Morphological Variation in Creosotebush, *Larrea tridentata*: Effects on Ecosystem Properties

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Abstract—Morphological characteristics of creosotebush canopies (angle of exterior stems), size of litter layer and sub-canopy soil chemistry were measured on several sites on the Jornada Experimental Range. Soils under canopies of inverted cone shaped shrubs had little or no litter layer and significantly lower total soil nitrogen and soil carbon than soils under canopies of hemispherically shaped shrubs. In Death Valley, creosotebushes growing in braided washes were predominately hemispherical in shape and those growing on a dry bajada were predominately inverted cone shaped. The morphological characteristics of creosotebushes appear to vary with soil type and with mean annual rainfall. The proportional distribution of different morphotypes of creosotebush affects the heterogeneity of creosotebush dominated ecosystems.

Creosotebush, *Larrea tridentata*, is the most widely distributed and most abundant shrub in the hot deserts of North America (Shreve 1942; Mabry and others 1977). *L. tridentata* is a small leafed, C3, evergreen shrub that dominates many desert ecosystems and determines the characteristics of those ecosystems. Several studies have focused on the physiological characteristics of this plant that contribute to its success (Lajtha and Whitford 1989; Fisher and others 1988; Oechel and others 1972).

Morphological characteristics of creosotebush have received less attention. The orientation of the branches of *L. tridentata* maximizes light interception in the early morning when moderate temperatures allow maximum photosynthesis (Neufeld and others 1988). The variation in canopy structure and foliage characteristics has been shown to affect the abundance and structure of the arthropod community living on the shrubs (Lightfoot and Whitford 1989).

Physiological studies have demonstrated that *L. tridentata* is limited both by water and by nutrients, especially nitrogen (Fisher and others 1988). Water availability is generally the most important factor limiting growth in arid ecosystems. The growth of an evergreen C3 shrub like *L. tridentata* is dependent upon water that is available for growth at the beginning of the growing season when temperatures are suitable for a plant with C3 physiology. In a summer rainfall desert such as the Chihuahuan Desert, winter and spring are frequently very dry. The early season growth of *L. tridentata* is therefore dependent upon water stored deep in the soil profile during the previous wet season. Stemflow and root channelization are potentially the primary source of that water (Martinez-Meza and Whitford 1995). These studies showed that stem angle was a significant factor in stemflow generation in *L. tridentata*. We hypothesized that creosotebushes growing in sites where rainfall is limited or on sites where most rainfall runs off would be characterized by an inverted cone canopy morphology.

In the northern Chihuahuan Desert, annual rainfall is between 200 mm and 250 mm with 60% of that rainfall as summer convectional storms. In this desert creosotebush morphology should be a compromise between optimization of water channelization to the root systems via stemflow and a canopy shape that enhances litter deposition under the canopy. In the driest part of the range, virtually all of the creosotebush should have conical shapes that optimize stem flow. Death Valley, at the northern edge of the Mojave Desert, is the driest area within the range of *L. tridentata* (average annual rainfall <50 mm). We hypothesized that a larger proportion of *L. tridentata* in Death Valley would have exterior stem angles greater than 45° than creosotebushes from habitats in the northern Chihuahuan Desert.

Nitrogen content, mineralization and nitrogen availability varies with the organic matter content of the soil and is related to the litter layer (Fisher and others 1990). The under shrub nutrient patches are characterized by horizontal and vertical gradients that are greatest under the shrub canopy near the stem and that decrease toward inter-shrub spaces (West and Klemmedson 1978; Crawford and Gosz 1982; Whitford 1986). In desert soils, nutrient concentrations, especially nitrogen, are correlated with soil organic matter content (Skujins 1981; Whitford and others 1987). The decomposition of organic litter accumulated under creosotebushes increases the nitrogen content of the undershrub soil as suggested by Parker and others (1982). Two factors affect the size of the litter accumulation layer under shrub canopies: (1) size of shrub and (2) the morphology of the shrub. Size and shape affect litter accumulation by affecting the wind turbulences that develop over and around canopies (Reichman 1984). In a landscape with scattered small shrubs, turbulence and the circular movement of dust and debris (eddy currents) result in fine particulate deposition under shrubs in addition to the deposition of dead

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leaves and other organic debris. The effectiveness of this deposition should be a function of shrub morphology. We hypothesize that hemispherically shaped creosotebushes should accumulate larger litter layers than those with a more conical shape.

