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Plant Spatial Pattern Predicts Hillslope Runoff and Erosion in a Semiarid Mediterranean Landscape

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ABSTRACT

The importance of the spatial pattern of vegetation for hydrological behavior in semiarid environments is widely acknowledged. However, there is little empirical work testing the hypothetical covariation between vegetation spatial structure and hillslope water and sediment fluxes. We evaluated the relationships between vegetation structural attributes (spatial pattern, functional diversity), soil surface properties (crust, stone, plant, and ground cover, and particle size distribution) and hillslope hydrologic functioning in a semiarid Mediterranean landscape; in particular, we tested whether decreasing patch density or coarsening plant spatial pattern would increase runoff and sediment yield at the hillslope scale. Runoff and sediment yield were measured over a 45-month period on nine 8 × 2-m plots that varied in vegetation type and spatial pattern. We grouped vegetation into functional types and derived plant spatial pattern attributes from field plot maps processed through a GIS system. We found that there was an inverse relationship between patch density and runoff, and that both runoff and sediment yields increased as the spatial pattern of vegetation coarsened. Vegetation pattern attributes and plant functional diversity were better related to runoff and sediment yield than soil surface properties. However, a significant relationship was found between physical crust cover and plant spatial pattern. Our results present empirical evidence for the direct relationship between the hydrologic functioning of semiarid lands and both the spatial pattern and the functional diversity of perennial vegetation, and suggest that plant spatial pattern, physical crust cover, and functional diversity may be linked through feedback mechanisms.

Key words: ecohydrology; spatial pattern; runoff; erosion; plant functional diversity; ecosystem functioning; surface properties; semiarid hydrology.

INTRODUCTION

It is widely accepted that vegetation strongly affects hydrologic processes. Many studies have shown the negative relationship between plant cover and runoff or sediment yield (see, for example, Elwell and Stocking 1976; Thornes 1990). Plant canopy and ground cover are the parameters that have most commonly been used in the study of the effect of vegetation on water and sediment fluxes. However, especially in drylands with patchy vegetation, other landscape metrics may have an important influence in the hydrologic behavior. Thus, strong ecohydrologic linkages between plant spatial pattern and runoff and erosion have been pointed out for several dryland environments (Abrahams and others 1995; Ludwig and Tongway 1995; Davenport and others 1998; Cammeraat and Imeson 1999; Wilcox and others 2003; Puigdefábregas 2005).

In arid and semiarid landscapes, the vegetation is commonly distributed in patches interspersed

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within a matrix of bare ground and low vegetation cover. In general, there are differences in soil properties between vegetation patches and open areas that may exert an important influence on soil and water fluxes. Soils beneath vegetation patches are commonly characterized by higher soil organic content, total porosity and soil aggregate stability, less developed mineral and biological soil crusts, and lower surface compaction than soils in the interpatch areas (Greene 1992; Bochet and others 1999; Puigdefábregas and others 1999; Schlesinger and others 1999; Maestre and others 2001, 2002). These differences commonly result in lower runoff and sediment yields, and higher soil moisture contents in vegetation patches than in open areas (Ludwig and Tongway 1995; Puigdefábregas and Sánchez 1996; Cerdà 1997; Bergkamp 1998; Reid and others 1999; Bhark and Small 2003; Bochet and others 2006). At hillslope and catchment scales, other hydrologic processes such as reinfiltration and concentration of surface runoff have to be taken into account. Vegetation patterns with high patch density can be expected to involve important obstructions to the surface flow and therefore increased opportunities for reinfiltration. In contrast, in low patch density patterns, the surface flow is more likely to present a higher concentration and thus a higher velocity because the bare surfaces are larger and potentially more connected (Tongway and Ludwig 1997; Cross and Schlesinger 1999). Moreover, feedbacks linking the spatial patterns of vegetation and soil properties can exacerbate the effect of plant pattern on water flows and erosion, as the surface soil degradation and the loss of water and nutrients resulting from enhanced runoff and erosion in low-density patterns may in turn adversely impact the vegetation and further reduce the patch density. Similar mechanisms have been considered in conceptual models that relate thresholds in soil erosion rates to the connectivity of interpatch areas (Davenport and others 1998). Recent simulation modeling has also shown that hillslopes with clumpy distributions of vegetation yield more runoff and erosion than identical hillslopes with spatially uniform distributions, although these differences decrease for storms of high magnitude (Boer and Puigdefábregas 2005). This simulation approach also shows that fine-grained vegetation patterns are more efficient than coarse-grained patterns in capturing water and sediment fluxes, as suggested by several previous field observations (Abrahams and others 1995; Wainwright and others 2000).

Plant spatial pattern has also been shown to be related to key structural variables as species richness and biodiversity (Bascompte and Rodríguez 2001; Maestre 2004), which in turn are thought to affect many ecosystem processes and services (Tilman 1999; Balvanera and others 2001). Morphological and physiological traits of plant species can have a substantial effect on the interaction between plants and water and sediment fluxes (Abrahams and others 1995; Reynolds and others 1997; Breshears and Barnes 1999; Foster and Brooks 2005; Bochet and others 2006); therefore, the number and diversity of plant functional groups, and the related variation in the structural complexity of the vegetation, can be expected to affect hydrologic processes. However, these relationships have been poorly explored (Casermeiro and others 2004).

