

Variation in Creosotebush (*Larrea tridentata*) Canopy Morphology in Relation to Habitat, Soil Fertility and Associated Annual Plant Communities

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ABSTRACT.—Differences in creosotebush (*Larrea tridentata*) crown morphology may reflect changes in the relative demand for water vs. nutrient resources, coinciding with shrub growth and development. Creosotebushes with inverted cone-shaped crowns were more abundant in water-limited environments whereas hemispherical shaped creosotebushes were more abundant in less water-limited environments. Cone-shaped creosotebushes accumulated substantially less litter under their canopies than did creosotebushes with hemispherical shaped crowns. Soil nutrient concentrations under conical shrubs were similar to those in intershrub spaces and both of these were significantly less than soil nutrient concentrations under hemispherical shrubs. In ecosystems where overland flow of water exerted a greater influence on the movement of organic litter than did wind, shrub shape had little effect on long-term litter accumulation. No persistent differences in the biomass or diversity of ephemeral taxa exploiting undershrub areas were found, probably because the positive effects of greater nutrient resources under hemispherical shrubs were offset by the limitations imposed by the larger, more dense canopies of hemispherical shrubs. Overall, creosotebush morphology affected litter accumulation patterns and soil nutrient patterns, and must be considered when assessing the heterogeneity of desert ecosystems in the southwestern USA.

INTRODUCTION

Creosotebush [*Larrea tridentata* (D.C.) Cov] is a xerophytic, evergreen, perennial shrub widely distributed and abundant in the hot deserts of North America (Shreve, 1942; Hunziker *et al.*, 1977). Creosotebush dominates many ecosystems in the Mojave, Sonoran and Chihuahuan deserts, and is important in determining the characteristics of those ecosystems. Many studies of creosotebush have focused on the physiological characteristics that contribute to its success in the extreme environments of hot deserts (*e.g.*, Franco *et al.*, 1994; Lajtha and Whitford, 1989; Fisher *et al.*, 1988; Reynolds, 1986; Oechel *et al.*, 1972). Morphological characteristics of creosotebush which may contribute to its success have received less attention. Creosotebush branches are oriented to maximize light interception in the early morning when moderate temperatures allow greatest photosynthetic rates (Neufeld *et al.*, 1988). In creosotebush, angles of external stems are probably determined by the rate of initiation and the rate of growth of new stems at the center of the shrub. Plants with access to sufficient water resources may have greater rates of new stem initiation and growth, resulting in the external stems being pushed further outward decreasing their stem angle relative to the horizontal plane. As new growth at the center of the shrub continues and external stem angle decreases, shrub morphology would change from the conical shape

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(Fig. 1A) to the hemispherical shape (Fig. 1B). Variations in creosotebush canopy structure and foliage characteristics have been shown to affect the abundance and structure of the arthropod community living on these shrubs (Lightfoot and Whitford, 1989).

Stem angle off the horizontal plane is a significant factor in the generation of stemflow in creosotebush, and stemflow coupled with root channelization in the soil is probably the primary source of water for early season growth (Martinez-Meza and Whitford, *in press*). Creosotebush stems with angles $> 45^\circ$ generate much more stemflow water (111.6 ± 94.6 mm) than do stems with angles $< 45^\circ$ (4.0 ± 1.7 mm; Martinez-Meza, 1994). The inverted cone morphology that results from creosotebushes having all primary external stems with angles $> 45^\circ$ should maximize their water collection ability on the basis of projected canopy surface area (Fig. 2). However, hemispherical crown creosotebushes, which have interior stems with angles $> 45^\circ$ and exterior stems with angles $< 45^\circ$, will collect and redirect a smaller fraction of the total rain falling on the shrub due to the reduced stemflow on the exterior stems (Fig. 2). Rainfall not redirected as stemflow ends up as throughfall onto undercanopy soil with a reduction in raindrop velocity and size, allowing some water retention in shallow soil layers, but a large proportion of this water is lost to the plant as runoff (Fig. 2; Martinez-Meza and Whitford, *in press*). From this we hypothesized that the inverted cone morphology would be most frequent in younger, less established shrubs in sites having low rainfall and where soil infiltration was minimal and run-off maximal.

Nitrogen content, mineralization and nitrogen availability vary with the organic matter content of the soil and are related to the amount of litter present (Fisher *et al.*, 1990). The under-shrub nutrient patches are characterized by horizontal and vertical gradients where nutrient concentrations are greatest under the shrub canopy near the stem (Whitford, 1986; Crawford and Gosz, 1982; West and Klemmedson, 1978). In desert soils, nutrient concentrations, especially nitrogen, are correlated with soil organic matter content (1987; Skujins, 1981; Whitford *et al.*). The decomposition of litter accumulated under creosotebushes increases the nitrogen content of the undershrub soil (Parker *et al.*, 1982).

Shrub canopy volume and shrub morphology affect the volume of litter that accumulates under shrub canopies. Shrub size and shape affect litter accumulation by affecting wind turbulences over, around, and beneath canopies (Reichman, 1984). In a landscape with sparsely scattered shrubs, turbulence and the circular movement of dust and debris (due to eddy currents) result in the deposition of fine particulate matter under shrubs in addition to the deposition of dead leaves and other organic debris (Friese and Allen, 1993). The effectiveness of litter deposition should be a function of shrub morphology. Predicted air stream patterns (Blevins, 1984) suggest that litter will accumulate under hemispherical shrubs (Fig. 3) due to local wind turbulences. These may bring about some mixing of the litter, but do not result in net loss of litter from under the shrub. Conversely, for inverted cone-shaped objects, the relative absence of local turbulence and the downward flow of wind and consequent acceleration of wind speed (Blevins, 1984) at the bases of conical shrubs should result in the disruption and then dispersal of much of the litter accumulated there. From this we hypothesized that creosotebushes with hemispherical crowns should accumulate more litter than should creosotebushes with a conical shape.

