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ARCHITECTURE, LIGHT INTERCEPTION, AND DISTRIBUTION OF *LARREA* SPECIES IN THE MONTE DESERT, ARGENTINA[1]

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Abstract. This paper analyzes the correlation between leaf orientation and the environmental conditions that prevail within the biogeographic range of each of the four South American *Larrea* species (*L. ameghinoi*, *L. cuneifolia*, *L. divaricata*, and *L. nitida*; Zygophyllaceae).

Data on the distribution of *Larrea* species were gathered from herbarium specimens. Measurements of leaf orientation were made throughout the Monte Desert, and in more detail in northern Patagonia, where the four species coexist. The direct solar radiation intercepted by the unshaded leaves of each species was estimated through a computer model and plotted as a function of the hourly time for the summer and winter solstices.

L. ameghinoi presents horizontal leaves and prostrate growth, characters which allow its development on sites that are exposed to the Patagonian westerlies. The species, however, is an inefficient light interceptor in winter and early spring, when moisture conditions are adequate in Patagonia. Its architecture is the result of selection for cushion-type, wind-resistant forms, at the expense of light interception. It is restricted to windy, open areas of the Patagonian steppe.

L. cuneifolia shows erect, east-facing leaves and branches, which maximize interception in the early morning and late afternoon, keeping noon interception at a minimum. It can tolerate very hot environments by physically evading the midday sun and intercepting more early morning and late afternoon light. It colonizes the hotter and drier parts of the Monte Desert.

L. divaricata has divaricate leaves with folioles uniformly distributed in all azimuthal directions, and showing an inclination of around 70°. Although it never shows maximum light interception efficiencies, it performs relatively well in all seasons and at all hours of the day. Its distribution is wide, not only in the arid Monte, but reaching also the Chaco woodlands and the Pacific coastal deserts.

L. nitida shows erect, north-facing leaves and branches. Its leaf orientation distribution allows the gradual warming of the leaf surfaces during the morning, with a maximum light interception near winter noons. The species grows in the Patagonian Monte and on the slopes of the Andes. Its general affinity with the colder west side of the Patagonian and Monte Deserts links its distribution with winter-type rains of Pacific origin.

The results suggest that the contrasting leaf orientations of the four South American *Larrea* species reflect the prevalent selective conditions endured under long periods in isolation, and that leaf orientation is an adaptive character that influences the habitat specificity of the different species.

Key words: geographic distribution; Larrea *spp.; leaf orientation; light interception; Monte Desert, Argentina; plant architecture.*

INTRODUCTION

South American *Larrea* species (Zygophyllaceae) show remarkable differences in leaf spatial arrangement and orientation. The hypothesis that leaf orientation is a selected trait that permits an adequate light

interception when air temperatures are more appropriate can be put forward. Owing to the large latitudinal span of the genus in South America (46°–22° S in the Monte Desert, plus a few sites around 15° S in Peru), environmental selective pressures should act differently on species inhabiting different portions of the climatic–latitudinal cline. In this paper the hypothesis is tested by answering the following questions: (a) how
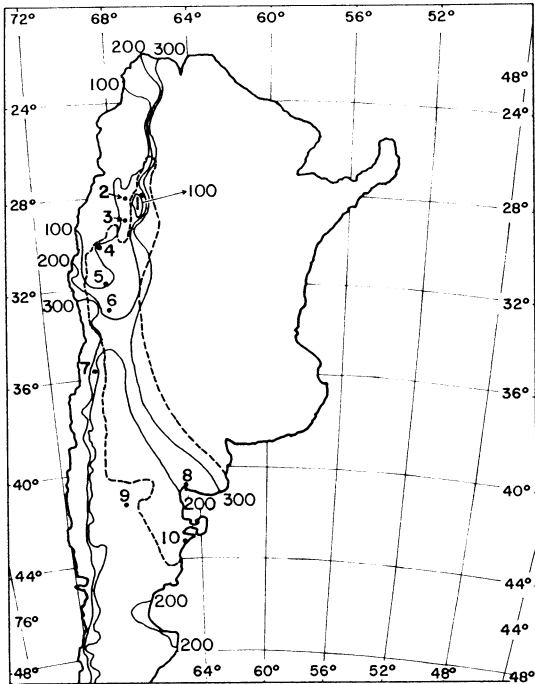
FIG. 1. Boundaries of the Monte Desert (– – –) according to Cabrera and Willink (1973) and Cabrera (1976). Isohyets for 300, 200, and 100 mm of annual precipitation are shown as ———. Meteorological stations are identified by a numbered dot. Name, location, and altitude of each station are as follows: (1) Andalgalá, 27°35′ S, 66°19′ W, 1072 m; (2) Tinogasta, 28°04′ S, 67°34′ W, 1201 m; (3) Chilecito, 29°10′ S, 67°31′ W, 1170 m; (4) Jáchal, 30°15′ S, 68°45′ W, 1165 m; (5) San Juan, 31°34′ S, 68°25′ W, 598 m; (6) Mendoza, 32°50′ S, 68°47′ W, 704 m; (7) Malargüe, 35°30′ S, 69°35′ W, 1423 m; (8) San Antonio Oeste, 40°44′ S, 64°57′ W, 7 m; (9) Maquinchao, 41°51′ S, 68°44′ W, 888 m; (10) Trelew, 43°14′ S, 65°18′ W, 39 m.