Despite recent evidence of increasing interest in the role of the vegetation pattern on runoff and soil erosion (see, for example, a review in Puigdefábregas 2005), there is still a lack of experimental fieldwork testing or quantifying the underlying key assumptions. In this study, we established a set of experimental field plots to examine the relationships between the vegetation spatial pattern and the hydrologic behavior in a semiarid Mediterranean landscape. The field plots varied in vegetation type and spatial pattern. We measured runoff and sediment yield in these plots under natural rainfall conditions over a 4-year period.

Plant spatial patterns can be described by using a variety of metrics and indicators, from simple patch attributes such as cover, number, shape, and orientation, and any combination of these (see, for example, Li and Archer 1997; Tongway and Ludwig 1997; Ludwig and others 2000), to more complex indices that measure the degree of fragmentation or connectivity of plant and soil spatial patterns (Wu and others 2000; Ludwig and others 2002). In this paper, the variables we used to describe the plant spatial pattern were the Directional Leakiness Index (DLI), developed by Ludwig and others (2002), and the patch density. The DLI is based on the distances between patches. It has been conceptually related to the connectivity of bare soil areas and the efficiency of the landscape to retain resources flowing across surfaces, and it has been proven to be sensitive to patch cover, shape and orientation (Ludwig and others 2002). We used DLI as an integrate indicator of the grain size and connectivity of bare soil pattern, and thereby of the degree of pattern coarsening. Plant functional diversity and a set of soil surface properties potentially related to plant spatial pattern and hillslope hydrology were also assessed.

In this work, we specifically addressed three questions. First, will a decrease in patch density or an increase in the grain size and connectivity of the open interpatch areas increase runoff and sediment yield? Second, if there were any relationships between patch pattern and runoff and sediment yield, how does the storm event size affect those relationship? Third, which plant and soil surface attributes are more related to the observed spatial pattern and hydrologic response?

METHODS

Study Site

The present work was conducted on the south-facing slopes of El Ventós Experimental catchment (38°28′N, 0°37′W), located in Alicante province, SE Spain (Figure 1). Previous research in the catchment was focused on the effect of vegetation type on the soil water balance and aquifer recharge, pointing to alpha grass (*Stipa tenacissima* L.) steppes as the most runoff-productive vegetation cover (Bellot and others 1998; Chirino and others 2006). The study site is characterized by steep hillslopes, with slope angles greater than 20% throughout most of the area, and very shallow soils (average soil depth = 12 cm). Soils are loamy–silty loam, Lithic Calciorthid, derived from Upper Cretaceous limestones and marls. The soil organic matter content (0–10 cm depth) ranges from 3.6 to 8.1% (E. Chirino, unpublished data). Mean annual rainfall is 270 mm and mean annual temperature is 18.2°C (Agost Meteorological Station, 1976–2005 period). Mean monthly rainfall ranges from 9 mm (July) to 35 mm (October), following a bimodal distribution with two rainy seasons, autumn and spring, and a dry period in summer. High rainfall variability between and within years is very common in the area. The maxima in monthly temperature and potential evapotranspiration occur in July or August and the annual potential evapotranspiration is approximately 1,350 mm (FAO–Penman–Monteith). The vegetation is a rather interspersed mosaic of open *S. tenacissima* steppes and dwarf shrublands with gradual transitions between them. These plant communities are widely distributed within the semiarid and dry areas of the Mediterranean basin (Le Houérou 2001) and derive from grasslands and woodlands that have been subjected to long-term exploitation and degradation by human activities such as fiber and wood harvesting, grazing, and repeated burning (Barber and others 1997; Puigdefábregas and Mendizábal 1998). The vegetation cover is arranged in vegetated patches of one or several plant individuals and species, separated by interpatches of bare ground. The main vegetation patches are single *S. tenacissima* tussocks, shrub individuals or clones (for example, *Quercus coccifera* L., *Rhamnus lycioides* L, and *Erica multifora* L.), subshrubs (for example, *Globularia alypum* L.), and single or mixed patches of sod-forming short grasses, mainly the sprouting perennial grass *Brachypodium retusum* (Pers.) P. Beauv., and chamaephytes (for example, *Teucrium pseudochamaepitys* L., *Fumana ericoides* L.). The interpatch areas have a high cover of rock fragments and physical and biological soil crusts dominated by cyanobacteria. Although the plant cover is highly constant throughout the whole study site, at around 40%, there is an important variation in the plant spatial pattern within the site, thus facilitating the analyses of the relationships between plant pattern and hydrologic response without the confounding effect of differences in plant cover.

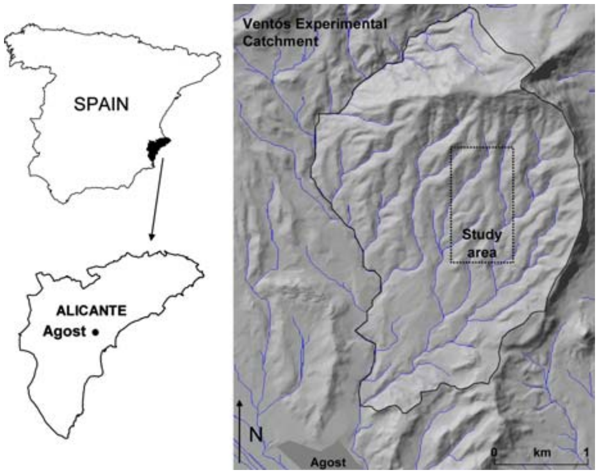

Figure 1. Location map of the study area.

