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Foliole movement and canopy architecture of *Larrea tridentata* (DC.) Cov. in Mexican deserts

Exequiel Ezcurra[1], Santiago Arizaga[1], Pedro Luis Valverde[2], Cristina Mourelle[1], and Arturo Flores-Martínez[1]

[1] Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70–275, 04510 – México, D.F., México
[2] Departamento de Biología, División CBS, Universidad Autónoma Metropolitana – Iztapalapa, Apartado Postal 55–535, 09340 – México, D.F., México

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Summary. The creosote bush *(Larrea tridentata)* is a common desert perennial with bifoliate, amphistomatic, divaricate leaves. The leaves can vertically close their folioles and vary their profile with respect to direct solar radiation. Field data from different Mexican deserts showed a significant correlation between foliole aperture and mean foliole inclination: in plants in which folioles were more open, the foliole surfaces were less vertical. In a series of field experiments in the Chihuahuan Desert, foliole aperture varied significantly with the water-status of the plant and the hour of the day. In moist plants, folioles opened in the early morning and closed in the afternoon. Water-stressed plants showed significantly lower foliole apertures. A simulation of the light interception patterns of the plants showed that foliole closure in water-stressed individuals reduces direct radiation interception by around 24%. Most (64%) of the reduction in interception was due to the vertical inclination of the photosynthetic surfaces induced by foliole closure in the water-stressed plants. The rest (36%) of the reduction in interception was due to differential self-shading between foliole pairs, which was higher in the closed folioles of the water-stressed plants, but operated more towards the early hours of the day.

Key words: *Larrea tridentata* – Mexico – Deserts – Canopy architecture – Foliole movement

Creosote bushes (*Larrea* spp., Zygophyllaceae) form one of the most characteristic genera of desert plants in the American Continent. In a previous paper (Ezcurra et al. 1991) it has been shown that leaf orientation is an important distinctive feature of the four South American *Larrea* species. In North America, the genus *Larrea* is represented by only one species, *L. tridentata,* which is morphologically similar to its South American ancestor, *L. divaricata* (Hunziker et al. 1972, 1977). Both these species present bifoliate, divaricate leaves with no azimuthal preference (Neufeld et al. 1988; Ezcurra et al. 1991). *L. tridentata,* however, shows planar leaf clusters with marked azimuthal orientation (Neufeld et al. 1988), a feature that is not observed in *L. divaricata* (Ezcurra et al. 1991). Additionally, both species present differences in habitat preferences. While *L. divaricata* grows in the less extreme deserts of South America, *L. tridentata* occupies extremely hot, dry deserts in Mexico or dry temperate deserts in the west-central United States (García et al. 1960; Barbour et al. 1974).

Two morphological characteristics seem to bear importance in the distribution of *L. tridentata.* Firstly, Neufeld et al. (1988) have shown that, although *L. tridentata* shows no azimuthal preference for the individual leaves, the leaf clusters do show azimuthal orientation (all *Larrea* species have opposite leaves produced along one single plane and the branches tend to be planar). Plants towards the north of its geographic distribution show southeast-facing leaf clusters, while towards the south of the distribution the leaf clusters show no preferential orientation. The orientation of leaf clusters seems to play a role in self-shading and protection against excessive radiation (Neufeld et al. 1988). Secondly, divaricate leaves can vertically close their folioles and regulate the amount of intercepted radiation (Fig. 1). This characteristic, first noted by Ashby (1932, see also Runyon 1934), has been neglected as an important feature of creosote bushes. In this paper we present observations from different Mexican deserts on the orientation of individual folioles and foliage clusters. We also present results from field experiments in which we evaluated (a) the amount of foliole movement present in creosote bushes, (b) how much of this movement is influenced by the water status of the plant, and (c) the influence of

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Correspondence to: E. Ezcurra

