

The role of vegetation patterns in structuring runoff and sediment fluxes in drylands

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Abstract

The dynamics of vegetation-driven spatial heterogeneity (VDSH) and its function in structuring runoff and sediment fluxes have received increased attention from both geomorphological and ecological perspectives, particularly in arid regions with sparse vegetation cover. This paper reviews the recent findings in this area obtained from field evidence and numerical simulation experiments, and outlines their implications for soil erosion assessment. VDSH is often observed at two scales, individual plant clumps and stands of clumps.

At the patch scale, the local outcomes of vegetated patches on soil erodibility and hydraulic soil properties are well established. They involve greater water storage capacity as well as increased organic carbon and nutrient inputs. These effects operate together with an enhanced capacity for the interception of water and windborne resources, and an increased biological activity that accelerates breakdown of plant litter and nutrient turnover rates. This suite of relationships, which often involve positive feedback mechanisms, creates vegetated patches that are increasingly different from nearby bare ground areas. By this way a mosaic builds up with bare ground and vegetated patches coupled together, respectively, as sources and sinks of water, sediments and nutrients.

At the stand scale within-storm temporal variability of rainfall intensity controls reinfiltration of overland flow and its decay with slope length. At moderate rainfall intensity, this factor interacts with the spatial structure of VDSH and the mechanism of overland flow generation. Reinfiltration is greater in small-grained VDSH and topsoil saturation excess overland flow. Available information shows that VDSH structures of sources and sinks of water and sediments evolve dynamically with hillslope fluxes and tune their spatial configurations to them.

Rainfall simulation experiments in large plots show that coarsening VDSH leads to significantly greater erosion rates even under heavy rainfall intensity because of the flow concentration and its velocity increase. Copyright © 2005 John Wiley & Sons, Ltd.

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Introduction

It is widely accepted that overland flow and sediment yield diminish with increasing plant cover and this relationship is used to formalize the effect of vegetation in erosion models. However, field and experimental evidence shows that both the form this relationship takes and the distribution of scattered individual observations can vary substantially.

The relationship between plant cover and erosion has been described as both linear and exponential. The former is used in the Universal Soil Loss Equation (USLE) (Wischmeier, 1959). The latter has been reported in experimental watersheds (Noble, 1965) and has been much used in later erosion models designed for natural environments (Elwell and Stocking, 1976; Thornes, 1990). In both cases, the experimental support of such relationships in sparse vegetation is rather weak, and some authors claim that with less than 10 per cent plant cover the effect is insignificant (Schumm, 1977; Abrahams *et al.*, 1988).

However, variations in the linear and exponential relationships mentioned above have also been reported. Experiments carried out (De Ploey *et al.*, 1976; Morgan *et al.*, 1986) show that under certain conditions erosion increases

with increasing vegetation cover. The same findings and wider variance with more plant cover in spontaneous semi-arid grasslands have been reported (Puigdefabregas *et al.*, 1996; Nicolau *et al.*, 1996). These authors explain their results because in low vegetation cover, most of the available sediments have already been exhausted. Results of laboratory experiments (Rogers and Schumm, 1991) show that a general exponential decrease in erosion occurs above certain levels of plant cover, while with lower cover, erosion trends may show an exponential increase, slower linear increase, reach a plateau or even a maximum followed by a decrease. Such variability is interpreted by the authors as due to the effect of flow turbulence caused by plant stems with low cover, although there is still a need for a general theory to explain how the flow turbulence is affected by the shape, structure and density of stems.

These interpretations of the variability observed in the relationship between erosion and plant cover, point out the effect of vegetation on spatial heterogeneity. In fact, the dynamics of vegetation-driven spatial heterogeneity (VDSH) and its function in structuring downhill runoff and sediment flux, are receiving increasing attention from both ecological and geomorphological perspectives, particularly in arid regions, with sparse plant cover.

In arid landscapes, and in general in stressed environments, VDSH can be observed in the field on two scales, which are associated with individual clumps of plants on one hand and the spatial distribution of these clumps on the other. In the following they are referred to as patch and stand scales.

The present contribution has two objectives: first, to review field observations and experimental results on how VDSH develops at the patch and the stand scales, and which are the effects on runoff and sediment yield patterns; and second, to discuss the relevance and challenges of VDSH in erosion assessment.

Patch-scale VDSH

Vegetation canopies modify important functions that affect the soil beneath them and contribute to its differentiation from the surrounding areas, a feature which in turn has strong implications for sediment redistribution. The most widely accepted results of the extensive research carried out on this subject are summarized below.

Effects of plant canopies on the underlying soil

Radiation and water balances. Canopies play a role in shielding the soil from radiation and rainfall. The first causes a milder thermal regime with less temperature oscillation in the soil beneath (Domingo *et al.*, 2000). The latter involves partition of rainfall into three components, interception, throughfall and stemflow, the proportions of which vary depending on canopy structure, pattern of rainfall intensity and atmospheric conditions. Intercepted water is evaporated back into the atmosphere and typically amounts to 20–30 per cent of the rainfall (Hamilton and Rowe, 1949; Navar and Bryan, 1990; Slatyer, 1965; Domingo *et al.*, 1994). The process of partitioning into throughfall and stemflow is less well understood. Reported stemflow values vary from less than 5 per cent to 40 per cent of rainfall (Pressland, 1973; Mauchamp and Janeau, 1993; Domingo *et al.*, 1998) depending on the architecture and surface characteristics of the branch system.

Interception diminishes net rainfall and stemflow concentrates water at the stem bases, facilitating deeper infiltration beyond the reach of direct evaporation (De Ploey, 1984; Nulsen *et al.*, 1986; Martinez-Meza and Whitford, 1996). Stemflow and a slower evaporation rate due to radiative shielding (Domingo *et al.*, 2001) make for greater water availability in the soil beneath canopies than in bare ground.

A collateral consequence of the canopy as a rainfall shield is the reduction of the effective drop-fall length, and thereby, of its kinetic energy (Wainwright *et al.*, 1999), although exceptions in some canopy architectures and leaf morphologies, mainly concerning tall trees, may cause canopy drip to have larger drops (Brandt, 1989).

Organic carbon balance. Compared to bare ground, the soil beneath vegetated patches receives much larger organic matter inputs in the form of plant debris. This flux helps to maintain more active and complex soil biotic systems that feed upon this organic matter transforming it into organic soil compounds.

This enhanced biological activity and its products contribute to building stable soil aggregates (Imeson and Vis, 1982; Imeson and Verstraten, 1989), which dramatically influence soil structure and its implications for soil hydrology, erodibility and fertility (Cammeraat and Imeson, 1998; Cerda, 1998; Puigdefabregas *et al.*, 1999; Barthes and Roose, 2002) that lead to increased water storage capacity, saturated hydraulic conductivity and to decreased soil erodibility. The soil aggregation process is well reported and has been formalized through system dynamics modelling (Bergkamp, 1996).

As a consequence of these structural changes and of the milder microclimate beneath plant canopies, mineral crusts, both at the surface and sub-surface or sieving crusts, are not as well developed as in open areas (Puigdefabregas *et al.*, 1999). The same phenomenon, concerning microphytic crusts, has been reported in several dryland environments, for

example in tussock grasslands of *Stipa tenacissima* in the Mediterranean region (Maestre and Cortina, 2002; Maestre *et al.*, 2002), in banded vegetation in the Sahel (Malam Issa *et al.*, 2001), in the shrub and grasslands of the Chihuahuan desert (Whitford, 2002) and in the Australian chenopod shrublands (Graetz and Tongway, 1986).

In all these cases microphytic crusts grow on bare ground, away from the competition of grasses or bushes (Belnap *et al.*, 2001) and taking advantage of the enhanced dewfall (Kidron *et al.*, 2002). Some of them are nitrogen fixing and they can be N sources for arid soils (Evans and Lange, 2001). In soils with sand fractions of 80 per cent or less they increase infiltration (Warren, 2001) while the contrary effect has been reported in more sandy soils (Yair, 2001). There is wide consensus that microphytic crusts reduce erosion rates (Warren, 2001; Alexander and Calvo, 1990; Canton *et al.*, 2001).

In some cases, the increase in organic matter in the uppermost soil layer gives rise to hydrophobicity phenomena. These have been observed in field experiments using rainfall simulation (Nicolau *et al.*, 1996) or fine time-resolution monitoring of soil moisture changes in natural conditions (Puigdefabregas *et al.*, 1998). In most cases, hydrophobic compounds are thought to originate from wild fires (Cammaraat and Imeson, 1999) although the influence of animals, such as ants' nests, under dry conditions (Cammaraat *et al.*, 2002) or accumulation of mammal (e.g. rabbit) dung beneath plant clumps (Contreras and Sole, 2003) has also been recently reported.

Nutrient balance. Nutrient storage and its availability to plants are much greater in the soil beneath canopies. An updated review of this phenomenon may be found in Whitford (2002). The enhanced biological soil activity just described helps to trap nutrients in organic structures as soon as they are freed. Thus losses are minimized, nutrients are locally reused within the plant–soil system and their cycles become more interwoven. Furthermore, atmospheric nitrogen fixation, either free or symbiotic, also contributes to enriching the system with nitrogen (Schlesinger, 1996; Cross and Schlesinger, 1999).

