

## DAM-FORMING CACTI AND NITROGEN ENRICHMENT IN A PIÑON-JUNIPER WOODLAND IN NORTHWESTERN ARIZONA

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**ABSTRACT.**—In a piñon-juniper woodland in northwestern Arizona, connected basal cladodes of a prickly pear cactus (*Opuntia littoralis* var. *martiniana*) form check dams that cause deposition of N-rich detritus in interspaces otherwise lacking litter. Seventy-eight percent of connected basal cladodes measured in transects grew at an angle (with respect to the slope contour)  $\leq 45^\circ$ —an orientation facilitating deposition of flood-borne debris.

Soil total N was significantly greater ( $P < 0.01$ ) and organic C was greater, but not significantly, above cactus dams compared to below cactus dams. Soil total N and organic C both above and below cactus dams were significantly greater ( $P = 0.0001$ ) compared to adjacent interspaces. Soil total N and organic C above cactus dams were equal to areas beneath canopies (tree and shrub combined). Net  $\text{NO}_3^-$  (0–5 cm depth) above cactus dams was significantly greater ( $P = 0.0001$ ) than below cactus dams, at interspaces, and beneath canopies. Net  $\text{NH}_4^+$  (0–5 cm soil depth) above cactus dams was significantly greater ( $P < 0.01$ ) than below cactus dams and interspaces, and was greater (but not significantly) than beneath canopies. At 5–10 cm soil depth, differences in net  $\text{NH}_4^+$  and net  $\text{NO}_3^-$  between sampling locations were not significant except for the difference in net  $\text{NO}_3^-$  above and below cactus dams ( $P < 0.05$ ). The litter layer above cactus dams had twice as much total N ( $P < 0.01$ ) as the litter layer beneath canopies (tree and shrub combined); differences in net mineralized N were not significant between litter layers. Over the course of a single rainy season, detritus depth behind cactus dams increased up to 23 cm, with a mean increase of 4.3 cm ( $s_{\bar{x}} = 0.625$ ,  $P = 0.0001$ ).

*Key words:* prickly pear cactus, nitrogen enrichment, growth habit, soil characteristics, check dams, detritus, runoff, bulk density, total nitrogen, organic carbon, mineral nitrogen, piñon-juniper woodlands, islands of fertility.

The growth habit of *Opuntia littoralis* var. *martiniana* (L. Benson) L. Benson consists of connected basal cladodes growing across woodland slopes roughly along the contour. Cladodes in contact with the ground sprout adventitious roots and become anchored. Sequentially anchored cladodes function as check dams during runoff events, causing deposition of flood-borne detritus including surface soil, animal feces, and litter of piñon pines, juniper, and oak.

Piñon-juniper woodlands occupy at least  $17 \times 10^6$  ha in the western U.S., with widespread distribution in Colorado, New Mexico, Arizona, eastern California, Nevada, and Utah (West 1988). These woodlands fall between mesic conditions that support closed-forest canopies and arid conditions in which plants are widely spaced. Compared with forests of wetter environments, piñon-juniper woodlands have low biomass, leaf area, and primary productivity (Grier et al. 1992). Woodland structure varies but can generally be described as single trees and shrubs and clumps of trees and shrubs surrounded by a network of interspaces (Lanner

1981). Litter occurs in patches due to the non-contiguous canopy cover, and soil N distribution corresponds to litter and canopy distribution (DeBano and Klopatek 1987, Tiedemann 1987). In mixed-species stands, patches may be mosaics of different litter components.

Interspace and canopy area soils usually differ in characteristics such as concentrations of nutrients, pH, bulk density, soil water, and in numbers and species of resident microorganisms and microarthropods (Everett and Sharrow 1985, Klopatek 1987, Klopatek and Klopatek 1987), although there are exceptions to this generalization (DeBano et al. 1987). Soil organic matter and nutrients are concentrated near the soil surface (West and Klemmedson 1978, Lyons and Gifford 1980, DeBano and Klopatek 1987), and runoff from storms can carry considerable amounts of detritus rich in organic matter and N (Fletcher et al. 1978).

Objectives of this study were (1) to characterize the angle of growth (relative to slope contour) of connected basal cladodes of *Opuntia littoralis* var. *martiniana*, (2) to compare litter and soil properties above and below cactus

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TABLE 1. Sites of measurement of angle (relative to the slope contour) of connected basal cladodes. (Samples for soil comparisons were taken only in the Hualapai Mountains [see Table 2].)

Location	Transect length (m)	Soil parent material	Elevation (m)	Aspect	Slope (%)	Piñon pine cover (%)
Cerbat Mountains <sup>a</sup>	401	granite	1930	S-SSE	10–25	10–30
Hualapai Mountains <sup>b</sup>	110	granite	1524	N	15–45	30–40
Music Mountains <sup>c</sup>	302	vesicular basalt	1712	E	30	40–70

<sup>a</sup>27 km NW of Kingman, AZ (lat.35°27', long.114°09'; T24NR18WS23nw).

<sup>b</sup>12 km SE of Kingman, AZ (lat.35°08', long.113°55'; T20NR16WS1sw).

<sup>c</sup>53 km NE of Kingman, AZ (lat.35°41', long.113°49'; T27NR36WS36ne).

dams, and (3) to compare litter and soil properties above and below cactus dams with inter-spaces and areas beneath canopies.

#### METHODS

Two distinct physiographic provinces come together in northwestern Arizona: southeast, west, and north of Kingman, Arizona, is the Basin and Range Province, characterized by north-trending fault-block mountain ranges separated by broad desert valleys; the Colorado Plateau lies to the east. This area is the interface of 3 deserts as well as a physiographic interface. North of Kingman is the Great Basin Desert, west is the Mojave Desert, and southwest is the Sonoran Desert. The climate of northwestern Arizona is semiarid (Sellers and Hill 1974). Precipitation is bimodal, occurring mostly in winter and summer months, with more rainfall during winter than summer.

Summer rain sometimes occurs as intense thundershowers (Sellers and Hill 1974).

