ECOHYDROLOGY OF A RESOURCE-CONSERVING SEMIARID WOODLAND: EFFECTS OF SCALE AND DISTURBANCE

Bradford P. Wilcox,[1] David D. Breshears,[2] and Craig D. Allen[3]

[1]*Rangeland Ecology and Management Department, Texas A&M University, College Station, Texas 77845-2126 USA*
[2]*Environmental Dynamics and Spatial Analysis Group, Mail Stop J495, Earth and Environmental Science Division, Los Alamos National Laboratory, Los Alamos, New Mexico 87545 USA*
[3]*U.S. Geological Survey, Midcontinent Ecological Science Center, Jemez Mountains Field Station, Los Alamos, New Mexico 87544 USA*

Abstract. In semiarid landscapes, the linkage between runoff and vegetation is a particularly close one. In this paper we report on the results of a long-term and multiple-scale study of interactions between runoff, erosion, and vegetation in a piñon–juniper woodland in New Mexico. We use our results to address three knowledge gaps: (1) the temporal scaling relationships between precipitation and runoff; (2) the effects of spatial scale on runoff and erosion, as influenced by vegetation; and (3) the influence of disturbance on these relationships. On the basis of our results, we tested three assumptions that represent current thinking in these areas (as evidenced, for example, by explicit or implicit assumptions embedded in commonly used models). The first assumption, that aggregated precipitation can be used as a surrogate for total runoff in semiarid environments, was not verified by our findings. We found that when runoff is generated mainly by overland flow in these systems, aggregated precipitation amounts alone (by year, season, or individual event) are a poor predictor of runoff amounts. The second assumption, that at the hillslope and smaller scales runoff and erosion are independent of spatial scale, was likewise not verified. We found that the redistribution of water and sediment within the hillslope was substantial and that there was a strong and nonlinear reduction in unit-area runoff and erosion with increasing scale (our scales were slope lengths ranging from 1 m to 105 m). The third assumption, that disturbance-related increases in runoff and erosion remain constant with time, was partially verified. We found that for low-slope-gradient sites, disturbance led to accelerated runoff and erosion, and these conditions may persist for a decade or longer. On the basis of our findings, we further suggest that (a) disturbance alters the effects of scale on runoff and erosion in a predictable way—scale relationships in degraded areas will be fundamentally different from those in nondegraded areas because more runoff will escape off site and erosion rates will be much higher; and (b) there exists a slope threshold, below which semiarid landscapes will eventually recover following disturbance and above which there will be no recovery without mitigation or remediation.

Key words: banded vegetation; dryland hydrology; ecohydrology; erosion; landscape ecology; pinyon; piñon–juniper; runoff; semiarid hydrology; vegetation patches; water yield.

INTRODUCTION

Ecological and hydrological processes are tightly interrelated, and the complex ways in which they interact represents an important research frontier—one that requires close collaboration between ecologists and hydrologists. Understanding these dynamics is crucial if we are to effectively address landscape change resulting from climate change and land use. Recent critiques of current hydrologic research have emphasized the need for more research at the interface of ecology and hydrology (Entekhabi et al. 1999, National Research Council 1999).

Ecological and hydrological processes are particularly tightly coupled in water-limited environments, or drylands, which encompass hyperarid, arid, semiarid,

and dry subhumid zones (Middleton and Thomas 1997). In these environments, a positive-feedback or self-reinforcing mechanism links water and vegetation (Cammeraat and Imeson 1999, Ludwig et al. 2000). In other words, how water is redistributed and where it becomes concentrated are important determinants of vegetation patterns; and conversely, vegetation patterns also directly modify the nature of runoff (Ludwig et al. 1997, Shachak et al. 1998, Bergkamp et al. 1999, Puigdefabregas et al. 1999, Valentin et al. 1999). These interactions are the focus of the emerging field of ecohydrology.

Understanding the linkages between vegetation and runoff processes takes on added importance in light of the current pace of change in both climate and land use. Both types of change are likely to engender nonlinear responses, with threshold conditions being important (Davenport et al. 1998, Imeson and Lavee 1998). The linkages between runoff and vegetation in

drylands, however, are complex (Hutjes et al. 1998). A conceptual framework (Ludwig et al. 1997) clarifies these linkages; it proposes that the redistribution of resources from source areas (bare patches) to sink areas (vegetation patches) is a fundamental process within drylands that may be disrupted if the vegetation patch structure is disturbed. "Resource-conserving" drylands are organized such that runoff is quickly captured by, and concentrated in, vegetation patches, minimizing the loss of resources. This concentration of resources increases the efficiency of their use and allows for higher net primary productivity. For example, when water from bare patches becomes concentrated in vegetated patches, it is stored at greater depths and is less subject to evaporation (Newman et al. 1997), which means more water is available to plants (Seghieri and Galle 1999, Galle et al. 2001).

The framework further proposes that if a disturbance, such as overgrazing, reduces the density and/or size of vegetation patches, the system will become "leaky" or "nonconserving"—less efficient at trapping runoff, leading to a loss of valuable water and nutrient resources (Ludwig and Tongway 2000). A positive-feedback loop may then reinforce the degradation process: the higher runoff rates will mean less water available to plants and higher erosion rates (see also Davenport et al. 1998). The degradation cycle may proceed whereby overland-flow runoff increases in both amount and energy, plant vigor declines, and the microclimate becomes more harsh. Although few studies have explicitly documented changes in overland runoff caused by disturbance, there is indirect evidence of such changes (Whisenant 1999).

Some of the fundamental assumptions of this framework, however, have not been tested or quantified, particularly in regard to the temporal and spatial nature of runoff. One of these assumptions is that some inherent relationships exist between spatial scale and runoff and erosion. For example, in a conserving system, unit-area runoff and erosion should dramatically decrease as scale increases, because runoff is quickly captured. For a degraded or nonconserving system, the decrease in unit-area runoff with increasing scale should be less precipitous, because capture is less efficient (Ludwig et al. 1997). Another assumption is that rainfall and the runoff it generates act as a trigger in the redistribution of resources. But for many or most dryland systems, neither the frequency nor the magnitude of runoff has been well quantified; and even though precipitation amounts are often used as a surrogate for runoff, for drylands the relationship is tenuous at best and requires further examination.

It is increasingly recognized that runoff is a fundamental ecological process in semiarid landscapes, but the spatial and temporal nature of runoff in these environments is not well understood. Major gaps in our knowledge, discussed below, are (1) the temporal relationships between precipitation and runoff (and as-

sociated erosion), including the frequency, magnitude, and timing of runoff and erosion; (2) the effects of spatial scale on runoff and erosion, including the relationships between redistribution of resources and resource losses; and (3) the effects of disturbance on these processes and relationships, in terms of both magnitude and persistence. The objective of our study was to evaluate, for each knowledge gap, common assumptions (explicit and implicit) related to that area. Using observations of runoff and erosion in a semiarid piñon–juniper woodland, we addressed knowledge gaps 1 and 3 with a long-term data set (8 yr) and knowledge gap 2 with a shorter term (26 mo), multiple-scale data set.

KNOWLEDGE GAPS AND ASSUMPTIONS

Temporal relationships between precipitation and runoff

Runoff prediction is often based on a simplified concept: that a given magnitude of runoff will be produced by a given amount of precipitation occurring over some period of time. One common methodology in hydrologic modeling, the curve number (Pilgrim and Cordery 1993, Arnold et al. 1998), predicts runoff volume in this way. It is employed in ecological models as well (e.g., Mauchamp 1994). Although reasonable for many humid environments, where runoff occurs as subsurface flow and is essentially that portion of precipitation greater than soil storage capacity, these precipitation–runoff relationships may not be appropriate for semiarid landscapes where runoff generally occurs as infiltration-excess overland flow. For these regions, the optimal period over which precipitation amounts should be aggregated is unknown; and even more important, runoff is strongly influenced by factors other than precipitation amount—such as surface infiltration characteristics, soil moisture, and precipitation intensity. In other words, data on precipitation alone may be insufficient for reliable prediction of runoff. Given the ecological importance of runoff in semiarid landscapes, gaining an understanding of the true relationship between precipitation and runoff is essential.

To address this knowledge gap, we evaluated the following assumption: In semiarid landscapes, runoff amounts can be predicted on the basis of precipitation amounts at any one of a number of temporal scales, ranging from that of an individual precipitation event to an annual total.

Effects of spatial scale on runoff

Very few studies have attempted to describe how naturally produced runoff and erosion at the vegetation-patch scale relate to those same processes at the hillslope scale. The limited data available for the hillslope scale suggest that, in semiarid environments, unit-area runoff decreases as scale increases from patch to hillslope (Abrahams et al. 1995, Puigdefabregas and San-

chez 1996, Bergkamp 1998, Reid et al. 1999). However, most modeling methodologies for predicting runoff from small watersheds do not explicitly take scale differences into account (Wood et al. 1990), except for a few models that incorporate the effects of channel transmission losses on runoff (Lane et al. 1980, Goodrich et al. 1997). Even if not explicitly expressed, the prevailing view is that runoff from small watersheds (where runoff generation is largely a hillslope process) is independent of scale.

To address this knowledge gap, we evaluated the following assumption: Runoff and erosion are independent of spatial scale for scales ranging from that of the individual vegetation patch to that of the hillslope.

Effects of disturbance on runoff

Although many studies have documented long-term vegetation dynamics following disturbance, few have tracked the long-term behavior of runoff following disturbance. Land disturbance, by changing vegetation and/or soil properties, can alter the spatial and temporal relationships among those properties in ways that may persist for decades or longer (Castillo et al. 1997, Belnap and Eldridge 2001). For example, when semiarid grasslands degrade into shrublands, the efficiency of runon on hillslopes is reduced. Water is routed off the hillslope in reticular fashion, via the interconnected intercanopy zones of relatively sparse vegetation cover. This mechanism, which has been well documented in creosote shrublands (former grasslands) in Arizona (Abrahams et al. 1995) and southern New Mexico (Schlesinger et al. 1999) and in sagebrush rangelands in Idaho (Seyfried 1991), favors the maintenance of the new shrubland conditions (Schlesinger et al. 1990). Over time, the intercanopy areas become progressively depleted of soil through erosion (both wind and water), lowering infiltration capacity and creating an increasingly harsh microclimate (Schlesinger et al. 1996, Aguiar and Sala 1999, Reynolds et al. 1999, Schlesinger et al. 1999). These studies suggest that severe disturbance, by reducing the size and density of vegetation patches, triggers a positive feedback loop that slows or even prevents a return of runoff and erosion to predisturbance levels.

To address this knowledge gap, we evaluated the following assumption: Increases in runoff and erosion that result from a reduction in the size and/or density of vegetation patches remain constant with time.