Plant canopies have been shown to be efficient traps of dry atmospheric deposition, including dust and chemical compounds. For example, most of the calcium input in some forests on acidic bedrock, in semi-arid areas of southeast Spain, has been shown to originate from nearby marls and limestone and to enter the system as dry deposition on the forest canopy (Domingo *et al.*, 1994).

This nutrient trapping phenomenon and the associated increase in nutrient storage enhances the development of the vegetated patches and hence the differentiation of their soil properties from adjacent clearings.

Sediment balance. Plant clumps are often associated with sediment deposition either in mounds below the canopy or in microfans uphill of them. The first, characterized by their fine texture, are the result of atmospheric dust trapped by the canopies as dry deposition or wind-transported sediment and organic debris (DeSoyza *et al.*, 1997) and also from differential splash, as postulated by several authors (Parsons *et al.*, 1992; Bochet *et al.*, 2002) as a consequence of the strong reduction of kinetic energy below shrub canopies, i.e. 70 per cent of open rainfall in *Larrea tridentata* (Wainwright *et al.*, 1999). Microfans are caused by reduction in overland-flow transport capacity due to the increased roughness caused by vegetation (Abrahams *et al.*, 1994; Valentin *et al.*, 1999; Puigdefabregas and Sanchez, 1996; Cammaraat and Imeson, 1999).

Mosaics of sources and sinks

The soil heterogeneity generated by plant clumps contrasts with the conditions in neighbouring bare ground and together they build up a spatial mosaic. The relevant issue of such mosaics is that their patches are not isolated but dynamically interdependent. Bare ground acts as a source of water and sediments that are trapped by vegetated patches, which act as sinks.

This source–sink structure and associated heterogeneity reinforces itself, as first described by American authors working in the semi-arid southern US shrublands of *Prosopis* sp. and *Larrea tridentata* (Virginia and Jarrell, 1983; Schlesinger *et al.*, 1990; Whitford, 2002). Their research was particularly concerned with enhanced soil fertility conditions favoured by nutrients trapped in the soil beneath shrubs and its increased biological activity. They coined the concept of 'resource island' to account for these features. Numerical simulation experiments in shrubland areas at the Jornada Experimental Range (New Mexico) confirm the importance of runoff infiltration below shrubs. Obtained values range between 15 per cent and <5 per cent of the total infiltration for 30 min storms of average intensity of 40 mm h⁻¹ and 70 mm h⁻¹ respectively (Howes and Abrahams, 2003). The highest mean runoff infiltration percentages were associated with an initially wet soil, a variable rainfall, and low mean rainfall intensity.

Similar relationships have been described on banded vegetation patterns in many semi-arid areas around the world, such as the Sahel (Valentin and d'Herbes, 1999), New South Wales, Australia (Dunkerley and Brown, 1999), or northern Mexico (Janeau *et al.*, 1999). All these cases share common properties such as fine-textured soils, low slope angles and vegetated bands (sinks) that are supplied with runoff water, nutrients and fine sediments coming from the inter-bands (sources). Moreover it has been shown that the latter provide safe places in the soil matrix for storing

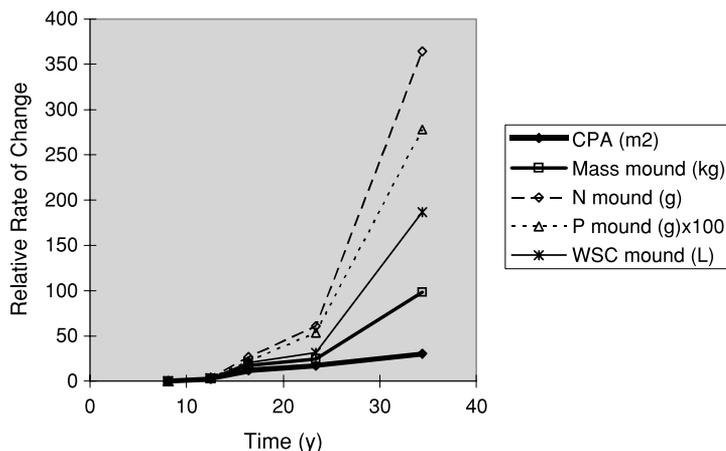


Figure 1. Relative rates of change of some soil properties in mounds under *Retama sphaerocarpa* bushes of different ages at the Rambla Honda field site (Almería, Spain). CPA, canopy projected area; WSC, water storage capacity; N, nitrogen; P, phosphorus. Reproduced from *Earth Science Review*, **48**, Puigdefábregas J, Sole A, Gutierrez L, del Barrio G, Boer M, 'Scales and processes of water redistribution in drylands: results from the Rambla Honda field site in southeast Spain', pp. 39–70, 1999, with permission of Elsevier Science.

nitrogen-rich organic matter, which is produced by the herbaceous ground layer on the strip's upper boundary (Guillaume *et al.*, 1999).

Source–sink coupling has also been demonstrated in the semi-arid Mediterranean region of Spain. Runoff exclusion experiments showed that growth of *Stipa tenacissima* tussocks is controlled by overland flow coming from patches of bare ground uphill (Puigdefábregas and Sanchez, 1996; Cerda, 1997). Similarly, the source–sink pattern of vegetated patches and bare ground has been found to match the topsoil moisture pattern along a climatic gradient in Israel (Pariente, 2002).

Observations on *Retama sphaerocarpa* bushes of different ages (Figure 1) illustrate the self-reinforcing process of 'resource island' formation (Pugnaire *et al.*, 1996). The increase of the soil mass stored beneath the bush results from the growth of the canopy and its effect on the interception of sediment. However, the water storage capacity, phosphorus and nitrogen stores beneath bushes grow at much faster rates than the soil mass, showing that they are outcomes from active processes that work as positive feedbacks in 'resource island' building. Increases in soil aggregation and soil organic matter content lead to a greater water storage capacity, while biologically tightened nutrient cycles and nitrogen fixation enhance organic phosphorus and nitrogen storage. Positive feedbacks in resource island formation via changes in water storage capacity, have been also described in tussock grasslands of *Stipa tenacissima* (Cerda, 1997) and in other vegetation types of arid environments (Holmgren *et al.*, 1997).

From an ecological perspective, two-phase mosaic structures of high and low plant cover patches have been claimed to be adaptive in arid ecosystems, because they allow for greater productivity than homogeneous distributions with the same rainfall rate, due to the source–sink effect on water and nutrients (Aguilar and Sala, 1999).

The source–sink concept has also been applied to forecast soil erosion on flat alluvial fans in central Australia (Pickup, 1985). The author introduced the concept of 'erosion cells', which consist of coupled erosion, transport and deposition areas, and uses these cells as the basic landscape unit for large-scale erosion assessment. In spite of the scale difference, the rationale underlying the 'erosion cell' is similar to that of the source–sink mosaics associated with VDSH.

Summary of the state of knowledge of VDSH at the patch scale

The local effects of vegetated patches on soil erodibility and hydraulic soil properties are well known. They are characterized by greater water storage capacity, increased soil organic carbon and larger nutrient inputs than adjacent clearings. Both features work together with an enhanced capacity of canopies to intercept water and windborne resources and a greater soil biological activity that leads to faster breakdown of plant debris and accelerated nutrient turnover.

This suite of properties often results from positive feedback mechanisms that cause vegetation patches to be increasingly different from nearby bare soil areas. In this way, bare ground and vegetated patches become coupled together in a landscape mosaic of sources and sinks of water, sediments and nutrients.

Stand-scale VDSH

VDSH is not only concerned with the differentiation of individual patches, but also with the spatial structure of these patches at the stand scale. Stand-scale VDSH may be expected to affect erosion patterns by working synergistically with the temporal heterogeneity of rainfall and interacting dynamically with downhill water and sediment fluxes.

VDSH synergy with rainfall temporal variability

Field evidence and numerical simulation experiments show that within-storm temporal variability of rainfall intensity works synergistically with spatial variability of soil hydrological properties, mostly associated with vegetation patterns, in modifying the opportunities for stand-scale infiltration and hence of the resulting runoff length.

Field observations and experiments. In arid and semi-arid areas it is claimed that runoff generation and rate are primarily controlled by the variation of surface properties related to infiltration rather than by the absolute amounts of annual rainfall (Yair and Kossovsky, 2002). Field observations and experiments with rainfall simulation in sparse plant covers (Yair and Lavee, 1985; Cerda, 1997; Bergkamp, 1998; Puigdefabregas *et al.*, 1999) led to the conclusion that the source–sink structure associated with VDSH is the underlying factor accounting for the strong decay of runoff coefficient with hillslope length that is observed in drylands. The short duration of the storms that prevail in these areas reduces the travel time of runoff before being infiltrated in the sinks of the mosaic patchwork.

