Runoff and Erosion in a Piñon–Juniper Woodland: Influence of Vegetation Patches

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ABSTRACT

In many semiarid regions, runoff and erosion differ according to vegetation patch type. These differences, although hypothesized to fundamentally affect ecological processes, have been poorly quantified. In a semiarid piñon–juniper woodland (Pinus edulis Engelm. and Juniperus monosperma (Engelm.) Sarg.) in northern New Mexico, we measured runoff and erosion from the three patch types that compose these woodlands: Canopy patches (those beneath woody plants), vegetated patches in intercanopy areas, and bare patches in intercanopy areas. The bare intercanopy patches exhibited the highest rates, followed by vegetated intercanopy patches and then by canopy patches. Large convective summer storms, though relatively infrequent, generated much of the runoff and most of the sediment; prolonged frontal storms were capable of generating considerable runoff but little sediment. A portion of the runoff and most of the sediment generated from bare intercanopy patches was redistributed downslope, probably to adjacent vegetated intercanopy patches, demonstrating connectivity between these two patch types. Our results indicate that there are significant and important differences in runoff and sediment production from the three patch types; that bare intercanopy patches act as sources of both water and sediment for the vegetated intercanopy patches; and that the transfer of water and sediment at small scales is both frequent enough and substantial enough to be considered ecologically significant.

Semiarid landscapes can be viewed as a mosaic of vegetation patches at practically every scale of observation. The different patterns formed by these patches generally reflect differences in soil water availability, which are traceable to myriad factors—such as aspect, slope, parent material, soil properties, microclimatic effects, and surface runoff characteristics.

The interrelationships between vegetation patterns and the distribution of surface runoff have been recognized in semiarid regions throughout the world, including Australia (Smith and Morton, 1990; Dunkerley and Brown, 1995; Ludwig et al., 1999), Mexico (Montaña et al., 1990; Cornet et al., 1992), Niger (White, 1971; Bromley et al., 1997), and the USA (Schlesinger et al., 1989; Seyfried, 1991; Wondzell et al., 1996; Schlesinger et al., 1999). These interrelationships have profound ecological implications, as outlined by Ludwig et al., 1997.

Redistribution of water and other resources by surface runoff may be especially important at small scales (<10 m²). In semiarid regions it is now recognized that at small scales, vegetation patches may function either as sources or sinks (Ludwig et al., 1997). Source areas, which generally have little or no vegetation, produce runoff; sink areas, located downslope of the source areas, receive and store the runoff and thereby become enriched and relatively productive. The results of several theoretical studies suggest that the transfer of water and nutrients through this process is important both ecologically and hydrologically (Maucler et al., 1994; Ludwig and Marsden, 1995; Reynolds et al., 1997; Dav-enport et al., 1998; Aguiar and Sala, 1999; Dunkerley, 1999; Klausmeier, 1999). Although widely recognized as important, the transfer and redistribution of water and sediment among vegetation patch types in semiarid landscapes have rarely been directly measured. Most of the information we have to date is based on indirect indicators of runoff or other ecologically relevant indicators, such as changes in soil water content (Cornet et al., 1992; Bromley et al., 1997) and in soil nutrients (Ludwig and Tongway, 1995), distribution of tree seedlings (Montaña et al., 1990), degree of plant water stress (Schlesinger et al., 1989; Anderson and Hodgkinson, 1997), and geomorphic characteristics (Greene, 1992; Hysell and Grier, 1996; Wondzell et al., 1996). Patch-scale measurements of runoff, but not of runon, in grasslands and desert shrub are presented by Schlesinger et al. (1999); the data are primarily from rainfall simulation but measurements from actual precipitation are also reported. Direct measurements of both runoff and runon from actual precipitation would provide a valuable complement to these studies. They would also enable runoff processes at the patch scale to be related to those at the hillslope scale.

Landscape ecologists are evaluating the health or functionality of semiarid rangelands on the basis of interactions between runoff and vegetation (Ludwig and Tongway, 1995; Ludwig et al., 1997). A fully functional semiarid ecosystem is defined as one in which only a very small part of the water and nutrients that enter the system are subsequently lost. Runoff, when it occurs, is redistributed within the system and effectively trapped and stored locally. A dysfunctional ecosystem is one from which a significant portion of the water and nutrients are being lost, generally because the network of vegetation patches is too spotty to trap surface runoff. Practices such as overgrazing can change a functional ecosystem into a dysfunctional one: As the number and size of vegetated patches are reduced, more and more water and resources are carried away from the system (Schlesinger et al., 1990; Ludwig et al., 1997, 1999; Schlesinger et al., 1999).