STUDY AREA AND METHODS

Our study was conducted in a semiarid piñon–juniper woodland, at a 5-ha site known as Mesita del Buey within the Los Alamos National Laboratory, on the Pajarito Plateau in northern New Mexico (2140 m, 35°50″58′ N, 106°16″20′ W). The site has a mean slope gradient of 5%. An integrated set of studies related to site ecology and hydrology have been carried out here over the past decade (Wilcox 1994, Davenport et al.

1996, Wilcox et al. 1996a, 1997, Breshears et al. 1997a, b, 1998, Newman et al. 1997, Breshears and Barnes 1999, Reid et al. 1999, Martens et al. 2000, 2001).

The semiarid, temperate, mountain climate has been described by Bowen (1996). The long-term mean annual precipitation at Mesita del Buey is ~400 mm/yr (varying with elevation from ~330 to 500 mm/yr) and displays a strong maximum in the months of July and August. Soils at the site are predominantly sandy loam or loam in texture and have developed in Bandelier-Tuff-derived alluvium and residuum (Davenport et al. 1996). The dominant tree species are Colorado piñon pine (*Pinus edulis* Engelm.) and one-seed juniper (*Juniperus monosperma* [Engelm] Sarg.), which together make up ~55% of the area's tree cover (Martens et al. 2000). The dominant herbaceous plant is the perennial grass blue grama (*Bouteloua gracilis* [H.B.K.] Lag.).

To conceptualize relationships between vegetation, runoff, and erosion, we used a hierarchical framework (Wilcox and Breshears 1995), the levels of which are distinguished on the basis of scale, vegetation cover, and topographic features (Fig. 1). In this paper we focus on three of these levels: the intercanopy unit, the patch, and the hillslope. At the intercanopy-unit level, we identify two categories, according to presence or absence of vegetation cover: vegetated units and bare units. The scale of each unit, in this case the slope length, is ~1–2 m. At the patch level, the two categories are the canopy and the intercanopy, for which the scale, or slope length, is ~2–5 m. The intercanopy patches comprise the vegetated and the bare units, which have distinct vegetation-cover characteristics and are hydrologically distinct from each other as well as from the canopy patches (Reid et al. 1999). Finally, the hillslope level encompasses the intercanopy and the canopy patches and may have a scale or slope length of up to several hundred meters. We measured runoff and erosion at four scales (microplot, long microplot, plot, hillslope), which correspond to the three hierarchical levels as outlined in Fig. 1. Results at the microplot and long-microplot scales have been reported in Reid et al. (1999).

Within this hierarchical framework, we tested assumption 1 (precipitation is a surrogate for runoff) and assumption 3 (effects of disturbance are constant over time) using the long-term data, covering an 8-yr period, at the plot scale. We tested assumption 2 (spatial scale does not affect runoff and erosion) using a shorter-term (26 mo) data set that was collected at all of the scales shown in Fig. 1. For assumption 1, we used regression analysis, and for assumptions 2 and 3, we used paired t tests with significance level at $P = 0.10$.

Precipitation measurements

Precipitation was measured at Mesita del Buey over the entire 8-yr period by means of a weighing-precipitation rain gauge equipped with a chart recorder and

HIERARCHICAL   SCALE-OF-MEASUREMENT
LEVEL   CATEGORY

I. Intercanopy unit   (1) Bare   (2) Vegetated

Bare   Vegetated
microplot   microplot
(1 × 1–3 m)   (1 × 1–3 m)

II. Patch   (1) Intercanopy   (2) Canopy

Canopy
microplot
(1 × 1 m)

Long
microplot
(1 × 6–8 m)
Plot
(3 × 10.7 m)

III. Hillslope   (1) Piñon–Juniper Woodland
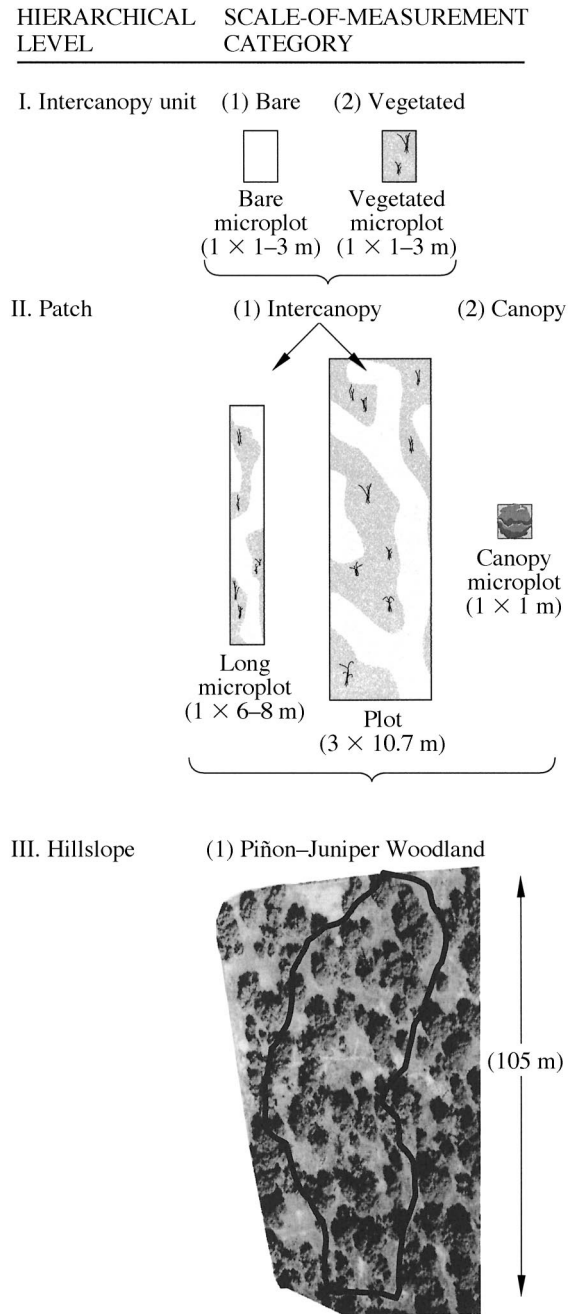
(105 m)

FIG. 1.   Hierarchical levels and the corresponding scale-of-measurement categories used for the Mesita del Buey study area. The four scales of measurement are microplot, long microplot, plot, and hillslope.

a snow shield. Beginning in August 1993, supplemental continuous precipitation data was collected via a tipping-bucket rain gauge and a ''precipitation well'' (for use when temperatures are below freezing). The precipitation well was constructed of 25 cm diameter aluminum tubing. It was inserted 3 m into the ground (which prevents the water from freezing) and extended 4 m above the surface.

Long-term, plot-scale data for assumptions 1 and 3

Naturally occurring runoff and erosion were monitored at the plot scale, on four adjacent 3 × 10.7 m plots, between 1991 and 1998 (these plots had been established in 1987 for rainfall simulation studies associated with development of the WEPP soil-erosion model [Simanton et al. 1991]). Two of the plots, U1 and U2 (undisturbed), were controls; the other two, D1 and D2 (disturbed), were stripped of all vegetation—including root crowns—biological soil crust, litter, and rock. We used data from the undisturbed plots to test assumption 1 and data from both the undisturbed and disturbed plots to test assumption 3.

Runoff was collected and manually measured in downslope tanks over the entire eight years. In 1994, we upgraded the installations to allow continuous measurement of runoff, with manual measurements continued as a backup. The upgrade included 100 L capacity wells equipped with pressure transducers, as well as 60° trapezoidal, 10 cm deep flumes through which overflow from the wells would be routed into collection tanks. We measured water volume after each runoff event and took two 1-L samples from each storage well to determine sediment concentrations.

Shorter-term, multiple-scale data for assumption 2

From July 1994 through August 1996, in addition to the plot-scale measurements described above, we collected data from 11 intercanopy microplots (1–2.8 m), three intercanopy long microplots (6–8 m), and the hillslope as a whole. Of the intercanopy microplots, four were vegetated units (>30% basal vegetation cover) and seven were bare units (<30% cover). The long microplots included both vegetated and bare areas. Runoff and sediment from each microplot and long microplot were collected in downslope storage tanks and measured in the same manner as for the long-term, plot-scale studies (see Reid et al. 1999 for a full description). We compared these runoff and erosion data with those from the canopy microplots, obtained from July 1995 to August 1996 and reported by Reid et al. (1999). Statistical tests for comparisons across scales were based on the data sets for the entire 26-mo period, thereby excluding the canopy microplot data.

During the same 26-mo period, runoff was monitored from a hillslope that was ~2000 m² in size. A 12 m long gutter was installed at the downslope end, perpendicular to the slope; surface runoff was routed from the gutter into a collection tank through a 17 cm deep trapezoidal flume. Sediment samples were not collected, but yields for a given runoff event were assumed to be equal to mean yields from the undisturbed plots (U1 and U2). An interflow collector, designed similarly to that described in Wilcox et al. [1997], was also installed, parallel to the surface runoff collector. Only trace amounts of interflow were recorded during the nearly three years of monitoring.

FIG. 2. Mean monthly precipitation measured at Mesita del Buey (1991–1998).
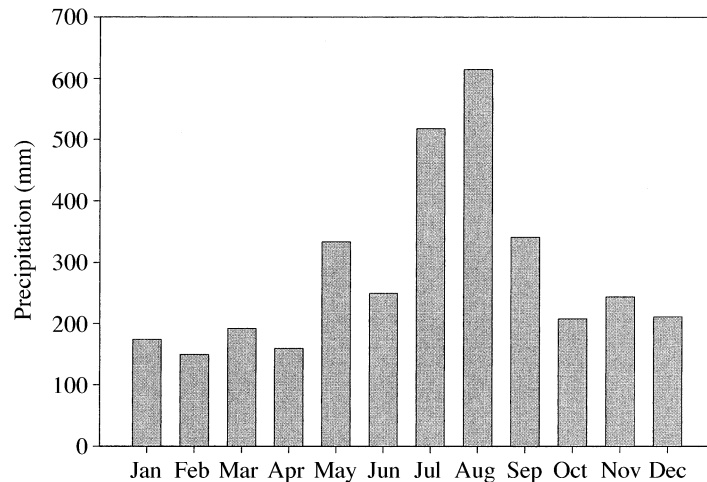
RESULTS

Knowledge gap 1—temporal relationships

Precipitation patterns at the site are typical of the mountain southwest, with a pronounced summer monsoon season in July, August, and September (Fig. 2). During the study period, annual precipitation ranged from 312 to 523 mm, and summer precipitation ranged from 150 to 322 mm (Table 1). Runoff from the undisturbed plots averaged 7% of the annual water budget, the contribution being as high as 14% in some years and as low as 2% in other years (Table 1). Over 90% of the associated erosion occurred in the summer. Winter erosion was minimal, even though close to 50% of the runoff occurred during winter months (Table 2).

