percentage of bare soil was higher in the open microsites (Table 1). Penetration resistance was significantly lower in the tussock microsites (Table 2). Concerning infiltration measurements, the analysed variables also showed a significant microsite effect (Table 2). Infiltration rate was higher in the tussock microsite, and the time required for the first drop to percolate was longer in the open microsite. Partial correlation analysis showed a significant negative relationship between the cyanobacteria cover and the infiltration rate, and both

Table 2
Effect of microsite on infiltration and penetration resistance. Data represent means ± SE ($n = 9$)

	Microsite		ANOVA results[a]		
	Tussock	Open	F	df	P
Infiltration rate (ml min^{-1})	6.5 ± 2.2	0.4 ± 0.2	46.95	1, 16	< 0.001
Time of first drop to fall (s)	4.3 ± 1.7	117.3 ± 22.1	69.66	1, 16	< 0.001
Penetration resistance (kPa)	257.3 ± 33.2	688.9 ± 29.0	67.73	1, 15	< 0.001

[a] For penetration resistance, we show the results of ANCOVA using soil moisture as a covariate.

Table 3
Partial correlations and *P*-values (in brackets) between cover of soil surface variables and penetration resistance (residuals from regression with soil moisture), infiltration rate (log-transformed) and time required for the first drop to fall (log-transformed). In all cases $n = 18$

	Penetration resistance	Infiltration rate	Time of first drop to fall
Cyanobacteria	0.471 (0.076)	−0.537 (0.039)	0.560 (0.030)
Mosses	0.259 (0.352)	−0.219 (0.432)	0.179 (0.522)
Lichens	0.257 (0.355)	−0.270 (0.331)	0.204 (0.467)
Bare soil	0.364 (0.182)	−0.512 (0.051)	0.515 (0.049)

the cyanobacteria cover and the percentage of bare soil showed a significant positive relationship with the time required for first drop to percolate (Table 3). The rest of the relationships were not significant, although marginally significant relationships between the cyanobacteria cover and the penetration resistance, and between the percentage of bare soil and the infiltration rate were also found.

Our results suggest the presence of a strong microsite effect on microphytic crust composition, infiltration and penetration resistance. *S. tenacissima* tussocks act as traps for water and sediments, improving soil surface structure in the upslope of the tussocks as compared to open areas (Puigdefábregas and Sánchez, 1996). In addition, reduction of radiation and soil temperatures under the canopy of tussocks (Maestre et al., 2001) attenuates harsh microclimatic conditions, allowing for the development of mosses. Our results suggest the presence of a facilitative relationship between *S. tenacissima* and mosses, and agree with general descriptions of moss distribution (Eldridge and Tozer, 1997), and with studies carried out at a higher scale in the same site (F.T. Maestre and J. Cortina, personal communication). Mosses are able to absorb large amounts of water during wet periods and to retain considerable amounts of water on the soil surface (Eldridge and Rosentreter, 1999). Thus, it may be possible that mosses developing under the canopy of *S. tenacissima* tussocks help to create a favourable microsite for the development of other species beneath its canopy (Maestre et al., 2001), although further research is needed to elucidate the effect of mosses on vascular vegetation, if any.

The formation, maintenance and dynamics of vegetated patches in semi-arid areas are strongly dependent on water, sediment, nutrient and seed fluxes from open areas to vegetated patches (Aguiar and Sala, 1999; Shachak et al., 1998). In our study area, open microsites were dominated by cyanobacteria and scaly lichens (Eldridge and Rosentreter, 1999). This kind of microphytic crust, together with physical crust, reduces infiltration and enhances runoff (West, 1990). Thus, microphytic crust that dominated the open microsites could play an important role in the generation of runoff for vegetated patches, and in the maintenance of vascular plants.

Despite that soil surface cover in both microsites was dominated by microphytic crusts, the role of other surface properties (microtopography and earthworm casts) and soil physical properties (texture and structure) cannot be underestimated when studying soil surface compaction and infiltration in these steppes. To infer the mechanisms involved and to clarify the relative importance of both biotic and abiotic components of soil crusts have in water infiltration and redistribution in *S. tenacissima* steppes, further manipulative experiments are needed. This study sheds some light on the source sink relationship between vascular plants and microphytic crusts in *S. tenacissima* steppes, and suggests that differences in the cover of microphytic crusts may help to redistribute water flows from open to vegetated patches.

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