Runoff and Erosion Measurements

Nine 8 × 2-m closed runoff plots were installed in the study area. The plots were distributed on three different slopes, covering a wide range of variation in vegetation-patch density and spatial arrangement. Slope angle (24°–26°), relative position on the hillslope (intermediate), and aspect (S–SW) were more-or-less similar between plots.

Surface runoff and sediment yields were measured after each natural rainfall event for a period of 45 months (March 2002–December 2005). The runoff from each plot was collected in a Gerlach trough connected to a 500-l tank, where it was measured. Sediments that had settled on the base of the trough were directly collected, taken to the laboratory, dried (60°C, constant weight), and weighed. The amount of sediments in the runoff was estimated by desiccation of the runoff samples taken from the collection tanks. Total runoff and total sediments produced on each plot during the study period were calculated by adding up the event-based data. Rainfall was measured with a tipping-bucket rain gauge at a standard meteorological station, located about 1.5 km from the experimental plots, which recorded rainfall with a temporal resolution of 5 min. During the study period, the spatial variation in total rainfall within the study area was considered to be negligible according to the rainfall data recorded from three pluviometers located next to the study plots and the rain gauge located at the weather station.

Measurements of Vegetation and Soil Properties

The perennial plant species were grouped into functional types based on the life-form and morphological characteristics that could affect rainfall partitioning, infiltration, and overland flow. We identified five functional groups: tussock grasses, sod-forming short grasses, chamaephytes, subshrubs and shrubs. The contribution of annual species to the plant cover in the study area was negligible. The canopies of the perennial plant patches within the runoff plots were visually outlined and mapped in the field and labeled as functional types. To reduce errors during mapping we established a mesh of 1 m^2 subplots, which were used as scale references. In our system, dominated by dense tussock and sod-forming grasses, the canopy cover approaches the plant ground cover. The minimum patch width for inclusion on the map was 4 cm, as we considered that this was the minimum size for an effective obstruction to the surface flow. The field maps of all plots were scanned and processed with the GIS system ArcView© (Environmental Systems Research Institute Inc., California). From each map, we derived patch cover, patch density, and the interpatch area directly connected to the trough (direct drainage). To calculate the DLI (Ludwig and others 2002), we converted the previous vector maps to raster-based maps, with 8-cm pixels classified as patches or interpatches, and applied the DLI Calculator© (A. Liedloff, Tropical Ecosystems Research Centre, CSIRO, Australia) to these maps. The DLI is obtained from an algorithm based on the distance between patches according to a given flow direction, reflecting the grain size and connectivity of bare interpatch areas. Due to the high inclination of the experimental slopes, we assumed that the main flow direction was downslope. When the flow direction is unknown, a variant of DLI called the multi-directional leakiness index (MDLI) can be applied. DLI ranges from 0 (minimum connectivity of bare interpatches, no leakiness, full retention) to 1 (maximum connectivity of bare interpatches, no retention, totally leaky). Perennial plant functional diversity was estimated by calculating Shannon's diversity index (Greig-Smith 1983) from the cover values of the various functional groups. The cover of stones, physical soil crust and outcrops was measured on each runoff plot by the point-intercept method. Point measurements of these variables were made every 10 cm along two parallel downslope transects on each plot. The stone cover was grouped into two positional classes: stones lying on the surface and stones partially embedded in the soil. Particle size distribution (pipette method) of surface soil was estimated from three soil cores (0–10 cm depth) sampled on each plot.

Statistical Analyses

We used Pearson's correlation to explore the covariation between the vegetation and pattern variables (total plant cover, functional diversity, patch density, direct drainage, DLI), soil variables (total ground cover, surface stone cover, embedded stone cover, outcrops cover, crust cover, and particle size distribution) and total runoff and sediment yields. Regression and partial correlation methods were used to analyze the relationships between the response variables (total runoff and sediment yields) and the best-correlated explanatory variables.

RESULTS

Rainfall, Runoff, and Sediment Yield

During the 45-month study period, the highest rainfall amount and intensity recorded were 50 mm and 56 mm h^{-1} (I_{15}max). Rainfall thresholds for runoff and sediment yields were low, about 3 and 6 mm, respectively. A large number of rainstorms (55 events) produced runoff on at least one of the experimental plots, and about half of them yielded sediments. However, most of the runoff and sediments were produced by a few rainfall events: six storms yielded more than 50% of the total runoff, and two storms yielded more than 50% of the total sediments measured during the study period. On average, total runoff accounted only for 1.5% of the annual water budget. On a event basis, plot runoff was linearly related to rainfall amount ($F_{1,54} = 13.6$, $r^2 = 0.61$, $P < 0.001$). Total runoff and sediment yield varied greatly