The undisturbed plots produced measurable summer or fall runoff (>0.1 mm) on 44 occasions (Fig. 3a). The 10 largest runoff events (four of which occurred in 1991), made up less than a quarter of the total number of events but accounted for >80% of total runoff. The cumulative distribution function, which calculates the probability of a given event being less than or equal to a specified value (Hirsch et al. 1992), was highly log-normal, which indicates a strong probability that any given runoff event will be small in comparison to the largest events.

Erosion produced by individual runoff events showed a more skewed distribution than that of the runoff events (Fig. 3b). Almost 80% of the erosion took place during the five largest runoff events, and we estimated that the largest event (22 July 1991) by itself was responsible for ~20% of the sediment leaving the plots. As shown by the cumulative distribution function, soil losses from the great majority of the runoff events (>80%) were below 50 kg/ha, most of them far smaller than that.

The correlation between precipitation and runoff was generally weak (Fig. 4). There was no correlation between precipitation and runoff when aggregated over a year or over a summer season (Fig. 4a and b). The

relationship for winter was significant ($P = 0.09$), with precipitation accounting for 68% of the variation. An examination of the winter pattern would suggest the existence of a precipitation threshold of ~150 mm that, if exceeded, will produce substantial winter runoff (>40 mm, Fig. 4c). At the finest temporal scale of individual events, the relationship was significant; however, precipitation volume accounted for only 32% of the variation in runoff (Fig. 4d). Generally, runoff was produced only when precipitation exceeded 15 mm. The greatest amount of runoff occurred for the intermediate-size precipitation events, which were mostly convectional thunderstorms. The larger events were the result of longer but less intense frontal storms.

Knowledge gap 2—effect of spatial scale

As the scale of measurement increased, both the frequency and especially the magnitude of runoff and erosion (on a unit-area basis) decreased (Fig. 5). The frequency of runoff was highest for the bare microplots, intermediate for the vegetated microplots and long microplots, and lowest for the plot and hillslope scales (Fig. 5a). For amounts of both runoff and erosion there were large differences across scales (Fig. 5b and c), with more than a 50-fold decrease in cumulative runoff with increasing scale (270 mm for bare microplots vs. 5 mm from the hillslope) and more than a 150-fold decrease in cumulative erosion (16 000 kg/ha from the bare microplots vs. 100 kg/ha from the hillslope). Variation in erosion was particularly high at the bare microplot scale. Statistical comparisons, based on the mean value at each scale for each event, indicated that runoff and erosion were significantly different for all comparisons with the exception of the vegetated microplot and the long microplot.

Runoff resulted most often from convectional thunderstorms. On only two occasions during the 26-mo observation period was runoff generated by fall frontal storms. Four of the events were large (>5 mm), five

BRADFORD P. WILCOX ET AL.

TABLE 1. Monthly precipitation (mm) and runoff (mm) at Mesita del Buey.

Month	1991	1992	1993	1994	1995	1996	1997	1998
a) Precipitation								
October	8	8	6	10	80	0	83	13
November	39	61	25	17	59	6	16	21
December	46	49	40	5	19	11	1	40
January	8	12	70	8	25	27	21	2
February	8	7	40	4	21	7	54	8
March	24	30	18	45	22	5	3	44
April	0	19	2	40	36	2	47	12
May	44	80	47	67	69	0	26	1
June	16	25	13	12	38	94	49	3
July	141	29	46	38	38	71	40	115
August	109	75	120	71	45	43	99	52
September	56	30	31	28	70	46	64	15
Total	499	425	460	347	523	312	503	326
b) Runoff from undisturbed plots								
October		0	0	0	t	0	2	0
November		0	0	0	t	0	0	0
December		0	0	0	0	0	0	0
January		2	23	0	t	0	t	3
February		55	21	0	6	t	7	t
March		t	3	0	0	0	0	t
April	0	0	0	0	0	0	0	0
May	0	1	0	t	t	0	0	0
June	0	t	0	0	t	5	0	0
July	22†	0	0	1	0	0	t	5
August	29	1	9	18	11	0	t	t
September	1	t	1	0	14	1	t	0
Total	52	59	57	19	32	6	9	9
% runoff	10	14	12	6	6	2	2	3
c) Runoff from disturbed plots								
October		0	0	0	4	0	6	t
November		0	0	0	1	0	0	0
December		0	0	0	0	0	0	0
January		9	28	0	1	t	1	8
February		65	31	0	13	t	14	0
March		t	15	0	0	0	1	t
April	0	0	0	0	0	0	0	t
May	0	1	0	t	t	0	0	0
June	0	t	0	0	1	11	t	0
July	33†	0	0	3	3	2	0	6
August	51	9	16	26	20	t	2	t
September	2	5	3	1	26	4	t	0
Total	87	90	94	30	70	17	23	14
% runoff	17	21	20	9	14	5	5	4

Note: A value of ''t'' designates runoff <1 mm.
† Equipment malfunction (see Wilcox 1994).

were medium (0.1–5 mm), and 28 were small (<0.1 mm). Both runoff and erosion decreased (per unit area) with increasing scale and with increasing vegetation cover, regardless of event size (Fig. 6).

Large runoff events showed considerably higher runoff efficiencies, which is explained by the very intense nature of the precipitation that produced them and also by the fact that antecedent soil moisture was high at the time the storms occurred (Fig. 6a). For the large runoff events, runoff at the scale of the microplots was comparable to the total amount of precipitation; that is, virtually all the precipitation ran off. Runoff efficiency was also very high at the long-microplot and plot scales. But at the hillslope scale, runoff dropped

off precipitously compared with that measured at the other scales, indicating that much of the runoff is stored within the hillslope. With respect to erosion produced by the large runoff events, the bare microplots produced much greater amounts of sediment than the vegetated ones, and much more than was measured at the other scales (Fig. 6b).

For comparison purposes, we have included an estimate of canopy runoff and erosion for the 26-mo period. This estimate is an extrapolation of the 14 mo of measurements (the canopy microplots were installed 12 mo later than the other microplots), based on the ratio of canopy microplot to bare microplot data (Reid et al. 1999). Runoff and erosion from canopy micro-

TABLE 2. Monthly erosion (kg/ha) at Mesita del Buey.

Month	1991	1992	1993	1994	1995	1996	1997	1998
a) Erosion from undisturbed plots								
October	0	0	0	0	4	0	39	0
November	0	0	0	0	0	0	0	0
December	0	0	0	0	0	0	0	0
January	0	2	41	0	0	0	0	14
February	0	69	37	0	17	0	23	0
March	0	0	5	0	0	0	0	0
April	0	0	0	0	0	0	0	0
May	0	2	0	1	1	0	0	0
June	0	0	0	0	2	117	0	0
July	548†	0	0	25	0	1	0	85
August	312	14	42	352	412	0	10	0
September	0	1	62	0	258	12	1	0
Total	860	88	188	378	694	131	73	99
b) Erosion from disturbed plots								
October	0	0	0	0	19	0	115	0
November	0	0	0	0	8	0	0	0
December	0	0	0	0	0	0	0	0
January	0	15	51	0	4	0	1	42
February	0	104	56	0	30	0	38	0
March	0	0	27	0	0	0	1	0
April	0	0	0	0	0	0	0	0
May	0	10	0	27	3	0	0	0
June	0	5	0	0	35	731	0	0
July	2186†	0	17	185	49	38	0	232
August	1187	108	126	798	926	11	61	18
September	3	64	163	23	548	25	5	0
Total	3376	305	440	1033	1622	806	223	292

† Equipment malfunction (see Wilcox 1994).

plots occurred only during large precipitation events and was less than that from bare microplots, vegetated microplots, and long microplots.

For the medium and small runoff and erosion events, there was a decline with scale. The nature of the decrease, however, appeared different from that for the large events, being more concave than convex (Fig. 6a, c, and e). At a given scale, runoff efficiency decreased from large to medium to small events. Erosion produced by the medium and small runoff events also declined with scale, in a concave manner similar to that for large events (Fig. 6b, d, and f).

Knowledge gap 3—effect of disturbance

For the 8-yr observation period, runoff from the disturbed plots was about twice as high as that from the undisturbed plots (Table 1). The frequency of runoff was greater for the disturbed plots as well, with a total of 72 summer and fall runoff events (compared with 44 from the undisturbed plots). In other words, disturbance lowered the precipitation threshold for generating runoff. Erosion was also higher from the disturbed plots (Table 2), averaging ~1000 kg/ha annually (vs. ~300 kg/ha from the undisturbed plots). Cumulative runoff and erosion were significantly greater from disturbed plots than undisturbed plots, with little variation within plot type (Fig. 7). Differences were significant for most years for both summer and winter runoff (Fig. 8). Although the vegetation on the dis-

turbed plots was severely altered, these plots have not developed rilling; all observed erosion is interrill in nature. The observations do not indicate any obvious recovery in infiltration capacity over the 11 years following disturbance. However, summer runoff was not significantly different between undisturbed and disturbed plots in 1998, which was the last year of observation and the only year there was no significant difference (Figs. 7 and 8).