The crown morphology of creosotebushes in a particular habitat should be a function of the relative abundance of water vs. nutrients in that habitat. To test this hypothesis we measured the relative abundance of conical vs hemispherical shaped creosotebushes from several creosotebush habitats in the northern Chihuahuan Desert and in the northern Mojave Desert of the southwestern United States. At selected sites within these desert habitats we also measured the accumulation of organic and inorganic soil nutrients, the accu-

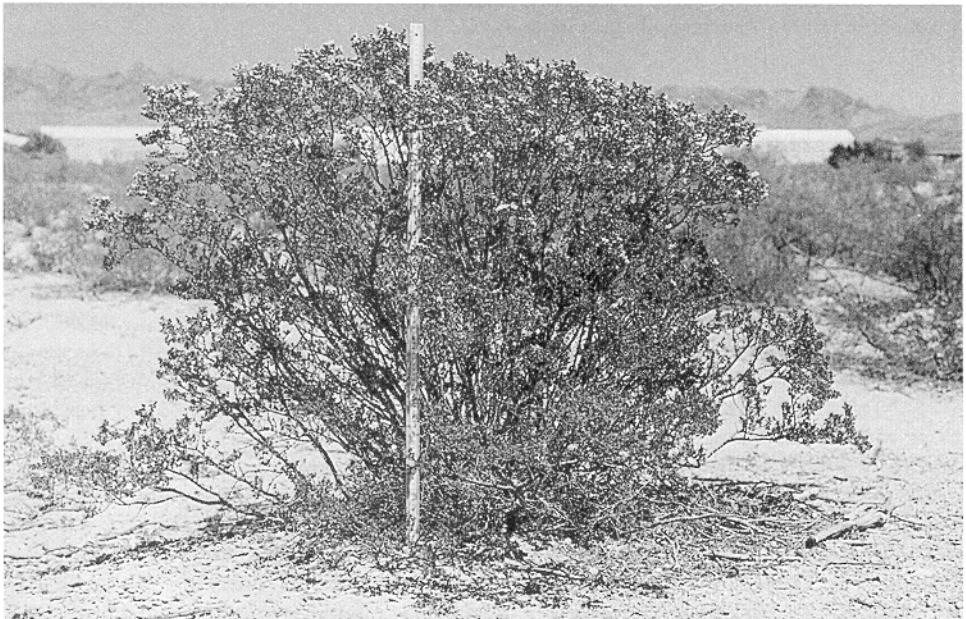
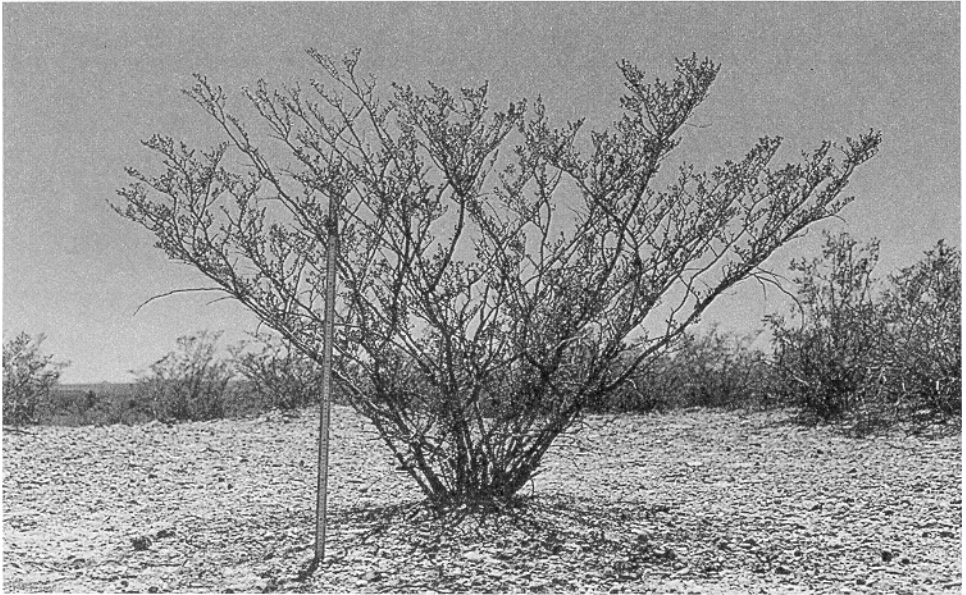


FIG. 1.—(Upper.) A creosotebush with an inverted cone (conical) shaped crown and (Lower) a creosotebush with a hemispherical crown. Note the substantial amount of litter accumulated under the hemispherical crown creosotebush

