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Intensity of ecohydrological interactions in reclaimed Mediterranean slopes: effects of run-off redistribution on plant performance

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ABSTRACT

We have conducted a field experiment to ascertain the role of ecohydrological interactions between run-off source areas and sink patches in the dynamics of artificial slopes derived from open cast coal mining in central-eastern Spain. We analysed the effects of run-off interruption on soil moisture, on the leaf water potential of woody species and on the herbaceous biomass in vegetation patches of three reclaimed slopes subjected to a different disturbance degree resulting from different overland flow volumes running down the slopes. Soil moisture and plant performance were seriously affected by run-off exclusion, and this effect was more intense as level of disturbance increased. In fact, run-off redistribution appeared to be determinant for plant performance in the more disturbed slope, whereas the presence of the shrub *Genista scorpius* appeared to be more determinant for plants in the less disturbed slope. Our results confirm the validity of the Trigger–Transfer–Reserve–Pulse model in artificial slopes during the aggradation process. These results point out the importance of run-off redistribution between vegetation patches in the evolution of artificial slopes by creating fertility islands that improve the performance of vegetation. Restoration practices in drylands may thus significantly improve if a 'run-off expert management' strategy is adopted. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS mining restoration; novel ecosystems; run-off interruption; leaf water potential; biomass

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INTRODUCTION

Ecohydrological interactions constitute a key process to understand how ecosystems work, especially in drylands where water is the main limiting factor for biological productivity (Aguiar and Sala, 1999; Porporato and Rodríguez-Iturbe, 2002). In the last years, many studies have highlighted the importance of run-off redistribution for the dynamics of arid and semiarid ecosystems worldwide, with examples from Africa (White, 1970; Seghieri *et al*., 1997), America (Cornet *et al*., 1992; Reid *et al*., 1999; Bhark and Small, 2003), Asia (White, 1969), Australia (Dunkerley and Brown, 1995; Ludwig and Tongway, 1995) and Europe (Puigdefábregas *et al*., 1999; Calvo-Cases *et al*., 2003; Imeson and Prinsen, 2004). These studies point out that the spatial pattern of vegetation produces a mosaic of patches in which run-off source areas (bare soil patches) are more or less coupled with run-off sink areas (vegetated patches) that may benefit from the extra water supply coming from upslope. The Trigger–Transfer–Reserve–Pulse model proposed by Ludwig *et al*. (2005) is a useful framework that explains the role of spatial redistribution of water in drylands and its impact on vegetation growth. According to this model, after rainfall events (Trigger), spatial redistribution of run-off (Transfer) increases water resources of vegetation patches (Reserve), which may produce an increase in plant growth (Pulse). This mechanism does not only improve the water efficiency of the ecosystem (Noy-Meir, 1973) but also increase its stability, as van de Koppell and Rietkerk (2004) have stated by showing that spatial interactions between vegetation patches (in terms of water flow) confer resilience and increase the adaptive capacity of arid ecosystems.

Spatial distribution of vegetation has been identified as an influential factor for the ecohydrological interactions in semi-arid ecosystems, even more decisive than vegetation cover *per se* (Wilcox *et al*., 2003; Bautista *et al*., 2007), as connectivity between run-off source patches may create leaky systems where water and soil resources easily flow out driving the ecosystem to a degraded state. It is no wonder that ecohydrology constitutes a major challenge for the international environmental agenda, especially for the rehabilitation of degraded arid and semiarid ecosystems (Hannah *et al*., 2007). Nevertheless, although the degradation process has been widely studied, our knowledge about the ecohydrology of the opposite phenomenon in semiarid areas, the 'ecosystem aggradation' process, is very scarce, especially for restored and artificial ecosystems. Cammeraat and Imeson (1999) studied the natural

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recovery of degraded areas of the Mediterranean Spain and concluded that vegetation patterns play a major role preventing water loss at the end of the slopes. However, we need a better understanding of the mechanisms involved in the ecohydrological interactions during the aggradation process to improve our management of restored ecosystems and the design of restoration projects (Newman *et al*., 2006; Wilcox and Thurow, 2006).

Mining-reclaimed landscapes can be included in the group of 'novel' or 'emerging' ecosystems whose functioning has been scarcely studied yet (Hobbs *et al*., 2006, 2009), and they constitute a great challenge for ecological restoration in drylands, as many restoration projects yield unsuccessful results (Moreno-de las Heras *et al*., 2008). Usually, these artificial ecosystems are characterized by poor soils with low infiltration capacity and scarce nutrients that make its vegetal colonization difficult, even more when climate imposes severe water limitations (Nicolau and Asensio, 2000). In these conditions, when vegetation cover is low, bare soil surfaces produce large amounts of run-off that usually trigger soil erosion processes governed by nonlinear dynamics (Moreno-de las Heras *et al*., 2009). Also, wrong topographic designs may result in the presence of water contributing areas upslope and in run-on inputs that intensify soil erosion processes with the formation of dense rill networks (Hancock and Willgoose, 2004). The development of rill networks maximizes the loss of run-off water from the slopes and drives the system to a highly degraded state in which costly efforts must be applied for its rehabilitation (Espigares *et al*., 2011; Moreno-de las Heras *et al*., 2011).