DISCUSSION

Assumption testing

Assumption 1: In semiarid landscapes, runoff can be predicted from precipitation at any one of a number of temporal scales.—Runoff cannot be predicted from precipitation when aggregated annually or during a summer season. We therefore reject this assumption for these time scales. Even on an event basis, the relationship between runoff and precipitation was only moderately predictive ($R^2 = 0.32$). Annual, summer, and single-event runoff are largely produced by convectional summer thunderstorms, with runoff occurring as infiltration-excess overland flow. For the winter the relationship was better, and there may be some opportunity for predicting winter runoff on the basis of precipitation. In the winter, the runoff process is fundamentally different: saturation-excess overland flow driven by a melting snowpack over frozen soils. Ob-
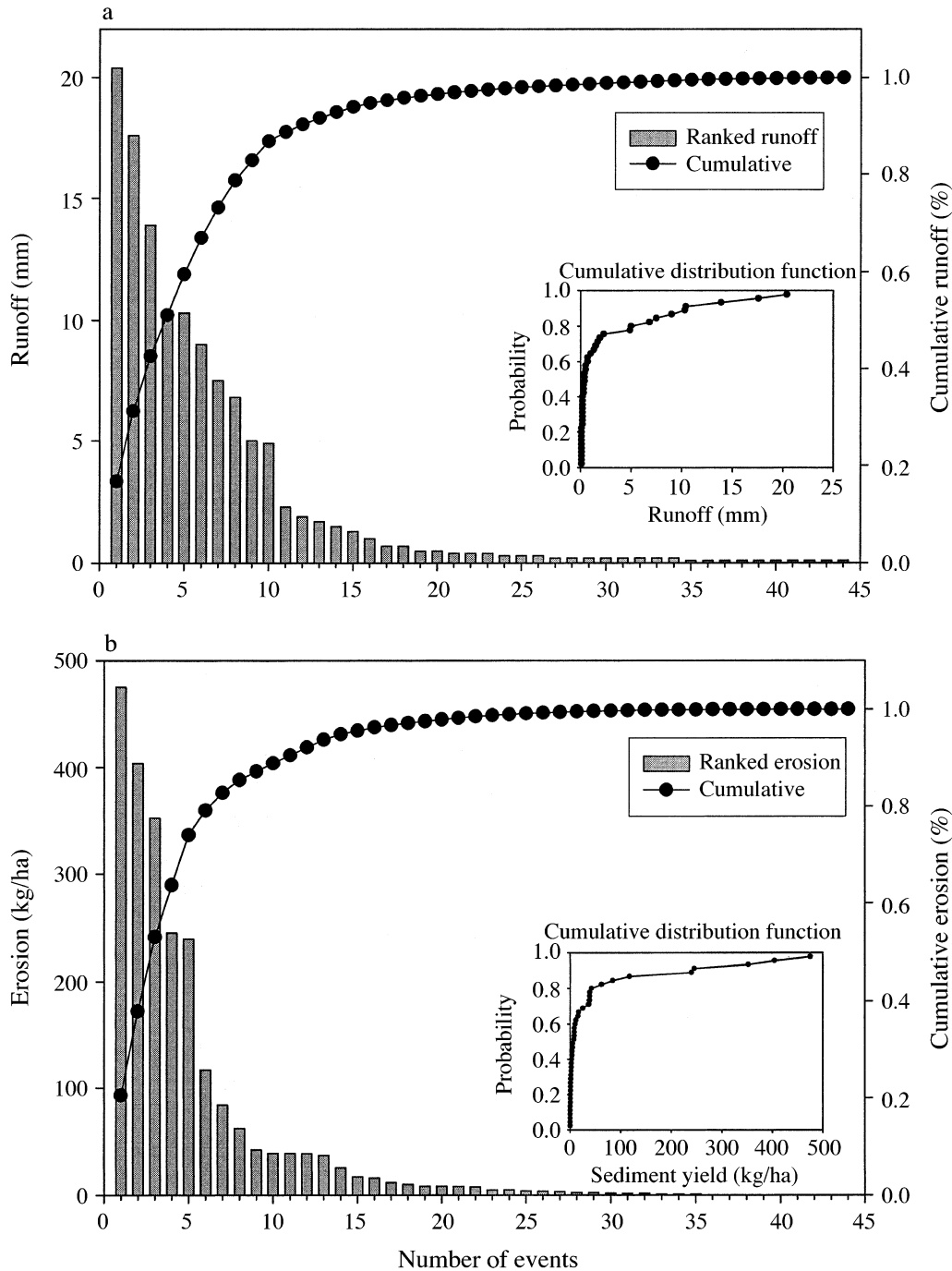
FIG. 3. A summary of mean (a) runoff and (b) erosion for the undisturbed plots. Events are ranked by magnitude (left axis); cumulative values are shown on the right axis. The cumulative distribution function is given in the inset for each.

viously, for this to happen there must be a sufficiently large winter snowpack, which occurs only in selected years (Breshears et al. 1997a). Our data do suggest that there may be a threshold value of winter precipitation, above which runoff is large and below which runoff is very small, although additional years of observation are needed to confirm this.

The generally poor relationship between aggregated precipitation and aggregated runoff that we observed likely applies to other areas where infiltration-excess overland flow is the dominant runoff process, as it is in most semiarid landscapes (Dunne 1978). Although not extensively documented, an analogous pattern has been noted by others. For example, Puigdefabregas et
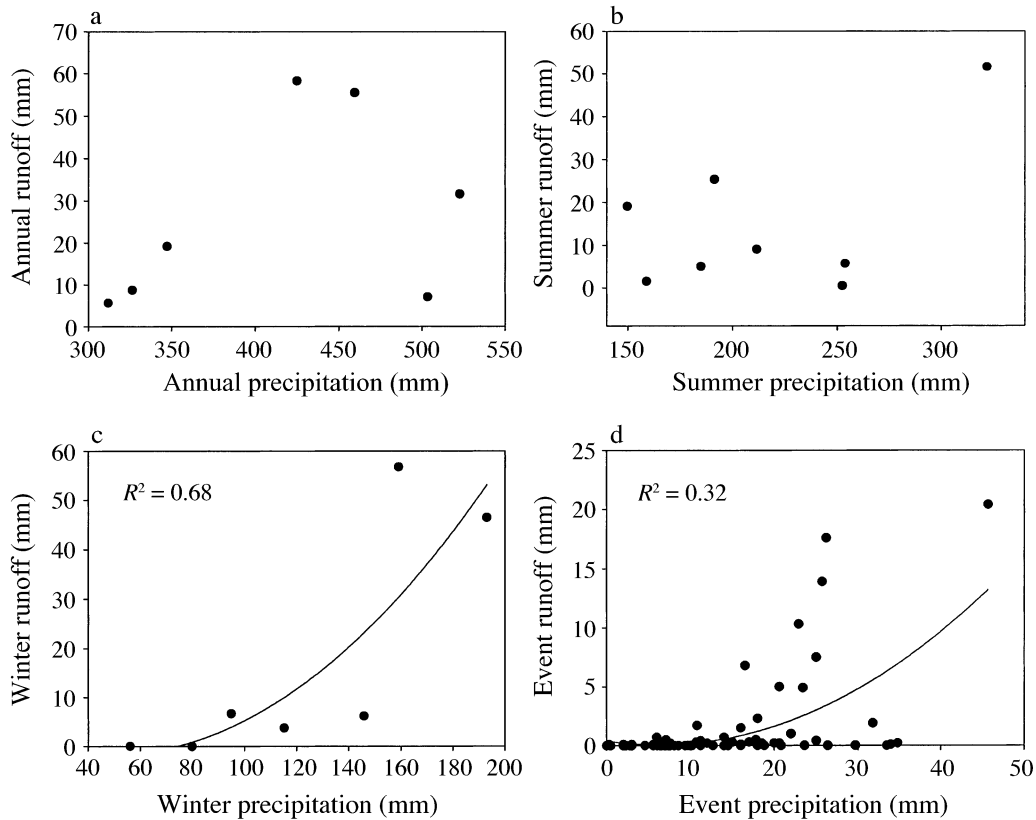
FIG. 4. The relationship between runoff and precipitation aggregated (a) annually, (b) by summer events, (c) by winter events, and (d) by total number of events.

al. (1999) recorded a relationship between event precipitation and runoff for semiarid Spain similar to that we observed. This is because for overland-flow-dominated systems runoff is controlled by the infiltration characteristics of the soil surface rather than the storage capacity of the soil (Beven 2001). In contrast, in other landscapes, particularly more humid environments, runoff occurs mostly as subsurface flow (or as saturation-excess overland flow) and is largely controlled by the ability of the landscape to store water. We would expect, then, that the amount of precipitation alone is much less predictive of runoff in semiarid regions than in humid ones. However, many modeling approaches used for calculating the water budget, for both ecological and hydrological applications, rely on aggregated precipitation as the primary variable for predicting runoff. Our results and those of others indicate that these predictions will have little relationship to reality for systems where runoff occurs primarily as infiltration-excess overland flow.

Assumption 2: Runoff and erosion are independent of spatial scale for scales ranging from that of the vegetation patch to that of the hillslope.—On the basis of our results, we reject this assumption. Our results from a conserving piñon–juniper woodland demonstrate how the relative importance of runoff in the water budget varies dramatically with the scale of observation. Most of the runoff measurable at the smaller scales is apparently captured by either herbaceous or possibly woody vegetation patches before it can exit at the hillslope scale. A large, high-intensity storm may generate runoff at the microplot scale (1- to 2.8-m slope length) with efficiencies very close to 100%; and yet the same storm will generate runoff at the hillslope scale with an efficiency of only 6%. Obviously, at the hillslope scale, large amounts of water are being stored. But by what means is the water stored? And exactly where does it end up?

The shape of the scale-dependent relationships (concave vs. convex; Fig. 6a, b, and c) provides insight into the scale at which storage is occurring for events of different sizes. In the case of small rainstorms, the concave shape suggests that most of the storage occurs at the patch level; whereas for the large rainstorms, the convex shape suggests that it is at the larger scales that storage is occurring. The differences in runoff and erosion between the intercanopy microplots and long microplots show that at small scales, water and sediment are being transferred from upslope bare patches to directly adjacent downslope vegetated patches (Reid et
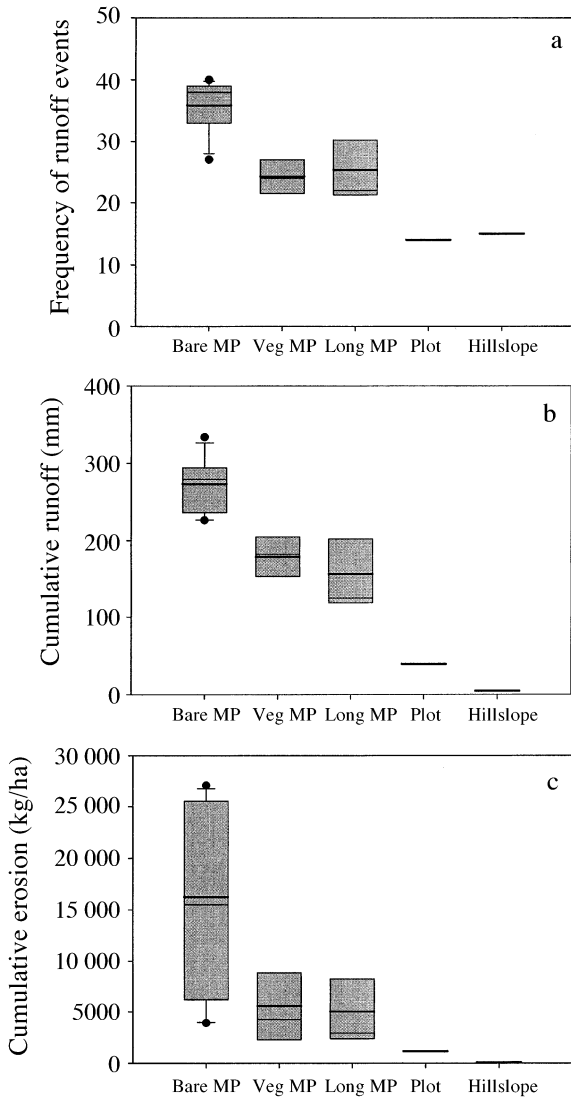
FIG. 5. Box-and-whisker diagrams showing the median, mean (thick line), 10th, 25th, 75th, and 90th percentiles for (a) frequency of runoff events; (b) cumulative unit-area runoff; and (c) cumulative unit-area erosion for bare microplots ($n = 7$), vegetated microplots ($n = 4$), long microplots ($n = 3$), plots ($n = 2$), and the hillslope ($n = 1$) during a consecutive 26-mo period (July 1994–August 1996).

al. 1999). When weighted according to the percentage of vegetation cover on the hillslope, the difference between runoff measured at the microplot scale and that measured at the hillslope scale is at least 20-fold. Although small-scale storage accounts for much of this difference, other storage sinks also appear to be important. Possible additional sinks include the canopy patches; and features such as micro dams, fallen logs, and subtle rises in the topography that impede the flow of water and cause it to pond behind and infiltrate into them (Tongway et al. 1989, Hysell and Grier 1996). The canopy patches, because of the accumulation of

litter and eolian material within them, tend to be slightly elevated with respect to the surrounding intercanopy patches; thus water may flow preferentially around them. This reticular flow pattern is typical of semiarid landscapes (Thornes 1994). To be captured in canopy patches, then, runoff water would have to attain the level of at least some of these patches (in all probability the upslope edge). A likely mechanism by which the water could attain this level is ponding behind larger-scale topographic features.