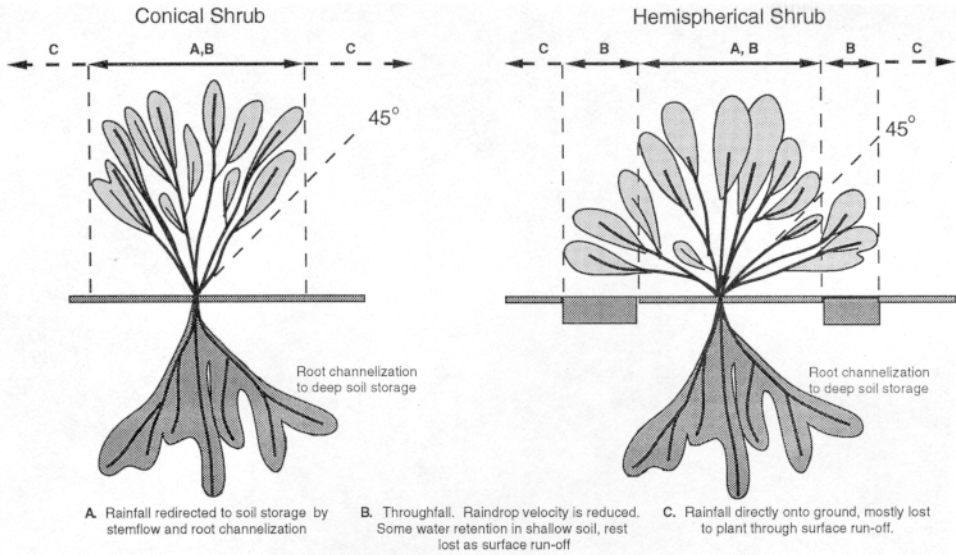


FIG. 2.—Diagram of the two shrub morphologies and their effects on stemflow and throughfall. Inverted cone (conical) shrubs have exterior stem angles $>45^\circ$ from the horizontal and hemispherical shrubs have exterior stem angles $<45^\circ$ from the horizontal

mulation of particulate matter, and the abundance of spring-flowering ephemeral plants under shrubs of the two morphologies.

MATERIALS AND METHODS

Study sites.—We sampled 12 sites in the Jornada Basin of the northern Chihuahuan Desert in southern New Mexico and three sites in the Mojave Desert (Table 1).

In the Jornada, six sites were on the E-facing slope of the Doña Ana Mountain Range 35–40 km NNE of Las Cruces, New Mexico. These sites were: (1) A sandy site (C-SAND) on a middle piedmont-slope; (2) a sandy site near the creosotebush-grassland (C-SAND-G) ecotone on a NE-facing mid-piedmont slope; (3) a site 2 km upslope from a dry lake basin (C-SAND-IL) and a loamy haplargid soil; (4) a gravelly site (C-GRAV) on a lower piedmont slope with a sandy loam soil texture; (5) a gravelly, fine sandy loam (C-GRAV-RIDGE) site, and (6) a site along the banks of the adjacent ephemeral stream (C-GRAV-WASH).

On the E side of the Jornada, five sites were on the W-facing mid-piedmont slope of the San Andres mountain range approximately 50 km NE of Las Cruces, New Mexico, and one site was on the W-facing piedmont slope of the Organ Mountain Range 5 km E of Las Cruces; (7) a loamy-sand alluvial fan ridge that was plowed in 1972 and in 1973 (C-RIDGE-RP), and (8) an adjacent ephemeral stream that was plowed at the same time (C-WASH-RP); (9) a ridge (C-RIDGE) that was not plowed (approximately 0.5 km N of C-RIDGE-RP), and (10) the banks and islands of the adjacent ephemeral stream bed (C-WASH); (11) a site heavily eroded by overland water-flow (C-EROD), on the lower piedmont slope of the San Andres range, and (12) a desert pavement site (C-PAVE) on the lower alluvial piedmont of the Organ Mountains.

The three sites in the Mojave desert were: (13) at the base of Death Valley in an area of braided washes (C-WASH-DV), 8 km NNE of Furnace Creek, California; (14) on a sandy