We first observed dam-forming cacti in the Hualapai Mountains (rising to over 2438 m, 12 km southeast of Kingman, Arizona) in the course of data collection for studies of piñon-juniper woodland productivity. We subsequently visited 2 nearby ranges (the Cerbat Mountains [over 2133 m at highest point] 29 km northwest of Kingman, and the Music Mountains [over 2011 m] 53 km northeast of Kingman) and found dam-forming cacti in these locations. To characterize the angle of growth of connected basal cladodes of prickly pear cacti (our 1st objective), we took angle measurements in July 1991 on all cacti intercepting straight-line transects in the 3 mountain ranges (Table 1). Starting points of line transects were randomly located, and direction of transects was along random azimuths. A total of 233 angle measurements were recorded. Sequentially connected

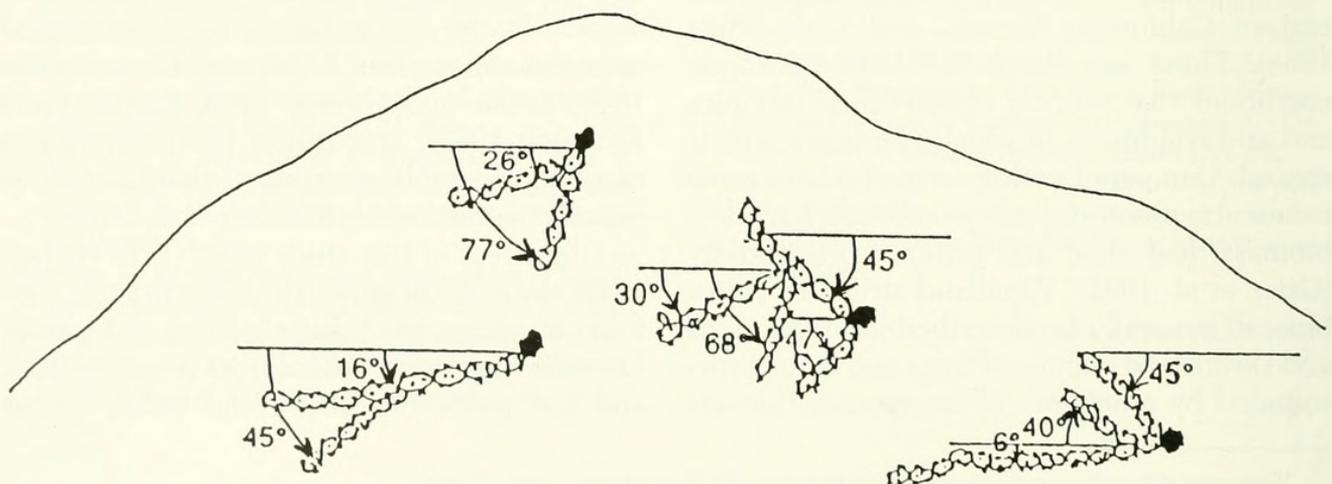


Fig. 1. Measurement of angle of growth of connected basal cladodes with respect to the slope contour. Point of origin indicated by solid cladode.

basal cladodes with series ranging from 0.4 m to 2.5 m in length were measured with an engineer's adjustable triangle as shown in Figure 1: a direction of growth parallel to slope contour was 0° while a direction of growth perpendicular to slope contour, either upslope or downslope, was 90°.

### Soil and Litter Sampling

**SITE DESCRIPTION.**—We restricted litter and soil sampling to 1 of the 3 transect locations (the Hualapai Mountains, 12 km southeast of Kingman [Table 2, Fig. 2]), to minimize confounding factors such as different soil types, site histories, and land-management practices. About 40% of the study site is open interspaces (combined data [unpublished] from eighteen 2 × 2-m plots using Daubenmire's [1968] coverage classes, and from 12 permanently marked 25-m-long line transects using methods described in Meeuwig and Budy [1981]). Interspaces are mostly bare soil and rock surface, with 3% grass cover (mostly *Bouteloua gracilis* [H.B.K.] Lag. ex Steudel and *B. curtipendula* [Michx.] Torr.) and traces of litter, herbs, and cryptogams. Shrubs, mostly scrub oak (*Quercus turbinella* Greene), cover about 30% of the study area. Piñon pines (*Pinus monophylla* var. *fallax* [Little] Silba) cover about 36% of the area and *Juniperus osteosperma* (Torr.) Little about 4%. The added cover of vegetation components is greater than total vegetation cover due to the presence of different vertical layers of shrub and tree canopies and aggregation of vegetation in clumps. Trees ranged in age from seedlings to about 260 yr (estimated from annual ring counts of cores [unpublished data]). Age estimates are approximate due to occurrence of false rings in wood of piñon pines and junipers.

Size range of soil surface patches covered by cacti and associated litter accumulations was estimated by measuring every cactus dam on a 25 × 25-m plot. We recorded length, width, and circumference for each cactus dam and associated litter accumulation (32 total). The area of soil surface covered by cactus dams and litter was calculated as the area of a circle plus 1/2 the difference between the area of a rectangle and a circle.

**SOIL AND LITTER SAMPLING APPROACH.**—Sampling was stratified by woodland microhabitats: above cactus dams, below cactus dams, interspaces, and beneath canopies. We took

TABLE 2. Characteristics of litter and soil sampling site in a piñon-juniper woodland in the Hualapai Mountains of northwestern Arizona. Records (1967–1991) of licensed livestock grazing show year-round grazing of cattle and horses with year-to-year variation in season of heaviest use and in number of animals (USDA BLM 1991).

Elevation: 1524 m (5000 ft)
% slope: 20-40
Aspect: north
Soil parent material: granite
Soil texture: sandy-loam
Soil classification <sup>a</sup> : Barkerville Series\
loamy, mixed, mesic, shallow\
Udorthentic haplustolls

Other soil characteristics<sup>b</sup>:

A1 horizon 10 cm deep, 39% coarse frag.
pH surface soil interspace—6.5
pH surface soil under canopy—8.0
non-calcareous throughout

Species and % cover<sup>c</sup>:

<i>Pinus monophylla</i> subsp. <i>fallax</i>	36.0%	$s_{\bar{x}}$ 5.7
<i>Juniperus osteosperma</i>	4.0%	$s_{\bar{x}}$ 1.6
<i>Quercus turbinella</i>	30.0%	$s_{\bar{x}}$ 6.2
<i>Yucca baccata</i>	4.0%	$s_{\bar{x}}$ 1.1
<i>Opuntia littoralis</i> var. <i>martiniana</i>	1.9%	$s_{\bar{x}}$ 1.1
<i>Rhus trilobata</i>	0.7%	$s_{\bar{x}}$ 0.4
<i>Ceanothus greggii</i>	0.4%	$s_{\bar{x}}$ 0.2
<i>Canotia holocantha</i>	0.3%	$s_{\bar{x}}$ 0.3
<i>Bouteloua gracilis</i>	2.9%	$s_{\bar{x}}$ 1.3
<i>Gutierrezia sarothrae</i>	<1%	

<sup>a</sup>Richmond and Richardson (1974).

<sup>b</sup>Unpublished data, this study.