In arid and semiarid shrublands and woodlands, a fundamental dichotomy exists between the areas beneath the canopies of woody plants and the intercanopy areas that separate them (Breshears and Barnes, 1999). The characteristics that differentiate canopy patches from intercanopy patches are well-documented: (i) the
physical presence of the canopy, which modifies both the intensity and the amount of precipitation that reaches the soil, thereby altering the microclimate of the canopy soils (Breshears et al., 1997b, 1998); (ii) the presence of litter beneath the canopy, which protects the surface and contributes organic matter to the soil, thereby enhancing infiltration capacity (Lfyord and Qashu, 1969; Blackburn, 1975; Johnson and Gordon, 1988; Schlesinger et al., 1999); and (iii) differences in soil morphology and soil faunal activity between these patch types (Greene, 1992; Bromley et al., 1997).

Within piñon–juniper woodlands, the intercanopy zone may be further subdivided into vegetated and bare patches (Wilcox and Breshears, 1995). We believe that it is within the intercanopy zones that most of the redistribution of resources takes place—the bare intercanopy patches acting as sources of water and sediment and the vegetated intercanopy patches acting as sinks. Anecdotal observations would support this belief; for example, we have frequently noted that during rainfall, water runs off the bare intercanopy patches and pools within the vegetated intercanopy patches.

There may also be some exchange of resources between the intercanopy and the canopy patches, particularly as the depth of water in the intercanopy increases (Dunne et al., 1991; Seyfried, 1991; Breshears et al., 1997b); but the microtopography and other surface features suggest that the canopy areas are not major collection areas for water and sediment generated from bare areas. These features suggest, instead, that runoff is usually routed around the canopy areas. Canopy patches, because of the addition of litter and perhaps eolian material, are slightly elevated and slope from the center toward the surrounding intercanopy patches. As a result, runoff produced on the hillslope (or larger) scale will tend to be routed around the canopy patches via a network of interconnected intercanopy patches—a pattern commonly observed in semiarid landscapes (Dunne et al., 1991; Seyfried, 1991).

An improved understanding of runoff and erosion dynamics among these three patch types may lead to an improved understanding of these processes at larger scales. Recently, Davenport et al. (1998) proposed a conceptual framework for relating runoff at the patch scale to that at the hillslope scale. They hypothesized that the spatial distribution and connectivity of the different patch types determine runoff and erosion at scales larger than that of the patch. In particular, small changes in patch abundance and spatial pattern can produce large changes in hillslope-scale runoff and erosion. To test these hypotheses, the connections among patch types, and particularly whether there are important hydrologic differences among them, must be determined.

To date, neither the differences in runoff and erosion by vegetation patch type nor the connections between patch types in piñon–juniper woodlands have been well-studied and quantified. This study, in which we measured runoff and erosion in a piñon–juniper woodland over a 26-mo period, was designed to:

1. Quantify the amount and frequency of runoff and erosion produced by each patch type (canopy, vegetated intercanopy, and bare intercanopy);
2. Quantify the precipitation characteristics that influenced runoff and erosion conditions within each patch type; and
3. Quantify the connections (transfer of runoff and sediment) between bare and vegetated intercanopy areas.

STUDY AREA

The study area is located in north-central New Mexico, within a 1.7-ha piñon–juniper woodland (35.85°N, 106.27°W) having an average elevation of 2150 m (Fig. 1). This site has been the focus of numerous other studies in hydrology (Wilcox, 1994; Wilcox et al., 1996a; Newman et al., 1997; Breshears et al., 1998), ecology (Padien and Lajtha, 1992; Breshears et al., 1997a; Breshears et al., 1997b; Martens et al., 1997), and soils (Davenport et al., 1996). The regional climate is semiarid, with mean annual precipitation of ~380 mm and a mean annual temperature of 16.5°C. On average, rain accounts for 70% of the precipitation and occurs from May to October. The monsoon-type rains that are typical from July through September account for ~40% of the annual precipitation (Bowen, 1990) and for most of the runoff generated by rainfall. Snow can accumulate between November and April; patterns of snow accumulation and snow-derived soil moisture are largely influenced by tree canopy cover (Breshears et al., 1997b).

