Landscape Ecology **17:** 587–597, 2002.

Microphytic crusts, shrub patches and water harvesting in the Negev Desert: the *Shikim* system

David J. Eldridge[1,2,*], Eli Zaady[2] and Moshe Shachak[3]
*[1]Centre for Natural Resources, Department of Land and Water Conservation, c/- School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, 2052, NSW, Australia; [2]Desertification and Restoration Ecology Research Centre, Ben-Gurion University of the Negev, Sede Boker Campus, 84990, Israel; [3]Mitrani Center for Desert Ecology, Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boker Campus, 84990, Israel; *Author for correspondence (e-mail: d.eldridge@unsw.edu.au)*

Received 27 March 2001; accepted in revised form 26 July 2002

Key words: Desert hydrology, Desert shrublands, Ecosystem services, Microphytic crust, Runoff and sediment production, Soil crust controls on ecosystem processes, Source-sink relationships, Water harvesting

Abstract

Human-made contour banks are a central component of the *Shikim* water harvesting system in Israel's Negev Desert. Efficient water capture depends on the presence of a stable microphytic crust which directs surplus surface runoff into the banks where it is stored. We used simulated rainfall to examine the impact of soil surface disturbance on runoff and sediment transport, and the effect of this on the efficiency of resource capture within the *Shikim* system. Two disturbance regimes: 1) removal of the microphytic crust only, and 2) removal of the crust and shrub patches by cultivation, were compared with an undisturbed control. In the undisturbed state, 32% of rainfall was redistributed as runoff. This runoff penetrated approximately 27% deeper under the shrub patches compared with the microphytic crust. When the microphytic crust was destroyed by simulated trampling, the runoff coefficient declined to 13%, and there was no significant difference in water penetration between shrub and crust patches. Complete destruction of the shrub hummocks and crust by cultivation resulted in a decline in the runoff coefficient to 6%. The result of sustained disturbance in these patchy Negev shrublands is a breakdown in spatial heterogeneity, a loss of ecosystem function, a reduction in ecosystem goods and services such as plant diversity and production, and ultimately a reduction in pastoral productivity. These results reinforce the view that microphytic crusts are critical for the efficient operation of the *Shikim* water harvesting system. Given that practices such as cultivation and trampling which disturb microphytic crusts result in enhanced infiltration, crusts should be left intact to maximise the water harvesting efficiency in these desert landscapes.

Introduction

In arid and semi-arid landscapes a combination of theoretical predictions and empirical data demonstrate that resources, particularly water, organic matter and nutrients, are patchily distributed in the landscape (Noy-Meir 1973; Tongway 1995). This patchy distribution of resources results in increased overall productivity (Noy-Meir 1973; Montaña et al. 2001) and manifests itself in a spatially discontinuous vegetation cover, with perennial plants and their associated fertile soils located within a matrix of less fertile soil.

Patchiness in the vegetation and soil resources exists at a range of spatial scales from the landscape or catchment scale (e.g. Macfayden (1950) and Dunkerley and Brown (1995), Mauchamp et al. (2001)) right down to the scale of the individual plants (Rostagno 1989; Bergkamp 1998; Bochet et al. 1999; Eldridge 1999). Resource distribution, regulated by vegetation and terrain, results in tight controls over landscape function, thereby influencing productivity and diversity (Yair and Shachak 1987; Ludwig et al. 1997; Hiernaux and Gérard 1999; López-Portillo and Montaña 1999). The discontinuous nature of the vegetation is thought to be controlled by processes of upslope water erosion and sedimentation, as well as complex interactions between the individual plants and the surrounding soil matrix (Puigdefébregas and Sanchez 1996; Cerdá 1997; Bochet et al. 1999; Reid et al. 1999).

Patchy or banded landscapes consist of two phases or patch types, one which is vegetated and the other which is essentially bare. The bare soil zone (often called the source or run–off zone) generates runoff (Peugeot et al. 1997; Reid et al. 1999) which travels downslope and is absorbed within the densely vegetated zone (runon or sink zone) which has a greater infiltration rate (Garner and Steinberger 1989; Rostagno 1989; Schlesinger et al. 1990; Greene 1992; Tongway and Ludwig 1994). The partitioning of resources between runoff and runon zones also occurs at differing rates depending on the scale and magnitude of rainfall, and hence water erosion and deposition rates. Some elements of spatial pattern are not involved in resource redistribution all of the time, and the mosaic of patches may operate intermittently. Furthermore, resources may not be delivered to particular patches, but may remain in transit between source and sink zones (Pickup 1985).

Within the northern Negev Desert of Israel, spatial heterogeneity in the shrub-dominated landscape is characterised by a matrix of soil hummocks supporting patches of perennial shrubs (shrub patches) separated by apparently bare soils dominated by microphytic crusts (crust patches). The microphytic crust of the inter-shrub matrix comprises cyanobacteria, bacteria, algae, mosses and some lichens (Verrecchia et al. 1995; Zaady et al. 1997). Microphytic crust surfaces are tightly structured, primarily due to the binding of soil particles by polysaccharides excreted by cyanobacteria (Schulten 1985; Malam Issa et al. 1999). Microphytic crusts trap rainfall, which either runs off and infiltrates into nearby shrub patches (Schlesinger et al. 1990; Shachak et al. 1999), evaporates, or eventually infiltrates elsewhere downslope. Physical soil crusts such as sieved structural, erosional or deposition crusts (Valentin 1991) which occur in association with microphytic crusts, accentuate this production of runoff. In contrast, the soil of shrub patches lacks a well-developed microphytic crust, and has a surface covered with loose soil particles. In the undisturbed state, this system functions efficiently through the capture, retention and movement of water and nutrients from crust patches to the shrub patches (Zaady and Shachak 1994; Shachak et al. 1999).

At the Sayeret Shaked Park near Beer Sheva in Israel's Northern Negev, a water harvesting system (termed the *Shikim* system) has been developed to trap runoff water, soil and nutrients originating from the upslope crust patches. Water trapped behind human-made contour banks sustains fruit trees, and provide a retreat for an expanding urban population seeking shady open space for recreation. These areas are in effect 'ecological parks', where recreation coexists with limited pastoralism and agri-forestry.