<sup>c</sup>Two methods were used to estimate cover: For all species, estimates were made on eighteen 2-m<sup>2</sup> plots according to coverage class ratings (Daubenmire 1968). Tree and shrub cover were estimated on 12 permanent 25-m line transects as % Cover = [(25\*3.14/Transect Length)] [Sum of crown diameters] (Meeuwig and Budy 1981). Values reported here for trees and shrubs are averages of both methods, and standard errors are from pooled variances.

paired samples 10.2 cm above (litter present) and below (little to no litter present) cactus axes to compare soil properties above and below cactus dams. We took additional samples from bare interspaces and from areas beneath tree and shrub canopies to compare these areas with the areas above and below cactus dam. Interspaces were considered to lie beyond the influence of canopies and associated litter and beyond the influence of cactus dams and associated litter. Vegetation and litter were scant to absent in interspaces. Beneath tree and shrub canopy, sampling included piñon pines, scrub oaks, junipers, and occasionally mixed-species canopies roughly in proportion to the presence of these components (as estimated by percent canopy cover) on the site (Table 2). The sampling location beneath canopies was at 2/3 canopy radius out from the stem or clump center. Litter of *Yucca baccata*

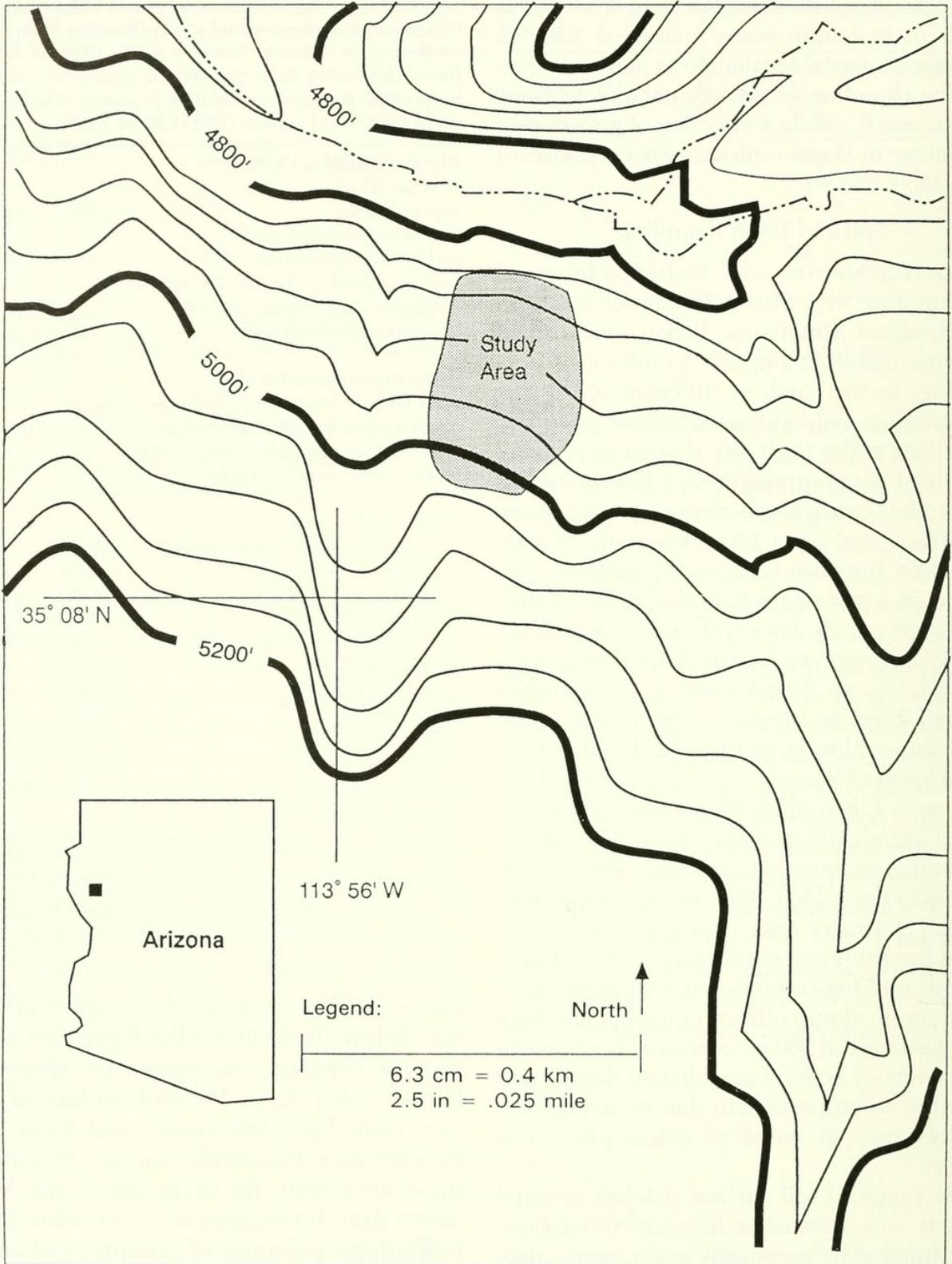


Fig. 2. Soil and litter sampling area in the Hualapai Mountains of northwestern Arizona. The contour interval is 12.2 m (40 ft). Enlarged from U.S. Geological Survey, Rattlesnake Hill, Arizona Quadrangle.

Torr. and a few other species was occasionally (though rarely) present in litter samples along with litter of the dominant species. With the exception of bulk density samples, soil and litter samples were composited within microhabitat strata by combining equal numbers of equal-

sized individual samples. Compositing followed guidelines in Peterson and Calvin (1986) and was suitable for the present study since we were not examining variation within microhabitats. As pointed out by Crépin and Johnson (1993), composite sampling can be used in

conjunction with stratification; i.e., the landscape can be divided into meaningful units and good averages of soil properties obtained by compositing samples within each unit. All soil and litter sampling was conducted in July 1991.

**BULK DENSITY.**—Bulk density was determined by the excavation method (Blake and Hartge 1986). Twenty-two paired samples were taken 10.2 cm above and below cactus axes, 10 samples were taken from interspaces, and 10 were taken from beneath tree and shrub canopies. Soil was excavated with a bulb planter (diameter 5.5 cm at cutting edge), creating a hole 7 cm deep. A thin, tough plastic bag was placed in the hole, filled with water, and then emptied into a graduated cylinder to determine hole volume. Extracted soil was dried at 105° C and weighed, resulting in a weight-to-volume measurement.

**TOTAL N, TOTAL ORGANIC C, AND SOIL TEXTURE.**—Thirty pairs of soil cores (mineral soil surface to 7 cm deep) were extracted with a bulb planter (diameter 5.5 cm at the cutting edge) adjacent to cactus axes (10.2 cm above and below cactus axes), 30 from beneath canopies, and 30 from interspaces. Samples were taken near each of the 6 satellite plots established for the net mineralization study (see below). Litter (all litter from surface to mineral soil) was retained for determination of total N. Samples were air-dried and stored in paper wrappers. Soil samples originally taken for determining bulk density (see above) were added to these soil samples for a total of 51 samples from each side of cactus dams, 40 samples from beneath canopies, and 40 from interspaces. One of the 22 paired bulk density samples was lost and could not be included.