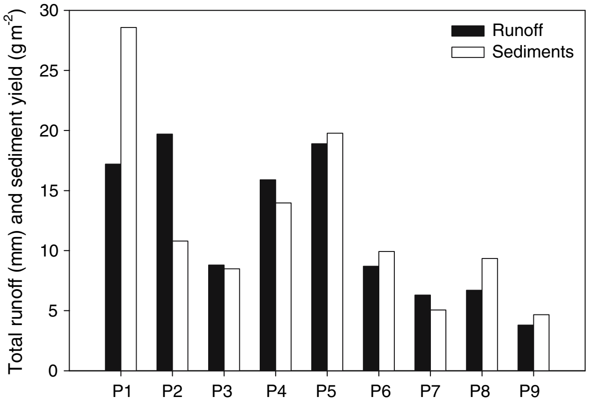

Figure 2. Total runoff and total sediment yield produced on the experimental plots during the study period (March 2002–December 2005).

between the experimental plots (Figure 2), ranging from 3.8 mm (P9) to 19.7 mm (P2), and from 4.7 g m^{-2} (P9) to 28.6 g m^{-2} (P1), respectively. Total sediment yield showed a positive exponential relationship with total runoff ($F_{1,7} = 13.6$, $r^2 = 0.66$, $P = 0.008$).

Surface Soil Properties, Vegetation Pattern, and Functional Diversity

Vegetation cover was below 50% on all of the plots (41% ± 3, average ± SD), and there were only slight variations between the plots in this respect (Figure 3). However, the proportion of bare soil was relatively low due to the high stone cover, which varied between 26 and 44%. Surface and embedded stone cover ranged from 18 to 35%, and from 3 to 16%, respectively. Physical crust cover was relatively low, ranging from 2 to 24%, but showed the highest variability. On some of the plots (for example, plots P5 and P6), most of the bare soil surface was covered by soil crusts, whereas soil was generally uncrusted on other plots (for example, P7, P8, and P9). Physical crusts were formed in the open spaces between plants and were commonly found together with biological crusts dominated by cyanobacteria. Outcrop cover was very small on most of the plots and nil on three of them. Particle size distribution of the surface soil slightly differed among plots, with silt content showing the highest values in all cases (Table 1).

Although plant cover was similar between plots, the size, shape, and spatial distribution of the vegetation patches varied greatly (Figure 4). Patch density varied from 1 to 8.5 patches per square meter, and the grain size and degree of bare soil connectivity, measured by the DLI, ranged from 0.21 to 0.55. The interpatch area draining directly to the trough (direct drainage) also showed a wide range of variation (0.44–3.04 m^2). Moreover, vegetation composition and functional diversity varied greatly between plots. On some plots, most plant individuals belonged to a single functional group (for example, plots P1 and P2) where the tussock grass *S. tenacissima* greatly dominated the plant cover. Conversely, plots P7, P8 and P9 showed a rather even distribution of functional groups, with an important contribution from sod-forming short grasses like *B. retusum*, subshrubs like *G. alypum* and *A. citysoides*, and chamaephytes. The rest of the plots showed an intermediate diversity of functional groups. Perennial plant functional diversity ranged from 0.6 to 1.3.

Pearson‘s coefficients of bivariate correlations between soil and vegetation properties are shown in Table 2. The two spatial pattern variables considered, DLI and patch density, were inversely correlated. Patch density was highly and positively correlated with plant functional diversity. DLI was positively correlated to crust cover and inversely correlated to plant functional diversity. The direct drainage area was positively correlated to DLI and inversely correlated to plant functional diversity. Except for crust cover, soil surface cover variables did not show any correlation with spatial pattern variables or functional diversity. Sand content was positively correlated with plant cover and embedded stone cover, and clay content was positively correlated with functional diversity (Table 2).

Soil and Vegetation Properties versus Runoff and Sediment Yield

Plant pattern-related properties and plant functional diversity showed significant correlations with the hydrologic response variables (Table 2). Both total runoff and sediment yield were positively correlated with DLI and inversely correlated with plant functional diversity. Patch density was negatively correlated to runoff, and direct drainage was positively correlated to sediment yield. Of the soil and vegetation variables considered, DLI was the most related to the hydrologic response of the experimental plots, showing a very significant linear relationship with total runoff ($F_{1,7} = 17.8$, $r^2 = 0.72$, $P = 0.004$) and a highly significant exponential relationship with sediment yield ($F_{1,7} = 27.9$, $r^2 = 0.80$, $P = 0.001$; Figure 5).

To determine the independent effect of DLI on runoff and sediment yield, we used partial correlation analysis, controlling for the effects of the variables correlated with DLI, that is, crust cover, patch density and direct drainage. Plant functional