The soils of the site are derived from rhyolitic tuff that was deposited about 1.4 to 1.1 million years ago (Goff et al., 1989). They are divisible into two main suborders: Typic Haplustalfs, which compose ~55% of the study area, and Lithic Ustochrepts, which compose ~35% (Davenport et al., 1996). The other 10% may consist of Typic Ustorthents, Typic Paleustalfs, Lithic Ustochrepts, or Lithic Haplustalfs. The average soil thickness ranges from 30 to 100 cm, with a mean of ~80 cm.

The dominant tree species are Colorado piñon pine (Pinus edulis Englem.) and one-seed juniper [Juniperus monosperma (Englem.) Sarg.]. Canopy patches, which cover 50% of the 1.7-ha site, are typically 4 to 5 m in diam. (Breshears et al., 1997b). Large piñons tend to be associated with small junipers and large junipers with small piñons (Martens et al., 1997).

Groundcover in the vegetated intercanopy patches includes blue grama (Bouteloua gracilis), bitterweed (Hymenoxys richardsonii), fringed sagebrush (Artemisia frigida), Navajo tea (Thelesperma filifolium), Indian paintbrush (Castilleja integra), cryptobiotic crust, plant and tree litter, and rocks (Wilcox, 1994). For at least the past 50 yr, the area has been free of animal grazing and fire damage (Allen, 1989).

Vegetation patterns in the intercanopy areas form an interesting mosaic of patches that are completely void of vegetation and patches having relatively dense vegetation cover. The bare patches usually exhibit a miniature erosion scarp along the upslope border. The bare patches are by and large not interconnected, and there
is little indication of channeling or rill formation on the hillslope. The major areas of storage of water and sediment appear to be the vegetated intercanopy patches downslope of the bare patches. As shown by Wilcox et al. (1996a), very little water escapes off-site in the form of runoff. According to the definitions of Ludwig et al. (1997), then, this site would be fully functional (most of the water and nutrient resources stay on-site).

**MATERIALS AND METHODS**

To quantify the differences in runoff and erosion among the canopy, vegetated intercanopy, and bare intercanopy patches, we set up experimental plots that encompassed all three, in ways that would allow the collection of several kinds of relevant data.

Three plots were located under tree canopies, on the downslope side of either a juniper ($n = 1$) or a piñon ($n = 2$) tree. Each canopy plot measured 1 m by 1 m, had an average gradient ranging between 6 and 12%, and was completely covered with tree litter.

Another three plots were located within intercanopy zones. In this case, each plot measured 2 m wide by 6 to 8 m long—large enough to encompass, lengthwise, both bare and vegetated patches (bare patches being upslope of vegetated patches) (Fig. 2). Two of the plots were selected to include bare patches displaying well-defined miniature erosion scarp (10–15 cm in height) at the upslope boundary. The third intercanopy plot possessed the remnants of such a scarp in the form of pedestaled vegetation. At its downslope end, each bare patch gradually transitioned into a vegetated patch.

Each of the three intercanopy plots was divided lengthwise into two 1-m wide subplots that were similar with respect to surface characteristics. One of these subplots was further subdivided crosswise into three or four patches on the basis of vegetation cover (Fig. 2). In other words, each intercanopy plot was designed for both long-slope measurements over an uninterrupted stretch of bare and vegetated patches and for short-slope measurements within individual bare or vegetated patches.

In this paper, the long-slope subplots are referred to as integrated subplots, because they integrate both bare and vegetated patches. Within the adjacent subplots, each of the short-slope patches is referred to as either a bare patch or a vegetated
tiplying the runoff volume (total water in each well) by the average sediment concentration found in the two samples from that well.

Precipitation was measured for each of the intercanopy plots by means of a wedge-type, graduated precipitation gauge; total precipitation was continuously recorded (at 1-min intervals) by an automated, tipping-bucket rain gauge located ≈200 m upslope of the plots.

Thus designed, this study allowed us to directly quantify runoff and erosion behavior as a function of patch type, as well as to quantify the amount of water and sediment supplied to vegetated patches from bare patches. Behavior as a function of patch type was quantified by comparing runoff and erosion from the canopy plots (representing canopy patches) with that from the vegetated portions of the intercanopy plots (representing vegetated intercanopy patches) and with that from the bare portions of the intercanopy plots (representing bare intercanopy patches). The amounts of water and of sediment supplied to the vegetated intercanopy patches from the bare intercanopy patches were calculated as (i) the difference between unit-area runoff from an integrated (long-slope) subplot and the cumulative runoff from the short-slope patches within its adjacent subplot; and (ii) the difference between unit-area erosion on an integrated subplot and the cumulative erosion measured on the short-slope patches within its adjacent subplot. With this approach we would expect, for example, that if the vegetated patches are acting as sinks, runoff and sediment from each integrated subplot would be less per unit area than cumulative runoff and sediment from the short-slope patches within the adjacent subplot.