The *Shikim* system comprises four parts (Figure 1). The upper part, which is 15–30 m wide and occupies up to 85% of the landscape, comprises a natural patchwork of shrub and crusted patches supporting a diverse native plant and animal community. This also provides runoff water, soil, organic matter and nutrients to the trees below. The second part is the cultivated strip about 2–4 m wide which is ploughed to remove the vegetation and reduce competition for water between the trees and the natural vegetation. The third part is a cultivated pit which collects and absorbs runoff, soil, organic matter and nutrients flowing downhill from the natural matrix. The last part of the *Shikim* system is a continuous ($\sim$ 500 m long) earthen mound or contour bank which prevents downslope leakage of materials from the pits. Although the distance between the banks is small, resulting in a small runoff contributing area, the *Shikim* system stores considerable amounts of water and nutrients which might otherwise be lost from the landscape (Shachak et al. 1998).

A practical consideration in relation to the management and functioning of the *Shikim* system is the impact of soil disturbance on the stability of the system, and, in particular, its effect on the flow of resources between the natural and the human-made parts of the system. In order to understand how the *Shikim* system functions and how it can be managed sustainably, we examined the movement of surface water, and changes in infiltration, runoff and sediment production, in relation to a range of disturbance regimes within the *Shikim* system. We did this by comparing soil hydrological properties on three surface treatments; i) the undisturbed natural patchwork of both shrub and crust patches ('control'), ii) a 'disturbed' system where only the crust was disturbed and the shrubs left intact ('disturbed'), and iii) a surface

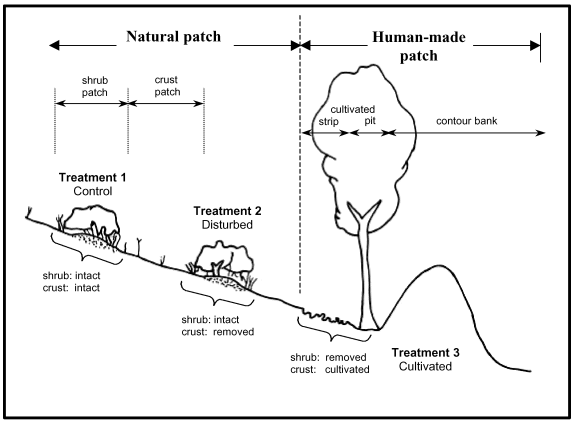

Figure 1. Diagrammatic representation the control, 'disturbed' and cultivated treatments in relation to the natural patchwork of crusts and shrubs, and the human made patches. Not to scale.

where both the crust and shrub patches had been completely removed by cultivation ('cultivation').

Materials and methods

Study area

The study site was at Sayeret Shaked Park near Beer Sheva in the Northern Negev of Israel (31°17′ N, 34°37′ E, Figure 2). Average annual rainfall is approximately 200 mm, most of which falls between November and March. The soil is loessial, about 1 m thick, with 14% clay, 27% silt and 59% sand (USA classification: loess soil with sandy loam texture – Calcixerollic, Xerochrepts (Dan et al. 1977) on Eocene bedrock. Salt content of the 0–25 cm soil layer is low, with electrical conductivity of 0.04 S m^{-1} (Teomim 1990).

The landscape comprised a series of discontinuous shrub mounds within a matrix of biologically crusted soils. The sub-circular shrub mounds supporting *Noaea mucronata* (Forssk.) Asherfon & Schweinf. and *Atractylis serratuloides* Cass. (Feinbrun-Dothan and Danin 1991) were less than 30 cm high and typically 20–30 cm across. The inter-mound surfaces were dominated by a microphytic crust of bacteria, cyanobacteria, algae, mosses and lichens. All rainfall simulations were carried out on a north-facing slope.

Experimental context and measurements

Within an area of approximately 40 m by 20 m, we selected fifteen 1 m^2 plots for detailed rainfall simulation experiments (see below). Five plots each were assigned to a control treatment (Treatment 1) and a 'disturbed' treatment (Treatment 2). A further five plots were located in the adjacent cultivated strip immediately upslope of three contour mounds (Treatment 3, see Figure 1). The cultivated strip was first cultivated in 1991, and again in August 1997 two months prior to the study. All plots were on similar slopes (mean ± standard error = 9.2 ± 0.6%).

Prior to simulated rainfall, approximately 25% of each of the five plots in Treatment 2 was treated with a wooden stake to simulate the trampling action of sheep hooves. Trampling was achieved by bringing down the stake from a height of approximately 10 cm in a circular arc motion, and dragging the leading edge of the stake through the soil crust for approximately 7 cm to mimic as closely as possible the dragging action of the hoof along the soil surface as the next step is taken.

Soil physical properties

Measurements of gravimetric soil moisture were taken immediately adjacent to the plots before simulation in the 0–20 mm depth layer within which most of the soil nutrients and soil crust occurs. A 500 g sample of the 0–20 mm layer of the soil was collected from the crust patch on all three treatments (including the completely cultivated treatment) for duplicate (n = 2) measurements of soil properties according to the following methods:

1. (a) pH and electrical conductivity (EC): a 1:5 soil water suspension shaken for 1 hour
2. (b) organic carbon: Walkley-Black wet combustion technique (Colwell 1969)
3. (c) particle size analysis on the < 2 mm fraction of the soil according to Loveday (1974) using dispersed samples.

Vegetation measurements

Projected foliage cover of all vascular plants was measured prior to simulation, by digitising coloured aerial photographs of each plot. Plant and litter biomass was measured by clipping, drying and weighing all above-ground vegetation after rainfall simulation.