Samples were combined to create composites: above cactus dams 51 samples of soil were composited to make 3 samples of soil, and 30 samples of litter were combined to make 3 litter samples. Below cactus dams (no litter present) 51 samples of soil were composited to make 3 soil samples. Beneath canopies 40 soil samples were composited to make 3 samples of soil, and 30 litter samples were composited to make 3 litter samples. From interspace areas (no litter present) 40 samples were composited to make 3 samples of soil. Analysis was by Utah State University Soils Testing Lab following the Kjeldahl method (Bremner and Mulvaney 1982) to determine percent total N, the Walkley-Black method (Nelson and Sommers 1982)

for percent organic C, and methods described by Gee and Bauder (1986) for particle-size analysis.

**NET MINERALIZED N.**—The total amount of N liberated from organic matter is "gross mineralization"; the quantity remaining after microbial immobilization is "net mineralization" (Carlyle 1986). Net mineral N, the N available for plant uptake, is an index of soil fertility. To compare soil N fertility among woodland sites, net mineral N was assessed by laboratory aerobic incubations (Binkley and Vitousek 1989).

Seven permanent plots were created on the study site, the 1st plot serving as a central point from which 6 satellite plots were created, each 32 m from the central point at 60° intervals beginning with a random azimuth. Because of topography, 1 plot was relocated 32 m from the center of a satellite plot. From each plot center 8 cacti (0.5 to 5 m from center) were selected at 45° intervals beginning with a random azimuth, for a total sample of 56 cacti.

Paired soil samples were taken 10.2 cm from cactus axes on all 7 permanent plots beginning from the easternmost cactus and moving clockwise. Samples were composited combining 4 individual samples into 1 composite sample. Compositing and field processing (see below) were performed immediately upon the extraction of 4 cores. For example, on the 1st plot 4 cores 10.2 cm above cactus axes in the 90°–270° hemisphere of the plot were taken, composited, and field processed before the next 4 cores were drawn. This ensured processing fresh soil. Fourteen composite sample pairs were prepared.

At approximately midpoints of the six 32-m lines creating satellite plots, 2 samples were taken beneath canopies (piñon pines sampled most heavily followed by scrub oak, mixed-species canopies, and juniper) and 2 from interspaces. Composites of 4 individual samples were prepared and field processing completed immediately as each set of 4 cores was drawn. Three composite samples were prepared.

Samples were taken with a 2-cm-diameter soil corer to a depth of 10 cm. Preparation of samples for analysis followed methods outlined in Vitousek et al. (1982): In the field cores were divided into 3 components (litter layer, top 5 cm of mineral soil, and mineral soil between 5 and 10 cm soil depth) and composited. Composite soil samples were sieved through a 2-

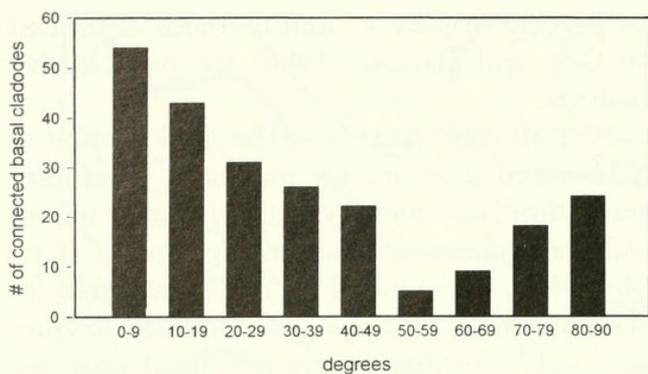


Fig. 3. Angle of growth of connected basal cladodes with respect to slope contour. Zero degrees is a direction of growth parallel to the slope contour; 90 degrees is a direction of growth perpendicular to the slope.

mm screen; litter was not sieved. Subsamples were sealed in bags for determination of moisture content, while a 2nd subsample of approximately 10 g was placed in 100 ml 1 N KCl adjusted with HCl to pH 2.5 with phenylmercuric acetate (PMA) added as a preservative. Solutions were refrigerated, transported to the laboratory, mixed frequently for 4 d, then allowed to settle for 48 h. After settling, the solution was removed with a pipette, and  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were determined at Bilby Research Facility at Northern Arizona University using methods described by Keeney and Nelson (1982).

The remainder of composited field samples (after removal of the above 2 subsamples) was transported to the laboratory and incubated aerobically following procedures in Vitousek et al. (1982): Soils were wetted to approximately field moisture capacity (assessed visually), placed in plastic-covered cups, each of which had a small air hole, and kept in a dark, moist chamber at a constant temperature of 22° C. During an 8-wk incubation period, samples received distilled water (applied as a fine mist to the surface with no mixing) as needed to maintain an approximately constant moisture content. So as not to disturb incubating samples, moisture content was assessed by visible soil color easily observable through the clear plastic incubation cups.

At the end of 8 wk, subsamples (approximately 10 g) of incubated samples were taken for determination of moisture content, and subsamples of approximately 10 g were placed in the KCl solution described above. These solutions were shipped to the soils testing lab-

TABLE 3. Size distribution of cactus dams and associated litter accumulations on a 25 × 25-m plot. The area measured was the soil surface covered by cactus dams and associated litter.

Size class (m <sup>2</sup> )	Number of cactus dams
0.05	1
0.1-1.0	16
1.1-2.0	6
2.1-3.0	6
3.1-4.0	2
10.30	1

oratory at Utah State University for determination of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  (U.S. EPA 1983).

CHANGE IN DEPOSIT DEPTH.—Depth of deposits above cactus dams (i.e., above connected basal cladodes) was measured before (July) and after (September) the rainy season of 1991 on 6 of the 7 plots designated for net mineralization sampling (see above). Two sampling points could not be relocated at the end of the rainy season, making a total sample size of 46 cactus dams (i.e., 6 plots, 8 cacti per plot, minus 2). Depth was measured from base to top of deposits in the area of greatest accumulation.

#### Statistical Analysis

A heterogeneity chi-square analysis followed by a chi-square analysis (Zar 1984) was performed with the 3 data sets of angle of cactus growth from the 3 mountain ranges.

SOIL AND LITTER ANALYSES.—Tests of normality were performed for each data set (above cactus dams, below cactus dams, interspaces, and beneath canopies) of each soil and litter characteristic sampled. A paired *t* test ( $\alpha = 0.05$ ) was used to compare means of soil characteristics above and below cactus dams, and to compare the depth of deposits at cactus dams before and after the rainy season. An analysis of variance *F*-test ( $\alpha = 0.05$ ) for unbalanced sample sizes (the GLM procedure in SAS software [SAS 1985]) was used to compare sample means of soil above and below cactus dams with beneath canopy and interspace sample means. Plots of residuals were generated to assess equality of variance. Significant differences between means were separated and ranked using a multiple comparison method

TABLE 4. Results of paired *t* tests comparing sample means of soil characteristics above and below cactus dams, and comparing depth of detritus above cactus dams between early July and mid-September. A minus B refers to the value above cactus dams minus the value below.