Lavee *et al*. (1998) described a shift in the ecohydrological behaviour of ecosystems along a climatic gradient: from arid systems with an abiotic control of water (run-off dominated) to Mediterranean ones in which biotic processes favour infiltration. Between both extremes, semi-arid ecosystems are described as a mosaic-like pattern containing arid–dry patches that produce run-off and humid–wet patches that receive it as run-on. Mediterranean constructed ecosystems can be classified as 'semi-arid azonal', as they often have to face such harsh conditions that they behave as if they were under semiarid conditions. Therefore, restoration efforts must drive the system to achieve a biotic control of water.

Merino-Martín *et al*. (2012a) proposed a model for the evolution of mining-restored ecosystems in which the intensity of ecohydrological interrelationships (understood as the functional coupling between run-off source and sink patches) varied along the gradient of run-off at the hillslope scale. In their model, the two extremes of the gradient showed the minimum intensity of ecohydrological interactions: on the one hand, degraded restored slopes in which abiotic processes (rill erosion) exert the control of water; on the other hand, wealthy slopes with high vegetation cover in which the control of water relies on biotic processes (plant facilitation, competition). According to this model, the maximum strength of ecohydrological interactions will coincide with an intermediate state of vegetation cover and disturbance. This conclusion agrees with Urgeghe *et al*. (2010) results, who claim for an intermediate source : sink ratio that will optimize the redistribution of water between patches and prevent intense erosion minimizing the loss of run-off at hillslope scale.

The main objective of this investigation is to demonstrate the validity of the TTRP model in constructed slopes derived from mining reclamation in Spain and to analyse the intensity of the ecohydrological interactions along a disturbance gradient (run-off at the hillslope scale). Specifically, we analysed the effect of the spatial redistribution of run-off on the performance of plant communities and how this effect changed at different volumes of run-off. For this purpose, we have conducted an experiment of run-off exclusion under field conditions that allowed us to explore the intensity of the ecohydrological interactions by measuring the ecological effects of the spatial redistribution of water through the answer of the following questions: (i) What is the contribution of the spatial redistribution of run-off to the increase of soil moisture in the run-off sink patches? (i) What is the contribution of the spatial redistribution of run-off to improve the performance of vegetation in the run-off sink patches? (iii) How do these processes vary along a gradient of run-off routing at slope scale?

Our hypothesis is that spatial redistribution of run-off will benefit vegetation patches that receive run-on water from interpatch areas upslope, so we expect a reduction in soil water and a worsening of plant performance in the patches subjected to run-off exclusion. Following Merino-Martín *et al*. (2012a) model, we expect minor ecological effects of the spatial redistribution of run-off in the slopes with low run-off at hillslope scale. It is important to highlight that low run-off at hillslope scale (measured at the foot of each slope) does not necessarily mean low movement of water along the slope because run-off produced at interpatch areas may be absorbed as run-on by vegetated patches downslope.

Our investigation provides empirical evidence of the importance of ecohydrological interactions during the aggradation process (i.e. the recovery of the ecosystemic structure and function) of artificial ecosystems, and also, it delves into the scarce knowledge of the functioning of this new but widely spread man-made ecosystems. Some practical implications for the restoration in drylands are also discussed.

METHODS

Study site

This study has been carried out in the *El Moral* reclaimed mine (50 ha), located within the *Utrillas* coalfield experimental site, in central-eastern Spain (40º47′50″N, 0º50′26″W), with a height of approximately 1100 m a.s.l. The climate in the area is Mediterranean-Continental, with a mean annual temperature of 14 °C (ranging from 6.7 °C in December to 23.1 °C in July). The local moisture regime is Mediterranean-dry according to Papadakis (1966), with a mean annual precipitation of 466 mm (mainly concentrated in spring and autumn) and a potential evapotranspiration of 759 mm. Thus, the main constraints for the biological activity in the area are a long frost period (from October to April) and the intense summer drought (from June to October).

The edaphic characteristics of the area were determined by the reclamation operations performed by the mining company *Minas y Ferrocarril de Utrillas S.A.* between 1987 and 1988, consisting in the construction of artificial hillslopes by means of covering the spoil bank with a layer of 100–250 cm of overburden substratum from the *Escucha* and *Utrillas* cretacic formations of *Albian* age (a nonsaline and clay–loam-textured spoil). Afterwards, the artificial slopes were revegetated by sowing cross-slope a mixture of perennial grasses (*Festuca rubra*, *Festuca arundinacea*, *Poa pratensis* and *Lolium perenne*) and leguminous herbs (*Medicago sativa* and *Onobrychis viciifolia*). All hillslopes were North faced and had a similar angle of 20º. Nowadays, the reclaimed area is composed of a set of hillslopes that have evolved very differently from the same original starting point, mainly driven by the effects of diverse amounts of overland flow derived from contributing areas upslope (channels and berms that produce run-on, or bare steep banks at the top of the slope) (Moreno-de las Heras *et al.*, 2008). In some cases, intense soil erosion processes have provoked rill networks that limit the development of soil and vegetation (Moreno-de las Heras, 2009; Moreno-de las Heras *et al.*, 2011; Espigares *et al.*, 2011), whereas in other cases, the constructed hillslopes are being colonized by woody species. For this study, we have avoided those slopes that followed a degradation trajectory (subjected to intense soil erosion), and we have selected three artificial hillslopes in the course of aggradation that have different run-off volumes (slope run-off coefficients ranging from 0.5% to 11.2% for a total precipitation of 550.67 mm during the study period). This run-off gradient constitutes a disturbance gradient along which we will test the intensity of the ecohydrological interactions.