This conclusion was mostly based on experimental studies using rainfall simulation and measurements of soil water measurements in the VDSH system. However, the rainfall forcing, in terms of temporal variability of rainfall intensity within storms, was not accounted for in an explicit way.

A field study addressing this issue from the perspective of the connectivity between the hillslopes and the channel was carried out at the Rambla Honda field site (southeast Spain), a mica-schist area with semi-arid climate and tussock vegetation and shallow low-permeability layers (Puigdefabregas *et al.*, 1998). Records of high temporal resolution for within-storm rainfall intensity, soil moisture and overland flow at the plot and microcatchment scales were used. It was shown (Figure 2) that while short-length overland flow (*c.* 10 m, the length of runoff plots used in the study) started quickly after rain began, widespread runoff that reached first-order channels required the combination of a slight increase in rainfall intensity and specific soil moisture conditions. Such 'reactive' conditions were created by the saturation of the shallow (15 cm) surface soil layer in bare ground patches, while the soil under grass tussocks (not shown in Figure 2) remained at *c.* 75 per cent of their water storage capacity.

This example refers to an upper layer saturation excess mechanism of runoff generation. In other areas with prevailing infiltration excess overland flow, the reactive condition described above is likely to occur earlier and to be of shorter duration. As a consequence, tighter coupling of rainfall and runoff pulses is to be expected.

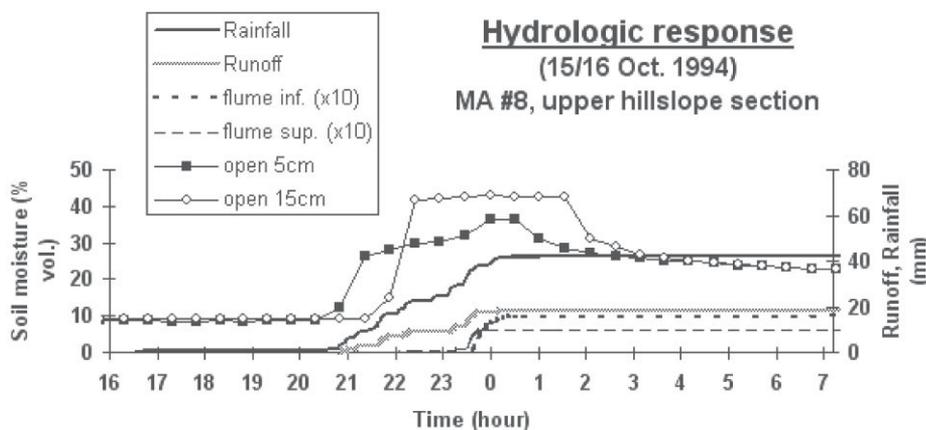


Figure 2. Cumulative time evolution of rainfall and hydrological responses of a tussock grassland microcatchment in the Rambla Honda field site (Almería, Spain) during the storm event of 15–16 October 1994. Runoff = overland flow from interrill $2\text{ m} \times 10\text{ m}$ plots; Flume inf & Flume sup = first-order channel channel discharge ($\text{mm} \times 10$) from the upper sector (0.0029 km^2) and the total catchment (0.046 km^2) respectively; open 5 cm, open 15 cm = inter-patch soil moisture at 5 cm and 15 cm depth, respectively). Reproduced from *Geomorphology*, 23, Puigdefabregas J, del Barrio G, Boer M, Gutierrez L, Sole A, 'Differential responses of hillslope and channel elements to rainfall events in a semi-arid area', pp. 337–351, 1998, with permission of Elsevier Science.

Numerical simulation experiments. The case study described above indicates how the within-storm temporal variability of rainfall intensity may control the spatial variability of runoff, but does not provide insight into the details of the VDSH control over the overland flow distribution. To gain further knowledge on these issues through experiments and observations is very difficult. Numerical simulation experiments, using distributed hydrological models, are therefore used as an alternative. This approach allows the manipulation of rainfall, terrain and surface properties in an easier and more rigorous way than in the field. The results obtained to date outline some consistent relationships.

During high-intensity storms, runoff variability in terms of volume and peak discharge is relatively independent of land surface heterogeneity (Castillo *et al.*, 2003), because rainfall intensity largely exceeds infiltration rates over the target area and runoff generation occurs homogeneously over the whole surface. During low-intensity storms, when maximum rainfall intensity is lower than the minimum infiltration rates, there is no runoff at all.

At intermediate storm intensities, runoff variability is greatest and is most strongly controlled by land surface heterogeneity, in terms of infiltration rates, which in turn are related to antecedent soil moisture and to saturated hydraulic conductivity (K_{sat}) patterns. Both variables are interrelated and strongly controlled by VDSH because in vegetated patches, water storage capacity and K_{sat} are greater than in bare ground (see section on 'Organic carbon balance'; Howes and Abrahams, 2003). Consequently, the duration of saturated conditions after rainfall intensity drops is shorter.

The sensitivity of runoff response to land surface variability depends on the prevailing runoff mechanism (Castillo *et al.*, 2003). In the case of infiltration excess overland flow, runoff is more uniform and less dependent on surface heterogeneity even at moderate rainfall intensities, because infiltration rates are quickly exceeded in large parts of the area. In the case of saturation excess overland flow, runoff is more controlled by the soil water content of the topsoil, which is more dependent on initial conditions and on VDSH.

The way in which VDSH controls runoff depends on its spatial structure. When the saturated hydraulic conductivity (K_{sat}) decreases along the flowpaths, either at the hillslope scale (Woolhiser *et al.*, 1996) or at the stand scale, between sources and sinks (Howes and Abrahams, 2003) runoff increases while the contrary occurs in reverse K_{sat} patterns. VDSH mosaics with coarse patchiness deliver larger runoff than fine-grained patchiness (Boer and Puigdefabregas, 2005).

An explicit analysis of the effect of rain variability within the storm on the runoff response was performed by Wainwright and Parsons (2002). These authors show that rainfall intensity alone controls the scale-dependency of runoff coefficients even when infiltration is both temporally and spatially uniform, provided that the infiltration rate is greater than the minimum rainfall intensity. Land surface heterogeneity adds some variability to the trend of decrease of runoff coefficients with slope length, but without reversals. It rather adds noise to the main trends. The authors conclude that considering rectangular storms with uniform average intensity risks underpredicting the runoff in substantial amounts.

VDSH interaction with downhill water and sediment fluxes

Field observations and experiments. Spatial mosaics generated by VDSH lead to heterogeneity in the spatial distribution of runoff and sediment fluxes. This is supported by many indirect field observations of the spatial distribution of topsoil textural properties, as well as direct flux measurements, though not as many, which are mostly obtained from rainfall simulations in the field (Abrahams *et al.*, 1989; Bergkamp, 1998; Bergkamp *et al.*, 1999; Cammeraat and Imeson, 1999; Galle *et al.*, 1999; Wainwright *et al.*, 2000) and less frequently using natural storm events (Lavee and Yair, 1990; Puigdefabregas and Sanchez, 1996). In general, it is found that depositional mounds build upstream of plant clumps, separated from each other by swales and proto-rills. Overland flow and sediment flux are largest in lateral swales and smallest both above and below plant clumps (Puigdefabregas and Sanchez, 1996). The overall effect of VDSH is to enhance reticular flow along microswales and microrills between vegetated patches (Thornes *et al.*, 1990), which increases flow depth and flow velocity in them (Abrahams *et al.*, 1989, 1995; Parsons *et al.*, 1996; Wainwright *et al.*, 2000). The consequence is stronger within-stand contrasts in erosive competence, and hence the shift to a more accelerated rill erosion.

In semi-arid climates on very gentle slopes (*c.* 0.2–0.7 per cent) with fine-textured soils, VDSH mosaics often become coarser and spatially structured in alternating bands of bare ground and bush-covered strips (Valentin *et al.*, 1999) (Figure 3). The spatial continuity of this kind of VDSH, also known as 'tiger bush' and 'vegetation arcs', is less affected by rill initiation because of the low slope gradient and the soil erosion protection of interbands by mineral and microphytic crusts (Malam Issa *et al.*, 1999). However, the characteristic VDSH coupling between sources (interbands) and sinks (bands) is maintained, as reported from the Sahelian zone, where the runoff generated in bare ground bands contributes up to 62 per cent of the water supply to bush strips (Galle *et al.*, 1999).