RESULTS

During the 26-mo study period, 95 rainstorms produced 790 mm of rain (82% of total precipitation—including snowfall—for the period, which was 960 mm). Long-term precipitation data indicate that this period was drier than average; at Bandelier National Monument during those 26 months total precipitation was 830 mm—130 mm less than the 69-yr average. The driest interval during our study was July 1995 to May 1996. During the fourteen months (July 1995—August 1996) that runoff and erosion from rainfall were measured from both the canopy and intercanopy patches, 43 rainstorms produced 297 mm of rain. (The total amount of precipitation, including snowfall, for this period was 373 mm.)

Table 1. Vegetation, slope and area characteristics in the study plots.

<table>
<thead>
<tr>
<th>Location no.</th>
<th>Category</th>
<th>Grass</th>
<th>Cactus</th>
<th>Forbs</th>
<th>Crypto.</th>
<th>Litter</th>
<th>Total veg</th>
<th>Area</th>
<th>Slope</th>
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<td>3</td>
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<td>2</td>
<td>4</td>
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<tr>
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<td>0</td>
<td>0</td>
<td>1</td>
<td>7</td>
<td>1.51</td>
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<td>48</td>
<td>97</td>
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<td>1</td>
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<td>1</td>
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<td>0</td>
<td>100</td>
<td>100</td>
<td>1.00</td>
<td>8.2</td>
</tr>
</tbody>
</table>

Fig. 2. Photograph of experimental plots.
Runoff Generation and Sediment Yields by Patch Type

The total runoff and sediment yield at each patch are presented in Fig. 3 and are arranged according to patch type and, within the intercanopy bare plots, by topographic position: upper slope, mid slope, and lower slope. Each topographic position had characteristic features that influenced sediment yield. For example, in the bare patches, the upper slope locations encompassed the miniature erosion scarp, and the lower slope locations were bare patches that graded into a vegetation patch. In Fig. 3, we also highlight the vegetated patches that were located at the lower portions of the intercanopy plots.

Total runoff was significantly different ($P < 0.01$) among the three patch types, being highest from the bare intercanopy patches, intermediate from the vegetated intercanopy patches, and lowest from the canopy patches (Fig. 3A). The topographic position of the bare intercanopy patches had little bearing on runoff production (percentage of precipitation converted to runoff), which, at the scales measured here, was quite high: 37% (138 mm). It was also quite high for the vegetated intercanopy patches (25%, or 93 mm) and for the canopy patches (8%, or 30 mm). The fact that runoff was gener-
Influence of Precipitation

The most frequently occurring \((n = 79)\) storms at the study area were small \((<15 \text{ mm})\); these accounted for about 45\% of the total rainfall during the study period. Storms producing \(>15 \text{ mm}\) occurred less frequently \((n = 16)\), but accounted for 55\% of the total rainfall. These larger storms were of two types: convective and frontal. The convective storms are considerably more intense than the frontal storms, but the frontal storms are of longer duration \(>5 \text{ hr}\).

Of the 95 rainstorms that were recorded during the 26-mo observation period, 18 (representing about 15\% of the rainfall) were omitted from the analysis because the data were incomplete. Using data for the 77 remaining storms (8 large convective storms, 7 large frontal storms, and 63 minor storms), we compared runoff and sediment yield from the intercanopy bare and vegetated patches for each of storm type. Some runoff occurred from at least one of the patches for every storm \(>4 \text{ mm}\); the smallest storm to produce runoff was a 1.8-mm event. Twenty-eight minor storms produced no runoff.

Most of the runoff measured during the study period was generated by large convective storms (Fig. 4A). Frontal storms also generated considerable runoff, while...
the minor storms produced very little. Differences between the bare and vegetated patches, although significant ($P < 0.05$), were relatively small. The striking feature of this comparison is the difference between runoff and precipitation for the three storm types. For the large convective storms, most of the precipitation was converted to runoff, while for the minor storms, only a small percentage of the precipitation ran off.