In each of the selected slopes, we have identified two types of zones: vegetation patches that function as run-off sink patches and interpatches, with a very low vegetation cover (less than 20%), that act as run-off sources (for a more detailed study of the hydrological behaviour of each zone, see Merino-Martín *et al.*, 2012b). Table I offers a general description of the main edaphic features of each zone in each slope. In slope 1, with the highest run-off volume, vegetation patches consisted of tussocks of *L. perenne* with scattered individuals of *Santolina chamaecyparissus*, with a mean cover of 67%. In slope 2, vegetation patches consisted of dense tussocks of *Brachypodium retusum* with a cover of 93%; and in slope 3, with the minimum run-off volume, vegetation patches are formed by shrubs of the leguminous *Genista scorpius*, with a mean cover of 81%. Interpatches consisted of bare soil areas with some scattered individuals of the chamaephytes *S. chamaecyparissus* and *Thymus vulgaris*, and small spots of *Dactylis glomerata* and *M. sativa*. An herbaceous community of annual plants also accompanied both type of patches.

Experimental design and field measurements

In each slope, we identified ten couples of adjacent run-off source and sink areas (a vegetation patch with an interpatch immediately upslope). Each couple was selected so that all run-off source and run-off sink areas were of similar sizes. In half of the couples of each slope, run-off flow between the vegetation patch and the adjacent interpatch upslope was interrupted by inserting 10 cm of a steel sheet (50 cm high) into the soil surface. Measurements of soil water

Table I. General features of the three slopes under study.

	Slope 1		Slope 2		Slope 3	
Total vegetation cover (%)	24.40 ± 2.81		43.94 ± 4.07		51.20 ± 4.16	
Vegetation patch cover (%)	21.79		10.69		18.18	
Interpatch cover (%)	78.21		89.31		81.82	
Run-off coefficient[a] (%)	11.17		2.04		0.50	
	Vegetation patch	Interpatch	Vegetation patch	Interpatch	Vegetation patch	Interpatch
pH[b] -H_2O;w/v:1/2-	8.21 ± 0.11	8.48 ± 0.15	8.41 ± 0.08	8.33 ± 0.03	8.17 ± 0.05	8.28 ± 0.17
EC[b] -w/v:1/2-(dSm^{-1})	0.04 ± 0.00	0.05 ± 0.00	0.08 ± 0.02	0.05 ± 0.01	0.07 ± 0.01	0.06 ± 0.01
Carbonates[b] (%)	10.10 ± 0.42	7.60 ± 2.96	9.43 ± 0.66	8.90 ± 0.90	8.00 ± 0.76	9.03 ± 0.64
Total Nitrogen[b] (%)	0.09 ± 0.01	0.05 ± 0.01*	0.12 ± 0.01	0.06 ± 0.01*	0.18 ± 0.04	0.12 ± 0.01
Organic matter [b] (%)	2.10 ± 0.16	0.31 ± 0.21*	2.84 ± 0.26	1.67 ± 0.65	4.31 ± 1.01	1.93 ± 0.57
C/N[b]	14.10 ± 0.68	4.40 ± 2.36*	13.83 ± 0.32	14.90 ± 2.99	13.90 ± 1.73	8.76 ± 1.63
Total Phosphorus[b] (%)	5.67 ± 0.33	4.33 ± 0.33	11.67 ± 1.33	3.67 ± 0.33*	13.67 ± 3.33	8.67 ± 2.18
Clay[b] (%)	12.33 ± 0.88	18.67 ± 2.03*	19.67 ± 0.88	17.67 ± 0.67	19.33 ± 0.33	20.00 ± 0.58
Silt[b] (%)	38.33 ± 6.12	48.33 ± 2.40	25.67 ± 3.18	43.00 ± 2.00*	29.00 ± 1.00	32.33 ± 0.67*
Sand[b] (%)	49.33 ± 6.64	33.00 ± 0.58*	51.33 ± 3.93	39.33 ± 2.67*	51.67 ± 1.20	47.67 ± 0.88*
AWC[b] (%)	8.07 ± 1.44	9.31 ± 0.52	8.52 ± 0.28	8.42 ± 0.85	6.40 ± 0.28	6.09 ± 0.48
Bulk density[c] ($g\,cm^{-3}$)	1.40 ± 0.03	1.51 ± 0.04	1.30 ± 0.05	1.48 ± 0.05*	1.13 ± 0.04	1.49 ± 0.02**
Soil surface strength[d] (kg)	4.53 ± 0.13	4.85 ± 0.11	5.05 ± 0.35	4.81 ± 0.09	2.22 ± 0.16	4.29 ± 0.11**

EC, electrical conductivity; w/v, relation weigh (soil)/volume (water); AWC, available water content for plants (difference in soil moisture between field capacity and wilting point).