Assumption 3: Increases in runoff and erosion that result from a reduction in the size and/or density of vegetation patches remain constant with time.—Our study, one of the few to monitor long-term effects of disturbance on runoff and erosion, supports this assumption for the first decade following disturbance. Others have found that the recovery of biological soil crusts, a key determinant of hydrologic response, can take decades in these environments (Belnap and Eldridge 2001). Although our results indicate that increases in erosion can persist for at least 11 years following disturbance, there have been signs of recovery: an increase in biological soil crust cover and a decrease in the percentage of bare ground between 1992 and 1998 (Breshears and Wilcox, *unpublished data*). There are also indications that runoff from the disturbed plots may be approaching predisturbance levels (1998 in Fig. 8a). For the first 5–6 years of the study, hydrographs from the two disturbed plots were virtually identical and generally larger than those of the undisturbed plots, whereas for the past 2 years of observation, runoff from one of the disturbed plots more closely matched that from the undisturbed plots. We see no evidence of the accelerated degradation that was observed on a moderately steep slope in semiarid Spain (Castillo et al. 1997).

Broader implications and conceptual framework

Hydrology of piñon–juniper woodlands.—Our findings, in concert with previous work (Wilcox 1994, Wilcox et al. 1996a, Reid et al. 1999), provide the basis for a more comprehensive understanding of runoff and erosion in piñon–juniper woodlands. Runoff at this site occurs as overland flow and may be generated by intense summer thunderstorms, prolonged frontal storms, or snowmelt (generally over frozen soils). It is the large, high-intensity thunderstorms that are the most important runoff-producing agent at all scales. Low-intensity frontal storms produce runoff relatively infrequently. Runoff from snowmelt occurs only at small scales and, unlike that from low-intensity frontal storms, does not usually contribute to stream or channel flow. Lateral subsurface flow, or interflow, rarely if ever occurs. These findings contrast with those from nearby ponderosa pine communities (Wilcox and Breshears 1997, Wilcox et al. 1997, Newman et al. 1998).
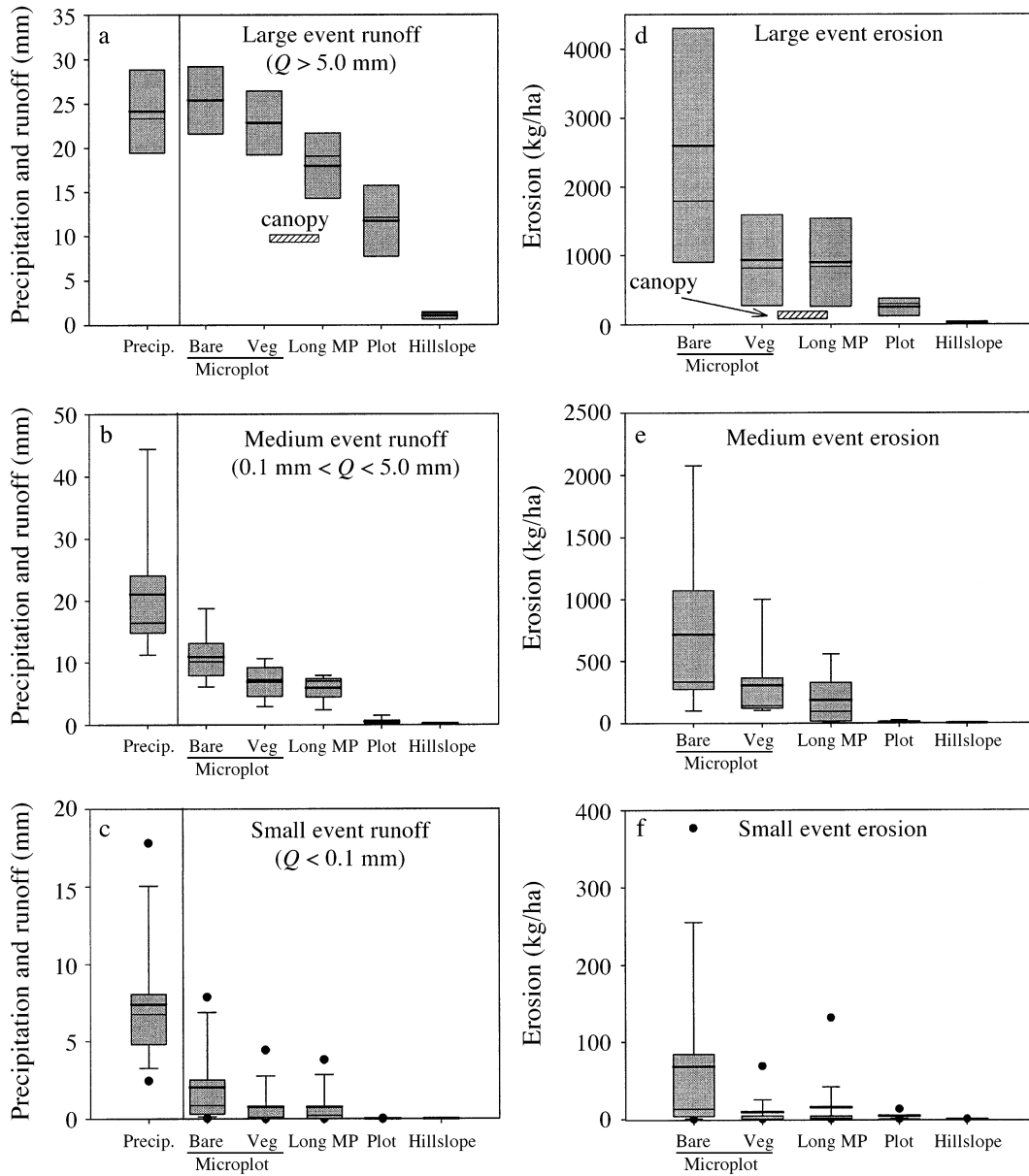
FIG. 6. Box-and-whisker diagrams showing the median, mean (thick line), 10th, 25th, 75th, and 90th percentiles for runoff and erosion produced by convectional storms: (a) large runoff events, (b) medium runoff events, (c) small runoff events, (d) erosion for large runoff events, (e) erosion for medium runoff events, and (f) erosion for small runoff events. For comparison, corresponding precipitation amounts are shown. Also for comparison, mean runoff and erosion from the canopy microplots is represented; this representation is an estimate for the 26-mo monitoring period based on the 14 mo of data actually collected and on the relative percentages of runoff and erosion from the canopy plots vs. those from the bare and vegetated microplots.

The general mechanisms of runoff generation observed at this site are assumed to be typical of other piñon–juniper areas of the southwest that are climatically, topographically, and edaphically similar. Conversely, they are distinct from the runoff mechanisms of regions in which a greater percentage of precipitation occurs in the winter. For example, in the juniper woodlands of the northwestern United States, runoff is generally produced by low-intensity winter rainstorms or melting snow, both of which result in quite low levels of erosion (Davenport et al. 1998). And in the piñon–juniper woodlands of northern Arizona, runoff occurs in both winter and summer, with winter runoff becoming more important as elevation increases (Collings and Myrick 1966, Clary et al. 1974, Baker 1984). Runoff mechanisms for most piñon–juniper woodlands in other regions have not been explicitly characterized (the most complete review of the hydrology of the relatively few
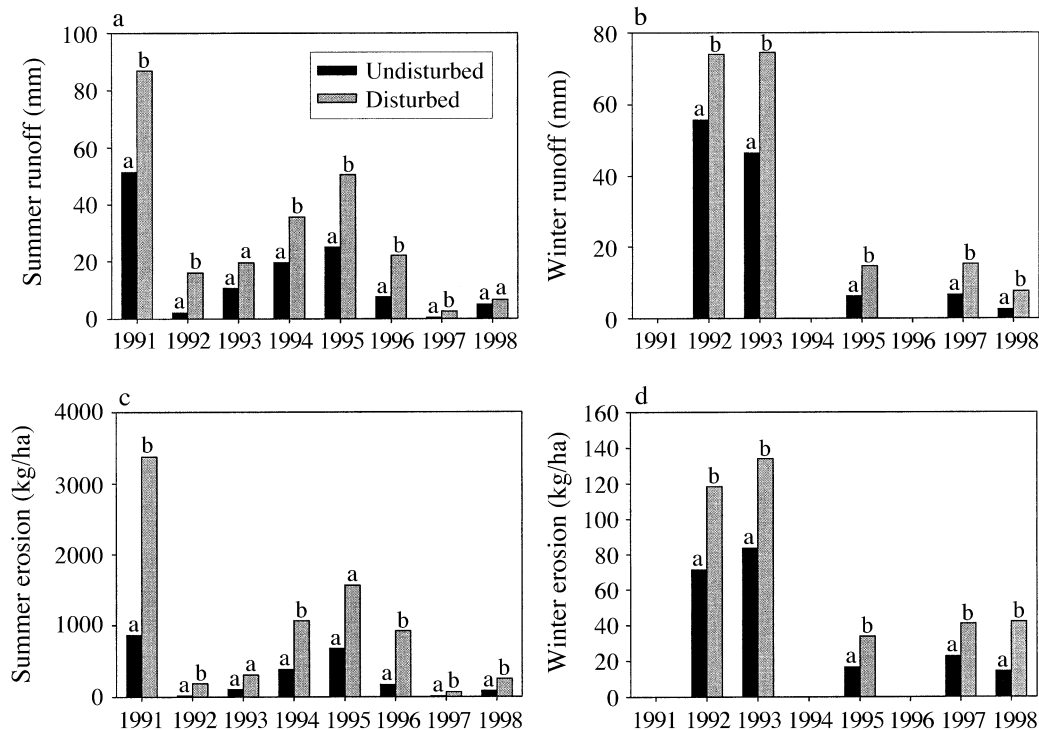
BRADFORD P. WILCOX ET AL.