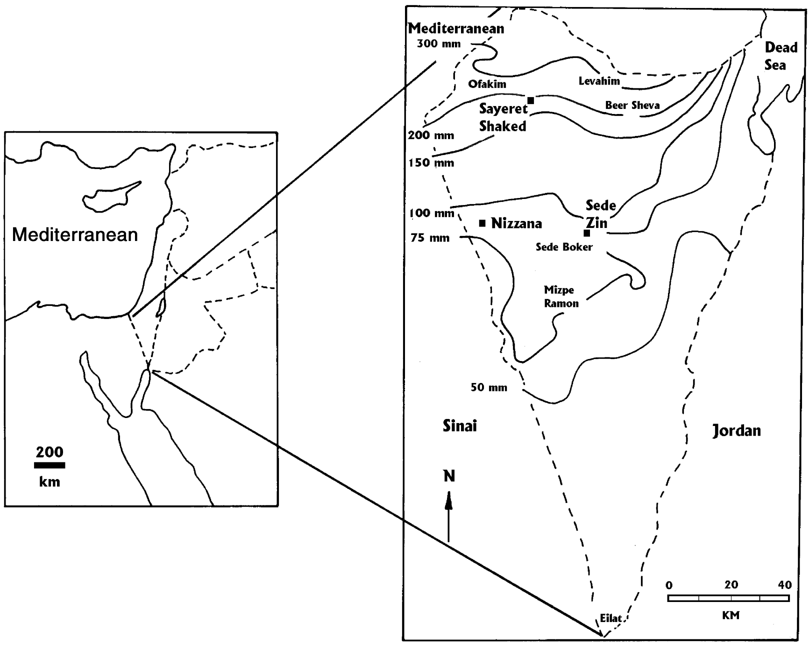

Figure 2. Location of the study site at Sayeret Shaked in the western Negev and the rainfall isohyets.

Additionally, during the spring of 1996 and 1997, plant biomass was measured on five 1 m^2 plots on the crust patches, the cultivated strip and the earthen mound, and the density of all annuals growing in five 1 m^2 plots on both the shrub and crust patches assessed.

Rainfall simulation measurements

Fifteen runoff plots were constructed by hammering sheets of steel into the soil to a depth of about 5 cm and placing a flume at the lower end of the plot for collecting runoff water and sediment. The plots were subjected to simulated rainfall with a rotating disc rainfall simulator using distilled water (Morin and Cluff 1980). The rainfall simulator nozzle delivers simulated raindrops from a standard height of 2.05 m producing rainfall with drop sizes of 2.5 mm diameter and with energy of approximately 30 kJ m^{-2} min^{-1} at a pressure of 60 kPa. Although the rainfall intensity was set at 37.5 mm h^{-1}, mean intensity (46.4 mm h^{-1}) varied slightly among plots due to varying in the local topography and hence the height above the ground (range 39.8–51.6 mm h^{-1}). Simulated rainfall was applied at a constant rate for 30 minutes, by which point the values for both infiltration and runoff had stabilised. The value at this point is defined as steady-state.

On each plot we measured time to ponding (Tp; time taken for water to accumulate over about 60% of the plot), the volume of rainfall required to initiate runoff, and the time taken for runoff to commence (Trun). The time elapsed between Tp and Trun depends principally on surface morphology and surface detention. The depth to water penetration was measured at 10 locations on each of the shrub and crust patches in the control and 'disturbed' plots, or at 10 random locations on the cultivated plots. This depth is governed principally by soil porosity, and predominantly by biopores constructed by invertebrates.

The volume of runoff was measured each minute using a vacuum pump attached to the lower end of each runoff plot. Samples of soil and water were bulked, but one minute sub-samples of runoff from 4–5, 9–10, 14–15, 19–20, 24–25 and 29–30 minutes were collected to assess changes in sediment concentration over time. Sediment was dried at 105° for 24 hours and expressed as either oven dry soil per litre of applied rainfall (sediment yield) or as sediment concentration in grams of sediment per litre of runoff water.

Simulated rainfall does not always reproduce the characteristics of natural rainfall. For example, natural rainfall is highly intermittent, often with short-duration high-intensity storms of less than a few minutes duration separated by rain-free periods of many min-

Table 1. Soil physico-chemical data from the top 0–20 mm of the surface from the three treatments. Mean values (± standard error) within a row followed by a different letter are significantly different at $P = 0.05$.

	Control	Disturbed	Cultivated
Initial soil moisture (%)	3.36 (0.30)[a]	3.30 (0.05)[a]	3.21 (0.07)[a]
pH (water)(1:5)	8.80 (0.01)[a]	8.84 (0.01)[a]	8.50 (0.05)[b]
Bulk density (Mg/m^3)	1.36 (0.03)[a]	1.40 (0.01)[a]	1.21 (0.001)[b]
EC (dS/m)	85.0 (1.75)[a]	93.7 (3.33)[a]	75.0 (1.57)[b]
Organic carbon (%)	1.88 (0.05)[a]	2.03 (0.03)[a]	1.91 (0.07)[a]
Clay (< 0.002 mm)(%)	12.7 (0.82)[a]	14.4 (0.39)[a]	14.8 (0.23)[a]
Silt (0.02–0.002 mm)(%)	9.9 (0.38)[a]	9.9 (0.22)[a]	7.3 (0.20)[b]
Sand (0.02–2.0 mm)(%)	77.4 (0.57)[a]	75.7 (0.46)[a]	77.9 (0.31)[a]
n	5	5	5

utes. Under natural rainfall, zones of ponding will develop, separated from other zones of high hydraulic conductivity, which do not normally pond due to abundant plant roots or faunal macropores. Consequently, during natural rainfall, runoff may often be short lasting and intermittent. Under simulated rainfall however, rainfall is pulsed and of uniform intensity, with often little or no temporal variability. Thus the pattern of ponding may not be contiguous across a plot. Therefore, rainfall simulation may produce greater runoff and therefore a higher runoff coefficient than would otherwise occur under natural conditions. Whilst there are obvious shortcomings with the use of rainfall simulation, it is nonetheless an effective technique for determining relative differences between treatments, and allowed us to examine differences in hydrological properties in an area of extremely variable rainfall.

Statistical analyses

One-way analysis of variance (Minitab 1994) was used to examine differences in vegetation, soil and hydrological properties after any transformations necessary to stabilise the variance.

Results

Soil physical and chemical properties

The most pronounced differences in soil physical and chemical properties occurred between the cultivated plots and the other two treatments (control and 'disturbed' plots), which were generally not significant differences ($P > 0.05$) from each other (Table 1). Predictably, bulk density was significantly less on the cultivated soils compared with the other treatments. Similarly, electrical conductivity was lower on the cultivated soils. Rainfall simulation on the cultivated plots resulted in a significant ($P < 0.05$) reduction in the silt content of surface soils (Table 1).