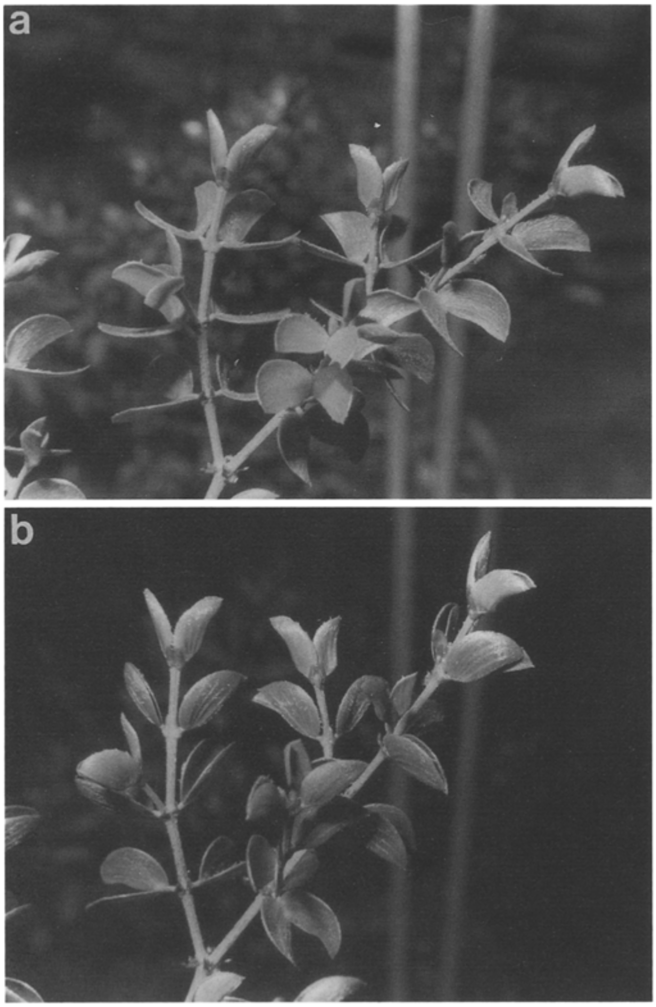

Fig. 1a, b. Foliole closure in *Larrea tridentata:* (**a**) a twig at 12.00, and (**b**) the same twig at 20.00. The younger leaves are more responsive than the older ones which move their folioles less

foliole movement on the interception of direct solar radiation.

Methods

Field observations

We studied *L. tridentata* in eight desert sites in Mexico (Fig. 2). In each site, two to three plants were selected and the inclination and azimuth of the folioles of 25 randomly selected leaves were measured. Additionally, the angular separation in the dihedron formed by the folioles was measured on another set of 20 randomly selected leaves. In some of the sites, the orientation (inclination and azimuth) of the plane formed by the broadest side of the foliage clusters was also measured, following the method described in Neufeld et al. (1988). To ensure that most of the variation was due to differences between plants and not induced by foliole movement along the day, all measurements were made between mid-morning to midday. The data were summarized using circular means and standard deviations (Batschelet 1981; Mardia 1972; we previously tested the independence between azimuths and inclinations). Differences between sets of angular values were tested through a X^2 analysis using log-linear models with the *G* statistic (McCullagh and Nelder 1983).

Field experiments

A series of field experiments were done at the Mapimí Biosphere Reserve in Durango, Mexico (26°41′N 103°45′W), in one of the most arid parts of the Mexican Chihuahuan Desert (Montaña 1988). Five experiments were performed, between May 15 and May 19, 1991, at the end of the dry season. The details of each experiment are described below (hour readings are given in local solar time).

Foliole aperture and water potential. On a loamy-gravelly pediment, 11 individuals of *L. tridentata* were sampled along a moisture gradient from the vicinity of a water reservoir to a distance of 50 m along the same contour line. Sampling was done on May 15, between 10.00 and 13.00. In each plant, water potential was measured with a PMS pressure chamber from a randomly selected twig, and foliole aperture was measured on 10 randomly selected leaves. The aperture angles were regressed against the water potential values.

Daily patterns of foliole aperture in relation to water potential. Six plants were chosen in the same gradient described above. Three of the plants (which will be referred to as the "moist" treatment) were 2–3 m from the edge of the reservoir and the other three (the "water-stressed" treatment) were 25–30 m away, along the same contour line. In May 16, every two hours from 5.00 to 19.00, plant water potential and foliole aperture in each of the plants was measured as described in the previous experiment, and total solar radiation was measured with a LICOR pyranometer.

Because the angle between folioles varied always between 0° and 100°, the difference between circular and conventional statistics was negligible. Thus, a nested analysis of variance was used to evaluate the effect of the variables under study (hour of the day, moisture treatment or plant water potential, and individual plants nested within treatments) on foliole aperture.

Foliole orientation and light interception. On the same plants of the previous experiment, the inclination and azimuth of the folioles of 10 randomly selected leaves were measured in May 17, every 3 h from 5.00 to 17.00. Total solar radiation was also measured at the same intervals. As in the case of the biogeographic field observations, the data were summarized using circular means and standard deviations, and the differences between angular values were tested through the *G* statistic.

A computer program was used to simulate the direct solar radiation intercepted by unshaded leaves in each treatment. The methodology is explained in detail in Ezcurra et al. (1991, the theory can be seen in Monteith and Unsworth 1990, and in Gates 1980). The simulation was done by feeding the program with different leaf-orientation data at each 3 h interval, as foliole orientation changes during the day. In the interval between two leaf measurements, the two simulations were linearly interpolated into one curve. This procedure estimated the direct radiation intercepted by the folioles if self-shading did not occur. A second simulation was done with a modified version of the program, in which, for each individual leaf, the shading of the sun-ward foliole onto the shaded one was calculated. For this purpose, foliole pairs were idealized as two triangles united along their bases. For each simulation time, each pair of folioles was projected onto a plane normal to the sun rays, and the shadow of one leaf-wing onto the other was computed as the overlap of both projections. This second analysis estimated the amount of radiation intercepted by the leaves when shading between foliole pairs is taken into account. By comparing the first simulation curves with the second ones, we estimated the amount of direct radiation that is avoided by the plants through self-shading between foliole pairs. The simulations were run for 26°41′N (the latitude of the Mapimí Reserve), and for the date of the experiment (May 17). Atmospheric transmittance was taken as 0.75, as this value gave the best fit between the radiation values predicted by the model (diffuse plus direct radiation) and the pyranometric values measured in the field (Fig. 5c). Solar declination for that day was 19°19′, and the solar elevation at noon was 82°38′.