FIG. 7. A comparison of runoff and erosion for the summer and winter months: (a) summer runoff, (b) winter runoff, (c) summer erosion, and (d) winter erosion. Different letters indicate that differences are significant at $P = 0.10$.

areas that have been studied may be found in Roundy and Vernon [1999]).

Erosion at Mesita del Buey is very low (~300 kg·ha^{-1}·yr^{-1} from the undisturbed plots and negligible amounts from the hillslope). Similar erosion rates are reported from stable piñon–juniper woodlands in Arizona (Clary et al. 1974, Heede 1987). Erosion from the disturbed plots was greater (~1000 kg·ha^{-1}·yr^{-1}), but was still substantially lower than that reported from other locations (Carrara and Carroll 1979, Gellis et al. 2001). The low erosion rates at Mesita del Buey are probably attributable to the low slope gradients. At a piñon–juniper hillslope site referred to as Frijolito, a 1-ha catchment within the Bandelier National Monument where we have also monitored runoff and erosion, the gradients are steeper (~10%, in contrast to the mean of <5% at Mesita del Buey). Following the drought of the 1950s, Frijolito has been undergoing severe and accelerated erosion (Allen and Breshears 1998), estimated at ~10 000 kg/ha annually (Wilcox et al. 1996b).

Scale dependency in conserving vs. nonconserving dryland ecosystems.—The cumulative data from our multiscale observations support a fundamental, if unstated, assertion of the Ludwig et al. (1997) framework: namely, that unit-area runoff will decrease as spatial scale increases because of the capture of runoff within the system. The decrease is expected to be more precipitous for a conserving system than for a nonconserving one with high erosion rates. On the basis of

these data, we propose an extended conceptual framework describing how unit-area runoff and erosion vary with scale between conserving and nonconserving conditions (Fig. 9). Differences between these conditions are due principally to differences in storage potential. The specific characteristics of a site, particularly vegetation patch structure and topographic features (rills, gullies, alluvial channels, and flood plains) determine its sinks or "threshold points"—points at which nonlinear changes in runoff and erosion are greatest (because of storage). These points may be modified by disturbance, particularly at the hillslope and smaller scales. For example, in the case of runoff (Fig. 9a), our work shows that for a conserving site, there is a strong nonlinear reduction in runoff as the scale of observation increases from microplot to hillslope, because of storage of runoff at the hillslope scale. For a nonconserving site, runoff should be less diminished with an increase in scale because of the limited small-scale storage, as observed by Wilcox et al. (1996b). Consequently, runoff from a nonconserving site is routed farther before being deposited in a sink area—be it a woody patch downslope (as in areas exhibiting banded vegetation) or an alluvial stream channel, as in many areas of the southwestern United States (Goodrich et al. 1997).

With respect to erosion (Fig. 9b), our results demonstrate that there is a very strong nonlinear reduction with increasing scale for conserving sites. At scales greater than those measured at our site, the number of
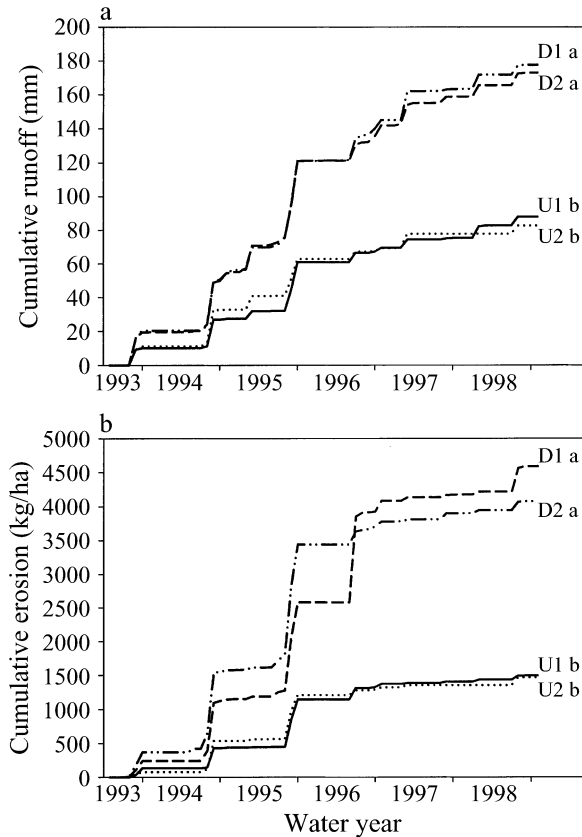
FIG. 8. Cumulative (a) runoff and (b) erosion for the two undisturbed plots (U1, U2) and the two disturbed plots (D1, D2) from August 1993 to December 1998.

sediment sinks or storage areas in the landscape increases with scale (Leopold et al. 1966, Osterkamp and Toy 1997). However, disturbance has the potential to dramatically alter this relationship. When a site becomes degraded through a loss of cover and soil compaction, it is likely that rill erosion and eventually even gullying will be initiated, which increase per-unit-area erosion as scale increases. However, at some larger scale, even within degraded sites, sediment will begin to be stored, and unit-area erosion or sediment yield will decrease. Osterkamp and Toy (1997) have reported such a threshold response for sediment movement and storage in southern Arizona.

The hydrologic response to disturbance will differ depending upon the resulting vegetation pattern (Fig. 10). Reduction of the density and/or size of vegetation patches, particularly those in the intercanopy, increases the connectivity of intercanopy areas, which facilitates loss of resources from the system (Davenport et al. 1998). On sites characterized by steeper slopes and stippled vegetation, the higher energy runoff will accelerate erosion, deflating the intercanopy areas, which further diminishes the opportunities for canopy patches to capture runoff (because of the increased difference in elevation between the two). In addition, as runoff

amounts and energy increase, microtopographic features that enhance the ability of the surface to store moisture may be destroyed, allowing for a relatively high net loss of resources from the system. Piñon–juniper and sagebrush are examples of the types of woodlands or shrublands that may degrade in this manner.

On other sites, generally characterized by less steep slopes and medium-textured soils, disturbance tends to create large intercanopy spaces that can carry large amounts of water downslope, to be captured by woody vegetation growing along the slope contour (Fig. 10), sometimes referred to as banded vegetation (Dunkerley 1997, Klausmeier 1999, Tongway and Ludwig 2001). Woody plants thus benefit from the reallocation of resources from intercanopy to canopy (Schlesinger et al. 1989). Degradation accentuating the banded vegetation does lead to increased runoff, but only up to the scale of the woody strip, where most if not all the upslope water will be captured (Bergkamp 1998, Greene et al. 2001). Examples of shrublands and woodlands that may degrade in this manner are mulga in Australia (Dunkerley and Brown 1995, Ludwig and Tongway 1995) and tiger bush in West Africa (Valentin and d'Herbes 1999, Valentin et al. 1999).

These scale dependencies in hydrological response have important ecological implications. The redistribution of water by runoff has been shown to affect plant water potential, herbaceous productivity, seedling establishment and germination rates, and plant mortality (Cornet et al. 1992, Montaña 1992, Hodgkinson and Freudenberger 1997, Seghieri et al. 1997, Noble et al. 1998, Seghieri and Galle 1999). More generally,
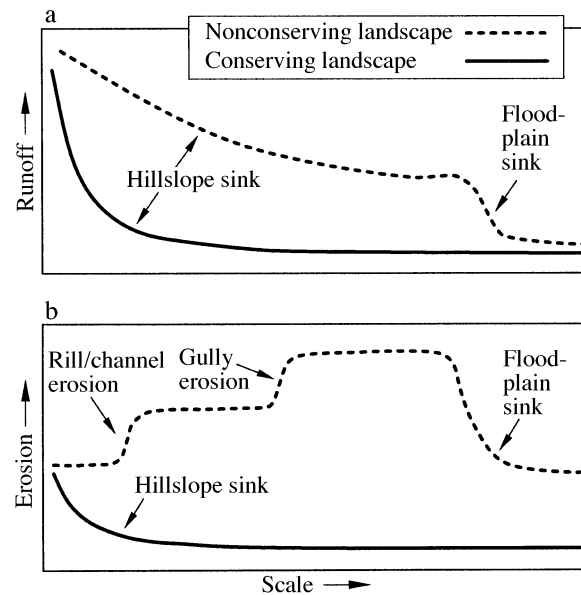

FIG. 9. Simplified conceptual model of the effects of scale on (a) unit-area runoff and (b) unit-area erosion in conserving vs. nonconserving semiarid systems.
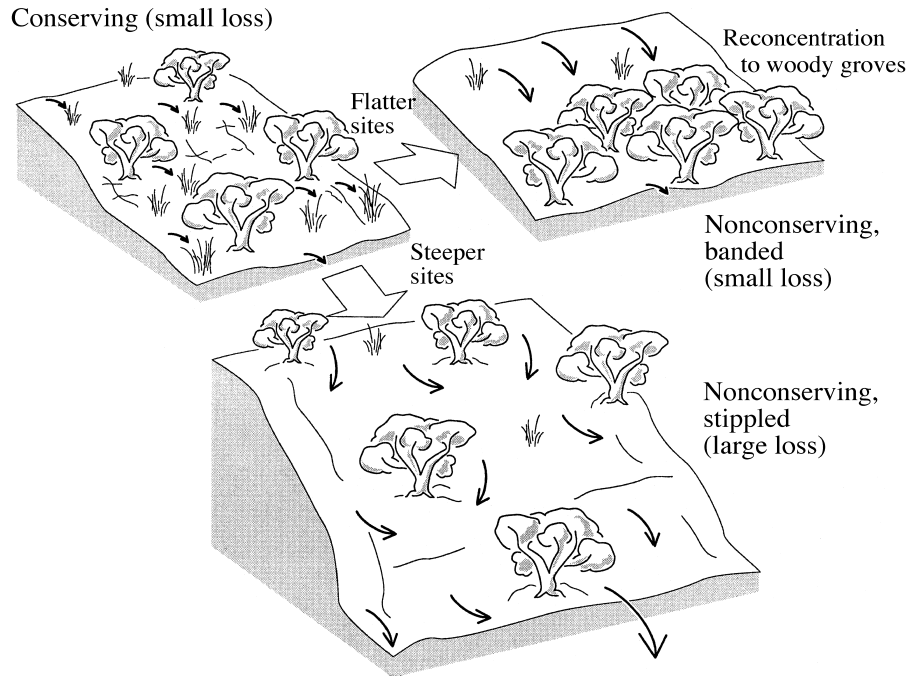
FIG. 10.   A conceptualization of runoff in conserving woodlands vs. runoff in nonconserving woodlands characterized by stippled or banded vegetation.

our results documenting how water is redistributed provide important support for Noy-Meir's (1973) basic concept about the importance, in more arid environments, of concentrating resources.