[a] Measured during the study period, by installing a collector at the foot of each slope where run-off was channelled through a cemented outlet.

[b] Measured in three composited samples (each formed of three subsamples) in each vegetation patch or run-off contributing area from the first 10 cm.

[c] Measured in 15 unaltered soil cores (3 cm height by 5 cm diameter) randomly distributed per vegetation patch and interpatch.

[d] Measured in 15 samples randomly distributed per vegetation patch or run-off contributing area.

*Values differ significantly at $\alpha = 0.05$. Tested using Mann–Whitney *U*-test.

**Values differ significantly at $\alpha = 0.01$. Tested using Mann–Whitney *U*-test.

content, leaf water potential of woody species and herbaceous biomass were taken in each vegetation patch (five control and five subjected to run-off exclusion in each slope) to ascertain the ecological impacts of run-off exclusion. The experiment lasted for the whole hydrologic year 2007–2008, with the installation of the sheets in August 2007, before the arrival of the autumn rains, until September 2008.

Soil moisture measurements were taken periodically (every 15 days without rain and 24 h after each rainfall event) in two points (the upper and lower parts) of each vegetation patch. We monitored the volumetric soil moisture (%) in the first 15 cm of the soil profile following the methodology proposed by Cassel *et al*. (1994), using a TDR instrument (Tektronix® 1502C), with an accuracy of 94% in the determination of soil moisture. Soil water data collection began in November 2007, with the first autumn rains that initiated the hydrologic year.

Leaf water potential of woody species was measured in the vegetation patches and in the interpatches in two campaigns: on 2 July and 3 September 2008 (early and late summer, respectively), coinciding with the period of maximum water deficit. In slope 1, only *S. chamaecyparissus* was monitored (the unique woody species in the slope), whereas in slope 3, we obtained data from *G. scorpius*, *S. chamaecyparissus* and *T. vulgaris* in the vegetation patches and only for the last two in the interpatches. No water potential measurements were taken in slope 2 as no woody species was present in the vegetation patches. Leaf water potential (Ψ_l, MPa) was determined using a pressure chamber (SKPM 1400, Skye Instruments®), following the methodology proposed by Brown and Tanner (1981). In each campaign, two measurements of water potential were taken at different moments, predawn (from 05:00 to 07:00 AM) and midday (from 02:00 to 04:00 PM), both on the same date. One measure of each species was obtained in each vegetation patch and interpatch.

Herb production was measured in late spring by clipping the aerial biomass in five quadrats (10 × 10 cm) randomly distributed in each vegetation patch. The samples were dried in an oven at 60 °C for 3 days and then weighed. Herb production was also measured in the same way in the interpatch areas of slope 3 to ascertain the role of *G. scorpius* canopy on herb biomass.

Data analysis

Bifactorial repeated measures ANOVAs were used to analyse the differences in soil water content between the vegetation patches along the hydrologic year, with time as within subject factor. We applied run-off treatment and slope as between-subject factors. To explore the differences in leaf water potential of the woody species, we performed repeated measures ANOVAs for each species in each slope and moment (predawn and midday). In this case, time (July and September campaigns) was the within subject factor, and treatment (control vegetation patch, run-off exclusion vegetation patch and interpatch) was the between-subject factor. Post hoc Tukey tests were used to determine differences on leaf water potentials between treatment groups.

Mann–Whitney *U*-tests were performed to analyse the differences in herb production between treatments. We also calculated the percentage of decrease in biomass produced by the run-off exclusion treatment by means of subtracting the biomass in control vegetation patches from that of their correspondent run-off exclusion patches in each slope. This new variable allowed us to analyse the magnitude of the impact of run-off exclusion between the three slopes by means of a Kruskal–Wallis test.

All statistics have been carried out with the STATISTICA 6.0 package (StatSoft Inc, 2001). Data analysed through ANOVA and Tukey tests fulfilled parametric assumptions, and nonparametric tests were used with those data that did not follow the assumptions needed to perform parametric analyses. For the multivariate analysis, we used the PC-ORD package (McCune and Mefford, 1997). The scientific names of the species are in accordance with *Flora Europaea* (Tutin *et al*., 1964–1980).

RESULTS

The study period was particularly humid, with a total precipitation of 550.67 mm (almost 20% above the historical records), mainly concentrated during the spring (from March to June), when 80% of the total precipitation occurred (Figure 1).