Plant clumps are not inert elements that merely interfere with downhill water and sediment fluxes according to their spatial distribution. They are also dynamic entities that grow and senesce in upward and downward cycles involving

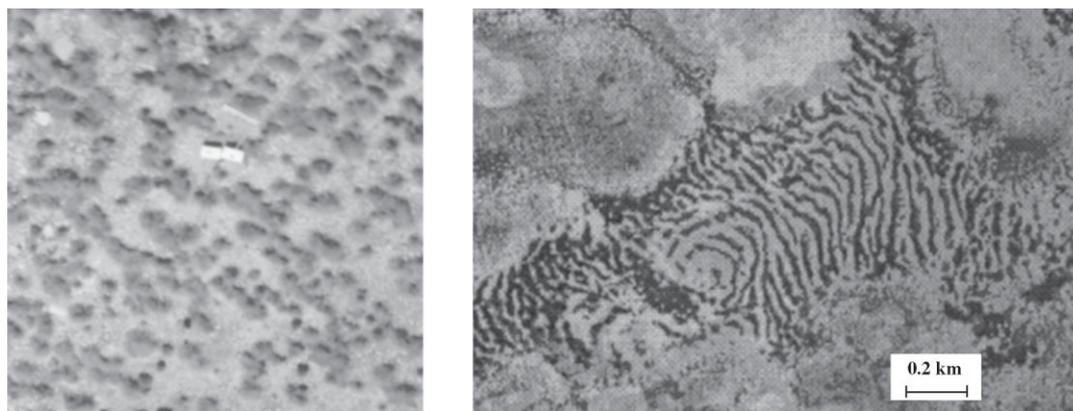


Figure 3. Aerial photographs showing the structural similarity between vegetation patterns of *Stipa tenacissima* tussocks at the Rambla Honda field site (left-hand photo), and the tiger bush pattern in Niger (right-hand photo). In the left-hand picture, the scale is given by the width of the runoff plot (2 m), the slope direction is NE–SW, with a 0.3 gradient, black spots show green tillers, dark grey patches indicate senescent parts of the tussocks with litter and fine sediment depositions, while light grey corresponds to denuded inter-tussock areas, with rock fragments (white) on the surface. In the right-hand picture, the higher topographic area is in the centre-SE of the image. Vegetation bands show downhill convexity, and sharp uphill boundary, which contrasts with its more irregular counterpart. Left-hand photo by J. Chadwick. Right-hand photo reproduced from Catena, 37(1–2), Valentin C, d’Herbes, JM, Poesen J, ‘Soil and water components of banded vegetation patterns’, pp. 1–24, 1999, with permission of Elsevier Science.

changes of shape and of place, as first described by Watt in his seminal paper on *Festuca ovina* in British grasslands (Watt, 1947).

The important issue to be stressed here is that plant clumps not only influence the spatial patterns of runoff and sediment redistribution, but that these patterns also produce feedback in the dynamics of vegetated patches. It has been demonstrated (Chappell *et al.*, 1999) that vegetated bands of tiger bush slowly migrate uphill (0.19–0.27 m a⁻¹ in the studied case) by regeneration of woody components on the upstream boundary, while they die out by senescence in the downstream sector, once available water has been exhausted (Galle *et al.*, 1999). Regeneration has even been described as being facilitated by a herbaceous upper belt that enhances fine sediment deposition and leads to a more favourable seedbed for woody plant seedling survival (Guillaume *et al.*, 1999).

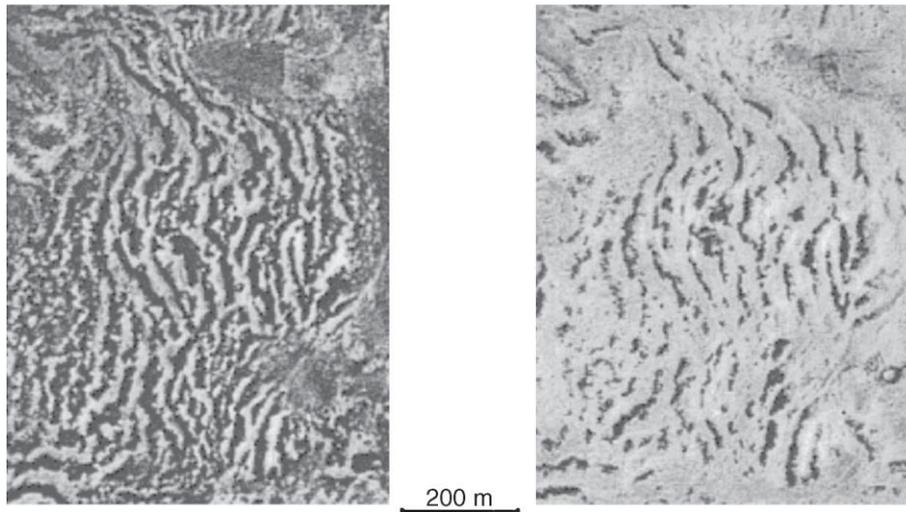
Structural similarities to the tiger bush have also been found in the Mediterranean tussock grasslands of *Stipa tenacissima* (Puigdefabregas and Sanchez, 1996). Here too, band-like structures perpendicular to the slope gradient have been reported, with uphill growing fronts and downhill decaying trails. The control of the runoff generated in interbands on the growth of tussock leaves has been shown (Puigdefabregas and Sanchez, 1996) but the senescence of the downhill sector of the tussocks as a result of water exhaustion by the uphill sector remains to be demonstrated.

The interaction between vegetation patchworks and downhill fluxes leads us to postulate that VDSH structures result from feedbacks between hillslope anisotropies and architectural and growth suites of plants. In the case of banded vegetation in Niger (Valentin and d’Herbes, 1999) it has been shown that the relative widths of bare and vegetated strips change with annual rainfall (Figure 4). Strips of bare ground become larger in dry spells, measured in a 15-year window, as the bush strips shrink.

In contrast, fine-scale vegetation patches have been found to decline in size and cover with increasing rainfall in Australian savannas while fetch-to-patch ratios become larger (Ludwig *et al.*, 1999). The explanation offered is that in higher rainfall savannas, mean spacing between patches disproportionately increased while mean patch size and cover declined. The cover of patches was negatively correlated with tree canopy cover, which significantly increased with rainfall. In the case of tussock grasslands of *Stipa tenacissima* in southeast Spain, it has also been reported (Puigdefabregas and Sanchez, 1996) that a banded pattern of tussocks, oriented along contours, develops within a range of length–slope factor (*LSF*) values, which are often taken as topographical surrogates of runoff transport capacity (Moore and Burch, 1986):

$$LSF = (A_s/22 \cdot 13)^n (\sin b/0.0896)^m$$

where A_s is the contributing area, b is the local slope angle and m , n are parameters. Below a lower threshold, these strips disappear and the pattern becomes a random distribution of circular tussocks. Above an upper threshold, runoff



Farantara 1962

Farantara 1992

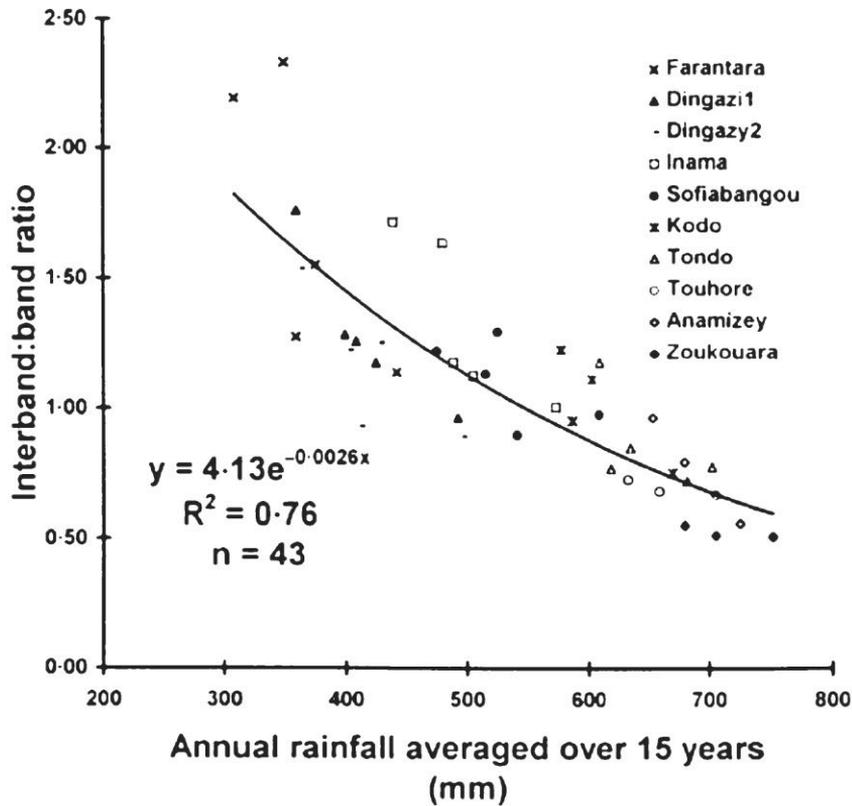


Figure 4. Dynamic response of the tiger bush pattern to annual rainfall in Niger. Aerial photographs from Farantara site (top). The interband–band ratio was increased from 1.13 in 1962, with $R_{15} = 426$ mm, to 2.3 in 1992, with $R_{15} = 315$ mm (R_{15} refers to the annual rainfall average during the past 15 years). The influence of R_{15} upon interband–band ratio (bottom) is shown using field measurements and aerial photographs of 1950, 1955, 1962, 1975 and 1992 from ten local transects across a regional transect in Niger. Reproduced from *Catena*, 37(1–2), Valentin C, d’Herbes JM, ‘Niger tiger bush as a natural water harvesting system’, pp. 217–229, 1999, with permission of Elsevier Science.

and sediment flux are strong enough to develop rill precursors that give rise to strips oriented in the direction of the slope.