Vegetation characteristics

There was no significant difference in mean (± standard error) projected foliage cover between the control plots (15.3 ± 1.7%) and the 'disturbed' plots (16.2 ± 2.5%; $P > 0.05$). Within both the control and 'disturbed' plots, shrub patches, comprising both shrubs and their associated mounds, occupied 22 ± 1.5% of the area (range 18–32%). Total above-ground plant biomass was higher on the control plots (223.7 ± 54.0 g m^{-2}) compared with the 'disturbed' plots (140.9 ± 28.7 g m^{-2}). However, the extensive within-treatment variability meant that there were no significant differences in biomass between the treatments ($P > 0.05$). The density of annuals was significantly greater in the shrub patches compared with the crust patches ($P = 0.013$; Figure 3A). Biomass was significantly greater on the contour bank, followed by the cultivated strip, and least on the crust patch ($P < 0.001$; Figure 3B).

Time to ponding, time to runoff and depth of wetting

Time to ponding, time to runoff and volume of rainfall to commencement of runoff increased significantly with increases in disturbance ($P = 0.001$; Table 2). On average, water took four to five times longer to pond and commence running off on the cultivated plots compared with the control plots. Simi-

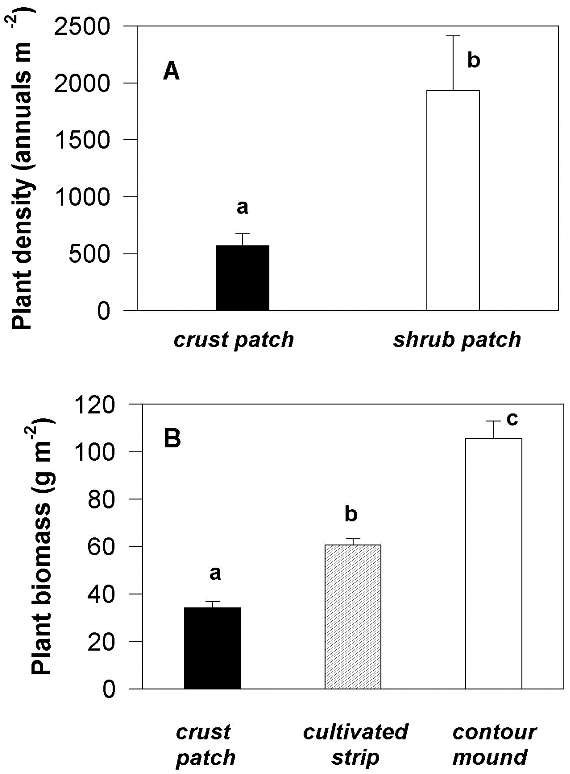

Figure 3. a) Density of annual plants (m^{-2}) on the crust and shrub patches, and b) plant biomass ($g\ m^{-2}$) on the crust, cultivated strip and contour bank. Different letters within a graph indicate a significant difference in the variable at $P < 0.05$.

larly, about five times more rainfall was required to initiate runoff on the cultivated compared with the control plots.

Pooled across both crust and shrub patches, there was no significant difference in water penetration between the control plots and the 'disturbed' plots ($P = 0.124$), but water penetration was significantly greater under the shrub patches compared with the crust patches ($P < 0.01$). There was a significant treatment (control vs 'disturbed') by patch (shrub vs crust) interaction ($P = 0.001$) indicating that water penetrated further (~ 27%) below the shrub patches on the control plots compared with the 'disturbed' plots, but between the shrubs on the crusted soil, there was no significant difference in water penetration between the control and 'disturbed' treatments (Table 2).

Steady-state runoff

Steady-state runoff (SSR) rates were significantly greater on the control plots compared with either the cultivated or 'disturbed' plots ($P = 0.027$), which were themselves not significantly different ($P > 0.05$). The high variability in runoff rates for the 'disturbed' and cultivated plots meant that runoff rate was generally not significantly different, except for the intermediate 8–14 minutes after commencement of simulations (Figure 4). The rate of increase in runoff was three times greater in the control plots (mean = 1.5 mm h^{-1} min^{-1}) compared with the other treatments (0.5 mm h^{-1} min^{-1}).

As we expected, the significantly greater runoff from the control plots equates with a low level of infiltration on these plots, assuming that surface detention and interception by vegetation are similar on both treatments. There was a general increase in steady-state infiltration (SSI) with the severity of soil disturbance. Approximately a third of all applied water was shed as runoff on the control plots. The coefficient of runoff (runoff as a proportion of applied rainfall), decreased significantly with the degree of disturbance ($P = 0.001$), though there was no significant difference in coefficients on the 'disturbed' and cultivated plots (Table 2) where generally more than 85% of applied rainfall infiltrated.

Sediment yield and sediment concentration

The sediment collected from the plots represented total contribution from rainsplash and flow-driven erosion processes. Sediment yield for the duration of the simulations ranged from 2.49 ± 0.50 g L^{-1} rainfall on the control plots to 3.30 ± 1.03 g L^{-1} rainfall on the cultivated plots. Sediment concentration (g/L runoff) followed a similar trend (Table 2). Sediment yield however varied considerably within any treatment, and was sometimes high on the control plots and sometimes low on the 'disturbed' and cultivated plots. Consequently, differences in sediment yield or sediment concentration between treatments were not significant ($P = 0.20$). Changes in sediment removal during the course of the simulations were markedly different both within and between treatments. There were no significant differences in average removal rates over time between treatments ($P = 0.37$), and rates ranged from 0.128–0.228 g L^{-1} min^{-1} on the control plots, to 0.58–16.3 g L^{-1} min^{-1} on the 'disturbed' and 0.06–3.6 g L^{-1} min^{-1} on the cultivated plots (Figure 5).

Table 2. Mean (± standard error) values for selected hydrological properties for the control, 'disturbed' and cultivated treatments. Different letters within a row indicate a significant difference in that variable at $P < 0.05$; n.a. not applicable.