Soil moisture

There were differences in soil moisture content in the first 15 cm between the control vegetation patches and those subjected to run-off exclusion (Figure 2), with significant effects of run-off exclusion treatment ($F_{1,22} = 5.07$; $p = 0.03$) and time ($F_{19,418} = 358.58$; $p < 0.01$). More water was found in control patches (12.61 ± 0.42, mean ± *SE*) than in those subjected to run-off exclusion (11.11 ± 0.61, mean ± *SE*). Regarding time, more water was found during the spring period. There was also a significant interaction between run-off treatment and slope ($F_{2,22} = 4.88$; $p = 0.02$),

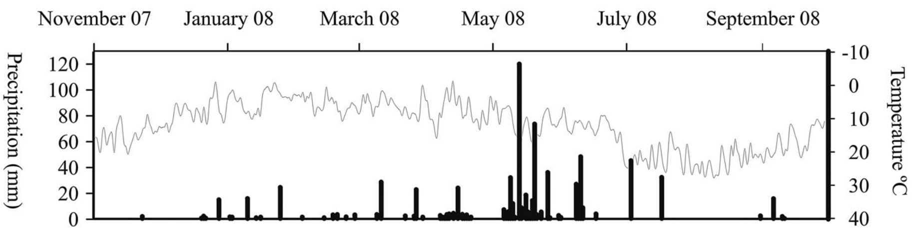

Figure 1. Distribution of temperature (line) and precipitation (bars) during the study period.

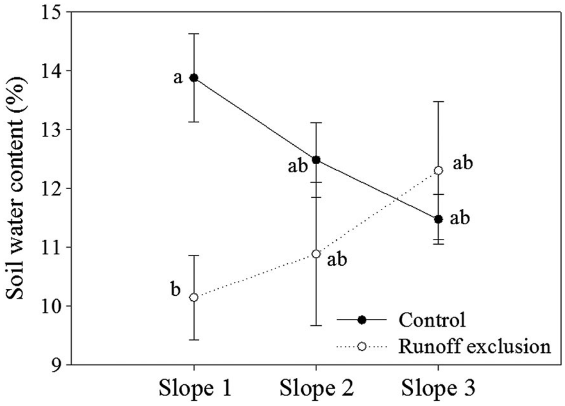

Figure 2. Mean soil water content in the first 15 cm in the vegetation patches subjected to run-off treatments in the three slopes. Vertical bars denote 0.95 confidence intervals. Different letters indicate significant differences with the post hoc Tukey tests ($p < 0.05$).

as differences between run-off treatments were deeper in slope 1 and decreased in slopes 2 and 3 (Figure 2).

Leaf water potential

Table II shows the results of the repeated measures ANOVAs performed with leaf water potential data of the woody species between treatments. In all cases, there were significant differences between the two campaigns, being consistently higher the water potentials of July than those of September (Figure 3). All species showed a significant effect of treatment, although this effect was not always statistically significant in both moments (predawn and midday, Table II). Whereas in slope 1 the minimum water potentials appeared in the vegetation patches subjected to run-off exclusion treatment, in slope 3 plants experienced the highest water stress in the interpatch areas (Figure 3). *G. scorpius*, the species that characterizes the vegetation patches of slope 3, showed a general reduction in leaf water potential under the run-off exclusion treatment, although this trend did not reach statistically significant levels (Figure 3). Soil moisture on the dates in which water potential measurements were taken showed significant differences between treatments only in slope 1 (Figure 4).

Herbaceous biomass

Herbaceous biomass was significantly lower in the vegetation patches subjected to run-off exclusion in slope 1 (Figure 5a). Slopes 2 and 3 showed a similar tendency but without statistical significance (Figure 5a). The percentage of biomass decrease between both run-off treatments was significantly different between slopes (Kruskal–Wallis test $H = 7.98$, $p = 0.02$), reaching its highest value in slope 1 and its minimum in slope 3 (Figure 5b).

Herb production in the vegetation patches of slope 3 (under the canopy of *G. scorpius* individuals) was significantly higher than in interpatches (Mann–Whitney $U = 3.00$, $p = 0.05$), with values of $281.9 \pm 34.9\ \mathrm{g\,cm^{-2}}$ (mean $\pm$ *SE*) under *G. scorpius* and $177.8 \pm 23.9\ \mathrm{g\,cm^{-2}}$ (mean $\pm$ *SE*) in interpatches.

DISCUSSION

Experimental manipulation of run-off flow between run-off source and sink areas in artificial slopes subjected to common water limitations of the Mediterranean zone allowed us to demonstrate the importance of such ecohydrological interactions for the dynamics of these ecosystems. In general, run-off coming from interpatches upslope improved soil water resources and plant performance in the vegetation patches that received this extra water as run-on. This result confirms that the Trigger–Transfer–Reserve–Pulse model (Ludwig *et al.*, 2005), initially proposed for natural ecosystems exposed to degradation processes, is also valid for artificial slopes that evolve towards a progressive aggradation. The run-off gradient incorporated in our experimental design allowed us to demonstrate that the intensity of this type of ecohydrological interaction is highly dependent on the total run-off volume routed along the slopes. In general, the ecological effects of run-off redistribution were higher in slope 1 (with the highest run-off rate at hillslope scale), thus confirming the model of Merino-Martín *et al.* (2012a) that predicts a decrease in the intensity of this interaction as the disturbance gradient decreases. In fact, a significant decrease in soil water content and in herb production provoked by run-off exclusion was only found in slope 1. Other authors have

Table II. Results of the repeated measure ANOVAs performed with leaf water potential data of the woody species in the different slopes and in both moments (predawn and midday).