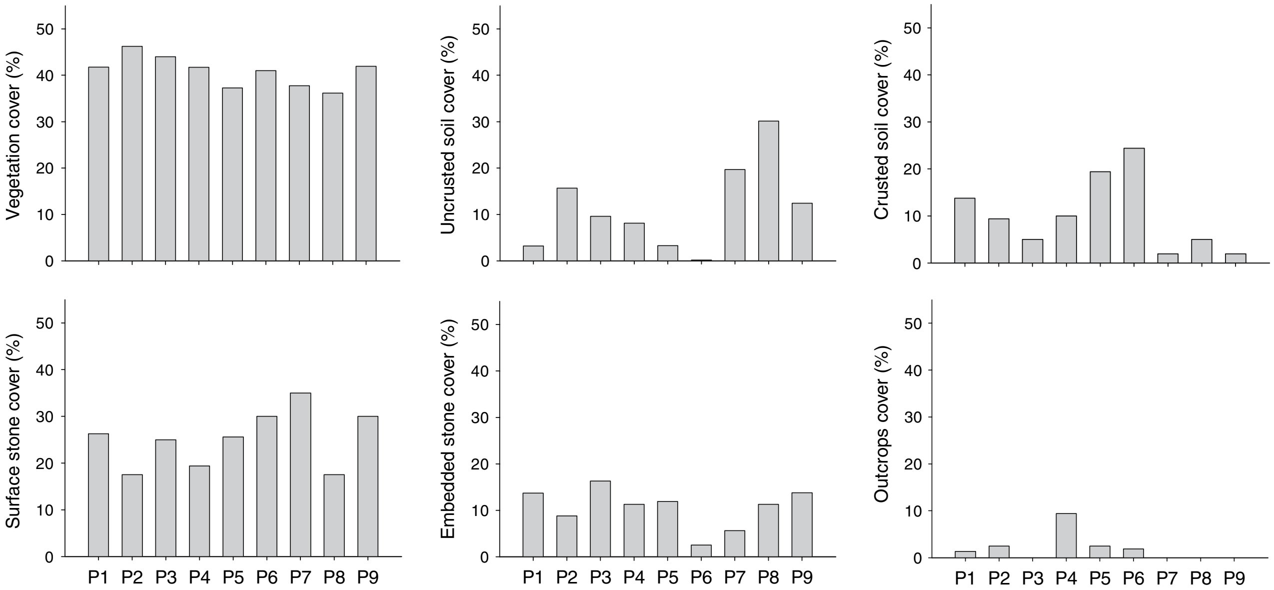

Figure 3. Cover values of vegetation and soil surface properties as a proportion of total cover on the experimental plots.

Table 1. Particle Size Distribution of the Surface Soil (0–10 cm Depth) on the Experimental Plots (P1–P9)

Plot	Sand (%)	Silt (%)	Clay (%)
P1	31.9 ± 1.3	42.4 ± 3.6	25.8 ± 2.3
P2	31.6 ± 4.6	44.5 ± 5.6	23.9 ± 2.3
P3	35.9 ± 5.5	42.8 ± 7.1	21.3 ± 1.8
P4	29.7 ± 3.3	47.0 ± 2.5	23.2 ± 1.2
P5	25.9 ± 1.0	51.8 ± 0.5	22.3 ± 1.4
P6	24.7 ± 2.7	52.5 ± 1.4	22.8 ± 1.9
P7	24.0 ± 1.0	47.2 ± 2.5	28.8 ± 2.6
P8	25.2 ± 4.1	47.1 ± 2.3	27.7 ± 3.0
P9	28.9 ± 0.7	45.6 ± 0.4	25.6 ± 1.4

Mean values ± SD.

diversity was not included in this analysis because it was highly correlated with patch density (Table 2). We found a positive independent effect of DLI on runoff ($r = 0.87$, $P = 0.026$, df = 4) but not on sediment yield ($r = 0.70$, $P = 0.120$, df = 4). We found similar results after controlling for crust cover, functional diversity, and direct drainage ($r = 0.83$, $P = 0.039$, df = 4, for runoff, and $r = 0.677$, $P = 0.140$, df = 4, for sediment yield).

We studied the role of event size in the effect of vegetation pattern on runoff by analyzing the relationships between DLI and two groups of runoff data: total runoff generated from the largest runoff events, responsible for 15% of the average total runoff during the study period ($n = 2$), and total runoff from the smallest runoff events, responsible for the same amount of runoff ($n = 37$). The accumulated runoff from the two largest runoff events during the study period was strongly related to DLI ($P < 0.001$). However, the accumulated runoff produced from the low magnitude events did not show any relationship with this index ($P = 0.191$; Figure 6).

Total ground cover (plant + stone + outcrop cover), plant cover, crust cover, and stone cover values (for total, surface and embedded stones) were not correlated with total runoff or sediment yields (Table 2). However, an exploratory analysis of these data suggested a direct covariation between crust cover and runoff and sediment yields which was not significant due to the particular behavior of plot 6 (Figure 7). None of the particle size classes was correlated with total runoff or sediment yields.

DISCUSSION

The potential for retaining resources, especially water, within the system is crucial to ecosystem functioning in semiarid and arid lands. According to recent theoretical and simulation modeling studies, ecosystem efficiency in retaining water and sediments becomes higher as the density and cover of perennial vegetation patches increase and the grain size of the vegetation pattern decreases (Tongway and Ludwig 1997; Boer and Puigdefábregas 2005). To our knowledge, our results present the first empirical evidence for the direct relationship between hydrologic functioning in