	Control	Disturbed	Cultivated
Time to ponding (min)	2.9 (0.67)^{a}	9.1 (1.69)^{b}	15.4 (2.36)^{c}
Time to runoff (min)	3.7 (0.59)^{a}	9.6 (1.67)^{b}	15.8 (2.35)^{c}
Rainfall to produce runoff (mm)	2.7 (0.43)^{a}	7.2 (1.45)^{a}	13.6 (2.02)^{b}
Wetting front (mm/25 mm rainfall)			
shrub patch	151.8 (3.35)^{a}	110.9 (3.55)^{b}	n.a.
crust patch	81.9 (5.11)^{a}	99.5 (2.60)^{a}	n.a.
cultivated	n.a.	n.a.	132.0 (4.26)
Steady-state infiltration (mm/h)	24.4 (3.27)^{a}	37.0 (2.77)^{a,c}	43.1 (2.66)^{b,c}
Steady-state runoff (mm/h)	19.3 (3.20)^{a,c}	10.2 (2.00)^{b,c}	8.3 (2.57)^{b}
Runoff coefficient (%)	31.9 (5.20)^{a}	13.3 (2.06)^{b}	6.1 (2.17)^{b}
Sediment concentration (g/L runoff)	8.3 (1.62)^{a}	40.4 (18.40)^{a}	96.9 (54.27)^{a}
Sediment yield (g/L rainfall)	2.49 (0.50)^{a}	2.96 (0.89)^{a}	3.30 (1.03)^{a}

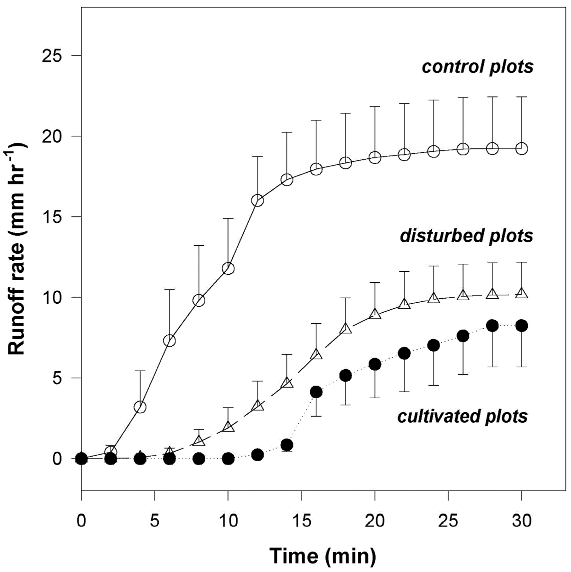

Figure 4. Runoff rate (mm h^{-1}) for the control (crust and shrub patches intact), disturbed (shrub patches intact, crust disturbed) and cultivated (shrub and crust patches removed) plots.

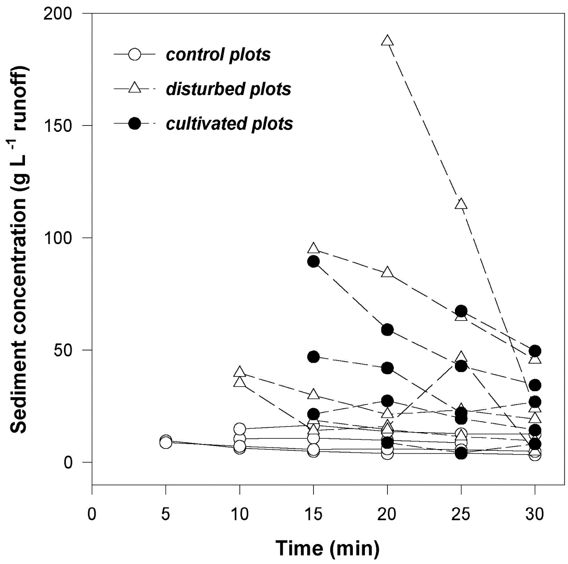

Figure 5. Sediment concentration curves (g L^{-1} runoff) for each of the five plots within each of the three treatments.

Discussion

The use of contour catchments to harvest both water and sediments from natural landscapes is a common management practice in drylands (Evenari et al. 1983; Bruins et al. 1986; Critchley et al. 1991). Contour catchments create water and nutrient enriched patches within natural landscapes, and are used to enhance yields and the reliability of production for humans, or to improve the value of the ecosystem for plants and animals. In the Negev these catchments provide primary production for livestock, sites for highly diverse native plant communities (Boeken and Shachak 1994), and sites for planting trees for firewood or shade. In similar landscapes, water harvesting systems such as the 'khadin' of the Thar desert in India (Kolarkar et al. 1983), the 'Khuskaba' in Pakistan (Sheikh et al. 1984), the 'teras' in the Sudan (Niemeijer 1998) and traditional systems in Morocco (Kutsch 1983), Tunisia (El-Amami 1977), Libya and Egypt (Reij et al. 1990) serve the same purpose.

The functioning of contour catchment systems is controlled by source-sink relationships among a hierarchy of patches at varying spatial scales. One level is the movement of water, soil and organic matter from the natural matrix to the human-made catchment. Within the natural matrix is the movement of water and materials between crust and shrub patches, and within the human-made patch is the movement of water and materials from cultivated strip to cultivated pit. In order to manage these contour catchment systems it is important to understand the factors controlling the retention of soil and water in the catchment, and therefore its productivity, and how this alters under different management regimes.

Crust-shrub relationships in the natural matrix

Efficient, sustainable production in patchy, crusted landscapes depends on the redistribution of water and sediments from the crusted bare surfaces to vegetated patches (Haase et al. 1996; Peugeot et al. 1997; Bergkamp 1998). In our studies in the western Negev, the movement of runoff water from crust to shrub patches was moderated by an extensive and stable cover of microphytic crusts. This crust was dominated by cyanobacteria (e.g. *Microcoleus vaginatus*, *Nostoc punctiforme*) and mosses (*Aloina bifrons*, *Crassidium crasinerv* var. *laevipilum*) which provide most of their soil protection within the top few millimetres of the surface. In patterned landscapes worldwide these microphytic crusts tend to be hydrophobic, and when associated with erosion crusts (Valentin 1991), enhance runoff by preventing the growth of vegetation through reduced seed capture and seedling emergence (Malam Issa et al. 1999; Veste et al. 2001). Despite their relatively low hydraulic conductivity (Eldridge et al. 2000), and poor ability to intercept overland flow on steep slopes even when undisturbed, some infiltration through the crusts occurs.