		Santolina chamaecyparissus		*Santolina chamaecyparissus*		*Thymus vulgaris*		*Genista scorpius*	
		Slope 1		Slope 3		Slope 3		Slope 3	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Predawn	Treatment	3.17	n.s.	6.25	**	4.31	*	2.35	n.s.
	Time	202.48	**	289.35	**	60.71	**	52.49	**
	Time*Treatment	1.31	n.s.	1.32	n.s.	5.30	*	2.21	n.s.
Midday	Treatment	4.34	*	2.78	n.s.	4.18	*	6.05	*
	Time	67.85	**	51.82	**	53.27	**	96.91	**
	Time*Treatment	3.15	n.s.	0.74	n.s.	0.82	n.s.	1.3	n.s.

Within-subject factor is Time (July and September campaigns); between-subject factor is Treatment (control patches, run-off exclusion patches and interpatches). Asterisks indicate significant differences (* at $\alpha = 0.05$ and ** at $\alpha = 0.01$).

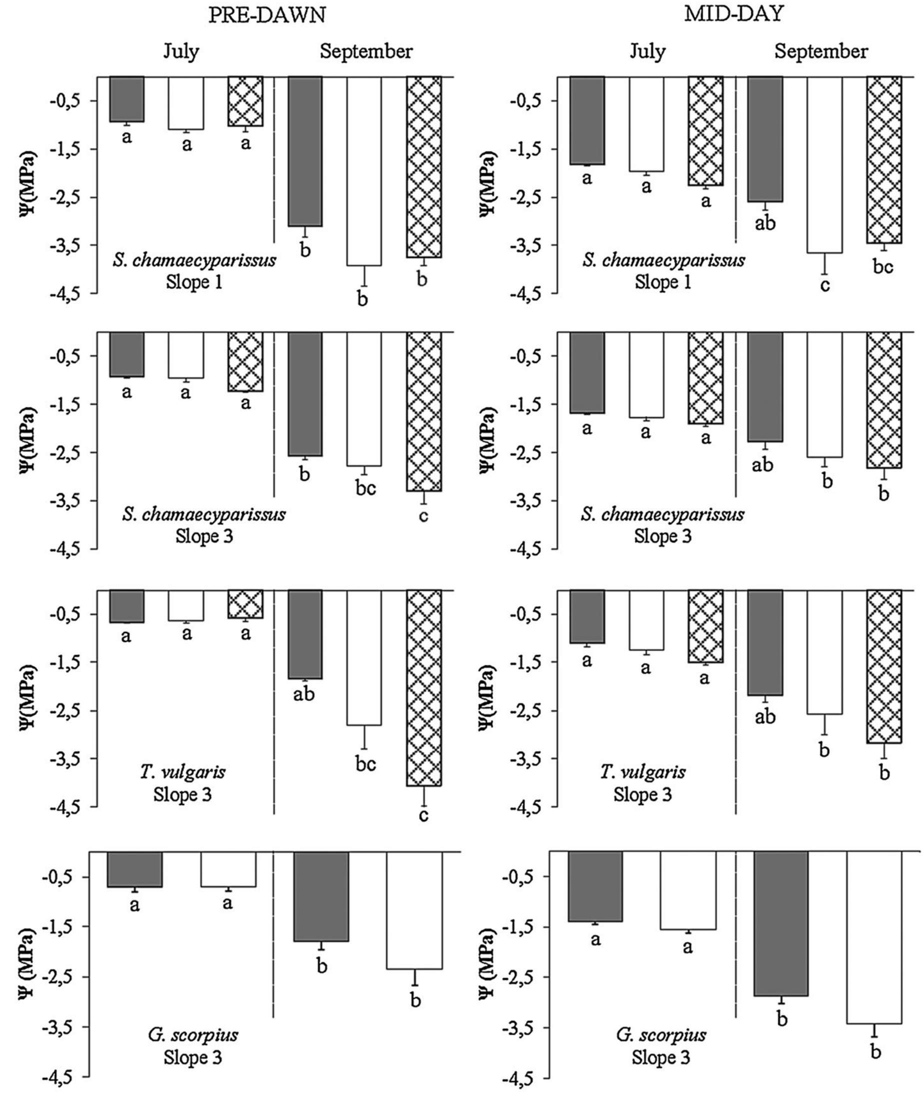

Figure 3. Mean leaf water potentials (whiskers indicate the standard error) of the woody species in the campaigns of July and September at predawn and midday. Grey bars, control; white bars, run-off exclusion treatment; grid bars, interpatch areas. Different letters indicate significant differences with the post hoc Tukey tests ($p < 0.05$).