Attribute	N	Paired <i>t</i> -test statistics			P
		Mean difference A minus B	$s_{\bar{x}}$	<i>t</i>	
Bulk density (g/ml) (natural log) 0-7 cm depth	22	-0.222	0.117	1.901	0.0711
Total N (%) 0-7 cm depth	3	0.043	0.003	13.000	0.0059
Organic C (%) 0-7 cm depth	3	0.933	0.231	4.035	0.0563
Net mineralized N (ug/g)					
0-5 cm depth NH <sub>4</sub> <sup>+</sup>	14	9.621	2.353	4.088	0.0013
0-5 cm depth NO <sub>3</sub> <sup>-</sup>	14	41.979	5.398	7.776	0.0001
5-10 cm depth NH <sub>4</sub> <sup>+</sup>	12	2.050	2.063	0.993	0.3418
5-10 cm depth NO <sub>3</sub> <sup>-</sup>	12	7.550	2.672	2.826	0.0165
Change in depth (cm) of detritus above cactus dams (natural log) 0-7 cm depth	46	1.240 <sup>a</sup>	0.124	10.038	0.0001

<sup>a</sup>Mean difference of September detritus depth minus July detritus depth.

(REGWF) cited as being compatible with the overall analysis of variance *F*-test (SAS 1985). A *t* test ( $\alpha = 0.05$ ) was used to compare sample means of total N and net mineralized N from the litter above cactus dams with the litter layer beneath woodland canopies.

## RESULTS

The pattern of angle of connected basal cladodes with respect to slope contour was similar in the 3 mountain ranges sampled; data were pooled based on results of a heterogeneity chi-square analysis. Analysis of pooled data ( $\chi^2 = 85.4$ ,  $P < 0.001$ ) indicated that orientation of connected basal cladodes of *Opuntia littoralis* var. *martiniana* was nonrandom: growth was most frequently parallel to the woodland slope contour (Fig. 3). The size range of cactus dams and associated litter on a 25 × 25-m plot at the Hualapai Mountains study area is given in Table 3.

SOIL AND LITTER ANALYSES.—The null hypothesis for normality was not rejected for most of the data sets; however, total N data

were nonnormal and were not normally distributed when transformed with standard transformations. Therefore, results of total N analyses should be interpreted with caution. Residual plots indicated equality of variance assumptions were reasonable.

Bulk density above and below cactus dams was not significantly different at  $P = 0.05$  (Table 4). Bulk density was significantly lower ( $P = 0.0001$ ) in soil deposits above cactus dams, below cactus dams, and beneath tree canopies, compared to soil from interspaces (Table 5, Fig. 4). Soil above and below cactus dams was also lower in bulk density than soil beneath tree canopies, although this difference was not significant at  $P = 0.05$ . There was little difference in soil texture among the 4 microhabitats (Table 5).

Soil total N above cactus dams was greater ( $P < 0.01$ ) than below cactus dams (Table 4). Organic C was not significantly different ( $P = 0.05$ ) above cactus dams compared to below cactus dams. Soil total N and organic C were 2-3 times greater ( $P = 0.0001$  in both cases) in soil above and below cactus dams than in interspace soil (Table 5, Fig. 4). Soil total N and

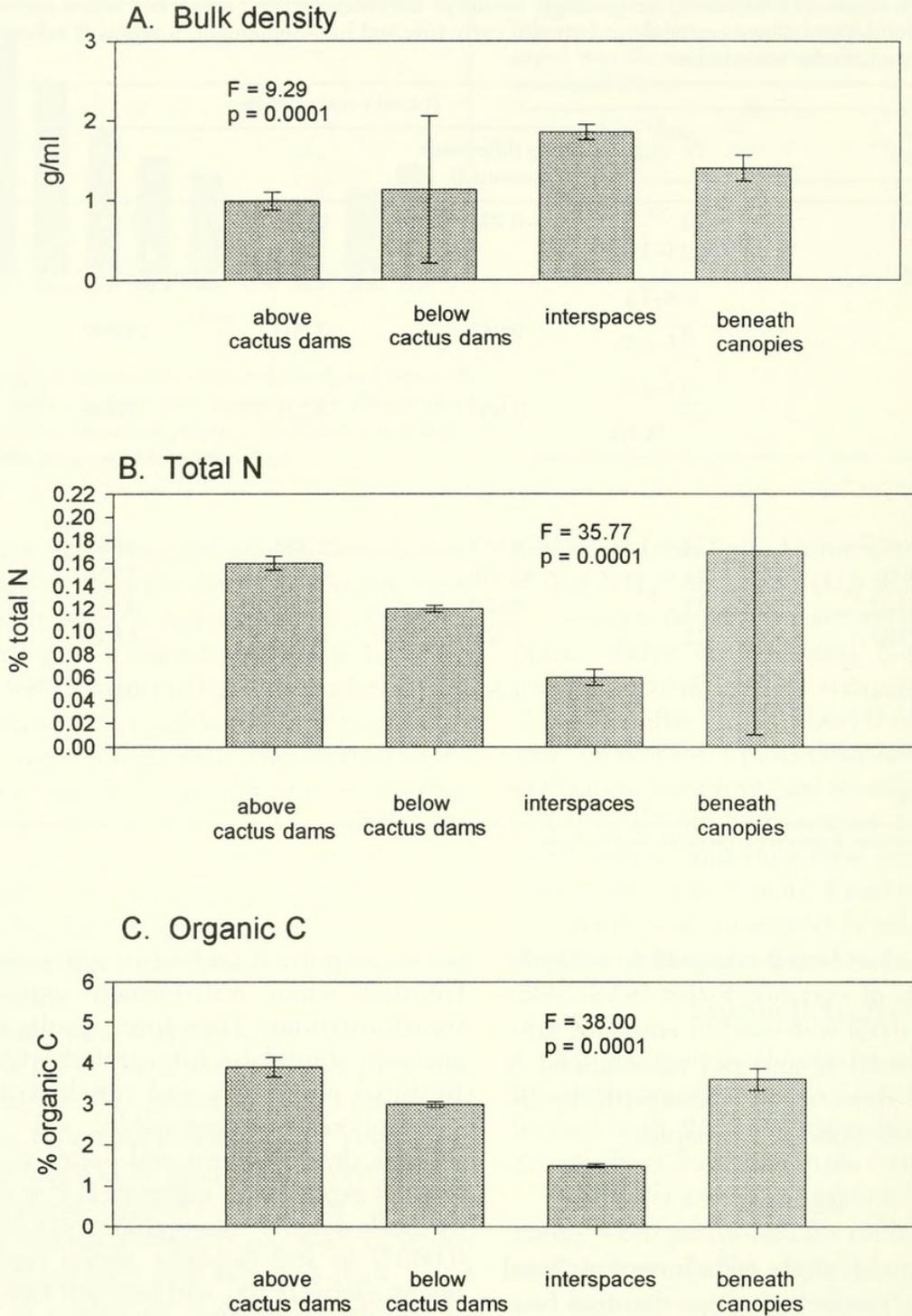


Fig. 4. Comparisons of soil characteristics above cactus dams, below cactus dams, beneath canopies (tree and shrub combined), and in bare interspaces.

organic C above cactus dams were equal to areas beneath canopies. Below cactus dams, soil total N was significantly lower than beneath canopies, and organic C was not significantly different compared to beneath canopies. While soil organic C and soil total N differed among woodland locations, the C:N ratio was similar between locations (Table 5).