Nutrient-enriched soil mounds under perennial shrubs such as *Noaea mucronata* and *Atractylis serratuloides* trap this runoff water and entrained sediment, creating highly productive patches compared with the surrounding relatively depauperate crust patches. Our results indicated that 32% (+ 5.2%) of applied water generated from simulated rainfall was shed from the natural matrix and redistributed to the shrub patches. Runoff coefficients for the control plots in our study were high (~ 33%, Table 2), but of similar magnitude to the highest runoff coefficients from natural rainfall calculated for 60 m^2 plots of a natural matrix in the same study area (Shachak et al. 1998). Similar high runoff coefficients have been reported for biologically crusted sand dunes at Nizzana in the Central-Western Negev (20–39%; Yair (1990)), and for bare inter-canopy patches within a piñon-juniper woodland in New Mexico (Reid et al. 1999). In studies in west Niger, catchment-scale runoff coefficients ranged from 30–44% whilst runoff plot values were 45–46% (Peugeot et al. 1997). In the present study, about 60–80% of the rainfall amount remained in the natural matrix to support its productivity and diversity, and therefore about 120–140% of normal rainfall is available for plant growth in the human-made patches. In other natural systems this water accumulation is sufficient to sustain the growth of trees and shrubs normally restricted to more mesic areas (Galle et al. 2001).

Disturbance and redistribution of water

Increased disturbance to the crust and shrubs in our study resulted in a decline in steady-state runoff rate (Figure 4, Table 2), with reduced water movement to the human-made patches. Disturbed microphytic crust within a shrub mosaic in the *Shikim* system induces two changes in the spatial distribution of water, and, consequently, the distribution of productivity. First, disturbance reduces water flow to the shrub patches, with obvious consequences for the herbaceous vegetation under the shrubs. Undisturbed mound soil under the shrubs traps and stores about 40% more water than undisturbed microphytic crust soils (Table 2). However, when only the crust is disturbed by trampling, infiltration under the shrub patches is not significantly different from that under the crust. A disturbed, crust-dominated patch will therefore be unable to sustain a highly productive and diverse assemblage of herbaceous plants in the shrub understorey.

Second, cultivation results in increased water penetration when the crusts are destroyed. We attribute this mainly to the destruction of the continuous polysaccharide sheaths in the crust, and exposure of macropores (foraging holes of termites and ants) beneath the crust (Elkins et al. 1989). Thus, disturbed microphytic crust reduces the water flow to the human-made pits, lowering the degree of resource enrichment in the pits. The net effect of this crust disturbance is a more uniform distribution of water in the landscape, which in drylands, results in reduced productivity (Noy-Meir 1973; Yair and Shachak 1987). Similar reductions in productivity have been described for patterned mulga (*Acacia aneura)* woodlands in eastern Australia (Noble et al. 1998; Ludwig et al. 1997) and *brousse tigrée* in Niger (Hiernaux and Gérard 1999; Seghieri and Galle 1999). Severe trampling can result in the formation of cattle or sheep tracks, and a concentration of water flow within rills and gullies which either flow through the vegetated patches or around them, resulting in water stress and eventually the death of trees and shrubs (Hiernaux and Gérard 1999).

Disturbance and the loss of ecosystem function

The impact of sustained disturbance on these patchy desert landscapes in a breakdown in spatial heterogeneity, a loss of ecosystem function, and concomitant reductions in ecosystem goods and services such as soil, nutrients, seeds, plant production and habitat. In the case of the *Shikim* system in the Negev, disturbance results in reduced capacity to harvest water and therefore reduced pastoral productivity, both in the human-made and natural parts of the system. As with other patterned arid and semi-arid systems, a reduction in patchiness at a range of scales has marked and long-term impacts on the capacity of the landscape to support plants, animals and human populations.

The pits can support a high diversity, biomass and cover of natural and introduced vegetation for a variety of human activities. They also provide grazing and shade for livestock, and shade, fruit and timber for humans. Disturbances that alter both the source strength of the natural matrix and therefore the spatial arrangement of patches, influence the balance between resource leakage and retention, and therefore the possibility of marked changes in ecosystem function. Grazing animals have the potential to alter the size, shape, number and configuration of patches (Shachak et al. 1999). Excessive overgrazing reduces the cover of shrubs, and productivity of the shrub hummocks, and increases runoff generation. Human disturbances also have an impact on the system, with shrub removal for firewood, cultivation and the use of motor vehicles pulverising the soil crust and impairing the functioning of the *Shikim* system. Depending on the requirements of crops or trees in the human-made patches, moderate levels of disturbance may be beneficial, however, to adjust the inputs of water and sediment redistributed to the pits. Thus the management of the *Shikim* system is an issue of patch management, and is a trade-off between the level of resources to be absorbed by the shrub patches and the level of resources to be redistributed to the human-made sinks.

Management of catchments

The first question in relation to patch management is how many human-made patches the landscape can support and where they should be located. Our results suggest that we should minimise the size of the human-managed part of the landscape in order to optimise the efficient use of water. As maximum runoff occurred on the undisturbed control plots, management that aims at maximising the ratio of matrix to human-made patches would result in efficient use of water in the human-managed part. Management for a high ratio of matrix to human-managed part could be achieved by having either many narrow strips along the slope, or a few wide strips. The selection between the two is essentially a matter of determining patch size and fetch (the distance between patches), which can be assessed using standard landscape survey techniques or landscape function analysis (see Ludwig et al. (1994)), and will depend on the water requirement of the plants in the human-made part. The selection of plant types for the human-made patches will depend on environmental factors such as slope and soil type as well as catchment to cultivated area ratios (Reij et al. 1990).

A second question is related to the management of the natural matrix in order to increase resources in the human-made parts. Additional runoff could be achieved by the strategic removal of shrubs and their associated mounds, provided that disturbance is minimal (Shachak et al. 1998). A decline in the number of shrub patches however will be at the expense of reducing the productivity and diversity of the natural matrix.

A third question relates to disturbances associated with the management and utilisation of the *Shikim.* Disturbances result from: construction of the human made pits, which destroys the natural matrix, repeated cultivation that destroys any regenerating crust in the pits, and livestock grazing that tramples the crust in the pits and the natural matrix. It is clear from our study that any disturbance to the soil crust outside the human-made pits affects the main process of redistribution of water. Therefore, the process of construction of the human-made part of the *Shikim* system should be restricted to the narrow strip of the pits. In addition, if the system is designed to support livestock, stocking rates should be managed so that disturbance of the soil crust is minimised. The only place where soil crust disturbance is beneficial is in the pits.