With respect to sediment yield, the interrelationships between storm type and vegetation patch type are quite dramatic (Fig. 4B): Almost all of the sediment yield resulted from the action of large convective storms on the bare patches. Neither the large frontal or minor storms produced much sediment.

**Connections between Patch Types**

**Runoff and Runon**

As is evident from Fig. 5, the three intercanopy plots differed from one another with respect to runon, that is, the amount of surface runoff captured or stored within the intercanopy plots as a result of depression storage capacity. Intercanopy Plots 1 and 2 were much more efficient with respect to the capture of runoff than was intercanopy Plot 3, regardless of storm type. For integrated Plot 1E, runon amounted to 129 mm, 19% of the precipitation from the 77 rainstorms; for integrated Plot 2E, runon was 104 mm, or 15%; and for integrated Plot 3E, runon was 23 mm (only 3%).

As noted above, most of the runoff was generated by large convective storms; and it was also in the wake of these storms that runon was greatest (it was next greatest in the wake of large frontal storms) (Fig. 5). At the same time, a higher percentage of the runoff water became runon in the wake of minor storms (Fig. 5C). In other words, the intercanopy zones seem to capture runoff more efficiently during smaller storms. On a storm-by-storm basis, runon within the intercanopy increases as precipitation increases, up to precipitation amounts of 30 mm. The increase in runon levels off at ~8 mm (Fig. 6) when >30 mm of precipitation is produced by a storm. These data suggest that the storage capacity of the intercanopy areas for runon is limited—we estimate to somewhere in the range of 6 to 10 mm.

**Sediment**

The redistribution of sediment from bare to vegetated patches, like the redistribution of runoff, differed among the three plots (Fig. 7). For example, for integrated Subplots 1E and 2E, we estimate that about 80% of the sediment generated from bare patches was redeposited in vegetated patches within the subplot. For integrated Subplot 3E, in which runon was relatively small, only about 20% of the sediment generated from the bare patches was redeposited within the boundaries of the plot. These differences were consistent for all three storm types. The largest quantities of redistributed sediment in downslope areas were measured following the large convective storms (Fig. 7A). On average, about 60% of the sediment within the three integrated subplots was redistributed, but the percentage was much higher for Plots 1 and 2. At these small scales, then, more than half of the sediment that is generated from the bare patches is redeposited—most likely in a vegetated patch—a few meters downslope.

**DISCUSSION**

The vegetation patch types that we isolated for study are, we believe, the fundamental hydrologic or functional units of piñon-juniper woodlands (Wilcox and
Breshears, 1995)—similar to those proposed for other semiarid ecosystems (Greene, 1992; Ludwig et al., 1997; Reynolds et al., 1997). In other words, each patch type should exhibit a consistent hydrologic behavior. If that is true, characterizing the nature of runoff and erosion in these patch types will aid our efforts at modeling these processes at the patch, as well as at larger scales (Seyfried and Wilcox, 1995), and provide useful information relative to ecological processes at the patch scale. Our study has demonstrated that there are important hydrologic differences between these patch types, as well as a significant exchange of material, both water and sediment, between them.

Our experimental design has advantages and limitations. One advantage is that we are directly measuring runoff and sediment from naturally-occurring events rather than relying on rainfall simulation or indirect indicators. One limitation, which must be considered when interpreting the data, is that our measurements are scale-dependent in that we have not taken into account effects from areas upslope of the bare patches (outside the intercanopy plot boundary). In other words, our design assumes that any water or sediment supplied via runoff and erosion to a vegetated patch comes exclusively from adjacent upslope areas—which may not be the case. Another limitation is that we cannot draw any positive conclusions about the exchange of water and sediment between canopy and intercanopy areas.

**Runoff and Erosion at the Patch Scale**

We were able to quantify distinct runoff and erosion properties for the three vegetation patch types: runoff and erosion were lowest for the canopy patches, higher for the vegetated intercanopy patches, and highest for the bare intercanopy patches. The bare patches, on average, generated about 3 times more sediment than the vegetated patches and about 24 times more sediment than the canopy patches. There was, however, considerable variability among bare patches delineated in this study, which is largely explained by topographic position. Even on relatively stable hillslopes, such as our study site, certain zones exhibit very high local erosion, marked by pedestaling of vegetation and miniature erosion scars. Those bare areas immediately upslope of a vegetated patch have relatively low rates of erosion.