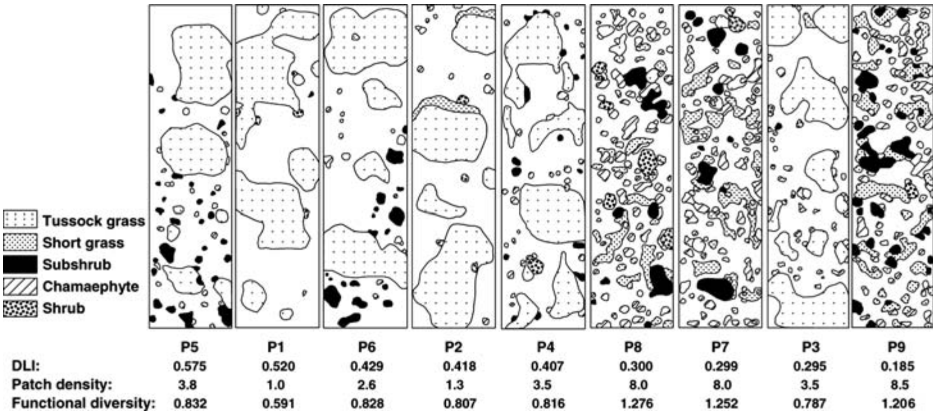

Figure 4. Maps of vegetation patches and interpatches on the experimental plots arranged from higher to lower Directional Leakiness Index (DLI) values, that is, from higher to lower leakiness, from *left* to *right*. The *shaded patches* are vegetation patches of different functional types.

semiarid lands and the spatial pattern and functional diversity of the perennial vegetation, and show that the spatial arrangement of vegetation patches alone can predict runoff and sediment yield at the hillslope scale.

A number of studies conducted in the northern Sonoran and Chihuahuan deserts reported an increase in overland flow and erosion rates linked to the replacement of grasslands by shrublands. This change in the hydrologic response has been attributed to changes in plant canopy spatial heterogeneity, with larger bare interpatch areas in shrublands than in grasslands (Abrahams and others 1995; Schlesinger and others 1999; Wainwright and others 2000). In semiarid rangelands of North Queensland, Australia, Bartley and others (2006) found large differences in runoff and sediment yield measurements from three hillslopes with similar total plant cover but different plant cover arrangements. The location of bare areas close to the flumes where the measurements were made, together with other co-occurring attributes such as hillslope topography and soil characteristics, were thought to explain the hydrologic response. Our results provide evidence for the relative importance of various pattern and structural attributes of vegetation and soil surface properties on hillslope hydrology and show that the grain size of the bare interpatch pattern is the attribute that best explains the hydrologic response in a water-limited landscape.

We found an inverse relationship between patch density and runoff, which confirms predictions of previous modeling studies. However, the grain size and connectivity of the interpatch pattern, measured as the leakiness index, DLI, was the variable that correlated best with the runoff and sediment yield. Therefore, even in the case of high patch density values, high runoff and sediment yields could be expected if plant patches were arranged in a clumped pattern that resulted in a coarse-grain pattern of bare areas. Indeed, after controlling for the effect of DLI on runoff, using partial correlation analysis, no relationship between patch density and runoff was found (data not shown).

The exponential relationship between DLI and sediment yield is consistent with the exponential relationship found between runoff and sediment yields, and suggests that runoff energy for erosion is increasingly enhanced on plots with larger interpatches as a result of higher water flow concentration and velocity. These hydraulic-parameter changes associated with coarser-grained plant spatial patterns have been reported previously in semiarid southwestern USA areas (for example, Wainwright and others 2000). Additionally, soil surface protection from raindrop impact is lower in coarse-grained patterns (Abrahams and others 1995), which may synergistically contribute to enhancing soil erosion.

Using a simulation modeling approach, Boer and Puigdefábregas (2005) found that the influence of vegetation pattern on the hillslope hydrologic response decreased with the size and intensity of the storm. The authors suggested that during high intensity storms (60–70 mm h^{-1}) both bare soil and vegetation patches work as runoff sources, masking the effect of the plant pattern. Conversely, we found a strong relationship between vegetation spatial pattern and the total runoff produced by the largest events. This disagreement could be attributed to the different ranges of storm magnitude used in both analyses, as the highest storm intensity recorded in our study was 38 mm h^{-1} (I_{15}max). However, a number of field experiments have shown that plant patches maintain their ability to act as runoff sinks under very heavy rainfalls (see, for example, Cerdá 1997), which is in agreement with our findings. On the other hand, the lack of relationship between DLI and total runoff when only small events were considered in the analysis, suggests that the average length of the

Table 2. Pearson's Coefficients of Bivariate Correlations between Vegetation, Surface Properties and Hydrological Variables

	Ground cover (%)[1]	Plant cover (%)	SS cover (%)[2]	ES cover (%)[2]	Outcrop cover (%)	Crust cover (%)	Sand (%)	Silt (%)	Clay (%)	Func. diversity[3]	Patch density	Direct drainage[4]	DLI[5]
Plant cover (%)	0.50												
SS cover (%)	0.42	−0.23											
ES cover (%)	0.43	0.19	−0.33										
Outcrops cover (%)	0.12	0.18	−0.42	−0.44									
Crust cover (%)	−0.15	−0.04	0.01	−0.39	0.28								
Sand (%)	0.58	0.79*	−0.33	0.71*	0.08	−0.22							
Silt (%)	−0.41	−0.54	0.22	−0.64	0.17	0.62	−0.79						
Clay (%)	−0.35	−0.49	0.23	−0.23	−0.37	−0.52	−0.50	−0.15					
Functional diversity	−0.35	−0.55	0.24	−0.20	−0.38	−0.62	−0.58	0.17	0.68*				
Patch density	−0.18	−0.58	0.30	−0.02	−0.38	−0.64	−0.50	0.12	0.62	0.96***			
Direct drainage	0.13	0.13	−0.01	0.01	0.18	0.52	0.13	−0.15	0.01	−0.68*	−0.66*		
DLI	−0.11	−0.60	−0.18	−0.09	0.37	0.79**	−0.04	0.31	−0.37	−0.72*	−0.74*	0.71*	
Total runoff	0.01	0.30	−0.48	0.12	0.53	0.49	0.29	−0.03	−0.42	−0.75*	−0.79*	0.61	0.85**
Sediment yield	0.11	−0.02	−0.20	0.30	0.26	0.53	0.22	−0.11	−0.19	−0.73*	−0.65	0.89**	0.83**