Our study indicates that cultivation increases both the infiltration and the depth to which water will penetrate, and therefore enhances the sink function of the pits. Soil crust disturbance may reduce the stability of the system if any eroded soil reduces the capacity of the pits to hold water. As shown in this study, the shrub patches can control soil erosion from the natural matrix to the human-made pits. By functioning as sinks for water and soil, the shrub patches play a dual role in the *Shikim* system, as 'islands' of high productivity and diversity in the natural matrix (*sensu* Garner and Steinberger (1989)), and as sinks for eroded soil, therefore preventing deposition of eroded soil in the pits.

Acknowledgements

We thank the Keren Kayemeth Leisrael for supporting this research which was conducted at the Desertification and Restoration Ecology Research Center laboratory at Sede Boker. We are grateful to Rami Garti and Yitsack Benyamini from the Erosion Research Station of the Ministry of Agriculture for the use of their portable rainfall simulator, and Efraim Fisik and his colleagues for their dedication and long hours of hard work in the field. We thank Geoff Pickup for comments on an earlier draft, the Keren Kayemeth Leisrael, the NSW Department of Land and Water Conservation and the Blaustein International Centre for supporting the senior author's visit to undertake the research. Publication CNR99.011 of the Centre for Natural Resources.

References

Bergkamp G. 1998. A hierarchical view of the interactions of runoff and infiltration with vegetation and microtopography in semiarid shrublands. Catena 33: 201–220.

Bochet E., Rubio J.L. and Poesen J. 1999. Modified topsoil islands within patchy Mediterranean vegetation in SE Spain. Catena 38: 23–44.

Boeken B. and Shachak M. 1994. Changes in desert plant communities in human-made patches in and their implications for the management of desertified landscapes. Ecological Applications 4: 702–716.

Bruins H.J., Evenari M. and Nessler U. 1986. Rainwater harvesting agriculture for food production in arid zones: the challenge of the African famine. Applied Geography 6: 13–32.

Cerdá A. 1997. The effect of patchy distribution of *Stipa tenacissima* L. on runoff and erosion. Journal of Arid Environments 36: 37–51.

Colwell J.D. 1969. Auto-analyser procedure for organic carbon analysis of soil. National Soil Fertility Project, Circular No. 5. CSIRO Division of Soils, Canberra, ACT, Australia.

Critchley W., Siegert K. and Chapman C. 1991. A Manual for the Design and Construction of Water Harvesting Schemes for Plant Production. Food and Agriculture Organisation of the United Nations, Rome, Italy.

Dan J., Yaalon D., Kundzimzinsky H. and Raz Z. 1977. The Soils of Israel. Bulletin No. 168, (in Hebrew). ARO Publication, Bet-Dagan, Israel.

Dunkerley D.L. and Brown K.J. 1995. Runoff and runon areas in a patterned chenopod shrubland, arid western New South Wales, Australia: characteristics and origin. Journal of Arid Environments 30: 41–55.

El-Amami S. 1977. Traditional technologies and development of the African environments, utilisation of runoff waters: the 'meskats' and other techniques in Tunisia. African Environment 3: 107–120.

Eldridge D.J. 1999. Distribution and floristics of moss- and lichen-dominated soil crusts in a patterned *Callitris glaucophylla* woodland in eastern Australia. Acta Oecologia 20: 159–170.

Eldridge D.J., Zaady E. and Shachak M. 2000. Infiltration through three contrasting biological soil crusts in patterned landscapes in the Negev, Israel. Catena 40: 323–336.

Elkins N.Z., Sabol G.V., Ward J.J. and Whitford W.G. 1989. The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. Oecologia 68: 521–528.

Evenari M., Shanan L. and Tadmor N. 1983. The Negev: the challenge of a desert. Oxford University Press, London, UK.

Feinbrun-Dothan N. and Danin A. 1991. Analytical flora of Eretz-Israel. Cana, Jerusalem, Israel.

Galle S., Brouwer J. and Delhoume J. 2001. Soil water balance. In: Tongway D.J., Valentin C. and Seghieri J. (eds), Banded Vegetation Patterning in Arid and Semiarid Environments: Ecological Processes and Consequences for Management. Springer-Verlag, New York, New York, USA, pp. 77–104.

Garner W. and Steinberger Y. 1989. A proposed mechanism for the formation of 'Fertile Islands' in the desert ecosystem. Journal of Arid Environments 16: 257–262.

Greene R.S.B. 1992. Soil physical properties of three geomorphic zones in a semi-arid mulga woodland. Australian Journal of Soil Research 30: 55–69.

Haase P., Pugnaire F.I., Clark S.C. and Incoll L.D. 1996. Spatial patterns in a two-tiered semi-arid shrubland in southeastern Spain. Journal of Vegetation Science 7: 527–534.

Hiernaux P. and Gérard B. 1999. The influence of vegetation pattern on the productivity, diversity and stability of vegetation: the case of ″brousse tigree″. Acta Oecologia 20: 147–158.

Kolarkar A.S., Murthy K. and Singh N. 1983. Khadin – a method of harvesting water for agriculture in the Thar Desert. Journal of Arid Environments 6: 59–66.

Kutsch H. 1983. Currently used techniques in rainfed water concentrating culture: the example of the Anti-Atlas. Applied Geography and Development 21: 108–117.

López-Portillo J. and Montaña C. 1999. Spatial distribution of *Prosopis glandulosa* var. *torreyana* in vegetated stripes of the southern Chihuahuan desert. Acta Oecologia 20: 197–208.

Loveday J. 1974. Methods of analysis of irrigated soils. Bureau of Soils Technical Communication No. 54.

Ludwig J.A., Tongway D.J. and Marsden S.G. 1994. A flow-filter model for simulating the conservation of limited resources in spatially heterogeneous, semi-arid landscapes. Pacific Conservation Biology 1: 209–213.

Ludwig J., Tongway D., Freudenberger D., Noble J. and Hodgkinson K. 1997. Landscape Ecology: Functions and Management. CSIRO, Australia.