Numerical simulation experiments. Field or laboratory experimental approaches to study the feedbacks of runoff and sediment redistribution to the spatial patterns of vegetation and the biological cycles of plant clumps are extremely difficult, mainly because of the long time spans involved. For this reason, as in the case of VDSH synergy with rainfall, numerical simulation modelling has started to be used.

The first attempts were based on cellular automata modelling in extreme environments, such as alpine (Gallart *et al.*, 1993) and semi-arid grasslands (Sanchez and Puigdefabregas, 1994). It was shown that the rate of sediment movement affects tussock shape and dynamics of tiller population within tussocks, as well as spatial patterns of tussock populations. It was also found that these spatial patterns represent stable configurations within relatively narrow ranges of sediment movement rates. Moreover these configurations could be qualitatively retrieved in real hillslopes. Results from these simulation experiments were difficult to generalize because they were highly case-specific.

Recently, new modelling approaches have been proposed as an aid to understanding the spatial vegetation patterns in semi-arid climates. They are based on the Turing instability concept (Turing, 1952; Glandsdorff and Prigogine, 1971) which was originally developed to explain spatial patterns in chemical systems as the outcome of spatially distributed functions such as diffusion–reaction or propagation–inhibition in the case of vegetation (Lejeune *et al.*, 1999; Couteron and Lejeune, 2001). Propagation includes all forms of vegetated patch expansion, either vegetative or by seed, while inhibition refers to within-patch competition for resources.

Lejeune *et al.* (1999) and Couteron and Lejeune (2001) found that patterns can be generated only biologically, even in isotropic environments, by the joint operation of these two functions when they work between certain thresholds. They can also be enhanced in anisotropic conditions, like hillslope gradients of overland flow or soil moisture that produce asymmetries in the propagation–inhibition functions. The authors also found that the intensity of the pattern is greater the shorter the propagation and the longer the inhibition distances are.

This is confirmed by the behaviour of tussock and caespitose plants, representative of the ‘phalanx’ and ‘guerrilla’ growth types respectively (Harper, 1985; Lovell and Lovell, 1985). ‘Phalanx’ growing plants have short internodal growth at the stem bases. They advance with ramets grouped tightly in a distinct front with short propagation distance and form sharp spatial patterns. In contrast, ‘guerilla’ growing plants spread through isolated exploring stolons or rhizomes with long internodal growth and show longer propagation distances and diffuse spatial patterns.

Simulation experiments using these models, parameterized in the tiger bush area (Lejeune *et al.*, 1999; Couteron and Lejeune, 2001) yield spatial configurations similar to those observed in the field. In particular they successfully predict pattern changes of spots, flexuous non-oriented bands and oriented bands, from isotropic (flat) to anisotropic (sloping) conditions.

Further developments of the propagation–inhibition functions have been used to explore the effect of rainfall variability on the spatial patterns of several vegetation functional types. They apply a hydrologically driven hierarchical competition–colonization model on a spatial frame using cellular automata (Fernandez-Illescas and Rodriguez-Iturbe, 2004). Simulation experiments parameterized in La Copita Research Site (Texas) suggest that the increase of interannual rainfall variability modifies the impact of local dispersal on the competitive interaction between woody plants (i.e. *Prosopis glandulosa*) and C₄ grasses (*Paspalum setaceum*). As a consequence, spatial patterns become coarser with big clusters of shrubs between large grass patches (Figure 5).

Is VDSH Relevant to Erosion?

In spite of the growing body of field observations that confirm the role of the spatial structure of vegetation in controlling the patterns of water and sediment redistribution over hillslopes, its relevance to erosion assessment at the regional scale still remains uncertain. It has often been argued (Bergkamp, 1998; Puigdefabregas *et al.*, 1998) that in heavy rainfall, topsoil reaches generalized saturation, and the resulting storm flow, in spite of being the main erosion driver, is little affected by vegetation patterns. This view has been supported by numerical simulation experiments (Wainwright and Parsons, 2002; Castillo *et al.*, 2003; Boer and Puigdefabregas, 2005) but conclusive field evidence is still lacking. Large-scale field experiments involving the manipulation of vegetation and rainfall patterns are difficult to carry out, because of both the cost and time required.

Experimental research has, however, been carried out at the Walnut Gulch Experimental Watershed, in the semi-arid southwestern USA (Abrahams *et al.*, 1995; Parsons *et al.*, 1996; Wainwright *et al.*, 2000) which provides relevant information on the subject. These authors reported a long-term shift from grassland to shrubland. This change, while it does not involve biomass or net primary productivity modification (Schlesinger *et al.*, 1990), entails an increase of

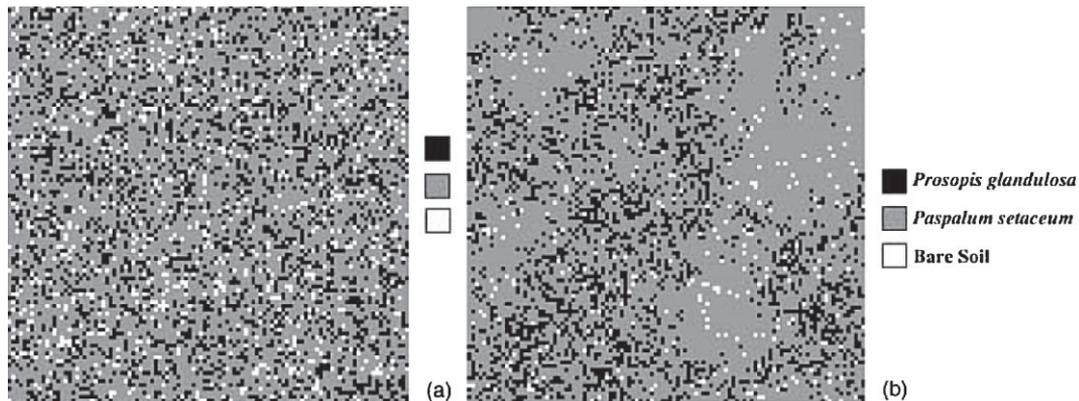


Figure 5. Modelled vegetation field of shrub–grass dynamics at timestep $t = 2477$ years: (a) without interannual rainfall variability, (b) with interannual rainfall variability. *Paspalum setaceum* disperses globally across the simulation field of 256 by 256 cells of 20 m², and *Prosopis glandulosa* disperses locally with a dispersal range of three cells. Reproduced from *Advances in Water Resources*, **27**, Fernandez-Illeras CP, Rodriguez-Iturbe I, 'The impact of interannual rainfall variability on the spatial and temporal patterns of vegetation in water-limited ecosystem', pp. 83–95, 2004, with permission of Elsevier Science.

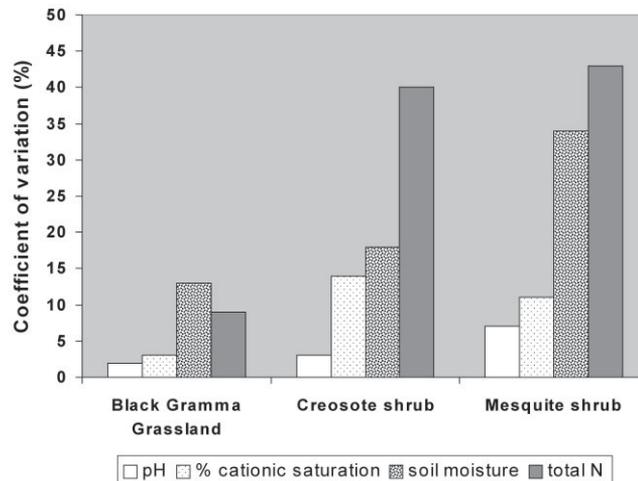


Figure 6. The shift from *Bouteloua eriopoda* (black gramma) grassland to *Larrea tridentata* (creosote) or *Prosopis glandulosa* (mesquite) shrubland in the semi-arid southwestern US leads to coarser-grained spatial distribution of vegetation and hence, to greater variability of topsoil attributes. Reproduced from *Science*, **147**, Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG, 'Biological feedbacks in global desertification', 1043–1048, 1990, with permission of Science Magazine (www.sciencemag.org).

VDSH (Figure 6) and coarsening of the spatial mosaic (Schlesinger, 1996). The causes of that shift remain obscure and several authors have summarized the main hypotheses (Schlesinger *et al.*, 1990; Whitford, 2002), but the purpose of the research was to find out whether the associated modification of spatial structure was accompanied by parallel changes in hydraulic parameters, overland flow and erosion rates. To this purpose, two rainfall simulation experiments were performed in two large experimental plots that were set up in shrubland (18 m wide \times 35 m long) and grassland (18 m wide \times 29 m long) areas respectively. Simulated rainfall intensity was 80 mm h⁻¹ during several time intervals going from 10 min to 77 min, of which 56 min are equivalent to the storm rainfall for a 100-year return period.