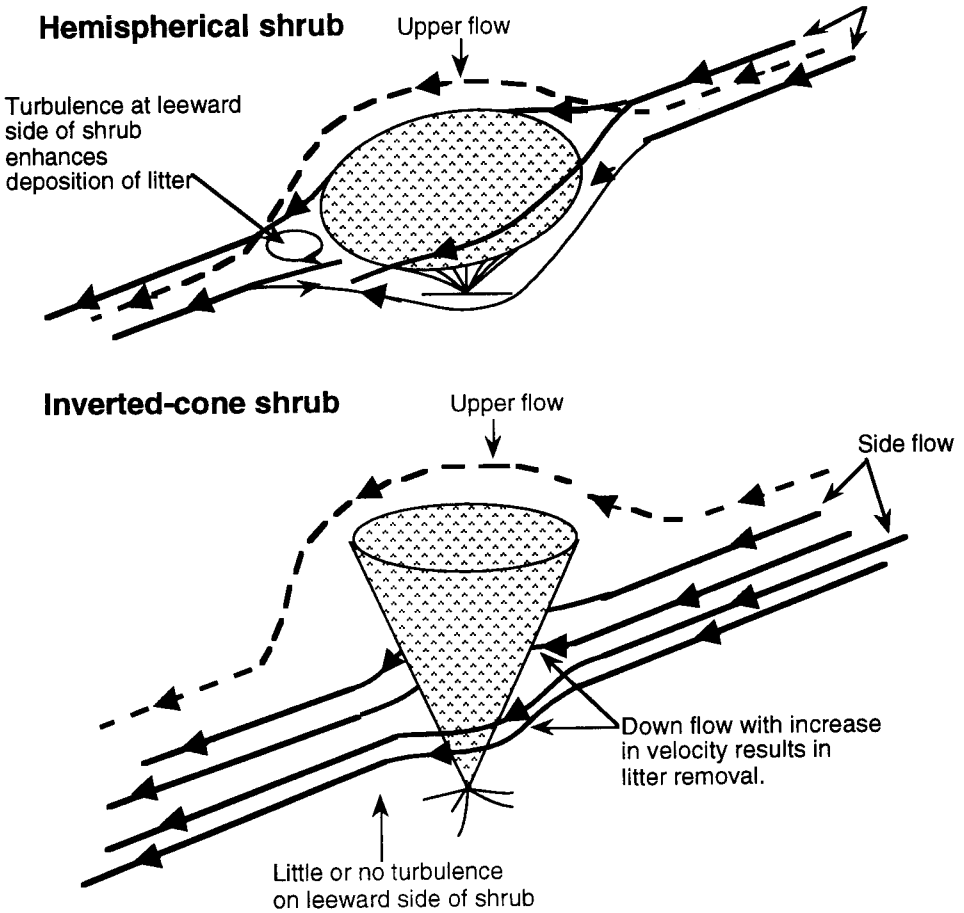


FIG. 3.—Flow paths of wind encountering shrubs with cone-shaped canopies vs. shrubs with hemispherical canopies. Turbulence on the leeward side of hemispherical crowns causes deposition of litter, whereas increase in wind velocity due to downflow at the base of conical shrubs causes litter to be blown away from under the shrub

bajada (C-BAJA-DV) at 1200 m elevation on the E side of the valley, 10 km NNE of Furnace Creek, California. (15) a volcanic cobble-covered piedmont (C-COBB) 10 km SSW of Henderson, Nevada. The average annual rainfall is 230 mm in the Jornada Basin in New Mexico, 40 mm at the Death Valley sites and 99 mm at Henderson, Nevada.

Shrub morphology.—Stem angles were measured on 50 plants at each of nine sites in the Jornada Basin and three Mojave Desert sites. Plants were sampled on the basis of having a single stem-crown at the soil surface, and on having a discrete canopy not touching neighboring plants. Measurements were made on plants meeting these criteria as they were encountered on line transects 50–100 m long. In each habitat transect lines were positioned 10 m apart and samples taken until a total of 50 plants were measured. The transects were positioned parallel to the axis of least slope. Plant stem-angles were calculated for exterior branches using the formula:

TABLE 1.—Locations and descriptions of study sites in the Chihuahuan and Mojave deserts

Location	Site code	Site-specific descriptions		
		Aspect	Slope	Soil
Piedmont slope of Mount Summerford of the Doña Ana Mountain Range in the Jornada del Muerto Basin 35–40 km NNE of Las Cruces, New Mexico	C-SAND	E	3%	sandy-pebbly-loam
	C-SAND-G	NE	2–3%	sandy-loam
	C-SAND-IL	E	1–2%	loamy-haplargid
	C-GRAV	NE	2%	sandy-loam
	C-GRAV-RIDGE	NE	2–4%	sandy-loam
Piedmont slope of San Andres Mountain Range in the Jornada del Muerto Basin 50 km NNE of Las Cruces, New Mexico	C-GRAV-WASH	NE	2%	sandy-loam
	C-RIDGE-RP	W	3–4%	sandy-loam
	C-WASH-RP	W	2–3%	sand
	C-RIDGE	W	3–4%	sandy-loam
	C-WASH	W	2–3%	sand
Piedmont slope of Organ Mt. Range, 5 km E of Las Cruces, New Mexico	C-EROD	W	1%	sandy-loam
	C-PAVE	W	1%	surface pavement gravelly-loam
Death Valley, approx 8 km and 10 km from Furnace Creek, California	C-WASH-DV	SW	3–4%	gravelly-sand
	C-BAJADA-DV	SW	3–4%	sand
A piedmont slope 10 km SSW of Henderson, Nevada	C-COBB	N	2–3%	volcanic cobble

$$\text{Stem-angle} = \arctan^* \frac{d_1}{d_2}$$

where:

d_1 = Vertical distance from the top exterior edge of the branch to the soil surface

d_2 = Horizontal distance from the base of the trunk to the point where it intersects the line of vertical distance.

Plants with all exterior primary stem angles over 45° from the horizontal were considered to have cone-shaped crowns (Fig. 2), while plants with all exterior primary stem angles less than 45° were considered to be hemispherical (Fig. 2). The choice of the 45° cut-off is based on the stemflow data of Martinez-Meza (1994) who found significantly greater stemflow on stems of angles $> 45^\circ$ from the horizontal.

Litter movement dynamics.—The aerodynamics of shrubs of the two shapes and the effect of those shapes on litter retention or litter deposition were examined by correlating predicted air stream flow lines around a hemispherical object and a conical object (Blevins, 1984) with litter accumulation. In order to determine whether there would be significant movement of litter among plants we used a simple model to calculate the wind speeds required to transport creosotebush organic litter in the form of leaf, stem or fruit tissue. In the field, there is no single threshold for lifting litter, because litter is not uniform in shape, size, density or mass per unit area. However, these values of entrainment threshold velocities, when evaluated in the context of prevailing wind conditions, indicate the importance of aeolian processes in litter redistribution.

Organic litter.—Soil surface area under the canopy of each shrub covered with organic litter (L_{SS}) was calculated from measurements of the major and minor axes through the center of each litter patch, assuming an elliptical distribution, using the equation:

$$L_{ss} = \frac{\pi}{4ab}$$

where a = length of the major axis and b = length of the minor axis.