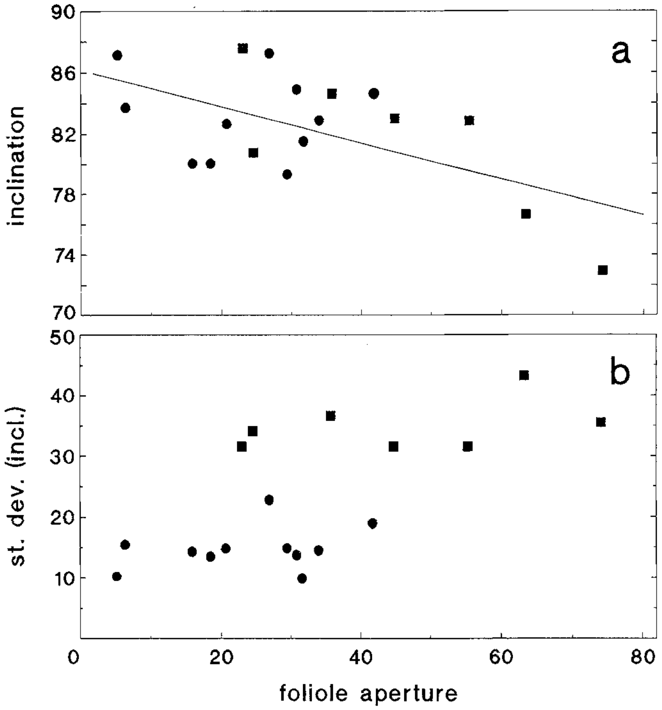

Fig. 3. (**a**) Correlation between mean foliole aperture and mean foliole inclination for 18 plants measured on the sites described in Fig. 2. ($r=0.59$, $P<0.01$). (**b**) Relationship between mean foliole aperture and circular standard deviation of foliole inclination for the same 18 plants. In both plots, plants from the Sonoran and Baja Californian coastal deserts are indicated by squares, and plants from the Chihuahuan, Querétaro and Hidalgan upland deserts are indicated by circles. Although there is a significant correlation between standard deviation and aperture ($r=0.67$, $P<0.01$), this correlation disappears when each data set is analyzed separately for each desert

Foliole aperture in response to artificial watering. On a loamy-clay bajada, 3 km below the pediment where the previous experiments were done, five individual creosote bushes were chosen within a radius of 50 m. The criteria for choosing each plant were (a) isolation to allow the individual watering of the plant, and (b) the existence of a neighbor in the vicinity (< 15 m) in similar conditions of isolation to use as a paired control. In the morning of May 15, each plant was given 0.6 m^3 of water, applied within a circle of 2.52 m radius (equivalent to 30 mm of rainfall).

Sampling was done 3 days later, on May 18. Every three hours, from 5.00 to 17.00, plant water potential and foliole aperture in each of the five watered plants and the five controls was measured as described in the previous experiments. An analysis of variance was