Modeling implications.—The scale-dependent non-linearity of runoff that we have described is likely a defining characteristic of many semiarid landscapes and therefore is important to consider when attempting to model runoff for these regions. Most hydrological modeling methodologies, however, do not explicitly take scale differences into account (Wood et al. 1990), which helps explain why these models generally do poorly when used to predict runoff under semiarid conditions. Even hydrological models that are both deterministic and spatially explicit have tended to yield poor results if they are not calibrated (Beven 1989, Wilcox et al. 1990). The reason for this has been much debated (Grayson et al. 1992, 1994, Smith et al. 1994). Some researchers suggest that it is incomplete input data concerning spatially distributed infiltration characteristics that result in poor predictions. However, as demonstrated by Loague and Kyriakidis (1997), supplying the model with more data does not necessarily improve its predictive capability. Others have suggested that the problem lies in the use of infiltration theory that is appropriate only at very small scales and for uniform soils (Beven 1989).

We would argue that a problem with deterministic hydrological models, at least as applied to semiarid landscapes, is failure to explicitly consider scale differences and the role of storage on the hillslope (Haw-

kins and Cundy 1987, Seyfried and Wilcox 1995). Our results indicate that scale-dependent runoff–runon processes exert much more control over runoff from a hillslope than does the spatial variability of point infiltration. Whether the primary modeling objective is ecological, hydrological, or a combination, it is important that scale dependencies be considered.

CONCLUSIONS

Our study examining the ecohydrology of a semiarid woodland contributes to an improved understanding in the three "knowledge gap" areas: (1) the temporal relationships between precipitation and runoff and erosion; (2) the effects of scale on runoff and erosion; and (3) how disturbance alters these relationships. Based on our results and comparisons with other studies, we conclude the following:

(1) Precipitation volume alone, irrespective of how it is aggregated temporally, is a poor predictor of runoff for semiarid landscapes in which infiltration-excess overland flow is the dominant mechanism of runoff generation.

(2) In a resource-conserving ecosystem, unit-area runoff and erosion decrease dramatically and nonlinearly from the patch to the hillslope scale.

In addition, we found that, following disturbance, both runoff and erosion amounts increased and remained at elevated levels for a decade; and the rates of runoff and erosion do not appear to have increased with time. These findings, along with our conclusions above and data from related literature, lead us to the

following two predictions regarding the effects of disturbance on runoff and erosion.

Disturbance will modify the effects of scale on runoff and erosion, both directly and via the modification of vegetation patterns.—Disturbance may modify surface topographical features and/or change the vegetation patch structure, either or both of which can substantially decrease storage within the hillslope. For example, when disturbance leads to a stippled or clumped pattern of shrubs with mostly bare interspaces, the ability of the hillslope to capture runoff is diminished, and therefore the degree to which runoff decreases with scale is diminished. Under these conditions, erosion may even increase with scale, owing to the formation of rills or gullies. When disturbance leads to a banded pattern of shrubby zones with relatively large and mostly bare areas upslope, the ways in which the effects of scale on runoff and erosion are modified will be very different: there should be little reduction in runoff with scale within the intercanopy areas, but as scale increases to the point of incorporating the banded zone, which will capture most of the runoff, net runoff will be at or close to zero.

There exists a threshold with respect to slope gradients, below which runoff and erosion will eventually return to predisturbance levels and above which runoff and erosion will remain at accelerated levels.—Our results suggest that, following disturbance, low-slope-gradient sites may eventually recover (runoff and erosion rates returning to predisturbance levels). Results from studies of steeper-slope sites show a different picture: that runoff and erosion actually increase with time following disturbance. Low-slope semiarid sites, in other words, are much more resilient following disturbance. On steeper-slope sites, then, if the redistribution pattern is altered, the runoff and erosion regime may shift to an accelerated mode and never recover.

In summary, the redistribution of water and sediment by runoff and erosion is a fundamental process by which water and nutrients become concentrated within semiarid landscapes and has profound ecological implications. This process is inherently scale-dependent and can be significantly altered by disturbance. Our findings reaffirm the fact that ecological and hydrological processes in semiarid landscapes are tightly coupled, and one cannot truly understand one without understanding the other.

Literature Cited

Abrahams, A. D., J. P. Anthony, and J. Wainwright. 1995. Effects of vegetation change on interrill runoff and erosion, Walnut Gulch, Southern Arizona. Geomorphology **13**:37–48.

Aguiar, M. R., and O. E. Sala. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology and Evolution **14**:273–277.

Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences (USA) **95**:14839–14842.

Arnold, J. G., R. Srinivasan, R. S. Muttiah, and J. R. Williams. 1998. Large area hydrologic modeling and assessment. Part I: model development. Journal of the American Water Resources Association **34**:73–89.

Baker, M. B. 1984. Changes in streamflow in a herbicide-treated pinyon–juniper watershed in Arizona. Water Resources Research **20**:1639–1642.

Belnap, J., and D. Eldridge. 2001. Disturbance and recovery of biological soil crusts. Pages 363–384 *in* J. Belnap and O. L. Lange, editors. Biological soil crusts: structure, function, and management. Springer-Verlag, Berlin, Germany.

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

Bergkamp, G., A. Cerda, and A. C. Imeson. 1999. Magnitude-frequency analysis of water redistribution along a climate gradient in Spain. Catena **37**:129–146.

Beven, K. 1989. Changing ideas in hydrology—the case of physically-based models. Journal of Hydrology **105**:157–172.

Beven, K. 2001. Runoff generation in semi-arid areas. Pages 57–105 *in* N. L. J. Bull and M. J. Kirkby, editors. Dryland rivers: processes and management in mediterranean climates. John Wiley and Sons, New York, New York, USA.

Bowen, B. M. 1996. Rainfall and climate variation over a sloping New Mexico plateau during the North American monsoon. Journal of Climate **9**:3432–3442.

Breshears, D. D., and F. J. Barnes. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landscape Ecology **14**:465–478.

Breshears, D. D., O. B. Myers, S. R. Johnson, C. W. Meyer, and S. N. Martens. 1997*a*. Differential use of spatially heterogeneous soil moisture by two semiarid woody species—*Pinus edulis* and *Juniperus monosperma*. Journal of Ecology **85**:289–299.

Breshears, D. D., J. W. Nyhan, C. E. Heil, and B. P. Wilcox. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. International Journal of Plant Sciences **159**:1010–1017.

Breshears, D. D., P. M. Rich, F. J. Barnes, and K. Campbell. 1997*b*. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecological Applications **7**:1201–1215.

Cammeraat, L. H., and A. C. Imeson. 1999. The evolution and significance of soil–vegetation patterns following land abandonment and fire in Spain. Catena **37**:107–127.

Carrara, P. E., and T. R. Carroll. 1979. The determination of erosion rates from exposed tree roots in the Piceance Basin, Colorado. Earth Surface Processes **4**:307–317.

Castillo, V. M., M. Martinezmena, and J. Albaladejo. 1997. Runoff and soil loss response to vegetation removal in a semiarid environment. Soil Science Society of America Journal **61**:1116–1121.

Clary, W. P., M. B. J. Baker, P. F. O'Connell, T. N. Johnson, and R. E. Campbell. 1974. Effects of pinyon–juniper re-

moval on natural resources products and uses in Arizona. USDA Forest Service, Fort Collins, Colorado, USA.

Collings, M. R., and R. M. Myrick. 1966. Effects of juniper and pinyon eradication on streamflow from Corduroy Creek Basin, Arizona. Professional Paper 491-B, U.S. Geological Survey.

Cornet, A. F., C. Montaña, J. P. Delhoume, and J. Lopez-Portillo. 1992. Water flows and the dynamics of desert vegetation stripes. Pages 327–345 in A. J. Hansen and F. di Castri, editors. Landscape boundaries: consequences for biotic diversity and ecological flows. Springer-Verlag, New York, New York, USA.

Davenport, D. W., D. D. Breshears, B. P. Wilcox, and C. D. Allen. 1998. Viewpoint: sustainability of piñon–juniper ecosystems—a unifying perspective of soil erosion thresholds. Journal of Range Management **51**:231–240.

Davenport, D. W., B. P. Wilcox, and D. D. Breshears. 1996. Soil morphology of canopy and intercanopy sites in a piñon–juniper woodland. Soil Science Society of America Journal **60**:1881–1887.

Dunkerley, D. L. 1997. Banded vegetation: development under uniform rainfall from a simple cellular automation model. Plant Ecology **129**:103–111.

Dunkerley, D. L., and K. J. Brown. 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.

Dunne, T. 1978. Field studies of hillslope flow processes. Pages 227–293 in M. J. Kirby, editor. Hillslope hydrology. John Wiley and Sons, New York, New York, USA.

Entekhabi, D., et al. 1999. An agenda for land surface hydrology research and a call for the second international hydrological decade. Bulletin of the American Meteorological Society **80**:2043–2058.

Galle, S., J. Brouwer, and J. P. Delhoume. 2001. Soil water balance. Pages 77−104 in D. Tongway, C. Valentin, and J. Segheri, editors. Banded vegetation patterning in arid and semiarid environments. Springer-Verlag, New York, New York, USA.

Gellis, A. C., A. Cheama, and S. M. Lalio. 2001. Developing a geomorphic approach for ranking watersheds for rehabilitation, Zuni Indian Reservation, New Mexico. Geomorphology **37**:105–134.

Goodrich, D. C., L. J. Lane, R. M. Shillito, S. N. Miller, K. H. Syed, and D. A. Woolhiser. 1997. Linearity of basin response as a function of scale in a semiarid watershed. Water Resources Research **33**:2951–2965.

Grayson, R. B., I. D. Moore, and T. A. McMahon. 1992. Physically based hydrologic modeling. 2. Is the concept realistic? Water Resources Research **28**:2659–2666.

Grayson, R. B., I. D. Moore, and T. A. McMahon. 1994. Reply to comment on ''Physically based hydrologic modeling. 2. Is the concept realistic?'' Water Resources Research **30**:855–856.

Greene, R. S. B., C. Valentin, and M. Esteves. 2001. Runoff and erosion processes. Pages 52–76 in D. Tongway, C. Valentin, and J. Segheri, editors. Banded vegetation patterning in arid and semiarid environments: ecological processes and consequences for management. Springer-Verlag, New York, New York, USA.

Hawkins, R. H., and T. W. Cundy. 1987. Steady-state analysis of infiltration and overland flow for spatially-varied hillslopes. Water Resources Bulletin **23**:251–256.