Soil nutrients.—At the C-SAND site (Table 1), samples of soil only from 0–15 cm soil depth were collected from three positions relative to the stem crown of creosotebushes: plant center, mid-canopy, and from the interspace between canopies of adjacent shrubs. Soil samples were placed in plastic bags, air-dried and sent to the New Mexico State University Soil and Water Testing Laboratory, where standard methods of chemical analysis (Page *et al.*, 1982) were used for the analysis of organic carbon (Walkley-Black procedure), total N (Kjeldahl method/autoanalyzer), P, Mg, K, Ca (atomic absorption) and electrical conductivity.

Soil mounds.—Also at the C-SAND site, the effect of shrub crown morphology on accumulation (and retention) of particulate matter was investigated by measuring mound height with a theodolite and calculating the mean height (relative to soil surface in shrub interspaces) of soil mounds [(minimum height + maximum height)/2] under shrub canopies.

Spring flowering ephemerals.—At four sites which had a significant number of spring flowering ephemerals during 1995 (C-SAND, C-GRAV-RIDGE, C-SAND-G AND C-PAVE) we measured the numbers of these plants growing under creosotebushes with the two crown morphologies. Adjacent pairs of creosotebushes with conical and hemispherical crowns were chosen using line transects. Along each transect we first selected a creosotebush of either canopy morphology (shrub A). We then identified a creosotebush with the alternate crown shape (shrub B) and of the same approximate size within a 5-m radius of the center of shrub A. If a suitable shrub B could not be found within the 5-m radius, shrub A was abandoned and another shrub A was selected from along the transect and the selection procedure for shrub B was repeated. In each case shrub A could be a hemispherical shrub or a conical shrub. Once a suitable pair of shrubs was identified, the number and size (height and diameter) of the spring-flowering ephemeral plant taxa within a square 0.25 m² quadrat under the S side of the canopy of both plants was measured. This process was repeated until 20 suitable shrub pairs were identified and the spring-flowering ephemerals under the shrubs were measured. The biomass of individual spring flowering ephemeral plants was calculated from species-specific regressions relating plant volume to aboveground biomass (Gutierrez and Whitford, 1987). Spring-flowering ephemerals were also censused under the S side of 20 pairs of plants at a piedmont site (C-COBB) in the Mojave Desert.

RESULTS

Shrub morphology.—At two sites, C-RIDGE and C-RIDGE-RP, creosotebushes were small and predominantly conical in shape (Table 2). Also notable was the absence of litter under the shrubs (Table 2). At the C-GRAV-RIDGE site plants were larger and a small proportion of these plants had developed hemispherical crowns. Most of these larger, hemispherical crowned shrubs had accumulated litter (Table 2). As predicted, a significantly greater number of creosotebushes in the adjacent drainage channel (C-GRAV-WASH) had hemispherical canopies (chi-square test, $P < 0.0001$). Litter accumulation at these sites was very variable, and not significantly related to canopy type at several sites (Table 2). The C-SAND, C-GRAV-RIDGE and C-GRAV-WASH sites had a significantly greater number of hemispherical shrubs with litter accumulations (Table 2). Data from the two Death Valley sites also supports the hypothesis that the relative importance of nutrients (as indicated by its surrogate litter quantity) vs. water affects crown morphology, with the more water-limited C-BAJADA-DV site having fewer hemispherical plants than the C-WASH-DV site (Table 2). The creosote-

TABLE 2.—Number of conical (CON) vs. hemispherical (HEM) creosotebush shrubs at nine sites in the Jornada Basin, and three sites in the Mojave Desert. Also shown is the number of plants at the Jornada Basin sites with measurable accumulations of litter under the canopy. Results of chi-squared tests on these data are also shown

Site	Shrub morphology (Number)		Chi- squared <i>P</i>	Percent shrubs with litter		G-test <i>P</i>
	CON	HEM		CON	HEM	
C-SAND	34	16	0.0109	6	25	0.0054
C-GRAV-RIDGE	42	8	<0.0001	12	63	<0.0001
C-GRAV-WASH	43	7	<0.0001	0	29	<0.0001
C-RIDGE-RP	50	0	<0.0001	0	0	N.A.
C-WASH-RP	37	13	0.0007	4	0	0.7658
C-RIDGE	49	1	<0.0001	0	0	N.A.
C-WASH	37	13	0.0007	57	54	0.7658
C-EROD	33	17	0.0237	0	0	N.A.
C-PAVE	38	12	0.0002	24	33	0.2672
C-WASH-DV	30	20	0.1573	None	None	N.A.
C-BAJADA-DV	40	10	<0.0001	None	None	N.A.
C-COBB	19	31	0.0897	None	None	N.A.
All sites	452	148	<0.0001	11	23	0.5676

bushes at C-COBB were predominantly hemispherical in shape (Table 2). At this site creosotebushes were sparsely distributed and soil water was augmented by run-off from the rock surfaces into the spaces where the shrubs were growing.

Litter movement dynamics.—A greater percentage of creosotebushes with hemispherical-shaped canopies accumulated litter than did conical-shaped shrubs (Table 2). Threshold wind velocities required to entrain the litter components of creosotebush in an air stream and transport that litter to another location were calculated based on mass-surface area relationships measured on 50 leaves, 50 stem segments and 50 fruits (Table 3). In the Jornada, wind velocities with the potential to move litter are common. For example, average daily wind velocities at approximately 2.25 m above ground level exceed 10 km h^{-1} on 150 days per year, and maximum daily wind velocities exceed 10 km h^{-1} on 302 days per year (data from the Jornada Long Term Ecological Research Program Weather Station). Of the nine sites at which we measured litter accumulation, four (C-GRAV-WASH, C-GRAV-RIDGE, C-SAND, and C-PAVE) had greater litter area under hemispherical crown plants vs. conical crown plants (Table 4).