Net mineral  $\text{NH}_4^+$  and  $\text{NO}_3^-$  at 0–5 cm depth were significantly greater ( $P = 0.001$  and  $P = 0.0001$ ) above cactus dams compared to below (Table 4). At 5–10 cm depth net mineral  $\text{NO}_3^-$  was significantly greater ( $P = 0.0165$ ) above cactus dams compared to below. Net mineral N in soil 0–5 cm deep above cactus dams was over 3 times that in interspace

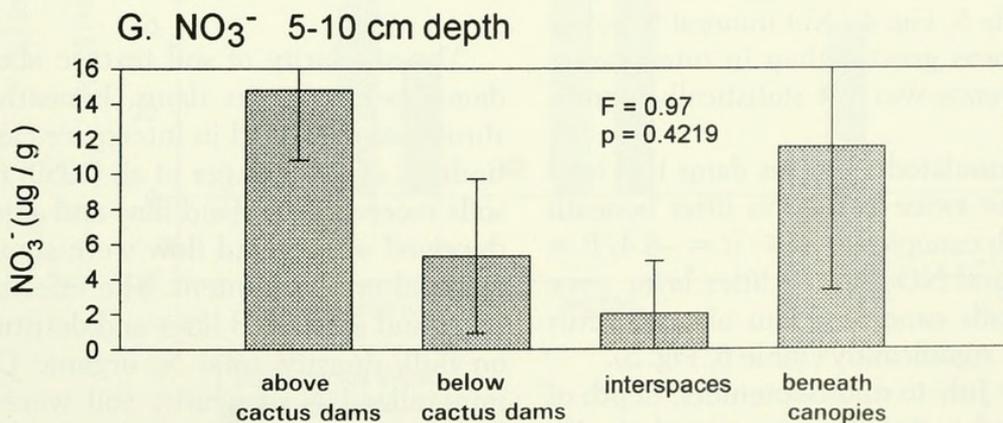
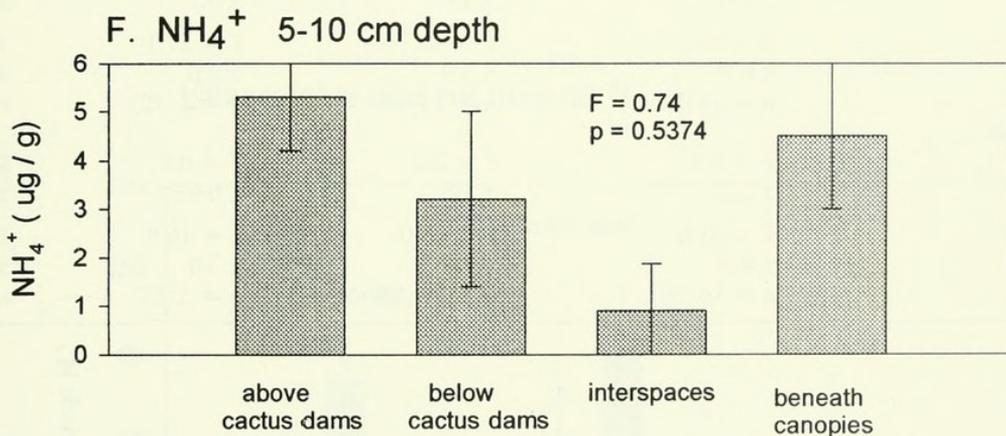
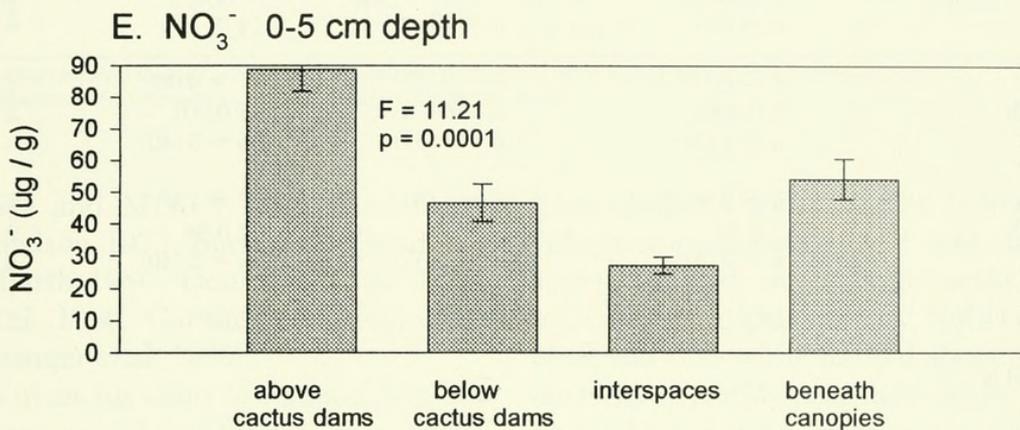
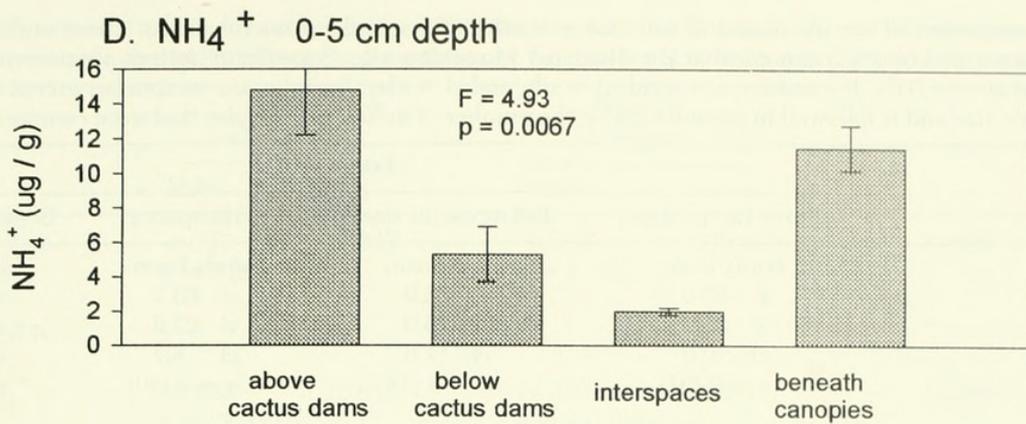


Fig. 4. Continued.