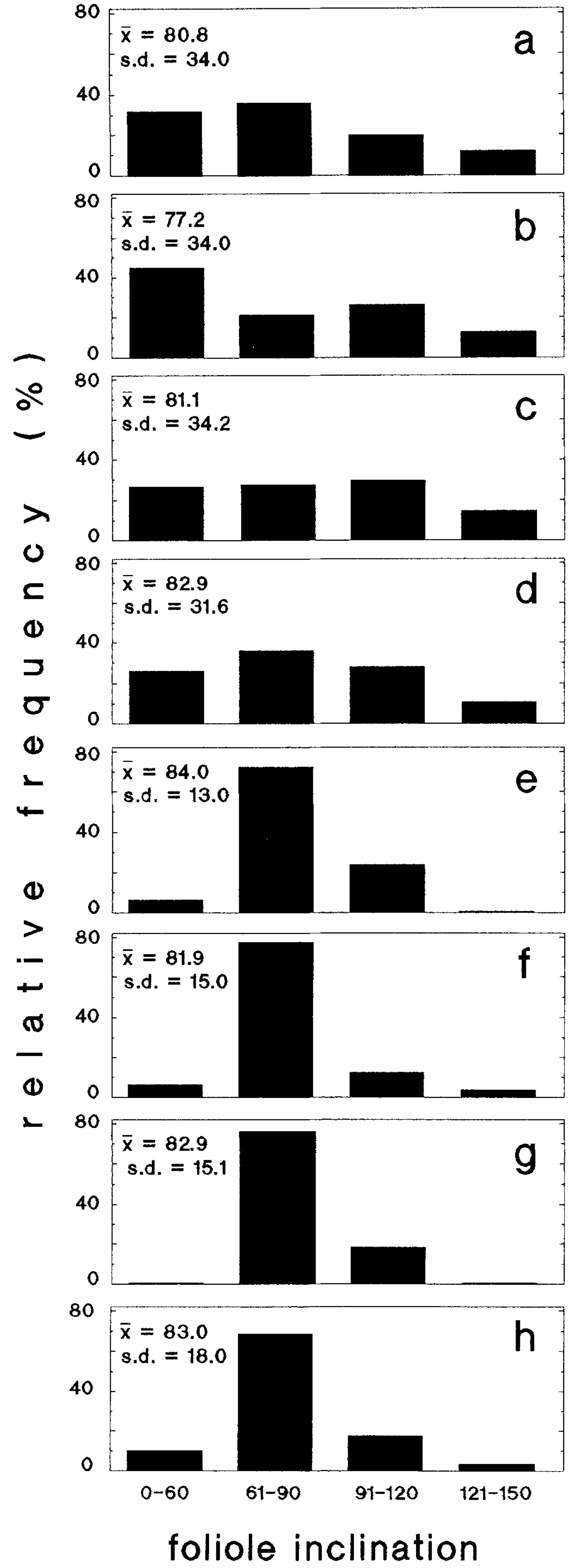

Fig. 2a–h. Frequency distribution of foliole inclinations for 18 plants in 8 sites arranged in latitudinal order from North to South. In each plant, the inclination of the folioles of 25 randomly selected leaves was measured, totaling 50 folioles per plant. The location, dates and sample size for the sites are as follows: (**a**) Pinacate (Sonoran Desert, 32°01′N 113°31′W, 3/30/89, 2 plants). (**b**) Gran Desierto (Sonoran Desert, 31°44′N 113°50′W, 3/23/89, 2 plants). (**c**) Quitovac (Sonoran Desert, 31°19′N 112°36′W, 3/31/89, 2 plants). (**d**) Vizcaíno (Baja California Desert, 27°33′N 113°12′W, 3/28/89, 2 plants). (**e**) Mapimí-Dunes (Chihuahuan Desert, 26°52′N 103°44′W, 1/29/89, 2 plants). (**f**) Mapimí-Bajada (Chihuahuan Desert, 26°41′N 103°45′W, 1/28/89, 2 plants). (**g**) Peña Blanca (Querétaro Desert, 21°02′N 99°49′W, 11/18/88, 3 plants). (**h**) Ixmiquilpan (Hidalgan Desert, 20°31′N 99°09′W, 1/21/89, 3 plants)

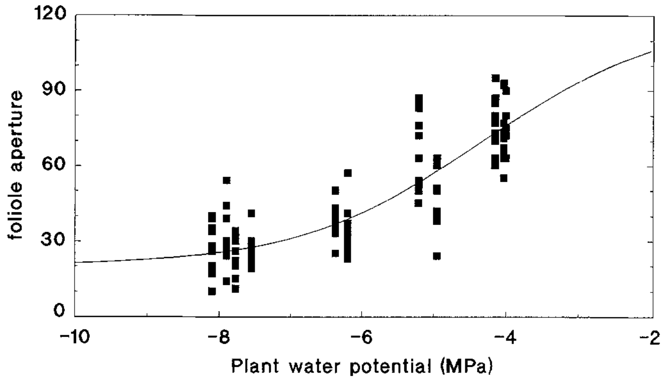

Fig. 4. Relationship between plant water potential and foliole aperture at midday in the Mapimí Reserve. A logistic regression model was used to impose a maximum and a minimum asymptote on foliole aperture. The values for maximum and minimum aperture were obtained, respectively, from well-watered greenhouse plants (mean foliole aperture 120°) and from plants in a nearby bajada, with water potentials below − 10 MPa (mean foliole aperture 15°)

used to evaluate the effects on foliole aperture of the hour of the day, the watering treatment, and the fixed differences between individual plants nested within the watering treatment.

Foliage orientation and self-shading. An optical grid was projected onto 11 plants from five different azimuths: E, SE, S, SW and W. This was done by viewing each plant from a fixed sighting device through a 1.2 cm × 1.2 cm wire-mesh, located 1.6 m away from the plant, and elevated 30° above the horizontal with respect to the center of the plant canopy. The projected grid defined a reticulum of aprox. 3 cm by 3 cm on the canopy. Twenty squares of the grid, in two rows of ten and separated one square from each other, were selected. The percentage of the area covered by leaves was visually estimated within each square for each of the five orientations in each plant. The values were arcsine transformed (to improve normality), and the variances of the foliage densities were compared using Bartlett's test (Sokal and Rohlf 1969). Pairwise multiple comparisons between variances of different orientations were done with F tests. Differences in foliage density between orientations were evaluated by means of a Kruskal-Wallis rank test (Hollander and Wolfe 1973). The variance/mean^2 ratio, an index of foliage clumping (Greig-Smith 1983), was calculated for each orientation. Additionally, the inclination and azimuth of the foliage clusters was also measured in eight randomly selected branches from five plants (40 branches in total). The data were classified into azimuthal categories.