TABLE 3.—Equations and calculation of entrainment threshold values for creosotebush litter based on mass-surface area relationships of 50 leaves, 50 fruits and 50 stem segments

Litter type	Equation	Threshold velocities
Leaves	$F_L = C_L (0.5 Y V^2 A_L)$	3.9 km h^{-1}
Fruits	$V^2 (9.97 \times 10^{-7}) - (W \times F_R)/r = 0$	6.12 km h^{-1}
Stem segments	$C_D (0.5 Y V^2 A_D) - (W \times F) = 0$	3.3 km h^{-1}

Where F_L = lifting force (kg), C_L = lifting coefficient (dimensionless), Y = air density (kg m^{-3}), V = wind velocity in m s^{-1} , A_L = lift projected area (m^2), W = average mass (kg), F_R = rolling resistance coefficient (dimensionless), r = radius (m), C_D = drag coefficient (dimensionless), A_D = drag projected area, W_L = average mass length $^{-1}$, and F = friction coefficient (dimensionless)

TABLE 4.—Accumulation of organic litter under conical vs. hemispherical shrubs. Due to the persistent skewness of some of the data the nonparametric Kolmogorov-Smirnoff (K-S) test was used in addition to one-way analysis of variance

Site	Mean area (cm ²) of litter under shrubs		ANOVA		K-S test P
	Conical	Hemispherical	F	P	
C-SAND	14	82	3.354	0.073	0.9029
C-GRAV-RIDGE	15	74	7.487	0.009	0.064
C-GRAV-WASH	0	65	0.101	0.752	0.746
C-RIDGE-RP	0	0	N.A.	N.A.	N.A.
C-WASH-RP	10.2	0	0.026	0.872	>0.999
C-RIDGE	0	0	N.A.	N.A.	N.A.
C-WASH	678	621	0.005	0.945	>0.999
C-EROD	0	0	N.A.	N.A.	N.A.
C-PAVE	150	461	2.294	0.137	>0.999
All sites	87	207	4.345	0.038	0.030

Soil nutrients.—Two patterns of soil nutrient accumulation related to the morphology of creosotebushes were found at the C-SAND site. The soils under canopies of hemispherical-shaped shrubs had significantly higher concentrations of organic carbon, organic matter and total nitrogen (Table 5). Electrical conductivity and cations were also higher in soils under hemispherical-shaped shrubs than in soils under inverted cone-shaped shrubs and intershrub soils (Table 5). However, there were no differences in concentrations of soil cations, soil carbon and soil organic matter in soils from below the canopy of cone-shaped shrubs and the soils of the intershrub spaces (Table 5).

Soil mounds.—Plants with hemispherical canopies were significantly more efficient than were conical plants at accumulating and/or retaining particulate matter, as seen by the greater mound height and litter accumulation under hemispherical plants (Table 6).

TABLE 5.—Comparisons of concentrations of nutrients in soils and soil characteristics from adjacent to the root crown (center) and at midcanopy (middle) of conical vs. hemispherical creosotebushes, and soils from shrub interspaces (outside). A t-test compared soil from (1) similar positions at conical vs. hemispherical crowned shrubs ($n = 5$, $* = P < 0.05$), and (2) soil from different positions under shrubs with the same crown morphology ($n = 5$, numbers in a row with different letters are significantly different at $P < 0.05$)

Soil characteristic	Conical crowns			Hemispherical crowns		
	Center	Middle	Outside	Center	Middle	Outside
Organic carbon (%)	0.58 ^a	0.49 ^a	0.43 ^a	0.79 ^{a,*}	0.64 ^{a,b}	0.48 ^b
Organic matter (%)	1.00 ^a	0.84 ^a	0.74 ^a	1.36 ^{a,*}	1.1 ^{a,b}	0.79 ^b
Total N (mg kg ⁻¹)	550.6 ^a	445.2 ^a	420.4 ^a	628.0 ^{a,b,*}	705.4 ^{a,*}	399.2 ^b
EC (mmhos cm ⁻¹)	0.52 ^a	0.37 ^a	0.30 ^a	0.70 ^{a,*}	0.98 ^{a,b,*}	0.30 ^b
P (mg kg ⁻¹)	11.0 ^a	11.3 ^a	9.74 ^a	14.6 ^{a,*}	17.1 ^{a,*}	8.0 ^b
K (mg kg ⁻¹)	22.4 ^a	19.4 ^a	10.8 ^a	37.0 ^{a,*}	38.8 ^{a,*}	9.4 ^b
Ca (meq l ⁻¹)	3.42 ^a	2.61 ^a	2.15 ^a	5.71 ^{a,*}	7.11 ^{a,*}	1.93 ^b
Mg (meq l ⁻¹)	0.70 ^a	0.54 ^a	0.45 ^a	1.11 ^{a,*}	1.58 ^{a,*}	0.44 ^b

TABLE 6.—Mean height of soil mounds, canopy area and litter area under conical (n = 12) or hemispherical (n = 13) shrubs. F value is for one-way ANOVA, df = 23, P < 0.05 in all cases

Plant characteristic	Crown shape		F
	Conical	Hemispherical	
Mound height (cm)	6.5	13.3	12.118
Canopy area (cm ²)	15,710	40,600	10.654
Litter area (cm ²)	1700	12,100	9.276