[1] *Plant + stone + outcrop cover (%).*

[2] *SS = surface stone cover; ES = embedded stone cover.*

[3] *Perennial plant functional diversity.*

[4] *Bare surface (m^2) directly connected to the plot trough.*

[5] *Directional Leakiness Index.*

**Significant correlation at the $P < 0.05$ level, **significant correlation at the $P < 0.01$ level, ***significant correlation at the $P < 0.001$ level ($n = 9$).*

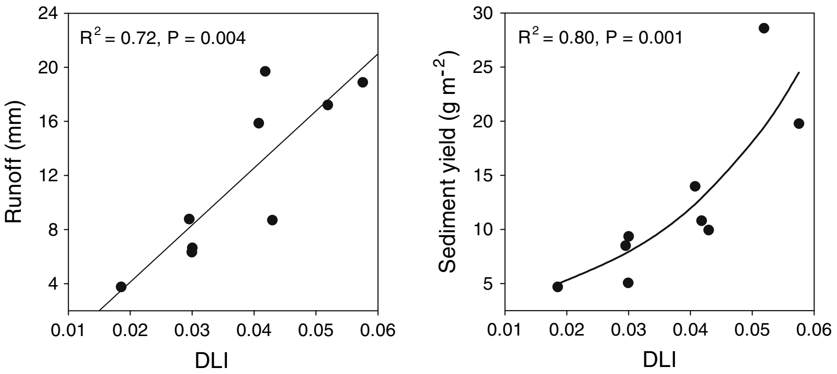

Figure 5. Total runoff (*left*) and sediment yield (*right*) versus the Directional Leakiness Index (DLI).

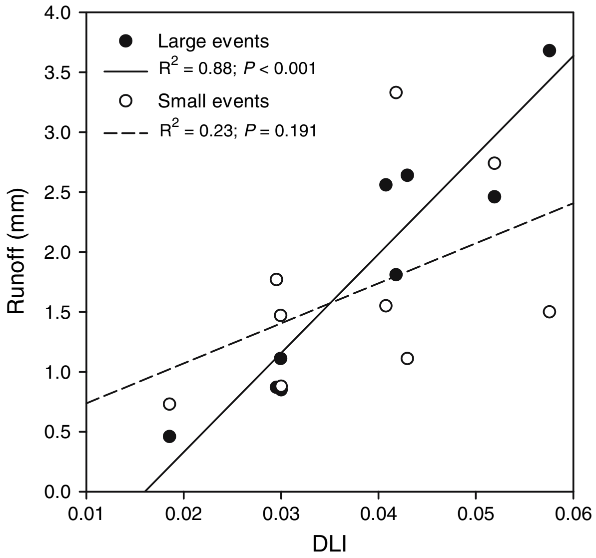

Figure 6. Total runoff generated from high magnitude and intermediate–low magnitude rainfall events versus the Directional Leakiness Index.

overland flow for the small runoff events was smaller than the average length of the bare soil interpatches. This contrasting response is in agreement with other studies (Bergkamp 1998; Calvo-Cases and others 2003) reporting that plot runoff produced by small rainfall events is mostly generated from bare areas close to the trough. The positive correlation between the sediment yield and the interpatch area directly connected to the trough suggests that vegetation patches acted as filters trapping part of the sediments transported by the runoff (Puigdefábregas and Sánchez 1996; Schlesinger and others 1999; Calvo-Cases and others 2003).

We found an inverse relationship between plant functional diversity and runoff and sediment yields. Despite the growing body of knowledge on the relationship between diversity and ecosystem functioning (Loreau and others 2001), the role of diversity in the hydrologic functioning of ecosystems remains unknown. It could be argued that differences in functional diversity may result in relevant differences in the range of plant community abilities to conserve water and soil in the system. However, there is little available evidence to either support or reject this hypothesis. Casermeiro and others (2004) analyzed as to which variables most influenced soil loss in scrubland communities in central Spain and found no relevant effect of plant diversity on soil erosion. In our case, the negative effect that increasing the functional diversity had on runoff and erosion may be mediated by the spatial pattern of vegetation. Distances between consecutive patches and patch density have been previously reported as explanatory variables for species diversity (Maestre 2004). Our results agree with this previous research and suggest that coarse-grain patterns of bare soil and low functional diversity may be linked through mechanisms that involve a reduction in the amount of suitable sites for plant establishment.