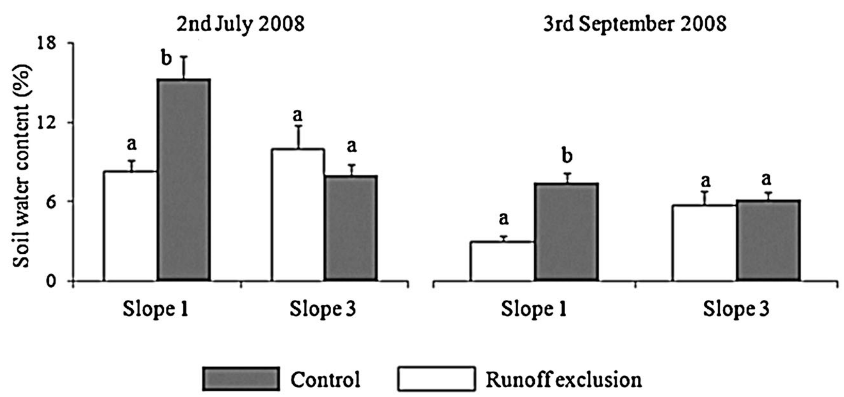

Figure 4. Mean soil water content in the sink patches subjected to both run-off treatments on the dates in which leaf water potential of woody plants was measured. Different letters indicate significant differences with Mann–Whitney *U*-tests for each slope and date ($p < 0.01$).

found similar results in natural ecosystems; for example, Noble *et al.* (1998) studied natural mulga woodlands of Australia and observed a depress in *Thyridolepis mitchelliana* (mulga grass) dry matter when the access of overland flow was prevented. Also, Schlesinger and Jones (1984) found less biomass and density of the shrubs *Larrea tridentata* and *Ambrosia dumosa* in areas of the Mojave desert that were isolated from overland flow by the ditches erected in 1936 during the construction of the Colorado river aqueduct. Although evidence for the importance of run-off

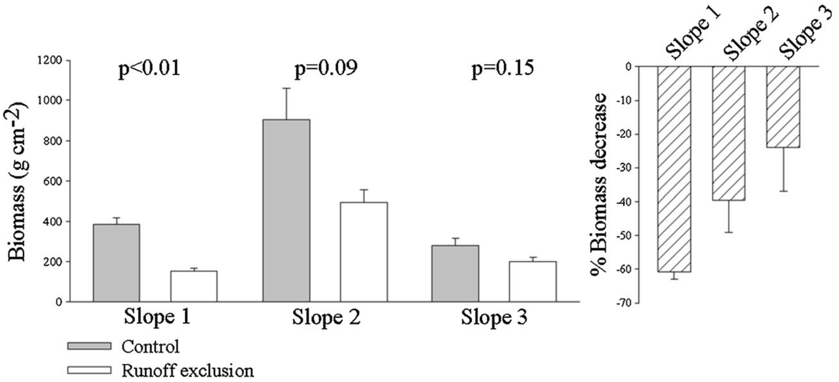

Figure 5. Left: Mean herbaceous production (whiskers indicate the standard error) in the vegetation patches subjected to different run-off treatments in the three slopes. *p*-values of Mann–Whitney *U*-tests are indicated. Right: Mean percentage of biomass decrease between control and run-off exclusion treatments in each slope.

redistribution between vegetation patches in the dynamics of semiarid ecosystems has been indicated by other authors (Ludwig *et al*., 2005; Wilcox *et al*., 2003), this is the first time in which empirical data on the effect of these interactions during the recovery process (aggradation) in artificial ecosystems is reported.

The analysis of leaf water potentials of woody plants at early and late summer allowed us to identify the conditions in which plants were more seriously affected by water stress. July conditions were much more benign than September ones because of the abundant rains occurred during spring; for that reason, no differences in water potential between treatments were found in that campaign, as soil moisture was high and plants experienced no water deficit. On the contrary, soil moisture in September was very low as expected after the long dry summer period, thus provoking conditions of water stress for plants. Here, we found significant differences between the slopes at both extremes of the disturbance gradient (total run-off at hillslope level). In slope 1, run-off exclusion created the least favourable conditions for plants, reaching plant water potential its minimum values under that treatment, especially at midday. Similar results were found by Seghieri and Galle (1999) in a run-off exclusion experiment in the banded vegetation of Niger: leaf water potentials of the dominant shrubs *Guiera senegalensis* and *Combretum micranthum* decreased in the plots subjected to run-off exclusion. However, in slope 3, the worst conditions for plants were not the run-off exclusion patches but the interpatches, as significant differences in water potential were found between control patches and interpatches (mainly at predawn), run-off exclusion patches having intermediate values between both. Thus, in this slope, a new factor modulating availability of water resources for plants must be considered: the presence of the shrub *Genista scorpius* that constitutes the principal species in the vegetation patches with the other species growing under its canopy.