Materials and Methods

Exterior branch stem angles were measured at three creosotebush sites on a piedmont slope on the Jornada Long Term Ecological Research Site 40 Km NNE of Las Cruces, NM. The caliche site is an erosional surface where more than 90 percent of soil surface has accumulations of calcium carbonate-coarse fragments in a discontinuous layer. The slope gradient is >4%, and creosotebush plants are mostly small with a sparse canopy. The sand site is a middle piedmont-slope with a 3-4% gradient. The surface layer of soil is an alluvial mantle composed primarily of sandy and pebbly or gravelly sediments. Most creosotebush plants grow in clumps of 4-5 shrubs. The gravel site is on a lower piedmont slope with a gradient <3% and soil texture of sandy loam. The creosotebushes form a stand with few clumps.

Measurements of stem-angle were also made at two sites in Death Valley, California, one at the base of the valley in an area of braided washes, and the other on a bajada at 1200 m elevation on the east side of the valley, 10 km from Furnace Creek, CA.

At the Jornada, three 50 m transects were randomly located at each site. All plants along transects were divided into one of two groups, those with all stem-angles greater than 45° and those with most (90%) of stem-angles less than 45°. The selection of 45° as a separation was based on the data on stemflow in Martinez-Meza and Whitford (1995). The average number of plants falling into these two groups were transformed into percentages and compared.

Stem-angles from the horizontal were measured with an inclinometer (1 square meter frame). This frame constructed with PVC was subdivided by placing several inclined strings crossing from one side to the right angle corner opposite that side. The strings were placed at angles of 75, 60, 45, 30, and 15 degrees. An estimate of exterior stem-angles of plants was obtained by placing the frame vertically on the ground and moving it around the plant to align stems with strings angles on the frame (Martinez-Meza and Whitford, 1985).

The stem-angles of plants sampled at two sites in Death Valley, California, were estimated by calculating stem-angles of exterior branches using the following:

$$\text{stem-angle} = \text{arctangent}\,\frac{d1}{d2}$$

where: d1 = Vertical distance from the top exterior edge of the branch to the soil surface.

d2 = Horizontal distance from the base of the trunk to the point where it intersects the line of vertical distance.

Litter area under the canopy of each shrub at the Jornada site was from two diameters through the center of the soil surface area covered with litter. To estimate the nitrogen concentrations both under shrub canopies and in the intershrub spaces, soil samples were collected from under mid-canopy and at the midpoint between the canopies of adjacent shrubs. These soil samples were placed in plastic bags and sent to the New Mexico State University Soil and Water Testing Laboratory for total N measurement.

Results and Discussion

The variability in morphology of *L. tridentata* in various topographic locations and soil types may be related to the importance of stemflow water to the shrub in any particular site. The highest percentage of *L. tridentata* plants with stem-angles greater than 45° was at the sand site, with the lowest percentage at the caliche site (fig. 1). Plants growing on the sand site were mostly large and well developed, whereas those growing on the caliche site usually were small and poorly developed. These results suggest the influence of characteristics of each site, such as slope and soil texture, on shrub morphology and distribution, which in turn affects the distribution of resources, for example, water and nutrient supplies.

The steeper slope gradient and a high accumulation of calcium carbonate-coarse fragments which may contribute to high erosional runoff at the caliche site, may explain the presence of the highest percentage of poorly developed plants with stem-angles less than 45° in that site. Creosotebushes at this site are characterized by shallow, lateral root systems (Brisson and Reynolds 1994). In contrast, the favorable conditions of topography and surface soil texture on the sand site results in creosotebushes with deep root systems (Virginia and others 1989). There is a wide size distribution of plants at this site and evidence that creosotebush has only recently established (unpublished data). The sand site is dominated by plants with stem-angles greater than 45°.

In Death Valley at the braided wash site, ten of the largest shrubs were adjacent to channels in the stream bed that exhibited evidence of recent flows. Those plants all had stem angels less than 35°. The average stem angle of the smallest shrubs (canopy radius <25 cm) was 59°. On the bajada site in Death Valley, there were no shrubs with stem angles <23°

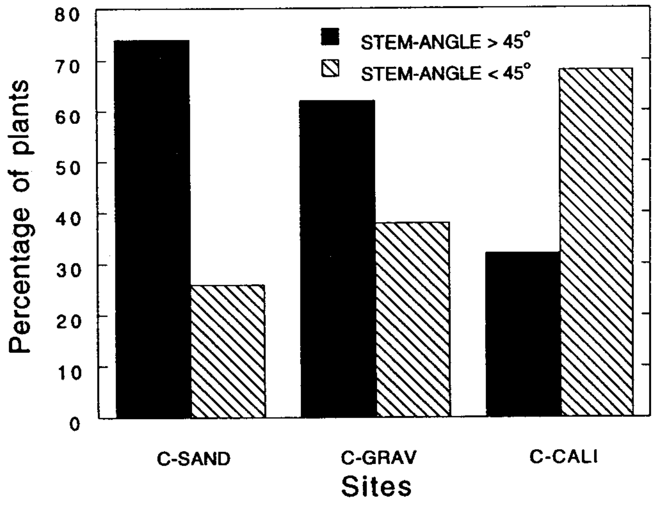

Figure 1—Percentage of *Larrea tridentata* plants with all stem angles greater than 45° and plants with exterior stem angles less than 45° at three sites in the Jornada Basin, New Mexico.