Results

Field observations

At all eight sites, the individual leaves were uniformly distributed in all azimuthal directions. Foliole inclination, however, varied significantly among sites ($G = 49.8$, d.f. $= 21$, $P < 0.001$). In some sites the folioles were more uniformly vertical (Fig. 2e–h), while in others they were more variable in their inclinations (Fig. 2a–d). No significant association was found between foliole azimuth and inclination.

Foliole aperture varied significantly ($P < 0.01$) between sites and between individual plants nested within sites. Significant correlations were found between foliole

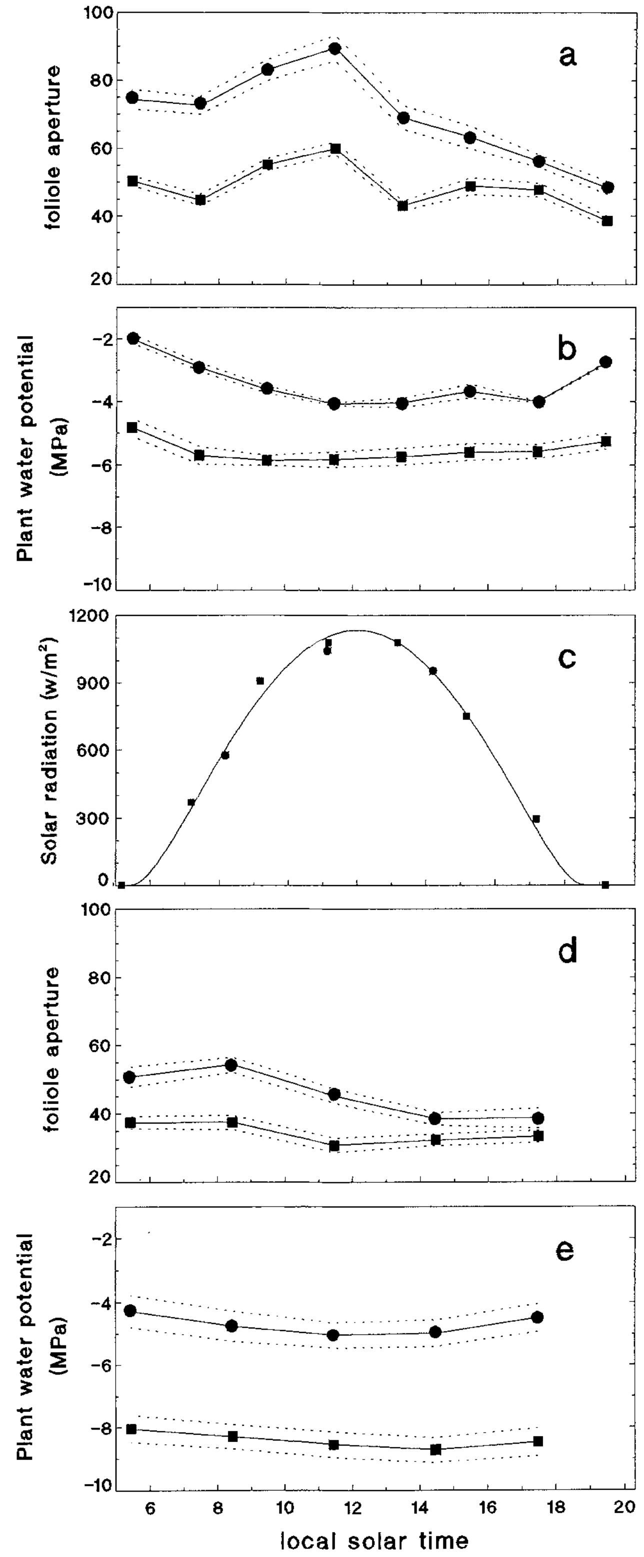

Fig. 5. (**a**) Daily variation in foliole angles for leaves of *Larrea tridentata* in the field. (**b**) Daily variation in water potential for plants of *L. tridentata* in the field. In both cases, the curves for plants growing in moist soil are shown by circles, and those for water-stressed plants by squares; standard errors are shown by dotted lines. (**c**) Daily radiation pattern measured on May 16 *(squares)* and May 17 *(circles)*. The curve shows the values calculated by the simulation model. (**d**) Daily variation in foliole angles in experimentally watered (circles) and non-watered plants *(squares)*. (**e**) Daily variation in water potential in watered and non-watered plants

Table 1. Inclination and azimuth of foliage clusters of *L. tridentata* in different Mexican deserts (n = number of foliage clusters sampled; the location of each site is given in Fig. 2). The Peña Blanca plants, which are within the tropics, showed no significant azimuthal preference in their leaf clusters