Patches of *G. scorpius* enhance performance of vegetation under its canopy. In fact, 63% more herb production was found in the understorey of *G. scorpius* shrubs than in interpatches in slope 3, and no significant differences were found in leaf water potentials of *T. vulgaris* and *S. chamaecyparissus* growing in the *G. scorpius* understorey between control and run-off exclusion treatments. Thus, *G. scorpius* patches would act as fertility islands (Garner and Steinberger, 1989) in the constructed slopes or, in more ecohydrological terms, as 'islands of hydrologically enhanced biotic productivity', according to Rango *et al.* (2006). In fact, differences in edaphic properties that improve water infiltration such as bulk density and soil surface strength have been found under *G. scorpius* canopies, and these vegetation patches have been classified as 'deep sinks' for its capacity to conserve against evaporation deep infiltrated water that can be used by *G. scorpius* and associated plants during dry periods (Merino-Martín *et al*., 2012b). This agrees with the conclusions of Maestre *et al.* (2009) about shrub encroachment in Mediterranean environments: shrubs with sprawling canopies that extend horizontally (like *G. scorpius*) enhance the resource sink behaviour of the ecosystem, in contrast with those shrubs that usually invade other semiarid areas of North America (e.g. mesquite, creosote bush).

Therefore, we observed that as total run-off decreases, the run-off–run-on interactions become less intense at the same time as plants seem to play a more determinant role in the spatial distribution of water resources. Our disturbance gradient of run-off at hillslope scale expresses the capacity of the system to retain water resources, and this capacity seems to be related to the fact that vegetation plays an active role in the mosaic-generation process. Thus, colonization of *G. scorpius* would initiate a 'nucleation' process where vegetated patches become hot spots of soil and vegetation change (Puigdefábregas *et al*., 1999). Turnbull *et al.* (2012) state that stabilizing feedbacks are generally associated with enhanced infiltration and the trapping of sediment and other resources that enable plant growth and continued retention of plant essential resources; in this sense, we can interpret the presence of *G. scorpius* patches as a signal of ecosystem recovery. Thus, *G. scorpius* can be considered a key species for the ecological succession in these reclaimed landscapes in a semiarid environment. Similarly, Maestre and Cortina (2004) have identified other shrubs as keystone species because of their role in infiltration and nutrient cycling in semiarid ecosystems of SE Spain (e.g. *Pistacia lentiscus*, *Quercus coccifera*). Therefore, it would be very convenient to introduce these species in early phases of restoration projects and avoid the mere revegetation with fast growing species that could afterwards ‘arrest’ the process of ecological succession (Moreno-de las Heras *et al*., 2008).

The analysis of the intensity of the ecohydrological interactions between vegetation patches in artificial slopes in a run-off gradient offers important implications for the design of restoration projects in semi-arid environments. In fact, Turnbull *et al*. (2012) point to the importance of ecohydrological feedbacks for the structure and function of drylands and conclude that understanding these processes may be crucial for their restoration, for example, by exploiting the strength of stabilizing ecohydrological feedbacks to increase the resilience or to push ecosystems towards a more desirable state. Some authors have stated that the best way to rehabilitate dysfunctional semiarid ecosystems is to restore vegetated patches like structures that best trap and store limited soil resources (Ludwig *et al*., 1999). One of the few experiences following this recommendation has been the establishment of run-off catcher structures in degraded *Acacia aneura* woodlands in Australia by means of piles of large tree branches and shrubs located along contour lines. This improved soil properties (Tongway and Ludwig, 1996) and increased perennial species abundance (Ludwig and Tongway, 1996). Also, Manu *et al*. (2000) described a successful project of restoration of degraded tiger bush vegetation in Niger with microcatchments run-off harvesters and the introduction of selected woody species. However, more investigation on the ecohydrological interactions during the recovery process in reclaimed ecosystems is needed to improve the efficiency of restoration practices in drylands.

CONCLUSIONS AND PRACTICAL IMPLICATIONS

We have demonstrated that run-off redistribution between run-off source and sink patches are crucial for the dynamics of artificial slopes in water limited environments, as improvements in the water status of soils and vegetation have been found. Also, the intensity of this ecohydrological interaction increases with the volume of run-off exported at hillslope scale, provided that thresholds that initiate intense soil erosion processes have not been surpassed. In the slope with low volumes of run-off at hillslope scale, we have also observed a shift from a passive to an active role of plants in the structuring of the mosaic of vegetation patches, mediated through the presence of the shrub *Genista scorpius* that creates islands of hydrologically enhanced biotic productivity. Some important implications for dryland restoration derive from these results, as run-off, which usually characterize the early phases of these artificial ecosystems, could be redirected to target nuclei in which introduced key species would benefit from this extra water supply. Through their capacity to improve soil properties and to enhance vegetation establishment, these shrub patches would accelerate the ecological succession while preventing the loss of water and soil resources produced by soil erosion. The concept of ‘run-off expert management’ emerges as an important issue for restoration, with implications for the design of topography, soil management and revegetation of reclaimed ecosystems.

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