The results from the canopy patches are especially interesting. Whereas runoff from piñon–juniper intercanopy areas has been documented elsewhere (Wilcox, 1994), as has runoff from areas encompassing both canopy and intercanopy patches (Wilcox et al., 1996a, 1996b), few if any studies have satisfactorily separated out the relative contribution of canopy patches. We found that runoff may occasionally be generated from canopy areas (always as the result of a large convective storm) and, surprisingly, that runoff production from a canopy patch can be at least as high as 8% of measured precipitation for an extended period. For individual storms it was obviously much higher.

The contribution to runoff of the various vegetation patch types varies hierarchically with rainfall characteristics. For the smallest storms, it is mainly the bare intercanopy patches that produce runoff. As rainfall amounts increase, the vegetated intercanopy patches contribute more. The intercanopy remains the sole contributor during the large frontal storms, which may upon occasion produce substantial amounts of runoff. It is only during large convective storms that all areas of the hillslope, including canopy areas, contribute runoff.

**Connectivity Among Intercanopy Patches**

We found that there can be a significant exchange of resources, especially sediment, within the intercanopy zones. We believe that the process is the same as that reported for other semiarid environments (Ludwig et al., 1997), with resource-depleted areas (bare intercanopy patches) acting as sources, especially for sediment, and the already-enriched zones (vegetated intercanopy patches) acting as sinks. Our experimental design does not allow us to state unequivocally that the water and sediment generated from the bare patches is deposited in the vegetated patches, only that these resources are being deposited downslope. Our field observations lead us to believe that it is the vegetated intercanopy patches that are the major sinks for the water and sediment. At the same time, we have evidence (our Subplot 3E) that not all vegetation patches operate as effective sinks (Fig. 5 and 7).

We found that at these scales, the process of runoff/runoff may account for between 3 and 20% of the water provided to sink areas. Our results are less dramatic than those of Bromley et al. (1997), who calculated that banded tiger bush vegetation in Niger receives 3.5 times more water than the surrounding areas of bare ground. In that system, the redistribution of water by surface runoff apparently created the banded patterns of woody plants. The quantities of runon we measured are smaller, but are still large enough to affect the spatial patterning of herbaceous plants. Our estimates of runoff for intercanopy patches that are bare (37% of precipitation) and vegetated (25% of precipitation) greatly exceed those reported for 2- by 2-m plots in semiarid grasslands (5.7% of precipitation) and for creosotebush scrub (18% of precipitation), reported by Schlesinger et al. (1999).

Each of the three storm types resulted in some runon within the intercanopy. The greatest amounts were measured during the large convective events, which generated the most runoff. But even small storms could initiate an important exchange of water between source and sink areas. And even small changes in volumetric water content resulting from runon can translate into large changes in soil water potential (site-specific relationships are reported in Breshears et al., 1997a) and, thereby, large changes in plant water potential. Sala and Lauenroth (1982) demonstrated that semiarid herbaceous species can respond to additions of water as small as 5 mm. Small changes in soil moisture content are also believed to have nonlinear effects on the likelihood that seedlings will germinate and become established (Lauenroth et al., 1987). Further, small additions of water have been shown to reduce plant water stress in...
woody plants (Schlesinger et al., 1989) and to increase seedling establishment at the upslope edges of vegetated patches, where runon should accumulate (Montaño et al., 1990).

We also found that at the vegetation-patch scale, the transfer and subsequent storage of sediment can be very substantial. Storage was greatest in the wake of the intense convective storms, which generated the bulk of the sediment, but sink areas proved to efficiently trap sediment generated by the less intense storm types as well. Our data would suggest that in stable semiarid woodlands, such as our study site, large amounts of sediment are redistributed. Sediment is removed from bare patches and deposited downslope in vegetated patches. This transfer is ecologically significant as well, because it translates to a redistribution of nutrients, as suggested by Ludwig and Tongway (1995). Obviously, such levels of resource depletion from the bare areas could not continue indefinitely. We imagine that within the intercanopy areas, there is a slow but continuous migration upslope of bare and vegetated patches. If that is the case, the importance of the vegetation patch in maintaining hillslope stability is obvious. For any given site, an intact network of vegetated intercanopy patches provides an important buffer against the losses of water, sediment, and nutrients that can ultimately bring about a dysfunctional ecosystem.