An important conclusion of this study was that the effects of a coarsened spatial structure, such as shrubland compared to grassland, may persist even under heavy storm rainfall conditions, by contributing to a decrease in overland flow resistance and increased velocity. As shown in Table I, while in grassland the downslope increase in the Reynolds number (Re) is accommodated equally by increases in depth and velocity ($f = m$) and by slightly diminished friction ($y = -0.22$), in shrubland they are entirely accommodated by increases in velocity ($f = 0$; $m = 1.00$), together with strongly diminished friction ($y = -1.56$).

Table I. Change from grassland to shrubland in southwestern USA. Downslope effects on overland flow hydraulic relations. The data used in this analysis come from the experiments indicated in Figure 7

Vegetation type	$d \propto Re^f$ f	$v \propto Re^m$ m	$ff \propto Re^y$ y
Grassland	0.50	0.50	-0.22
Shrubland	0.00	1.00	-1.56

Source: Abrahams *et al.* (1995) (Walnut Gulch, Southern Arizona). d = Overland flow depth; v = Overland flow velocity; ff = Darcy-Weisbach friction factor; Re = Reynolds number; f , m , y are the parameters of the relationships.

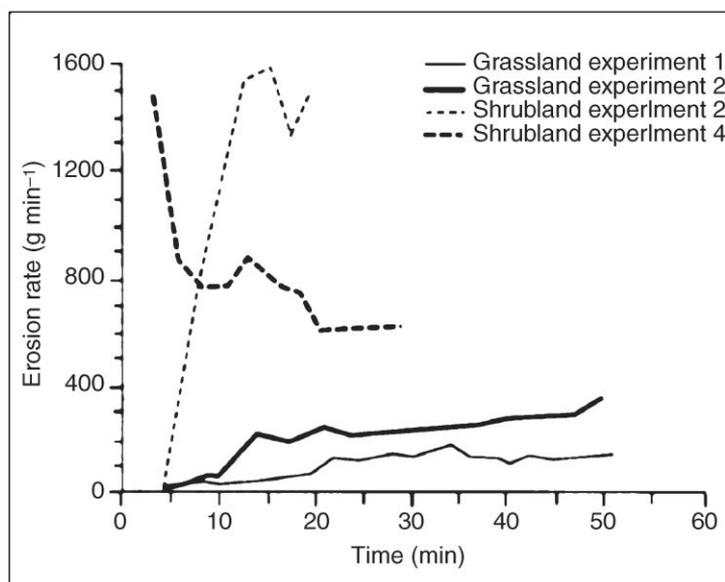


Figure 7. Change from grassland to shrubland in the southwestern USA. Photo shows natural overland flow pattern in a shrubland stand. Reproduced from *Engineered Information Systems for Natural Resources*, Hillslope Erosion Model: <http://eisnr.tucson.ars.ag.gov/hillslopeerosionmodel/>, 2002, with permission of USDA-ARS Southwest Watershed Research Center, Tucson, Arizona. Graph shows erosion rate against time for large plot experiments that attained equilibrium runoff. Reproduced from *Hydrological Processes*, 14, Wainwright J, Parsons AJ, Abrahams AD, 'Plot-scale studies of vegetation, overland flow and erosion interactions: case studies from Arizona and New Mexico', pp. 2921–2943, 2000, with permission of John Wiley & Sons, Ltd.

The final outcomes are that, compared to grassland, shrubland presents a greater downslope concentration of flow in fewer threads (Figure 7) which means higher erosion rates and development of desert pavements in inter-shrub areas.

VDSH Implications on Soil Erosion Assessment

The effects of VDSH structure concern not only runoff coefficients and infiltration of overland flow, but also changes in surface resistance and flow velocity. Both factors are important for erosion assessment at medium and high rainfall intensity respectively and both work at resolutions much finer than those used by models designed for regional assessment of runoff and erosion. This raises the challenge of how to account for spatial structures of VDSH at subgrid resolutions and for temporal structures of rainfall variability at resolutions finer than the model time step.

Remotely sensed vegetation density is the most usual source of information about VDSH. However at the resolution of imagery that is commonly used at regional scales (30 m – 1 km) most of the VDSH structure is lost, and hence soil erosion is underpredicted. Methods for retrieving subgrid-scale information of vegetation density are aimed either at increasing the spatial resolution of remotely sensed imagery (Atkinson, 1997) or at downscaling the frequency distribution of plant cover (Zhang *et al.*, 1998). The first approach requires preliminary regionalization and calibration of the spatial dependence of vegetation density at finer scales. The second (Zhang *et al.*, 1998) is more robust and easy to downscale but it loses the information of spatial structure.

As shown above, within-storm temporal variability of rainfall intensity is a dominant factor in the control of overland flow infiltration and runoff decay with hillslope length. If this factor is not accounted for, runoff is likely to be underestimated (Wainwright and Parsons, 2002). The usual time scale of rain intensity bursts (*c.* 10 min) is determined by the microphysical cloud processes of drop formation and release (Peters and Christensen, 2002). Rainfall data bases at the regional scale are usually at much lower temporal resolutions (*i.e.* daily, monthly). As suggested by Wainwright and Parsons (2002), improving runoff predictions calls for rainfall models that replicate the temporal patterns of intensities at resolutions finer than the time required for the flow to traverse a model cell, in our case, the autocorrelation length of the VDSH pattern.

Feedback of rainfall patterns and hillslope fluxes of water and sediments to VDSH is required for assessing long-term trends of runoff and erosion. This requires the coupling of ecological and hydrological models, which is currently an active subject of research (Lejeune *et al.*, 1999; Coueron and Lejeune, 2001; Fernandez-Illescas and Rodriguez-Iturbe, 2004) but standard procedures to be included in regional erosion assessment are not yet available.

Conclusions

Field evidence shows that the influence of vegetation on spatial structuring of runoff and sediment fluxes is more noticeable in extreme environments, where plant cover is scattered. Under such conditions, vegetation-driven spatial heterogeneity (VDSH) of soil properties concerned with resource storage leads to mosaic-like structures of sources and sinks with variable degree of interconnection. Vegetated patches act as sinks, and show significant feedback mechanisms that increase their sink power over time.

While vegetation density is controlled by water and resource availability, its spatial configuration is tuned to storm time patterns together with anisotropies induced by topography or gradients of soil properties. Such tuning indicates that each VDSH configuration is stable only within restricted ranges of its driving forces, but it is liable to change outside of them.

Within-storm temporal variability of rainfall intensity is a main control of infiltration and runoff length, particularly in events of moderate intensity. Land surface heterogeneity enhances this effect, particularly in areas where topsoil saturation excess is a significant mechanism of overland flow generation.

Field evidence shows that fine-grained VDSH is more efficient than coarse-grained patterns in controlling the redistribution lengths of water and sediments, as well as enhancing the on-spot use of resources. This effect is more conspicuous in storms of small to medium intensity, although it persists even in strong storms because its greater roughness controls overland flow velocity better, and hence its erosive power.

The effect of VDSH on structuring runoff and sediment fluxes raises two main challenges in hydrological and erosion modelling at regional scales. The first concerns the spatial and temporal scaling, because VDSH–rainfall interaction takes place at greater spatial and temporal resolutions than those applied by regional models. The second is related to the feedbacks of fluxes to VDSH itself, and is essential for long-term runoff and erosion predictions.

References

- Abrahams AD, Parsons AJ, Luk SH. 1988. Hydrologic and sediment responses to simulated rainfall on desert hillslopes in southern Arizona. *Catena* **15**: 103–117.
- Abrahams AD, Parsons AJ, Luk SH. 1989. Distribution of depth of overland flow on desert hillslopes and its implications for modelling soil erosion. *Journal of Hydrology* **106**: 177–184.
- Abrahams AD, Parsons AJ, Wainwright J. 1994. Resistance to overland flow on semi-arid grassland and shrubland hillslopes, Walnut Gulch, southern Arizona. *Journal of Hydrology* **156**: 431–446.
- Abrahams A, Parsons AJ, Wainwright J. 1995. Effects of vegetation change on interrill runoff and erosion, Walnut Gulch, southern Arizona. *Geomorphology* **13**(1–4): 37–48.
- Aguiar MR, Sala OE. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *TREE* **14**(7): 273–277.