does leaf orientation vary among species?, (b) how does the amount of light intercepted by the different species vary according to latitude, time of day, and season?, and (c) how does the leaf orientation pattern of each species correlate with its biogeographic distribution?

Larrea is possibly the most widespread genus of desert shrubs on the American Continent. One species (*L. tridentata*) occurs in most of the hot arid areas of North America, while in South America four other species (*L. ameghinoi, L. cuneifolia, L. divaricata,* and *L. nitida*) are found on different parts of the Monte Desert in Argentina. *L. divaricata,* morphologically very similar to the North American *L. tridentata,* is found throughout the Monte. It is also present in the semiarid regions of the Chaco forest and in arid areas of Chile, Bolivia, and Peru. According to Wells and Hunziker (1977, see also Hunziker et al. 1972), the genus evolved in South America, and the present *Larrea tridentata* is a derivation of an ancestral *L. divaricata* that probably arrived in North America during the late Wisconsin or early Holocene. During the Holocene interglacial it expanded its range and simultaneously differentiated

by autoploidy into the present three cytogeographical races (Yang 1970).

All the species of the genus *Larrea* are microphyllous shrubs with resinous cuticles and small stomata, showing high stomatal resistance and stomatal closure at midday during dry seasons (Morello 1955*b*). The leaf morphology of *Larrea* allows the efficient use of water but has an attached metabolic cost. Because of low transpiration rates in desert xerophylls and succulents, temperature regulation of the chlorenchyma by means of evaporative cooling is not completely attainable, particularly during droughts (Walter and Stadelmann 1974, Solbrig 1977). As these species do not lose their photosynthetic tissues when soil water is scarce, other characters evolved that minimize the overheating problem. Some species (desert microphylls) have developed small leaf sizes as a partial solution to this problem. In desert succulents it has been found that spatial orientation of the chlorenchymatous tissues is of importance in the regulation of photosynthetic temperature (Nobel 1988). A recent study on *L. tridentata* in Mexico and the United States (Neufeld et al. 1988) has shown that the azimuth and inclination of foliage clusters in this species are nonrandom, a fact which suggests that leaf and branch orientation may also be important for desert microphylls.

METHODS

Biogeographical analysis

Data on the geographical distribution of *Larrea* species were gathered from herbarium specimens at the Museo Botánico of the Universidad Nacional de Córdoba (Argentina), Instituto Darwinion (Buenos Aires, Argentina), and Instituto Argentino de Investigaciones en Zonas Aridas (Mendoza, Argentina). The collection sites reported on the herbarium labels for each species were registered. Altitude and geographic coordinates, when available, were also extracted from the labels and checked on topographic maps. Climatic data for 10 selected Monte localities were gathered from the Servicio Meteorológico Nacional (Buenos Aires, Argentina).