Macfayden W.A. 1950. Vegetation patterns in British Somalilands. Nature 165: 121.

Malam Issa O., Trichet C., Défarge J., Couté A. and Valentin C. 1999. Morphology and microstructure of microbiotic soil crusts on a tiger bush sequence (Niger, Sahel). Catena 37: 175–196.

Mauchamp A., Rambal S., Ludwig J.A. and Tongway D.J. 2001. Multiscale modelling of vegetation bands. In: Tongway D.J., Valentin C. and Seghieri J. (eds), Banded Vegetation Patterning in Arid and Semiarid Environments: Ecological Processes and Consequences for Management. Springer-Verlag, New York, New York, USA, pp. 146–166.

Minitab 1994. Minitab Reference Manual, Release 10.1. Minitab Inc., State College, Pennsylvania.

Montaña C., Seghieri J. and Cornet A. 2001. Vegetation dynamics: recruitment and regeneration in two-phase mosaics. In: Tongway D.J., Valentin C. and Seghieri J. (eds), Banded Vegetation Patterning in Arid and Semiarid Environments: Ecological Processes and Consequences for Management. Springer-Verlag, New York, pp. 132–145.

Morin J. and Cluff C.B. 1980. Runoff calculation on semi-arid watersheds using infiltration equations determined from rotodisk rainulator. Water Resources Research 16: 1080–1093.

Niemeijer D. 1998. Soil nutrient harvesting in indigenous Teras water harvesting in eastern Sudan. Land Degradation and Development 9: 323–330.

Noble J.C., Greene R.S.B. and Müller W.J. 1998. Herbage production following rainfall redistribution in a semi-arid mulga (*Acacia aneura*) woodland in western New South Wales. Rangeland Journal 20: 206–225.

Noy-Meir I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4: 25–51.

Peugeot C., Estéves M., Gale S., Rojot J.L. and Vandervaere J.P. 1997. Runoff generation processes: results and analysis of field data collected at the east central supersite of the HAPEX-Sahel experiment. Journal of Hydrology 188–189: 179–202.

Pickup G. 1985. The erosion cell – a geomorphic approach to landscape classification in range assessment. Australian Rangeland Journal 7: 114–121.

Puigdefébregas J. and Sanchez G. 1996. Geomorphological implications of vegetation patchiness on semi-arid slopes. In: Anderson M.G. and Brooks S.M. (eds), Advances in Hillslope Processes. Vol. 2. Wiley, Chichester, UK, pp. 1027–1060.

Reid K.D., Wilcox B.P., Breshears D.D. and MacDonald L. 1999. Runoff and erosion in a piñon-juniper woodland: influence of vegetation patches. Soil Science Society of America Journal 63: 1869–1879.

Reij C., Mulder P. and Begemann L. 1990. Water Harvesting for Plant Production. Technical Paper Number No. 91. Vol. 1. World Bank, Washington, DC, USA.

Rostagno C.M. 1989. Infiltration and sediment production as affected by soil surface condition in a shrubland of Patagonia, Argentina. Journal of Range Management 42: 382–385.

Schlesinger W.H., Reynolds J.E., Cunningham G.L., Huenneke L.E., Jarrell W.M., Virginia R.A. et al. 1990. Biological feedbacks in global desertification. Science 247: 1043–1048.

Schulten J.A. 1985. Soil aggregation by cryptogams of sand prairie. American Journal of Botany 72: 1657–1661.

Seghieri J. and Galle S. 1999. Run-on contribution to a Sahelian two-phase mosaic system: soil water regime and vegetation life cycles. Acta Oecologia 20: 209–217.

Shachak M., Sachs M. and Itshak M. 1998. Ecosystem management of desertified shrublands in Israel. Ecosystems 1: 475–483.

Shachak M., Pickett S.T.A., Boeken B. and Zaady E. 1999. Managing patchiness, ecological flows, productivity, and diversity in dry lands: Concepts and applications in the Negev desert. In: Hoekstra T. and Shachak M. (eds), Arid Lands Management – Toward Ecological Sustainability. University of Illinois Press, Urbana, Illinois, USA, pp. 254–263.

Sheikh H.I., Shah B.H. and Aleeh A. 1984. Effect of rainwater harvesting method on the establishment of tree species. Forest Ecology and Management 8: 257–263.

Teomim N. 1990. Soil survey of the Sayeret Shaked Park. Jewish National Fund, Gilat, Israel.

Tongway D.J. 1995. Monitoring soil productive potential. Environmental Monitoring and Assessment 37: 303–318.

Tongway D.J. and Ludwig J.A. 1994. Small-scale patch heterogeneity in semi-arid landscapes. Pacific Conservation Biology 1: 201–208.

Valentin C. 1991. Soil crusting in two alluvial soils of northern Niger. Geoderma 48: 201–221.

Verrecchia E., Yair A., Kidron G.J. and Verrecchia K. 1995. Physical properties of the psammophile cryptogamic crusts and their consequences to the water regime of sandy soils, north western Negev Desert, Israel. Journal of Arid Environments 29: 427–437.

Veste M., Littman T., Breckle S.W. and Yair A. 2001. The role of biological soil crusts on desert sand dunes of the north-western Negev (Israel). In: Breckle S.W., Veste M. and Wucherer W. (eds), Sustainable Land Use in Deserts., Heidelberg, Germany, pp. 357–367.

Yair A. 1990. Runoff generation in a sandy area – the Nizzana Sands, western Negev, Israel. Earth Surface Processes and Landforms 15: 597–609.

Yair A. and Shachak M. 1987. Studies in watershed ecology of an arid area. In: Berkovsky L. and Wurtele W. (eds), Progress in Desert Research. Rowman and Littlefield, Totowa, New Jersey, USA, pp. 145–193.

Zaady E. and Shachak M. 1994. Microphytic soil crust and ecosystem leakage in the Negev Desert. American Journal of Botany 81: 109.

Zaady E., Gutterman Y. and Boeken B. 1997. The germination of mucilaginous seeds of *Plantago coronopus*, *Reboudia pinnata*, and *Carrichtera annua* on cyanobacterial soil crust from the Negev Desert. Plant and Soil 190: 247–252.