The lack of a relationship between the soil properties analyzed and the runoff or sediment yield was unexpected, as there is a large set of experimental evidence for the role of soil texture (for example, Bradford and others 1987), rock fragment cover (Poesen and others 1990), and soil physical and biological crusts (Morin and others 1981; Eldridge and others 2000; Belnap 2006) in controlling water and sediment surface flows. In our study, the soil texture and the rock fragment cover varied only slightly between plots, and their potential effects on the hydrologic response could have been masked by the effect of other explanatory variables. Conversely, crust cover greatly varied between plots. The lack of a relationship between this variable and the runoff or sediment yield was highly determined by the particular case of plot 6 (Figure 6), which included a transverse strip of *S. tenacissima* tussocks close to the trough

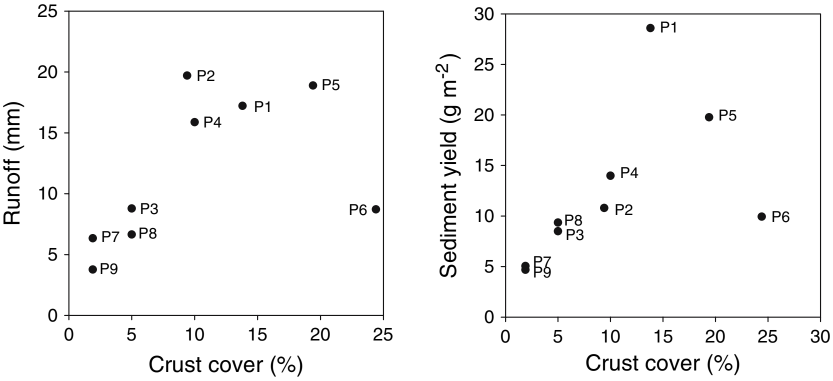

Figure 7. Total runoff (*left*) and sediment yield (*right*) versus crust cover.

(Figure 3), which probably trapped most of the runoff and sediments flowing downslope. The relationships found between crust cover and plant spatial pattern indicate that the effect of raindrop impacts on the soil surface could have been less effectively dissipated as the grain size and connectivity of the bare soil increased and the patch density decreased. The effects of biological soil crusts on hydrologic variables depend on the biological crust type (Belnap 2006). In our case, the biological component of the soil crust was dominated by cyanobacteria, which have been reported to decrease infiltration and enhance runoff (Maestre and others 2002).

As we expected, the small variation in vegetation cover did not explain the plot variation in runoff and sediment yields. Semiarid vegetation communities with similar low plant cover values but different size, shape, and/or density of vegetation patches are common in semiarid landscapes (see, for example, Abrahams and others 1995; Bartley and others 2006). This fact suggests that for a given climatic condition plant spatial pattern may be more sensitive to disturbances and degradation-driving factors than to total plant cover, which highlights the strength of our results. Although differences in plant cover are controlled by climate and resource availability, plant spatial pattern is probably caused by the interacting effects of historic spatial variations in land use and disturbance and the background environmental heterogeneity of semiarid landscapes, further enhanced by feedback mechanisms (Pickett and White 1985; Puigdefábregas 2005).

A number of patchiness metrics can be used to describe the plant spatial pattern (Gustafson 1998; Bastin and others 2002). We used an integrate indicator of resource retention—the DLI—to quantify the grain-size and connectivity of the bare interpatch areas, and therefore the potential of the system for conserving water and soil. Our results show that the DLI correlates very well with patch density and functional diversity, is highly sensitive to small differences in bare soil connectivity, and is a good explanatory variable for runoff and sediment yields; it therefore provides field evidence for the potential of this type of metrics based on the distance between patches as indicators of the hydrologic functioning of semiarid hillslopes. Besides plant pattern, the connectivity of surface flows is also affected by the topography. For example, surface microdepressions acting as water-ponding and sediment-trapping areas may involve the loss of connectivity; soil mounds associated with plant patches can also affect the convergence or divergence of surface flows. Thus, when topographic data are available, the use of indicators that combine vegetation pattern and topographic data, as the recently developed leakiness index, LI (Ludwig and others 2007), could greatly improve the predictions of runoff and sediment yields.

CONCLUSIONS

Our results present empirical evidence for the relationship between the hydrologic response of semiarid lands and both the spatial pattern and the functional diversity of perennial vegetation. Decreasing the patch density or coarsening the spatial pattern of the patch-interpatch system will lead to an increase in runoff and sediment yields. Feedbacks involving functional diversity and soil surface crusting seem to contribute to these relationships between spatial pattern and hydrologic functioning. Our results suggest that increasing functional diversity has a positive effect on soil and water conservation, and thereby on general ecosystem functioning, which may be mediated by the spatial pattern of the vegetation. In general, plant structural attributes are better explanatory variables for runoff and erosion than soil surface attributes.

Plant cover and biomass are the most common vegetation properties used for hydrologic modeling.

The results of this study suggest that these variables alone are not sufficient to predict runoff and sediment yields in patchy semiarid landscapes, where other patch metrics like patch number and grain-size pattern could be better hydrologic indicators than patch cover. Integrated indexes based on the distance between patches, such as the DLI, have great potential as surrogates for the hydrologic functioning in semiarid landscapes. These indices, as well as many other patch metrics, can be easily obtained from aerial photographs and incorporated into hydrologic and erosion models at the hillslope and catchment scales.

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