Site	n	Incl. (±SD)	Azim. (±SD)
Pinacate	20	52.1 (±13.4)	146.0 (± 34.8)
Quitovac	39	44.9 (±13.9)	169.5 (± 24.4)
Vizcaíno	25	50.2 (±12.8)	175.8 (± 33.0)
Mapimí	31	42.0 (± 7.3)	157.4 (± 31.1)
Peña Blanca	38	52.0 (±10.5)	38.5 (±118.3)

aperture and inclination (Fig. 3a), and between foliole aperture and the standard deviation of foliole inclination (Fig. 3b), but this second correlation disappeared when the plants from the two deserts were considered separately. That is, in plants in which folioles were more open, the leaf surfaces were less vertical. The plants with more open folioles and with high variability in foliole inclination were located in the Sonoran and Baja California coastal deserts (Fig. 2a–d), while the plants with more closed and uniformly vertical folioles were located in the Chihuahuan, Querétaro and Hidalgan upland deserts (Fig. 2e–h).

Finally, significant azimuthal preferences were found for leaf clusters (Table 1). As reported by Neufeld et al. (1988), we found a biogeographic gradient, with plants in the more northern deserts showing southeast orientations, and plants in the southern, tropical deserts showing no azimuthal preference.

Field experiments

Foliole aperture and water potential. A significant relationship was found between foliole aperture at midday and the water potentials of the plants ($R^2 = 0.74$, $P < 0.001$, Fig. 4). The lower the water potential, the more closed the folioles remained during the day.

Daily patterns of foliole aperture in relation to water potential. A significant relationship was found between foliole aperture and both the hour of the day ($F_{(7,460)} = 35.6$, $P < 0.0001$) and the moisture treatment ($F_{(1,4)} = 18.3$, $P = 0.01$). A significant relationship was also found between foliole aperture and water potentials ($F_{(1,454)}) = 280.9$, $P < 0.0001$). The folioles from the moister plants were significantly more open than those from the drier plants. Folioles were already well open at sunrise, and the angles between them kept increasing until noon (Fig. 5a). After 12.00, the folioles started to close, and kept reducing their aperture until sunset. A significant ($F_{(4,7)} = 6.8$, $P = 0.02$) interaction was found between hour and moisture, water-stressed plants were less responsive in time. Finally, significant differences were found between individual plants ($F_{(4,460)} = 17.9$, $P < 0.0001$), although these were quantitatively less important than the variation associated with moisture and hour of the day. This indicates that there are individual differences in the response to moisture: at the same hour, given similar water potentials, some plants will show higher foliole apertures than others.

Plants from the moist treatment showed significantly higher water potentials than plants from the dry treatment ($F_{(1,28)} = 1148.4$, $P < 0.0001$), and a significantly higher variability in their daily patterns ($F_{(7,28)} = 7.9$; $P < 0.0001$), a fact that indicates that their stomatal activity is higher than in waterstressed creosote bushes (Fig. 5b).

Foliole orientation and light interception. The plants from the moist treatment showed significant variation in foliole inclination during the day ($P < 0.001$). Their mean inclination was 53°40′ in the morning, but changed to a steeper inclination (62°05′) in the afternoon. The plants from the dry treatment, however, did not show a significant variation in inclination along the day, and their mean inclination (73°20′) was significantly higher than that of the moister plants ($P < 0.0001$). In both treatments the individual leaves were uniformly distributed in all azimuthal directions, and leaf inclination was independent of leaf azimuth. The distributions of foliole inclinations in the moister plants were significantly different ($P < 0.001$) from the inclinations found for the Sonoran Desert plants (Fig. 2a–d), both for the morning and the afternoon, and for the pooled data set.

The radiation pattern during both experiments (foliole aperture on May 16 and foliole orientation on May 17) was similar. The predictions of the model for an atmospheric transmittance value of 0.75 explained 99.3% of the measured variation in radiation (Fig. 5c). The simulation of direct solar radiation intercepted by unshaded leaves (Fig. 6a) showed that there is a trend for leaves of the moist treatment to maximize light interception in the morning. The interception curve for water-stressed plants did not show this shift towards the morning, but showed instead a midday decrease. The integral under the curve (i.e. the total radiation intercepted by unshaded leaves) yielded 18.4 MJ/m^2 for leaves from the moist treatment, and 15.8 MJ/m^2 for leaves from the dry plants (a 14% reduction). The differences between the light interception regime of the two treatments was more marked between 10.00 and 12.00, when the dry plants showed a 30% reduction.

The curves obtained in the simulation when self-shading between foliole pairs was taken into account showed a qualitatively similar trend as the first simulation, but lower interception values in general (Fig. 6b). These lower values were due to a considerable reduction in interception by the adaxial sides of the folioles, which were affected by self-shading. Also, the morning differences between treatments became more pronounced, as in the morning the folioles of the water-stressed individuals were more closed and hence more subject to self-shading. The integral under the curves yielded 16.7 MJ/m^2 for leaves from the moist treatment, and 12.8 MJ/m^2 for leaves from the dry plants (a 24% reduction induced by foliole closure and self-shading together).