Spring ephemerals.—The spring-flowering annual plant communities differed greatly among sites (Table 7). However, at the Jornada sites there were few differences in densities and biomass of individual species (Table 7) that could be attributed to differences in soil properties. Soil under hemispherical shrubs supported a greater total biomass of spring-flowering ephemeral plants at the C-SAND site (ANOVA, P < 0.01) and at the C-SAND-IL and C-PAVE sites (ANOVA, P < 0.05). With the exception of the C-SAND-IL site, hemispherical-shaped plants had a greater diversity of spring-flowering ephemeral taxa, as indicated by Shannon's index of diversity (Shannon, 1948; Brower *et al.*, 1989; Table 7). At the C-COBB site in the Mojave, species richness was 4 under conical shrubs and 6 under hemispherical shrubs. The density of spring-flowering ephemerals was 83 plants m⁻² under conical shrubs and 128 plants m⁻² under hemispherical shrubs. Species richness (2) and density of spring annuals (22 plants m⁻²) was lowest in the intershrub spaces at this site. A characteristic of this site was the large number of shrubs, 17% of the total compared to 0–3% at the other sites, where rodents had made burrows under shrubs with hemispherical canopies. Under these shrubs species richness (6.7) and density of spring annuals (210 plants m⁻²) were highest. With the exception of the C-SAND-IL site, species richness and diversity

TABLE 7.—Mean density of common ephemeral taxa under conical (C) vs. hemispherical (H) shrubs. Also shown are descriptors of the entire ephemeral community under the two shrub shapes at the four sites

Species	Density of annuals under shrubs (plants m ⁻² shrub ⁻¹)							
	C-SAND		C-SAND-IL		C-SAND-G		C-PAVE	
	C	H	C	H	C	H	C	H
<i>Chaenactis stevioides</i>	0	0	0	0	3.8	3.2	0	0
<i>Cryptantha micrantha</i>	14.4	14.7	0.4	0.2	0.2	0.4	0	0
<i>Descurainaea pinnata</i>	9.9	73.3	27.2	25.8	0	0	6.0	6.4
<i>Eriogonum abertianum</i>	0.3	2.1	0	5.4	3.6	6.8	0	0
<i>Eriastrum diffusum</i>	134.1	179.2	1.2	3.8	48.0	39.6	0.2	0
<i>Eriogonum rotundifolium</i>	0.3	0	18.6	17.4	0	0	0	0.2
<i>E. trichopes</i>	0	1.1	33.4	36.8	0.2	0	0	0
<i>Lesquerella gordonii</i>	0	0	0	0	24.8	31.4	0	0
<i>Lepidium lasiocarpum</i>	3.7	9.6	0	0	8.0	5.6	0	0
<i>Lupinus brevicaulis</i>	0	0	0	0	4.2	3.4	0	0
<i>Phacelia coerulea</i>	0	0	0.8	2.4	0	0	15.0	19.4
Species richness (S)	9	10	15	14	9	13	7	9
Total biomass (g)	31.6	54.3	70.4	78.6	99.2	94.1	22.7	28.8
Diversity index (H')	16.7	18.2	26.3	22.5	13.0	25.5	8.8	16.1

were lower under the canopies of conical-shaped shrubs than under hemispherical-shaped shrubs. Differences in densities of annuals were greatest at the C-SAND site (Table 7).

DISCUSSION

Variability in the proportions of conical- and hemispherical-shaped shrubs in a landscape is a function of the topography of the landscape and of the size, density and spatial distribution of the shrubs. These variables together with soil type determine the run-off characteristics of a site and the effectiveness of wind redistribution of soil particles and litter fragments. Studies have shown that creosotebush growth is initially dependent upon water and subsequently limited by nitrogen availability (Lajtha and Schlesinger, 1986; Fisher *et al.*, 1988; Lajtha and Whitford, 1989). In creosotebush there may be trade-offs, reflected in the morphology of the shrubs, between increasing deep water stores that the shrubs can tap when ambient temperatures are suitable for growth and accumulating sufficient soil organic matter associated nitrogen to support high growth rates.

Our data show that soils under conical-shaped shrubs have concentrations of organic carbon, nitrogen, and the essential ions of P, K, Ca and Mg that are the same as soils in the intershrub spaces. The absence of soil nutrient differences in intershrub spaces suggests that soil nutrients at the C-SAND site are distributed homogeneously except in the immediate vicinity of shrubs (Table 5). This suggests that even though litter may not have been present under all hemispherical-crowned shrubs at the time of measurement (Table 2), there is a greater overall accumulation of nutrients under shrubs of this canopy type at the C-SAND site. Soils under hemispherical-shaped shrubs have significantly greater nutrient concentrations than have soils under conical-shaped shrubs or soils in intershrub spaces. Much of the spatial heterogeneity of soils at a sandy creosotebush-dominated site may therefore be due to the spatial distribution of the two shrub morphotypes, in particular to increased litter and soil accumulation under the hemispherical shrubs. Litter transportation and deposition by fluvial processes are harder to predict and are little affected by the shape of shrub canopies. Thus the absence of litter accumulation, even under the large number of hemispherical plants at the severely water-eroded C-EROD site (Table 2), was probably due to fluvial transport of litter during a recent overland flow event.