Plant architecture

Study area. — The whole Monte Desert (Fig. 1) was traveled between March and June 1986, from its northern boundary down to the transition with the Patagonian steppe. The trip helped verify and complete the biogeographic data, and added new collection sites on areas that had been poorly collected. Additionally, measurements of leaf and branch orientations of plants belonging to the different *Larrea* species were made at selected sites. For each species present in a site, 4 plants and 10 leaves per plant were randomly selected. The azimuth and inclination of each leaf were measured. As the biogeographic ranges of the different *Larrea* species seldom overlap, the observation sites rarely

contained more than two species. For this reason, statistical comparisons in leaf orientations between the four species are not valid, as the different sites are not true replicates (differences in plant architecture between the species could be attributed to the effect of the different sites).

To eliminate pseudoreplication, the biogeographical information obtained in this sampling trip was used to select a site that contained all four *Larrea* species in the same area. A second trip was made in August 1986 to San Antonio, in the Patagonian Monte near the Atlantic coast. In the vicinity of this area, around 42° S, the four *Larrea* species are found within a radius of 50 km. Leaf and branch orientations of the four species were measured on this site.

Sampling procedure.—Sixteen plants were chosen within the study area, four belonging to each of the different *Larrea* species. The individuals of each species were selected for their contrasting environmental situations. In the case of the prostrate *L. ameghinoi,* two of the plants were selected from high, wind-exposed ridges, while the other two were chosen from relatively wind-protected depressions. In the case of the other three species, two individual plants of each species (which we shall refer to as the "unstressed" individuals) were chosen by their apparently adequate moisture conditions, as indicated by a low and protected topographic position, a greener foliage, and a moist soil profile. The other set of individual plants (the "stressed" group) was chosen by the presence of opposite indicators (a high and exposed position, a yellowish foliage, and a dry soil profile).

The inclination and the azimuth of 50 mature, fully developed leaves were measured on each plant. Inclination was measured with a clinometer and azimuth with a field compass. The leaves were chosen randomly by sorting a main branch, a secondary branch within it, and a leaf within the secondary branch. In the case of *L. divaricata,* in which the two folioles present different orientations, only 25 leaves were chosen on each plant, and the orientation of each foliole was registered independently.

Statistical analysis and simulation of light interception.—Mean azimuth and inclination were calculated using circular statistics (Batschelet 1981). Circular standard deviations were calculated following Mardia (1972, see also Batschelet 1981: 35). Additionally, the leaves were classified into inclination and azimuth classes (five inclination classes of 30° each and eight azimuth classes of 45° each), and leaf frequencies for each individual plant were arranged in a two-way inclination-by-azimuth contingency table. Differences in leaf orientation between plants, or between groups of plants, were evaluated by means of a *G* test (Sokal and Rohlf 1969).

Standard astronomical equations were used to calculate the position of the sun for the different hours of the day, and for any day of the year. The light inter-

ception efficiency (LIE) was defined as the projection of the leaf area on a plane orthogonal to the direction of the light, divided by the leaf area, and calculated as the spherical sine of the angle of incidence of the sun rays on the leaf surface (Ehleringer and Werk 1986).

$$LIE = \cos(I)\cdot\sin(e_h) + \sin(I)\cdot\cos(e_h)\cdot\cos(A - a_h),$$

where I and A are the inclination and azimuth of the leaf surface, and e_h and a_h are the elevation and azimuth of the sun for a given time (h).

The total LIE for all the unshaded leaves of a single plant was estimated as the sum of all individual leaf LIEs, divided by the total number of sampled leaves. This procedure is based on the fact that the maximum possible LIE for a whole plant, at any given time, will occur if every individual leaf were normal to the sun rays, i.e., if the individual leaf LIE was equal to unity for every single leaf. If all leaves have a similar area, then the LIE for the unshaded leaves in the whole plant would be equal to

$$LIE(plant) = \frac{(\text{sum of actual individual leaf LIEs})}{(\text{sum of maximum individual leaf LIEs})}$$

which simplifies to

$$LIE(plant) = \frac{(\text{sum of actual individual leaf LIEs})}{(\text{number of leaves})}.$$

A program was supplied with data describing the azimuth and inclination of the leaves in each of the sampled species, plus the latitude and the date to be simulated. The position of the sun was calculated from sunrise to sunset at 10-min intervals, and the LIE of each individual leaf in the sample set was estimated. The program could detect, at any given hour of the day, if each individual leaf received light on the adaxial or abaxial face. Total plant LIE, described in the above equation, was calculated in two ways: (a) for all leaves independently of the face which receives light, and (b) by summing only leaves receiving light in the adaxial face. Obviously, LIE(total) = LIE(adaxial) + LIE(abaxial).