Although the vertical distribution of soil moisture has been a very useful predictor of broad-scale vegetation patterns in semiarid ecosystems (Coffin and Lauenroth, 1990; Sala et al., 1997), several recent modeling studies have indicated that taking into account the horizontal redistribution of soil moisture via runoff should further improve our ability to predict vegetation dynamics (Mauchamp et al., 1994; Ludwig and Marsden, 1995; Thiery et al., 1995; Reynolds et al., 1997; Aguiar and Sala, 1999; Dunkerley, 1999; Klausmeier, 1999). Our results complement these modeling studies by providing field documentation of the importance of the horizontal redistribution of water in semiarid environments.

**Scale Relationships**

A comparison of our results with those of large-scale studies conducted at the same site (Wilcox et al., 1996a) is instructive with respect to hydrologic scale relationships. At the small scales of measurement used in this study, the frequency and amount of runoff are striking and contrast sharply with those reported from the larger-scale studies. At the hillslope scale, runoff was found to be infrequent and to make up a small fraction of the water budget; in one study, runoff from a 2000-m² piñon–juniper hillslope within our study area was found to be less than 2% of precipitation (Wilcox et al., 1996a). In contrast, at the patch scale, runoff from the bare patches was about 31% of total precipitation and that from the vegetated patches was about 21%. Clearly, at the larger scales, most of the runoff generated is not measured because it never reaches the collection trenches farther downslope. The intercanopy vegetation patches on the hillslope certainly function as sinks, but other, larger-scale features such as topographic lows or obstacles that may impede hillslope flow (such as fallen tree limbs or other debris) probably act as sinks as well. Soil moisture data suggest that canopy areas may also act as sinks (Breshears et al., 1997b). As the water level in the intercanopy rises, the potential for it to infiltrate into adjacent canopy patches increases.

Percolation models may be a useful tool for expressing and predicting runoff at multiple scales. The percolation model proposed by Davenport et al. (1998), for relating runoff at the patch scale to that at the hillslope scale, predicts that runoff at the hillslope scale is much less per unit-area than that at the patch scale because of storage within the hillslope. It further predicts that the magnitude of the scale-dependent difference depends on the proportion and spatial arrangement of patches, and that thresholds between low and high rates of runoff and erosion at the hillslope scale result from small changes in the number and spatial arrangement of vegetated patches.

Our results support two underlying assumptions of this percolation model: (i) that there are discrete functional patch types, and (ii) that storage occurs within vegetated intercanopy patches. Further study will be required to more directly quantify the connectivity between intercanopy bare patches and canopy patches. In addition, validation of the percolation model will require simultaneous measurement of runoff at the patch and hillslope scales. The development and application of spatially explicit models that incorporate the three basic functional units that we have isolated will, we believe, lead to an improved understanding of vegetation, water, and sediment dynamics in semiarid ecosystems and to improved predictive capabilities. Such an understanding is needed to address issues related to vegetation and ecosystem responses to changes in climate and land use (Walker and Steffen, 1999), which can be particularly rapid and dramatic in semiarid environments (Allen and Breshears, 1998).

**CONCLUSIONS**

Over a period of 26 mo, we have monitored runoff and erosion produced by rainfall on three different vegetation patch types within a piñon–juniper woodland (which represent the three fundamental functional units of these semiarid environments). These detailed measurements have allowed us to document and quantify the important differences in runoff and erosion between the functional units and, on that basis, to draw the following conclusions that are relevant, we believe, to many semiarid woodlands and shrublands:

- Each vegetation patch type displays distinct runoff and erosion properties (canopy lowest, bare highest), with the bare patches acting as sources and the vegetated ones as sinks.
- The runoff and erosion behavior of the different vegetation patch types depends on the type of rainstorm and, to some extent, on the spatial arrangement of the groundcover. High-intensity convective storms generate most of the runoff and sediment.
• The redistribution of water and sediment via runoff and erosion from the bare to vegetated intercanopy patches is ecologically significant. Large quantities of sediment, even on relatively stable hillslopes, are internally redistributed within the hillslope.

• Sediment production within the intercanopy is highly variable but is largely governed by topographic position.

• At the vegetation patch scale, both the frequency and amounts of runoff are much greater than at larger scales, and greater than previously thought.

• More generally, an intact network of vegetated intercanopy patches provides an important buffer against losses of water, sediment, and nutrients for any given site. The dynamics of this network are important to consider in evaluating ecosystem responses to changes in climate and land use.

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REFERENCES