- Alexander RW, Calvo A. 1990. The influence of lichens on slope processes in some Spanish Badlands. In *Vegetation and Erosion*, Thornes JB (ed.). J. Wiley & Sons: Chichester; 385–398.
- Atkinson PM. 1997. Mapping sub-pixel boundaries from remotely sensed images. In *Innovations in GIS4*, Kemp Z (ed.). Taylor & Francis: London; 166–180.
- Barthes B, Roose E. 2002. Aggregate stability as an indicator of soil susceptibility to runoff and erosion; validation at several levels. *Catena* **47**(2–2): 133–149.
- Belnap J, Büdel B, Lange OL. 2001. Biological soil crusts: characteristics and distribution. In *Biological Soil Crusts: Structure, Function and Management*, Belnap J, Lange OL (eds). Springer-Verlag: Berlin Heidelberg; 3–30.
- Bergkamp G. 1996. *Mediterranean geocosystems: Hierarchical organisation and degradation*. Thesis, University of Amsterdam.
- Bergkamp G. 1998. A hierarchical view of the interactions of runoff and infiltration with vegetation and microtopography in semiarid shrublands. *Catena* **33**(3–4): 201–220.
- Bergkamp G, Cerda A, Imeson AC. 1999. Magnitude-frequency analysis of water redistribution along a climate gradient in Spain. *Catena* **37**(1–2): 129–146.
- Bochet E, Poesen J, Rubio JL. 2002. Influence of plant morphology on splash erosion in a Mediterranean matorral. *Zeitschrift für Geomorphologie* **46**(2): 223–243.
- Boer M, Puigdefábregas J. 2005. Effects of spatially structured vegetation patterns on hillslope erosion in a semiarid Mediterranean environment: a simulation study. *Earth Surface Processes and Landforms* **30**: 149–167; this issue.
- Brandt CJ. 1989. The size distribution of throughfall drops under vegetation canopies. *Catena* **16**: 507–524.
- Cammeraat LH, Imeson AC. 1998. Deriving indicators of soil degradation from soil aggregation studies in southeastern Spain and southern France. *Geomorphology* **23**(2–4): 307–321.
- Cammeraat LH, Imeson AC. 1999. The evolution and significance of soil-vegetation patterns following land abandonment and fire in Spain. *Catena* **37**(1–2): 107–127.
- Cammeraat LH, Willott SJ, Compton SG, Incoll JD. 2002. The effects of ants' nests on the physical, chemical and hydrological properties of a rangeland soil in semi-arid Spain. *Geoderma* **105**(1–2): 1–20.
- Canton Y, Sole-Benet A, Puigdefábregas J. 2001. Hydrological and erosion response of a badland system in semiarid SE Spain. *Journal of Hydrology* **252**(1–4): 65–84.
- Castillo VM, Gómez-Piñaza A, Martínez Mena M. 2003. The role of antecedent soil water content in the runoff response of semiarid catchments: a simulation approach. *Journal of Hydrology* **288**(1–4): 114–130.
- Cerda A. 1997. The effect of patchy distribution of *Stipa tenacissima* L. on runoff and erosion. *Journal of Arid Environments* **36**(1): 37–51.
- Cerda A. 1998. Soil aggregate stability under different Mediterranean vegetation types. *Catena* **32**(2): 73–86.
- Chappell A, Valentin C, Warre A, Noon P, Charlton M, d'Herbes JM. 1999. Testing the validity of upslope migration in banded vegetation from south-west Niger. *Catena* **37**(1–2): 217–229.
- Contreras S, Sole A. 2003. Hidrofobicidad en suelos mediterráneos semiáridos: implicaciones hidrológicas para una pequeña cuenca en el SE ibérico. *Cuaternario y Geomorfología* **17**(1–2): 29–45.
- Couteron P, Lejeune O. 2001. Periodic spotted patterns in semi-arid vegetation explained by a propagation-inhibition model. *Journal of Ecology* **89**: 616–628.
- Cross AF, Schlesinger WH. 1999. Plant regulation of soil nutrient distribution in the northern Chihuahuan Desert. *Plant Ecology* **145**: 11–25.
- De Ploey J. 1984. Stemflow and colluviation: Modelling and implications. *Pedologie* **34**: 135–146.
- De Ploey J, Savat J, Moeyers D. 1976. The differential impact of some soil loss factors on flow, runoff creep and rainwash. *Earth Surface Processes* **1**: 151–161.
- DeSoyza AG, Whitford WG, Martinez-Meza E, Van Zee JW. 1997. Variation in Larrea tridentatabush (*Larrea tridentata*) morphology in relation to habitat, soil fertility and associated annual plant communities. *American Midland Naturalist* **137**: 13–26.
- Domingo F, Puigdefábregas J, Moro MJ, Bellot J. 1994. Role of vegetation cover in the biogeochemical balances of a small afforested catchment in South East Spain. *Journal of Hydrology* **159**: 275–289.
- Domingo F, Sánchez G, Moro MJ, Brenner A, Puigdefábregas J. 1998. Measurement and modelling of rainfall interception by three semi-arid canopies. *Agricultural Meteorology* **91**: 275–292.
- Domingo F, Villagarcía L, Brenner AJ, Puigdefábregas J. 2000. Measuring and modelling the radiation balance of a heterogeneous shrubland. *Plant, Cell and the Environment* **23**: 27–38.
- Domingo F, Villagarcía L, Boer MM, Alados-Arboledas L, Puigdefábregas J. 2001. Evaluating the long-term water balance of arid zone stream bed vegetation using evapotranspiration modelling and hillslope runoff measurements. *Journal of Hydrology* **243**: 17–30.
- Dunkerley DL, Brown KJ. 1999. Banded vegetation near Broken Hill, Australia: significance of surface roughness and soil physical properties. *Catena* **37**: 75–88.
- Elwell HA, Stocking MA. 1976. Vegetation cover to estimate soil erosion hazard in Rhodesia. *Geoderma* **15**: 61–70.
- Evans RD, Lange OL. 2001. Biological soil crusts and ecosystem nitrogen and carbon dynamics. In *Biological Soil Crusts: Structure, Function and Management*, Belnap J, Lange OL (eds). Springer-Verlag: Berlin Heidelberg; 263–280.
- Fernandez-Illescas CP, Rodriguez-Iturbe I. 2004. The impact of interannual rainfall variability on the spatial and temporal patterns of vegetation in a water-limited ecosystem. *Advances in Water Resources* **27**: 83–95.
- Gallart F, Puigdefábregas J, del Barrio G. 1993. Computer simulation of high mountain terraces as interaction between vegetation growth and sediment movement. *Catena* **20**: 529–542.

- Galle S, Ehrmann M, Peugeot C. 1999. Water balance in a banded vegetation pattern. A case study of tiger bush in western Niger. *Catena* **37**(1–2): 197–216.
- Glandsdorff P, Prigogine I. 1971. *Thermodynamic Theory of Structure, Stability and Fluctuations*. John Wiley & Sons: Chichester.
- Graetz RE, Tongway DJ. 1986. Influence of grazing management on vegetation, soil structure and nutrient distribution and the infiltration of applied rainfall in a semiarid chenopod shrubland. *Australian Journal of Ecology* **11**: 347–360.
- Guillaume K, Abbadié L, Mariotti A, Nacro H. 1999. Soil organic matter dynamics in tiger bush (Niamey, Niger). Preliminary results. *Acta Oecologica* **20**(3): 185–196.
- Hamilton EL, Rowe PB. 1949. *Rainfall interception by chaparral in California*. Publications of the California Range and Forest Experimental Station.
- Harper JL. 1985. Modules, branches, and the capture of resources. In: *Population Biology and Evolution of Clonal Organisms*, Jackson JBC, Buss LW, Cook RE (eds). Yale University Press: New Haven; 1–33.
- Holmgren M, Scheffer M, Huston MA. 1997. The interplay of facilitation and competition in plant communities. *Ecology* **78**: 1966–1975.
- Howes DA, Abrahams AD. 2003. Modeling runoff in a desert shrubland ecosystem, Jornada Basin, New Mexico. *Geomorphology* **53**: 45–73.
- Imeson AC, Verstraten JM. 1989. The microaggregation and erodibility of some semi-arid and Mediterranean soils. In *Arid and Semi-arid Environments – Geomorphological and Pedological Aspects*, Yair A, Berkowicz S (eds). Catena Suppl. **14**(1–2). Catena Verlag: Cremlingen; 11–24.
- Imeson AC, Vis M. 1982. Factors influencing the aggregate stability of soils in natural and semi-natural ecosystems at different altitudes in the Central Cordillera of Colombia. *Zeitschrift Für Geomorphologie N.F. Suppl. Bd.* **44**: 94–105.
- Janeau JL, Mauchamp A, Tarin G. 1999. The soil surface characteristics of vegetation stripes in Northern Mexico and their influences on the system hydrodynamics. An experimental approach. *Catena* **37**: 165–173.
- Kidron GJ, Herrnstadt J, Barziley E. 2002. The role of dew as a moisture source for sand and microbiotic crusts in the Negev Desert, Israel. *Journal of Arid Environments* **52**(4): 517–533.
- Lavee H, Yair A. 1990. Spatial variability of overland flow in a small arid basin. *International Association of Scientific Hydrology Publications* **189**: 105–120.
- Lejeune O, Abbadié L, Mariotti A, Nacro H. 1999. Short range co-operativity competing with long range inhibition explains vegetation patterns. *Acta Oecologica* **20**(3): 171–184.
- Lovell PH, Lovell PJ. 1985. The importance of plant form as a determining factor in competition and habitat exploitation. In *Studies on Plant Demography: A Festschrift for John L. Harper*, White J (ed.). Academic Press: London; 209–221.
- Ludwig JA, Tongway DJ, Eager RW, Williams RJ, Cook GD. 1999. Fine-scale vegetation patches decline in size and cover with increasing rainfall in Australian savannas. *Landscape Ecology* **17**: 557–566.
- Maestre FT, Cortina J. 2002. Spatial patterns of surface soil properties and vegetation in a Mediterranean semi-arid steppe. *Plant and Soil* **241**: 279–291.
- Maestre FT, Huesca M, Zaady E, Bautista S, Cortina J. 2002. Infiltration, penetration resistance and microphytic crust composition in contrasted microsites within a Mediterranean semi-arid steppe. *Soil Biology and Biochemistry* **34**: 895–898.
- Malam Issa O, Trichet J, Défarge C, Couté A, Valentin C. 1999. Morphology and microstructure of microbiotic crusts on a tiger bush sequence (Niger, Sahel). *Catena* **37**(1–2): 175–196.
- Malam Issa O, Le Bissonnais Y, Defarge Trichet J. 2001. Role of a cyanobacterial cover on structural stability of sandy soils in the Sahelian part of western Niger. *Geoderma* **101**(3–4): 15–30.
- Martinez-Meza E, Whitford W. 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. *Journal of Arid Environments* **32**: 271–287.
- Mauchamp A, Janeau JL. 1993. Water funnelling by the crown of *Flourensua cernua*, a Chihuahuan Desert shrub. *Journal of Arid Environments* **25**: 299–306.
- Moore ID, Burch GJ. 1986. Physical basis of the Length-slope factor in the Universal Soil Loss Equation. *Soil Science Society of America Journal* **50**(5): 1294–1298.
- Morgan RP, Finney HJ, Lavee H, Merritt E, Noble CA. 1986. Plant cover effects on hillslope runoff and erosion: evidence from two laboratory experiments. *Hillslope Processes*, Abrahams AD (ed.). Binghamton Symposia in Geomorphology 16. Allen and Unwin: St Leonards, Australia; 77–90.
- Navar J, Bryan R. 1990. Interception loss and rainfall redistribution by three semi-arid growing shrubs in Northeastern Mexico. *Journal of Hydrology* **115**: 51–63.
- Nicolau JM, Sole A, Puigdefábregas J, Gutierrez L. 1996. Effects of soil and vegetation on runoff along a catena in semi-arid Spain. *Geomorphology* **14**: 297–309.
- Noble EL. 1965. *Sediment reduction through watershed rehabilitation*. US Department of Agriculture Miscellaneous Publications **970**: 114–123.
- Nulsen RA, Blight KJ, Baxter IN, Solin EJ, Imrie DH. 1986. The fate of rainfall in a mallee and heath vegetated catchment in southern western Australia. *Australian Journal of Ecology* **11**: 361–371.
- Pariente S. 2002. Spatial patterns of soil moisture as affected by shrubs in different climatic conditions. *Environmental Monitoring and Assessment* **73**: 237–251.
- Parsons AJ, Abrahams AD, Simanton JR. 1992. Microtopography and soil-surface materials on semi-arid piedmont hillslopes, southern Arizona. *Journal of Arid Environments* **22**: 107–115.