Based on the fact that the pathway of the solar beam through the atmosphere becomes shorter as the sun approaches the zenith, the proportion of direct solar radiation (DSR) that is dampened by the air mass was calculated as a function of the angular elevation of the sun above the celestial horizon (Ross 1981). The estimations were done following Gates' (1980, see also Nobel 1988) method, which calculates DSR at a given hour of the day (S_h, measured in watts per square metre), by calculating the relative pathway length of the solar beam through the atmosphere, so that

$$S_h = S_0 t^{[1/\sin(e_h)]}$$

where $S_0 = 1380$ W/m^2 is the solar constant, t is the air transmittance (a value ranging theoretically between 0 for a perfectly opaque atmosphere and 1 for
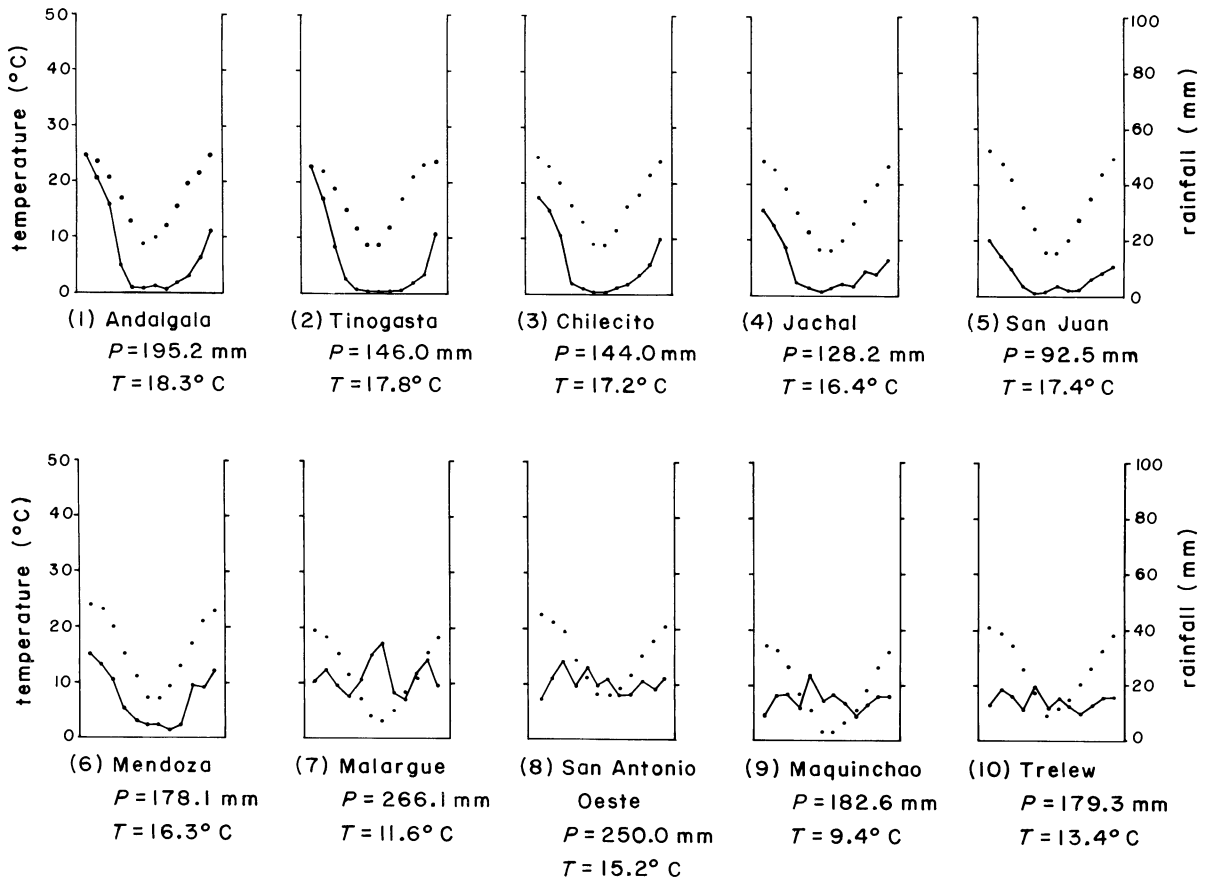
FIG. 2. Climatic diagrams of the 10 selected meteorological stations. Latitude, longitude, altitude, and station number as described in Fig. 1. The P and T values under each diagram indicate mean annual precipitation and mean annual temperature, respectively. Data from 1951 to 1980, except for Andalgalá (temperature 1901–1960, precipitation 1910–1980). Tinogasta (temp. 1941–1980, precip. 1910–1980), Chilecito (temp. 1941–1970, precip. 1910–1978), San Juan (temp. and precip. 1901–1966), and Malargüe (temp. 1954–1980). ····· = mean monthly temperature, •——• = mean monthly rainfall.