TABLE 5. Comparison of sample means of soil characteristics at 4 woodland microhabitats (above and below cactus dams, interspaces, and beneath canopies) at the Hualapai Mountains site. Superscript letters separate means significantly different at  $\alpha = 0.05$ . For texture, s = sand, sl = silt, and cl = clay. Samples are composites except for bulk density.  $N$  = sample size and is followed in parentheses by the number of individual samples that were composited.

Attribute	Location			
	Above cactus dams	Below cactus dams	Interspaces	Beneath canopies
Soil texture	sandy loam	sandy loam	sandy loam	sandy loam
% separates	s 65.0 sl 25.0 cl 9.0 $n = 3$ (51)	s 63.0 sl 26.0 cl 11.0 $n = 3$ (51)	s 63.7 sl 27.6 cl 8.7 $n = 3$ (40)	s 62.7 sl 28.3 cl 9.0 $n = 3$ (40)
Bulk density (g/ml)	$\bar{x} = 0.99^b$ $\pm 0.11$ $n = 22$	$\bar{x} = 1.13^b$ $\pm 0.92$ $n = 22$	$\bar{x} = 1.85^a$ $\pm 0.10$ $n = 10$	$\bar{x} = 1.40^b$ $\pm 0.16$ $n = 10$
Total N (%) 0-7 cm depth	$\bar{x} = 0.16^a$ $\pm 0.006$ $n = 3$ (51)	$\bar{x} = 0.12^b$ $\pm 0.003$ $n = 3$ (51)	$\bar{x} = 0.06^c$ $\pm 0.007$ $n = 3$ (40)	$\bar{x} = 0.17^a$ $\pm 0.16$ $n = 3$ (40)
Organic C (%) 0-7 cm depth	$\bar{x} = 3.9^a$ $\pm 0.24$ $n = 3$ (51)	$\bar{x} = 3.0^a$ $\pm 0.07$ $n = 3$ (51)	$\bar{x} = 1.5^b$ $\pm 0.04$ $n = 3$ (40)	$\bar{x} = 3.6^a$ $\pm 0.26$ $n = 3$ (40)
C:N ratio	24.4	25.0	25.0	21.2
Net mineralized N (ug/g)				
0-5 cm depth				
$\text{NH}_4^+$	$\bar{x} = 14.8^a$ $\pm 2.6$	$\bar{x} = 5.3^b$ $\pm 1.6$	$\bar{x} = 2.0^b$ $\pm 0.2$	$\bar{x} = 11.5^a$ $\pm 1.3$
$\text{NO}_3^-$	$\bar{x} = 88.7^a$ $\pm 6.9$ $n = 14$ (56)	$\bar{x} = 46.7^{bc}$ $\pm 5.9$ $n = 14$ (56)	$\bar{x} = 27.1^c$ $\pm 2.6$ $n = 3$ (12)	$\bar{x} = 54.2^b$ $\pm 6.4$ $n = 3$ (12)
5-10 cm depth				
$\text{NH}_4^+$	$\bar{x} = 5.3$ $\pm 1.1$	$\bar{x} = 3.2$ $\pm 1.8$	$\bar{x} = 0.9$ $\pm 0.97$	$\bar{x} = 4.5$ $\pm 1.5$
$\text{NO}_3^-$	$\bar{x} = 31.6^a$ $\pm 4.0$ $n = 14$ (56)	$\bar{x} = 24.0^b$ $\pm 4.4$ $n = 14$ (56)	$\bar{x} = 16.6$ $\pm 3.0$ $n = 3$ (12)	$\bar{x} = 30.9$ $\pm 8.2$ $n = 3$ (12)

soil and almost twice that in soil beneath tree canopies (Table 5, Fig. 4). Net mineral N below cactus dams was greater than in interspaces, but the difference was not statistically significant.

Litter accumulated at cactus dams had total N (0.74%) over twice as high as litter beneath tree and shrub canopies (0.32%) ( $t = -8.4$ ,  $P = 0.01$ ).  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in the litter layer were greater beneath canopies than above cactus dams, but not significantly (Table 6, Fig. 5).

From early July to mid-September, depth of detritus behind cactus dams increased significantly ( $P = 0.0001$ ) from -2 cm to +23 cm, with an average of +4.3 cm ( $s_{\bar{x}} 0.625$ ; Fig. 6).

## DISCUSSION

The similarity of soil texture above cactus dams, below cactus dams, beneath tree and shrub canopies, and in interspaces agrees with findings of Schlesinger et al. (1989) that desert soils receiving overland flow and adjacent soils deprived of overland flow were similar in fine material or clay content. The effects of cactus dams and associated litter and detritus deposits on bulk density, total N, organic C, and net mineralized N of nearby soil were expected based on a number of studies in shrub lands and woodlands documenting islands of fertility, i.e., localized areas of nutrient enrichment

TABLE 6. Comparison of total N and net mineralized N in the litter layer beneath canopies with litter accumulations above cactus dams. *N* = sample size and is followed in parentheses by the number of individual samples that were composited.

Attribute	Above cactus dams		Beneath canopies		<i>t</i>	<i>P</i>
	Mean	<i>s<sub>x</sub></i>	Mean	<i>s<sub>x</sub></i>		
Total N (%)	0.737 <i>n</i> = 3 (30)	0.047	0.320 <i>n</i> = 3 (30)	0.015	-8.4275	0.0095
Net mineralized N ( $\mu\text{g/g}$ )						
$\text{NH}_4^+$	60.233 <i>n</i> = 2 <sup>a</sup> (12)	15.018	84.550 <i>n</i> = 12 <sup>b</sup> (48)	11.250	1.2929	0.2426
$\text{NO}_3^-$	-2.108 <i>n</i> = 2 (12)	6.410	40.050 <i>n</i> = 12 (48)	34.950	1.1865	0.4398

<sup>a</sup>Three composites were prepared; however, initial (before incubation) net mineral N values were not obtained for 1 sample.

<sup>b</sup>Values before incubation were not obtained for 2 of the original 14 composited samples.

(Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973, Barth and Klemmedson 1978, Barth 1980, Doescher et al. 1984, Everett et al. 1986, Garner and Steinberger 1989, Schlesinger et al. 1990).

Deposits at cactus dams of *Opuntia littoralis* var. *martiniana* raised soil total N from 0.06% (interspace soil) to 0.16% above connected

basal cladodes and to 0.12% below (Table 4). Nitrogen enrichment and soil amelioration associated with deposits at cactus dams may increase cactus productivity. Nobel et al. (1987) observed that while annual aboveground productivity of prickly pear cacti can be high under optimal conditions, cacti productivity is often limited by low levels of soil N (Nobel et al.