In the northern Chihuahuan Desert, creosotebush has spread from the well-drained ridges down the piedmont slopes and on to the flat plains in some locations (Buffington and Herbel, 1965). Creosotebush-dominated ecosystems began to establish in these areas sometime between the 1880s and early 1900s. The age distribution and encroachment of creosotebush into new areas undoubtedly affects the distribution of morphotypes and the development of fertile islands under shrub canopies. The growth of young shrubs with smaller and shallower root systems is water-limited, making the conical crown morphology which enhances water redirection into the rhizosphere (Martinez-Meza and Whitford, *in press*) important for survival and growth. As these plants grow and access more reliable sources of water from distant (deeper) sources, their continued growth becomes nutrient-limited. Our data show that the hemispherical crown morphology enhances litter accumulation and the development of fertile islands under the shrub canopy. Since hemispherical shrubs would continue to generate significant amounts of stemflow water via their inner, more vertical stems, the major role of the outer stems appears to be the trapping of organic litter, thereby reducing nutrient (nitrogen) limitation of growth.

In many desert ecosystems, islands of fertility develop under shrubs because of litter accumulation and nutrient enrichment of below canopy soils by stemflow and throughfall (Garcia Moya and McKell, 1970; Charley and West, 1975; Parker *et al.*, 1982; Virginia and Jarrell, 1983). The morphology of shrub canopies obviously affects the strength of the

islands of fertility effect. Wind velocities near the ground will be substantially less due not only to initial velocities but also to the effects of the density, shape and size of surrounding vegetation (e.g., Vogel, 1981). However, the frequency at which high wind velocity occurs is an indication of the importance of wind in redistributing plant litter in this desert ecosystem. High winds are common in the Jornada Basin, particularly during spring. When threshold wind velocities and airflow patterns around plant canopies are taken into consideration, and if other vegetation in the vicinity has only minimal effect on wind velocity and turbulence, there should be little or no litter accumulation under shrubs with conical crowns. While other factors, such as the role of soil organisms in burying litter or cementing litter to the soil surface have not been taken into account here, most of these factors should act equally at both shrub types. For much of the year wind velocity should be great enough to move leaf, fruit and stem litter away from under conical crowns. However, while aeolian processes may dominate in many arid ecosystems, in others such as the ephemeral streams (washes), fluvial processes may confound the interpretation of litter accumulation processes. Fluvial processes were important at three sites (C-WASH, C-WASH-RP and C-EROD), and this may explain the divergence from predicted patterns of litter accumulation. In this context, knowledge of the time and intensity of water flow in washes with respect to sampling time is essential.

The data presented here on creosotebush morphology support the prediction that shrubs growing in sites assumed to be highly water-limited such as well-drained piedmont slopes or ridges should have large exterior stem angles. This would maximize rainfall stem flow and deep water storage (Martinez-Meza and Whitford, *in press*). Shrubs growing in areas where run-off water accumulates or in deep sandy soils where infiltration rates are high were hypothesized to have a more hemispherical shape that will enhance soil and litter accumulation under the canopy. These predictions were largely supported by our data with a few notable exceptions. In the arid Mojave Desert, volcanic cobble site (C-COBB), most of the creosotebushes were hemispherical. At this site much of the precipitation is probably not lost through surface run-off. Instead, water drains from the surface rock layer into the soil under the rocks where it is stored and available for use by plants. Creosotebush genotypic ploidy level is $4n$ in the Mojave Desert and $2n$ in the Chihuahuan Desert (Hunziker *et al.*, 1977), and there may be a genotypically determined propensity for hemispherical-shaped canopies. However, also in the Mojave, the C-BAJADA-DV site had a significantly greater number of conical plants (Table 2), suggesting that creosotebush genotypic ploidy does not change the canopy shape development response to environmental conditions.

Desert annual plants respond to both water and nitrogen (Gutierrez and Whitford, 1987). Since the morphology of a shrub affects both the redistribution of precipitation and the concentrations of soil nutrients, we predicted large differences in species composition, density and biomass of annual plants under the two shrub types. The data did not support this prediction. While there were consistent patterns in species richness and diversity at most sites (reduced under conical-shaped shrubs), at one site (C-SAND-IL) this was reversed. This is the only site at the base of an alluvial fan. The soils there were deep sandy loams (Bullock and Neher, 1988). At this site, because of the dense stands of shrubs, wind redistribution of litter and soil particles is probably only a minor factor in the variability of soils associated with shrubs of different shaped canopies. *Descurainaea pinnata*, a winter annual that occurred at high densities under hemispherical shrubs at the C-SAND site, achieves highest density and biomass in sites with high soil nitrogen and its absence or low density at other sites suggests that soil N accumulations are lower at those sites (Gutierrez and Whitford, 1987). In the Jornada Basin it is not unusual to find clumps of 3–10 creosotebushes with overlapping canopies and/or with grasses and other perennials within the

clump. Such clumps reduce wind velocity at the soil surface at the base of adjacent shrubs. Shrub clumps also act to obstruct overland flow of water. At sites with numerous clumps, the effects of morphology on litter accumulation and soil fertility may be greatly modified and reduced.

One of our sites, C-RIDGE-RP was plowed in 1972 and 1973. The plowing eliminated all shrubs from this site. Shrubs present at this site in 1994 had established in the previous two decades. All of the shrubs encountered at this site had exterior stem angles greater than 45°. This supports the hypothesis that newly established shrubs should have a morphology that enhances water capture and storage. Development of a more hemispherical shape should occur after a shrub is well established and has access to sufficient water in the deep soil profile to support growth during periods of favorable temperatures. Temporal variables and spatial variables undoubtedly affect the composition of the annual plant communities that develop under the canopies of creosotebush and modify the effects of the morphology of the shrubs. Shrub morphology is obviously an important variable affecting the composition, density and biomass of the subcanopy annual plant community. Considering the effects of morphology on litter accumulation patterns, water redistribution patterns, and soil nutrient patterns, it is clear that the morphology of creosotebush must be considered when assessing the heterogeneity of these ecosystems.

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