a perfectly transparent air mass, and in practice ranging between 0.5 and 0.8 in most desert areas), and the term $[1/\sin(e_h)]$ is a measure of the relative pathway length of the solar beam for a given solar elevation (e_h). All the simulations were done for $t = 0.75$.

Finally, the mean DSR intercepted by the unshaded leaves of each species was estimated by multiplying at each 10-min interval the LIE of each sampled species by the calculated DSR values (S_h). The calculated values of intercepted radiation were then plotted as a function of the local solar time. The simulations were run for 42° S, the latitude of the Monte Desert where the four species coexist, and for two different dates, the summer and the winter solstices.

RESULTS

Biogeographical analysis

The boundaries of the Monte Desert follow approximately the 200-mm annual isohyet (Fig. 1). Although annual rainfall is relatively constant throughout the

Monte, the distribution changes from monsoon-type summer rains in the north to a more regular monthly distribution in the southern Atlantic coast, or to a winter rainfall peak near the Patagonian Andes (Fig. 2).

L. divaricata is the most widely distributed species of the group (Fig. 3c), whereas *L. ameghinoi* has the narrowest distribution and is restricted to northern Patagonia (Fig. 3a). *L. cuneifolia* occupies most of the latitudinal span of the Monte (Fig. 3b), and its distribution follows quite closely the boundaries of this desert. *L. nitida* is abundant in northern Patagonia and the southern Monte, but it also goes northwards throughout the west of the Monte up to around 28° S (Fig. 3d). The wide latitudinal range of *L. nitida,* however, is accompanied by marked altitudinal changes. The