Litter total N and net mineral N

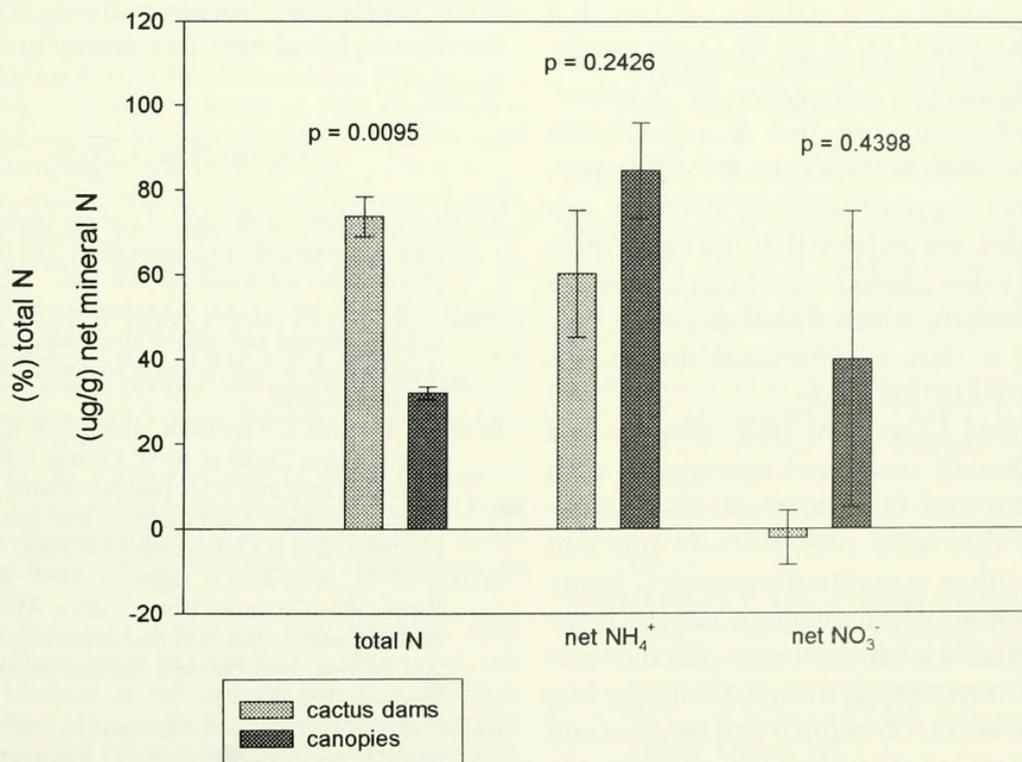


Fig. 5. Nitrogen in the litter accumulated above cactus dams compared with the litter layer beneath canopies (trees and shrubs combined).

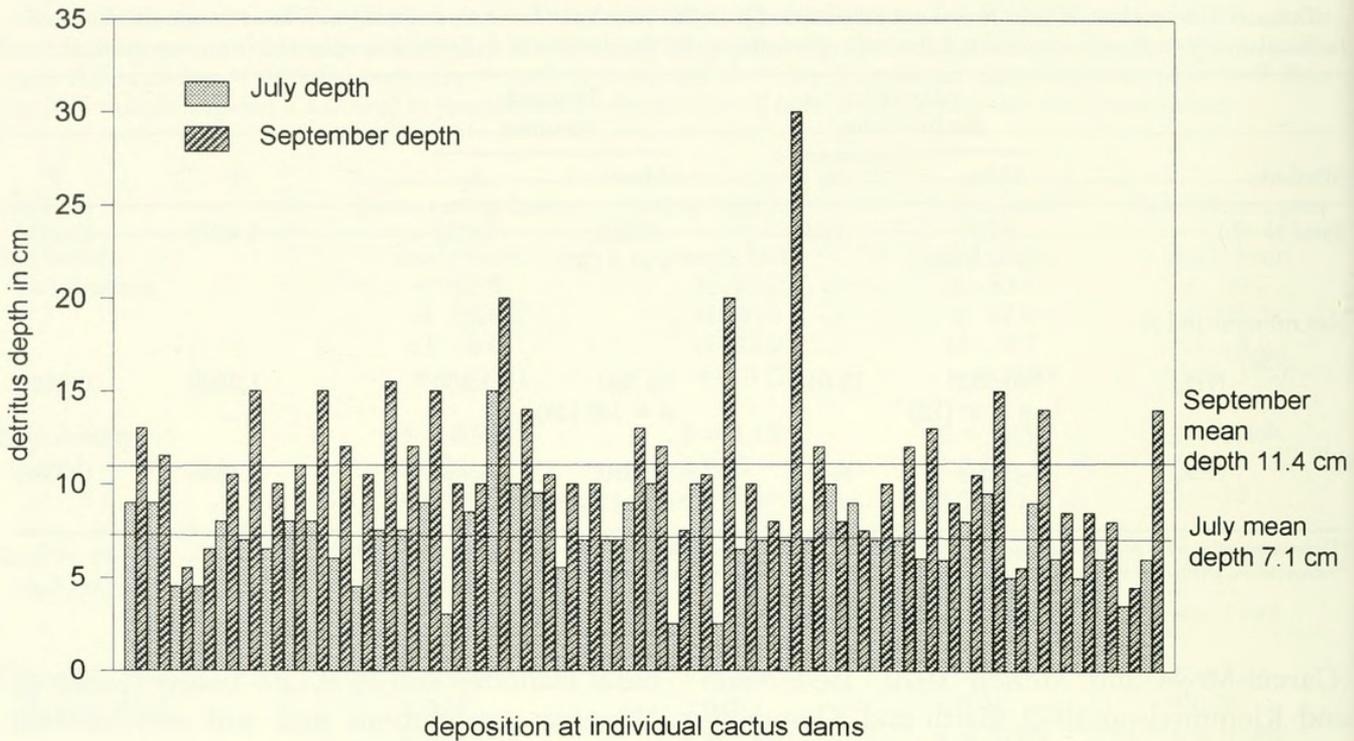


Fig. 6. Deposition at cactus dams during 1 season of summer thundershowers: depths of detritus accumulations at 46 cactus dams in July and in September.

1987, Nobel 1989). Increased productivity in desert prickly pear cacti is positively correlated with both number of new cladodes produced and cladode size (Nobel et al. 1987). We do not know if similar patterns occur in woodland species of prickly pear. Additionally, Nobel (1988) describes a tendency for "daughter" cladodes to replicate the orientation of "mother" cladodes and points out that if a particular direction of growth is favorable, it may be perpetuated. This happens because favorably oriented cladodes are expected to be more productive than other cladodes and produce more and larger similarly oriented cladodes. This may be occurring in dam-forming cacti, but it was not investigated in this study.

Cactus dams lower soil bulk density and enrich patches of woodland interspace with organic matter, total N, and net mineral N, suggesting that they may play roles in nutrient cycling and other ecosystem processes. Some possible functions of cactus dams are to (1) increase woodland detritus storage, (2) increase the rate of N turnover, (3) mitigate nutrient loss in interspace areas, (4) reduce soil erosion and dampen effects of disturbances, (5) provide seedbeds, and (6) provide habitat for other organisms.

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