(table 1). A larger proportion of the shrubs in the Death Valley sites had exterior stem angles >45° than the creosotebushes from the Jornada sites in the Chihuahuan Desert (table 1).

The distribution of stem angles in *L. tridentata* appears to be related to the predominant limiting factor for the shrubs in a given location or to soil limitation of root depth. Obviously *L. tridentata* shrubs growing at the edge of active wash channels have access to more water (transmission loss water stored in stream bed sediments) than plants growing at a distance from a run-off channel. For shrubs with access to stream bed sediments, enhanced stem flow is less critical for growth than is availability of soil nutrients. Growth of *L. tridentata* that have adequate available water is rapidly limited by nitrogen availability (Fisher and others 1988). Plants with low stem angles trap and retain litter under the canopy which results in nutrient enhancement of soil beneath the canopy. Virtually all of the *L. tridentata* growing on the bajada in Death Valley had stem angles greater than 45°. Only 12% of the creosotebushes at this site had stem angles less than 45°.

These data suggest that the morphology of creosotebushes varies considerably among sites within a region and among regions. Creosotebushes growing in microsites with enhanced water (run-on sites and edges of arroyos) tend to be more hemispherical in shape. This facilitates retention and accumulation of litter and nutrient enrichment of soils under the canopy.

At sites where water is limited by climate and topography (Death Valley piedmont) or dry microsites (run off sites), creosotebushes tend to be conical in shape. This shape enhances stemflow which is channelized to the deep roots (Martinez-Meza and Whitford In Press). The distribution of morphologies of creosotebush within a region or site therefore probably reflects the spatial pattern of redistribution of water at that location.

The aerodynamics of shrubs of different shapes and the effect of those shapes on litter retention or litter deposition was examined by correlating air stream flow lines around a hemispherical object and a conical object (Blevins 1984). These object shapes approximate the shapes of *L. tridentata* shrubs with exterior stem angles > and <45°. For shrubs approximating a hemispherical shape, wind flows around and above the canopy causing small local turbulances (primarily under the canopy) and deposition on the downwind side of the canopy (fig. 2). This local turbulence may result in some mixing of litter but will not reduce the litter layer under the shrub. For shrubs of a conical shape, the wind flows around the base of the cone with no reduction in velocity or turbulence. Also some of the lateral flow has a down flow component which accelerates the wind speed at ground level (fig. 2).

Table 1—Morphological characteristics of *L. tridentata* from two sites in Death Valley, California.

	Braided wash 0 m elevation	Bajada 1230 m elevation
Average stem angle	48°	51°
Percent >45°	63%	88%
Percent >60°	33%	23.5%
Percent <23°	6%	0%

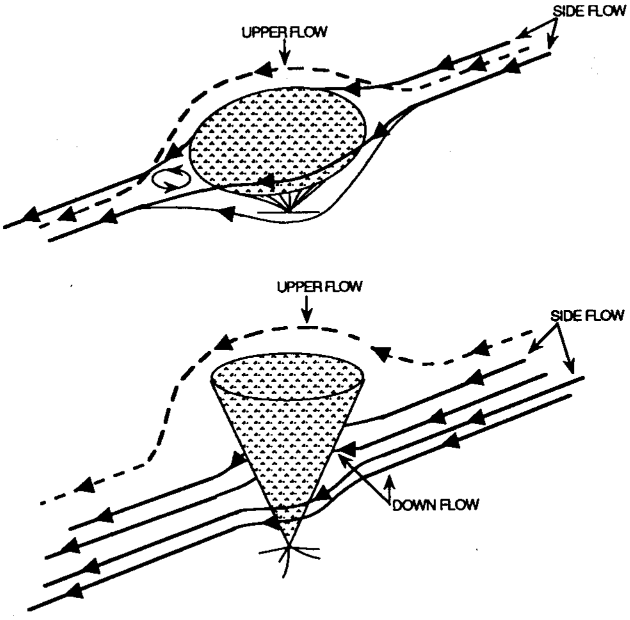

Figure 2—The movement of wind and development of eddy currents around shrubs with a hemispherical shape (top panel) and shrubs with a conical shape (bottom panel).