Finally, by subtracting the curve for water-stressed plants from the curve for moist plants in Fig. 6b, a curve

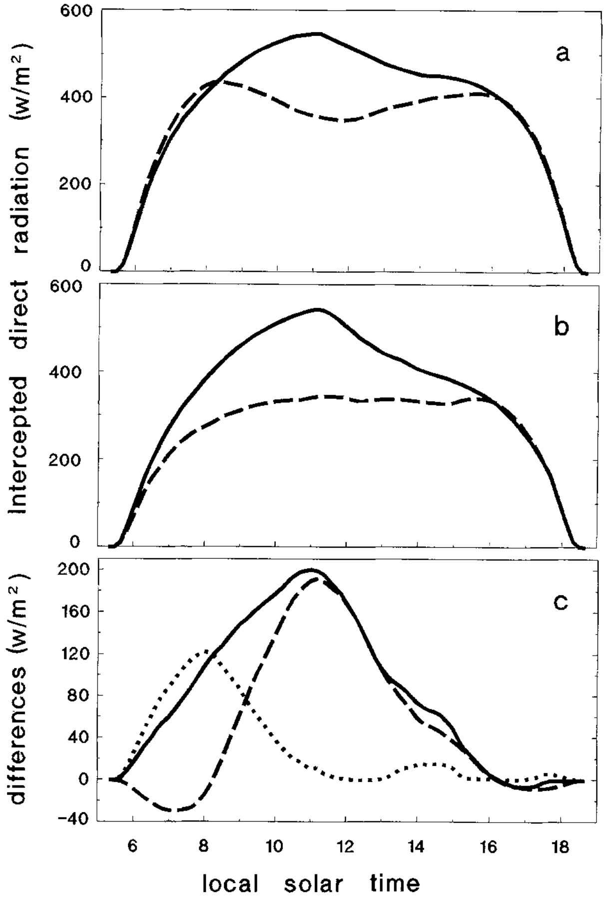

Fig. 6. (**a**) Computer simulation of direct solar radiation intercepted by unshaded folioles in moist and water-stressed plants. Moist plants are indicated by continuous lines, water-stressed plants by broken lines. (**b**) Simulation of direct radiation intercepted by folioles in moist and water-stressed plants when self-shading between foliole pairs is taken into account. Symbols as in **a**. (**c**) Differences in intercepted direct radiation between moist and water-stressed plants. Symbols are as follows: (———) total differences between both treatments; (– – – –) differences due to foliole inclination; (· · · · ·) differences due to self-shading

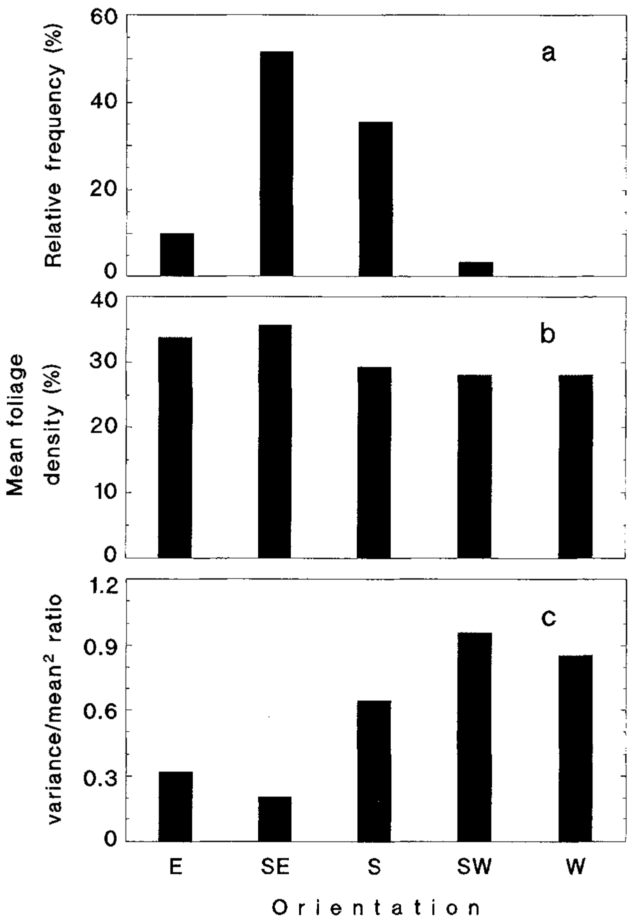

Fig. 7. (**a**) Azimuthal orientation of leaf clusters ($n = 31$ branches). No branches with N, NE or NW azimuths were found. (**b**) Mean relative foliage density when the canopy is viewed from different azimuths (the branches were not viewed from the N, NE or NW as the sun at the latitude of Mapimí never shows Northern azimuths). (**c**) Variance/mean² ratio as a measure a foliage clumping, when the canopy is viewed from different azimuths