- Parsons AJ, Abrahams AD, Wainwright J. 1996. Responses of interrill runoff and erosion rates to vegetation change in southern Arizona. *Geomorphology* **14**: 311–317.
- Peters O, Christensen K. 2002. Rain: Relaxations in the sky. *Physical Review E* **66**(036120): 1–8.
- Pickup G. 1985. The erosion cell – A geomorphic approach to landscape classification in range assessment. *Australian Rangeland Journal* **7**: 114–121.
- Pressland AJ. 1973. Rainfall partitioning by an arid woodland (*Acacia aneura* F. Muell) in South-western Queensland. *Australian Journal of Botany* **21**: 235–245.
- Pugnaire FI, Haase P, Puigdefábregas J, Cueto M, Clark SC, Incoll LD. 1996. Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos* **76**: 455–464.
- Puigdefábregas J, Sanchez G. 1996. Geomorphological implications of vegetation patchiness in semi-arid slopes. In *Advances in Hillslope Processes*, Anderson M, Brooks S (eds). John Wiley & Sons: Chichester; 1027–1060.
- Puigdefábregas J, Aguilera C, Brenner A, Clark S, Cueto M, Delgado L, Domingo F, Gutierrez L, Incoll L, Lazaro R, Nicolau JM, Sanchez G, Sole A, Vidal S. 1996. The Rambla Honda Field Site. Interactions of soil and vegetation along a catena in semi-arid SE Spain. In *Mediterranean Desertification and Land Use*, Brandt CJ, Thornes JB (eds). John Wiley & Sons. Chichester.
- Puigdefábregas J, Barrio del G, Boer M, Gutierrez L, Sole A. 1998. Differential responses of hillslope and channel elements to rainfall events in a semi-arid area. *Geomorphology* **23**: 337–351.
- Puigdefábregas J, Sole A, Gutierrez L, del Barrio G, Boer M. 1999. Scales and processes of water redistribution in drylands: results from the Rambla Honda field site in southeast Spain. *Earth Science Reviews* **48**: 39–70.
- Rogers RD, Schumm SA. 1991. The effect of sparse vegetation cover on erosion and sediment yield. *Journal of Hydrology* **123**: 19–24.
- Sánchez G, Puigdefábregas J. 1994. Interaction between plant growth and sediment movement in semi-arid slopes. *Geomorphology* **9**: 243–260.
- Schlesinger WH. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**: 364–374.
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks. In *Global Desertification. Science* **247**: 1043–1048.
- Schumm SA. 1977. *The Fluvial System*. John Wiley and Sons: Chichester.
- Slatyer RO. 1965. Measurements of precipitation interception by an arid zone plant community (*Acacia aneura*, F. Muell). *Arid Zone Research* **25**: 181–192.
- Thornes JB. 1990. The interaction of erosional and vegetation dynamics in land degradation: spatial outcomes. In *Vegetation and Erosion*, Thornes JB (ed.). John Wiley and Sons: Chichester; 41–53.
- Thornes JB, Francis CF, Lopez Bermudez F, Romero Diaz A. 1990. Reticular overland flow with coarse particles and vegetation roughness under Mediterranean conditions. In *Strategies to combat desertification in Mediterranean Europe*, Rubio JL, Rickson RJ (ed.). Commission for the European Communities: Brussels; 228–245.
- Turing AM. 1952. The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society of London, Series B* **237**: 37–72.
- Valentin CD, d'Herbes JM. 1999. Niger tiger bush as a natural water harvesting system. *Catena* **37**(1–2): 231–256.
- Valentin C, d'Herbes JM, Poesen J. 1999. Soil and water components of banded vegetation patterns. *Catena* **37**(1–2): 1–24.
- Virginia RA, Jarrell WM. 1983. Soil properties in a *Prosopis* sp.-dominated Sonora Desert ecosystem. *Journal of American Soil Science Society* **47**: 138–144.
- Wainwright J, Parsons AJ. 2002. The effect of temporal variations in rainfall on scale dependency in runoff coefficients. *Water Resources Research* **38**(12): 7-1–7-9.
- Wainwright J, Parsons AJ, Abrahams AD. 1999. Rainfall energy under creosotebush. *Journal of Arid Environments* **43**(2): 111–120.
- Wainwright J, Parsons AJ, Abrahams AD. 2000. Plot-scale studies of vegetation, overland flow and erosion interactions: case studies from Arizona and New Mexico. *Hydrological Processes* **14**: 2921–2943.
- Warren SD. 2001. Synopsis: influence of biological soil crusts on arid land hydrology and soil stability. In *Biological Soil Crusts: Structure, Function and Management*, Belnap J, Lange OL (eds). Springer-Verlag: Berlin Heidelberg; 349–362.
- Watt AS. 1947. Pattern and process in the plant community. *Journal of Ecology* **35**: 1–22.
- Whitford W. 2002. *Ecology of Desert Systems*. Academic Press: San Diego.
- Wischmeier WH. 1959. A rainfall erosion index for a universal soil-loss equation. *Proceedings of Soil Science Society of America* **23**: 246–249.
- Woolhiser DA, Smith RE, Giraldez JV. 1996. Effects of spatial variability of saturated hydraulic conductivity on Hortonian overland flow. *Water Resources Research* **32**(3): 671–678.
- Yair A. 2001. Effects of biological soil crusts on water redistribution in the Negev Desert, Israel. In *Biological Soil Crusts: Structure, Function and Management*, Belnap J, Lange OL (eds). Springer-Verlag: Berlin Heidelberg.
- Yair A, Kossovsky A. 2002. Climate and surface properties: hydrological response of small arid and semi-arid watersheds. *Geomorphology* **42**(1–2): 43–57.
- Yair A, Lavee H. 1985. Runoff generation in arid and semiarid zones. In *Hydrological Forecasting*, Anderson MG, Burt TP (eds). John Wiley: New York; 183–220.
- Zhang X, Drake N, Wainwright J. 1998. Downscaling land surface parameters for global soil erosion estimation using no ancillary data. *Proceedings of the 3rd International Conference on GeoComputation*, University of Bristol (UK), Abrahart RJ (producer). GeoComputation CD-ROM.