Threshold velocities required to entrain the litter components of *L. tridentata* 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. The threshold velocity for leaves was calculated using the aerodynamic equation:

$F_L = C_L (1/2\, Y V^2 A_L$, where:
$F_L =$ lifting force (kg),
$C_L =$ lifting coefficient (dimensionless),
$Y =$ air density (kg/m^3),
$V =$ wind velocity (m/s),
and $A_L =$ lift projected area (m^2).

The threshold velocity for rolling fruits was calculated from:

$V^2 (9.97 \times 10^{-7}) - (w \times f)/r = 0$, where:
$V =$ wind velocity (m/s),
$w =$ average mass,
$f =$ rolling resistance coefficient,
$r =$ radius (m).

The threshold velocity for stem segments was calculated from:

$C_D (1/2\, Y V^2 A_D) - (w \times f) = 0$, where:
C_D is the drag coefficient,
$Y =$ air density,
$V =$ wind velocity,
$A_D =$ drag projected area,
$w =$ average mass/length (kg/m)
$f =$ friction coefficient.

For leaves, the threshold velocity was calculated to be 3.9 km/h, for seed - 6.12 km/h and for a 25 mm length stem segment - 3.3 km/h. These low threshold velocities demonstrate that creosotebush litter can be moved on a large fraction of days in a year. Average daily wind velocities exceed 10 km/hr 150 days per year (unpublished data, Jornada Long Term Ecological Research Program).

The data on threshold wind velocities and on air streams and shrub shapes lead to the prediction that there will be little or no litter accumulation under shrubs with a conical shape if there is no other vegetation in the immediate vicinity that affects the turbulence and velocity of the wind.

The canopy characteristics of the *L. tridentata* shrubs of conical and hemispherical shapes under which litter accumulations differed in average canopy diameter and exterior stem angles. The conical shrubs had an average canopy diameter of 132 ± 24 cm, average height of 111 ± 20 cm and average exterior stem-angle of 59 ± 4°. The hemispherical shrubs had an average canopy diameter of 209 ± 47 cm, average height of 116 24 cm and average exterior stem angle of 24 ± 6°. The average area of litter accumulation under the conical shrubs was 126 ± 427 cm^2. Only 2 of the 20 shrubs with stem angles of 45° or larger had a measurable accumulation of litter. The average area of litter accumulation under the hemispherical shrubs was 16473 ± 8263 cm^2 with a range of 2971 –30481 cm^2. All of the hemispherical shrubs had measurable litter accumulations.

The difference in litter accumulations under shrubs that differed in exterior stem angles was reflected in the soil chemistry under the shrub canopy (table 2). The most obvious difference in soil nutrients was total nitrogen. Nitrogen may enter the system via rainfall or dry-fall that is subsequently washed into the soil via stemflow and throughfall and from the decomposition of dead leaves and other detritus that accumulates under the canopy of the shrub. The differences in soil nitrogen are probably the result of the differences in quantities of organic material available for decomposition and subsequent mineralization. Differences in concentrations of other nutrients were not as consistent. Elements like calcium enter the system as dust (dryfall) and are washed from the leaf surfaces via stemflow and throughfall. While most throughfall infiltrates into the soil, much of the rainfall that hits the intershrub space is lost in runoff. This probably accounts for most of the differences in table 2.

Considering the data presented herein, it is evident that the morphology of creosotebush based on exterior stem angles has important effects on the redistribution of rainfall (Martinez-Meza and Whitford 1995) and on the accumulation and retention of litter under the canopy. The accumulation and retention of litter plus the transport of adhering dust from the stems and leaves during rain events produces the "fertile islands" that have been described for desert shrubs. The relative abundance and spatial distribution of the morphotypes of creosotebush therefore affects the spatial heterogeneity of *Larrea tridentata* dominated ecosystems. The health of a shrubland ecosystem is in part determined by the ability of that system to retain and efficiently use scarce resources such as water and soil nutrients. The distribution of morphologies of the shrubs within an ecosystem provides information about the use and retention of critical resources within a site.

Table 2—Comparisons of concentrations of nutrients in soils from under mid-canopy of *Larrea tridentata* (creosotebush) shrubs with exterior stem angles >45° and exterior stem angles <45° and soils open, unvegetated, intershrub spaces. Numbers in a row followed by different letters are significantly different ($p < 0.05$).

	Exterior stem angles		
	<45°	>45°	Open
N_{total} ppm	571.1a	416.7b	350.8c
P ppm	10.4a	9.8a	8.5b
K ppm	46.6a	43.4a	26.2b
$C_{organic}$ %	0.5a	0.4b	0.3c
Mg meq/l	1.2a	1.0a	0.85b
Ca meq/l	5.5a	5.1a	3.0b

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