indicating how much direct radiation is avoided by the water-stressed treatment was calculated (Fig. 6c). Likewise, from the curves in Fig. 6a we estimated how much direct radiation is avoided by the water-stressed treatment when foliole inclination alone is taken into account. The difference between both estimates yielded a third curve that evaluates how much direct radiation is avoided by the stressed plants due to their higher level of self-shading. Integrating the areas under these three curves, we estimated how much radiation is avoided in stressed plants by the two mechanisms: foliole inclination and self-shading. According to the model, at the end of the day the water-stressed plants intercepted 3.9 MJ/m² less than the moist plants; 64% (2.5 MJ/m²) of this reduction in intercepted radiation was due to differences in foliole inclination, and 36% (1.4 MJ/m²) was due to the higher level of self-shading in the water-stressed plants.

Foliole aperture in response to artificial watering. Three days after artificial watering, there was a significant difference in foliole aperture ($F_{(1,8)} = 12.9$, $P < 0.01$) and plant water potential ($F_{(1,8)} = 581.8$, $P < 0.0001$) between watered and non-watered plants (Fig. 5d, e). Watering increased water potential by ca. 2 MPa, and increased foliole aperture in the morning by approx. 15°. The differences in foliole aperture between treatments diminished and became non-significant after 14.00. Significant differences in the response of individual plants were also found in this experiment ($F_{(8,482)} = 6.0$, $P < 0.0001$).

Foliage orientation and self-shading. As with the biogeographic data, a significant preference was found for leaf clusters with a SE azimuth ($G = 34.9$, d.f. $= 4$, $P < 0.001$; Fig. 7a). Likewise, relative foliage density was significantly higher, and the variance of the foliage density was significantly lower (indicating a more regular spatial distribution) when the plants were viewed from the Southeast (Kruskal-Wallis' $H = 15.7$, d.f. $= 4$, $P < 0.01$ for foliage density, Fig. 7b; Bartlett's $B = 54.7$, d.f. $= 4$, $P < 0.001$ for foliage variances; the clumping indexes are shown in Fig. 7c). The SE orientation of the planar leaf clusters and the higher foliage density towards the SE indicate that self-shading and interference between leaves are minimum around mid-morning.

Discussion and conclusions

The biogeographic relationship between foliole aperture and inclination was confirmed by the field experiments, which also showed a close relationship between foliole aperture in the morning and water stress. Vertical folioles in the water-stressed plants alter the interception of direct solar radiation in two ways. On the one hand, vertical folioles reduce light interception at midday (Fig. 6a). On the other, self-shading between foliole pairs is greater when the leaf is closed (Fig. 6b and c). In a completely closed leaf, the adaxial sides of both folioles are facing each other and all of the light interception is done by the abaxial sides, reducing the effective leaf surface by 50%. Both mechanisms operate in a complementary manner: self-shading has more effect in the morning while inclination has more effect towards midday.

A vertical inclination of the photosynthetic tissues will tend to minimize the interception of direct radiation during the hotter hours of the day (Nobel 1982, 1988) and will also allow a more conservative water use (Ehleringer and Werk 1986). *L. tridentata,* like the other *Larrea* species, is an amphistomatic plant with palisade tissue in both sides of the leaves (Runyon 1934, Pyykkö 1966; Ragonese 1960). Thus, foliole closure will still allow photosynthesis to proceed through the abaxial surface during the early hours of the day. When water is available, the folioles open in the morning and intercept additional light until the afternoon, when they close again irrespectively of the water status of the plant. Under these conditions the plant will use more water, as the leaf surface is increased, but it will also intercept more light. Thus, creosote bushes can regulate through foliole movement their water use and light interception strategy.

Although, in general, foliole aperture affects the inclination of the photosynthetic surface, a significant difference existed between the Sonoran tetraploid and the Chihuahuan diploid populations described by Yang (1970) in the variability of their inclinations (Fig. 3b). The Sonoran foliages were always more variable, even when compared to the different moisture treatments at Mapimí. Thus, the higher variability of Sonoran plants cannot be attributed to moisture conditions. Although under adequate moisture conditions the Chihuahuan creosote bushes will tend to reduce their foliole inclination and approximate the observed Sonoran architectures, a certain amount of the observed differences between both deserts seems to be fixed at the ecotypic level.

Creosote bushes in northern Mexico show distinct south-southeastern orientation in their leaf clusters, indicating a trend to minimize self-shading (and hence maximize light interception) in the mornings and midday, particularly during the colder and often moist winter months, when the sun is lower above the horizon. Towards the tropical desert areas, where the sun does not always present southern azimuths, and where winters are hotter and drier, this orientation is lost. These results are consistent with those reported by Neufeld et al. (1988), who discuss this phenomenon in detail.

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