Heede, B. H. 1987. The influence of pinyon–juniper on microtopography and sediment delivery of an Arizona watershed. Pages 195–198 in I. G. Poppoff, C. R. Goldman, S. L. Loeb, and L. B. Leopold, editors. International mountain watershed symposium—subalpine processes and water quality. Tahoe Resource Conservation District, South Lake Tahoe, California, USA.

Hirsch, R. M., D. R. Helsel, T. A. Cohn, and E. J. Gilroy. 1992. Statistical analysis of hydrologic data. Pages 17.11–17.55 in D. R. Maidment, editor. Handbook of hydrology. McGraw-Hill, New York, New York, USA.

Hodgkinson, K., and D. Freudenberger. 1997. Production pulses and flow-ons on rangeland landscapes. Pages 23–34 in J. Ludwig, D. Tongway, D. Freudenberger, J. Noble, and K. Hodgkinson, editors. Landscape ecology, function and management: principles from Australia's rangelands. CSIRO, Collingwood, Australia.

Hutjes, R. W. A., et al. 1998. Biospheric aspects of the hydrological cycle. Journal of Hydrology **213**:1–21.

Hysell, M. T., and C. C. Grier. 1996. Dam-forming cacti and nitrogen enrichment in a pinon–juniper woodland in northwestern Arizona. Great Basin Naturalist **56**:211–224.

Imeson, A. C., and H. Lavee. 1998. Soil erosion and climate change—the transect approach and the influence of scale. Geomorphology **23**:219–227.

Klausmeier, C. A. 1999. Regular and irregular patterns in semiarid vegetation. Science **284**:1826–1828.

Lane, L. J., V. A. Ferreira, and E. D. Shirley. 1980. Estimating transmission losses in ephemeral stream channels. Pages 193–202 in Hydrology and water resources in Arizona and the Southwest. Proceedings of the 1980 meeting of the Arizona section, American Water Resources Association. Las Vegas, Nevada, USA.

Leopold, L. B., W. W. Emmett, and R. M. Myrick. 1966. Channel and hillslope processes in a semiarid area, New Mexico. Geological Survey Professional Paper 352-G, U.S. Department of the Interior.

Loague, K., and P. C. Kyriakidis. 1997. Spatial and temporal variability in the R-5 infiltration data set—deja vu and rainfall–runoff simulations. Water Resources Research **33**: 2883–2895.

Ludwig, J. A., and D. J. Tongway. 1995. Spatial organization of landscapes and its function in semi-arid woodlands, Australia. Landscape Ecology **10**:51–63.

Ludwig, J. A., and D. J. Tongway. 2000. Viewing rangelands as landscape systems. Pages 39–52 in O. Arnalds and S. Archer, editors. Rangeland desertification. Kluwer Academic, Dordrecht, The Netherlands.

Ludwig, J. A., D. J. Tongway, D. Freudenberger, J. Noble, and K. Hodgkinson. 1997. Landscape ecology function and management: principles from Australia's Rangelands. CSIRO Publications, Collingwood, Australia.

Ludwig, J. A., J. A. Wiens, and D. J. Tongway. 2000. A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. Ecosystems **3**:84–97.

Martens, S. N., D. D. Breshears, and F. J. Barnes. 2001. Development of species dominance along an elevational gradient; population dynamics of *Pinus edulis* and *Juniperus monosperma*. International Journal of Plant Sciences **162**:777–783.

Martens, S. N., D. D. Breshears, and C. W. Meyer. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. Ecological Modelling **126**:79–93.

Mauchamp, A., S. Rambal, and J. Lepart. 1994. Simulating the dynamics of a vegetation mosaic: a spatialized functional model. Ecological Modelling **71**:107–130.

Middleton, N. J., and D. S. G. Thomas. 1997. World atlas of desertification. Edward Arnold, London, UK.

Montaña, C. 1992. The colonization of bare areas in two-phase mosaics of an arid ecosystem. Journal of Ecology **80**:315–327.

National Research Council. 1999. Hydrologic science priorities for the U. S. Global Change Research Program. National Academy, Washington, D.C., USA.

Newman, B. D., A. R. Campbell, and B. P. Wilcox. 1997. Tracer-based studies of soil water movement in semi-arid forests of New Mexico. Journal of Hydrology **196**:251–270.

Newman, B. D., A. R. Campbell, and B. P. Wilcox. 1998. Lateral subsurface flow pathways in a semiarid ponderosa pine hillslope. Water Resources Research **34**:3485–3496.

Noble, J. C., R. S. B. Greene, and W. L. Müller. 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.

Osterkamp, W. R., and T. J. Toy. 1997. Geomorphic considerations for erosion prediction. Environmental Geology **29**:152–157.

Pilgrim, D. H., and I. Cordery. 1993. Flood runoff. Pages 9.1–9.42 *in* D. R. Maidment, editor. Handbook of hydrology. McGraw-Hill, New York, New York, USA.

Puigdefabregas, J., and G. Sanchez. 1996. Geomorphological implications of vegetation patchiness of semi-arid slopes. Pages 1027–1060 *in* M. G. Anderson and S. M. Brooks, editors. Advances in hillslope processes. John Wiley and Sons, New York, New York, USA.

Puigdefabregas, J., A. Sole, L. Gutierrez, G. del Barrio, and M. Boer. 1999. Scales and processes of water and sediment redistribution in drylands: results from the Rambla Honda field site in Southeast Spain. Earth-Science Reviews **48**:39–70.

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

Reynolds, J. F., R. A. Virginia, P. R. Kemp, A. G. de Soyza, and D. C. Tremmel. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecological Monographs **69**:69–106.

Roundy, B. A., and J. L. Vernon. 1999. Watershed values and conditions associated with pinyon–juniper communities. Pages 172–187 *in* S. B. Monsen and R. Stevens, co-ordinators. Ecology and management of pinyon–juniper communities within the Interior West. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Schlesinger, W. H., A. D. Abrahams, A. J. Parsons, and J. Wainwright. 1999. Nutrient losses in runoff from grassland and shrubland habitats in Southern New Mexico: I. Rainfall simulation experiments. Biogeochemistry **45**:21–34.

Schlesinger, W. H., P. J. Fonteyn, and W. A. Reiners. 1989. Effects of overland flow on plant water relations, erosion, and soil water percolation on a Mojave Desert landscape. Soil Science Society of America Journal **53**:1567–1572.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. E. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology **77**:364–374.

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

Seghieri, J., and S. Galle. 1999. Run-on contribution to a Sahelian two-phase mosaic system: soil water regime and vegetation life cycles. Acta Oecologica—International Journal of Ecology **20**:209–217.

Seghieri, J., S. Galle, J. L. Rajot, and M. Ehrmann. 1997. Relationships between soil moisture and growth of herbaceous plants in a natural vegetation mosaic in Niger. Journal of Arid Environments **36**:87–102.

Seyfried, M. S. 1991. Infiltration patterns from simulated rainfall on a semiarid rangeland soil. Soil Science Society of America Journal **55**:1726–1734.

Seyfried, M. S., and B. P. Wilcox. 1995. Scale and the nature of spatial variability: field examples having implications for hydrologic modeling. Water Resources Research **1**:173–184.

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

Simanton, J. R., M. A. Weltz, and H. D. Larsen. 1991. Rangeland experiments to parameterize the water erosion prediction project model: vegetation canopy cover effects. Journal of Range Management **44**:276–282.

Smith, R. E., D. R. Goodrich, D. A. Woolhiser, and J. R. Simanton. 1994. Comment on ''Physically based hydrologic modeling. 2. Is the concept realistic?'' Water Resources Research **30**:851–854.

Thornes, J. B. 1994. Catchment and channel hydrology. Pages 257–287 *in* A. D. Abrahams and A. J. Parsons, editors. Geomorphology of desert environments. Chapman and Hall, London, UK.

Tongway, D. J., and J. A. Ludwig. 2001. Theories on the origins, maintenance, dynamics and functioning of banded landscapes. Pages 20–31 *in* D. J. Tongway, C. Valentin, and J. Segheri, editors. Banded vegetation patterning in arid and semiarid environments: ecological processes and consequences of management. Springer-Verlag, New York, New York, USA.

Tongway, D. J., J. A. Ludwig, and W. G. Whitford. 1989. Mulga log mounds: fertile patches in the semi-arid woodlands of eastern Australia. Australian Journal of Ecology **14**:263–268.

Valentin, C., and J. M. d'Herbes. 1999. Niger tiger bush as a natural water harvesting system. Catena **37**:231–256.

Valentin, C., J. M. d'Herbes, and J. Poesen. 1999. Soil and water components of banded vegetation patterns. Catena **37**:1–24.

Whisenant, S. G. 1999. Repairing damaged wildlands: a process-oriented, landscape-scale approach. Cambridge University Press, Cambridge, UK.

Wilcox, B. P. 1994. Runoff and erosion in intercanopy zones of pinyon–juniper woodlands. Journal of Range Management **47**:285–295.

Wilcox, B. P., and D. D. Breshears. 1995. Hydrology and ecology of pinyon–juniper woodlands: conceptual framework and field studies. Pages 109–119 *in* Desired future conditions for pinyon–juniper ecosystems. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Flagstaff, Arizona, USA.

Wilcox, B. P., and D. D. Breshears. 1997. Interflow in semi-arid environments—an overlooked process in risk assessment. Human and Ecological Risk Assessment **3**:187–203.

Wilcox, B. P., B. D. Newman, C. D. Allen, K. D. Reid, D. Brandes, J. Pitlick, and D. W. Davenport. 1996*a*. Runoff and erosion on the Pajarito Plateau: observations from the field. Pages 433–439 *in* Geology of the Los Alamos–Jemez Mountains region. New Mexico Geological Society, Albuquerque, New Mexico, USA.

Wilcox, B. P., B. D. Newman, D. Brandes, D. W. Davenport, and K. Reid. 1997. Runoff from a semiarid ponderosa pine hillslope in New Mexico. Water Resources Research **33**:2301–2314.

Wilcox, B. P., J. Pitlick, C. D. Allen, and D. W. Davenport. 1996*b*. Runoff and erosion from a rapidly eroding pinyon–juniper hillslope. Pages 61–71 *in* M. G. Anderson and S. M. Brooks, editors. Advances in hillslope processes. John Wiley and Sons, New York, New York, USA.

Wilcox, B. P., W. J. Rawls, D. L. Brakensiek, and J. R. Wight. 1990. Predicting runoff from rangeland catchments: a comparison of two models. Water Resources Research **26**:2401–2410.

Wood, E. F., M. Sivapalan, and K. Beven. 1990. Similarity and scale in catchment storm response. Reviews of Geophysics **28**:1–18.