altitude reported in herbarium labels for this species was negatively correlated with latitude (Fig. 4b). For every degree of latitude towards the equator there is an increase of ≈200 m in its mean altitude. In contrast, the altitude of collection sites for *L. cuneifolia* was uncorrelated with latitude (Fig. 4a). The altitude–
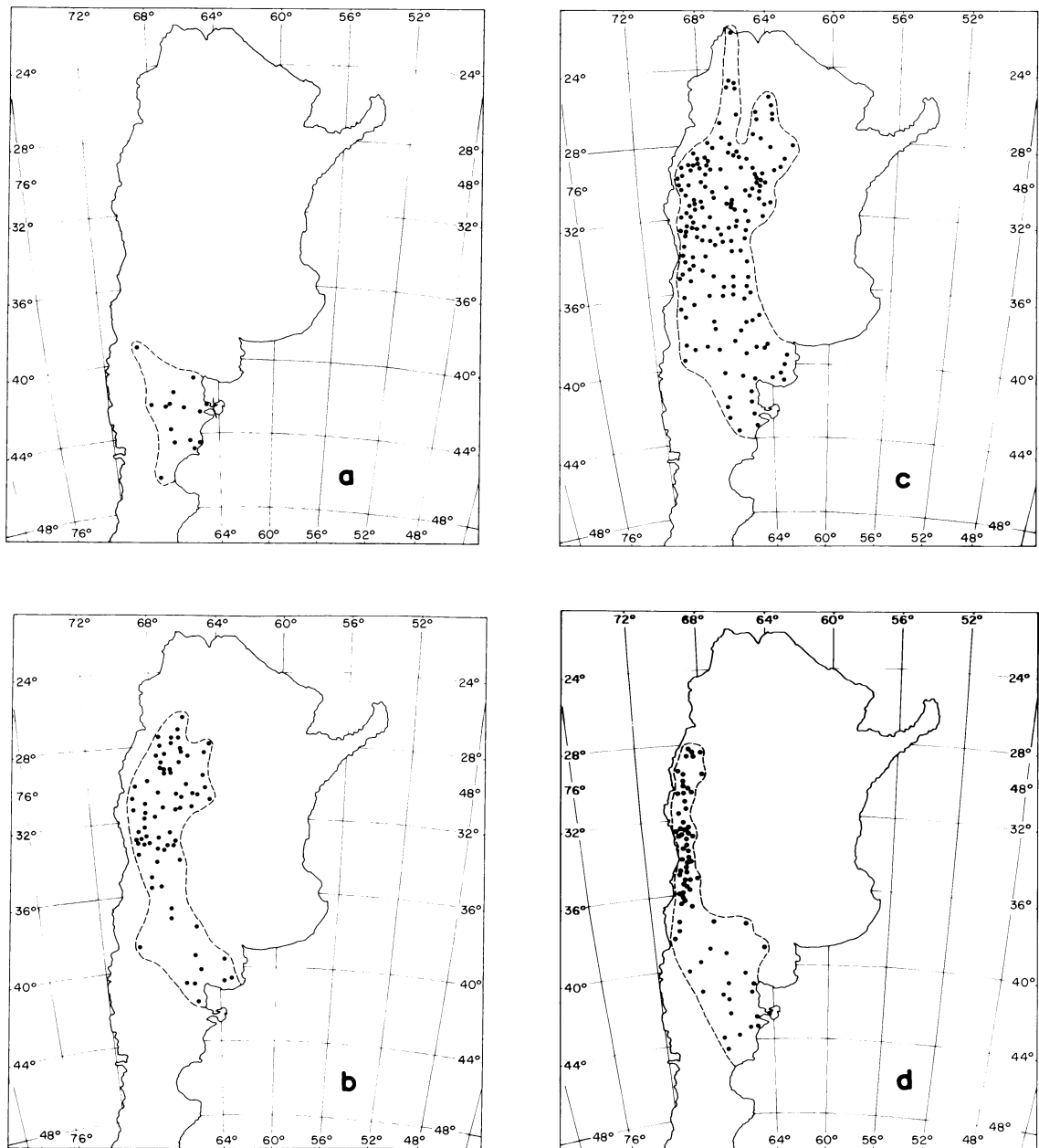
FIG. 3. Geographic distribution of (a) *L. ameghinoi*, (b) *L. cuneifolia*, (c) *L. divaricata*, and (d) *L. nitida*. Dots indicate collection locations from herbarium specimens.

latitude relationship for *L. divaricata* was even weaker than for *L. cuneifolia*, mostly due to its extensive presence in the low-latitude, low-elevation Chaco plains.

Although the different species often grow in the same region and sometimes hybridize in the field (Hunziker et al. 1969), they possess distinctly different habitat preferences (Barbour et al. 1974). Mixed *Larrea* shrubs are uncommon; the species tend to replace each other in space in an abrupt way. In the northern, subtropical part of the Monte Desert, where monsoon-type rains fall during the extremely hot summer season, *L. cu-*

neifolia colonizes the drier bajadas, while *L. divaricata* behaves as a riparian species, growing along washes, arroyos, and playas (Morello 1955a). In the semiarid Chaco woodlands, however, *L. cuneifolia* is not observed while *L. divaricata* is found growing on the bajadas and plains in areas with up to 700 mm of annual precipitation (Morello 1955a, 1958, García et al. 1960). In the middle of the Monte (36°–40° S), *L. cuneifolia* is found occupying the lowest altitudes, and the northern aspects of dry, rocky hills. The more mesophytic *L. divaricata* occupies a second altitudinal
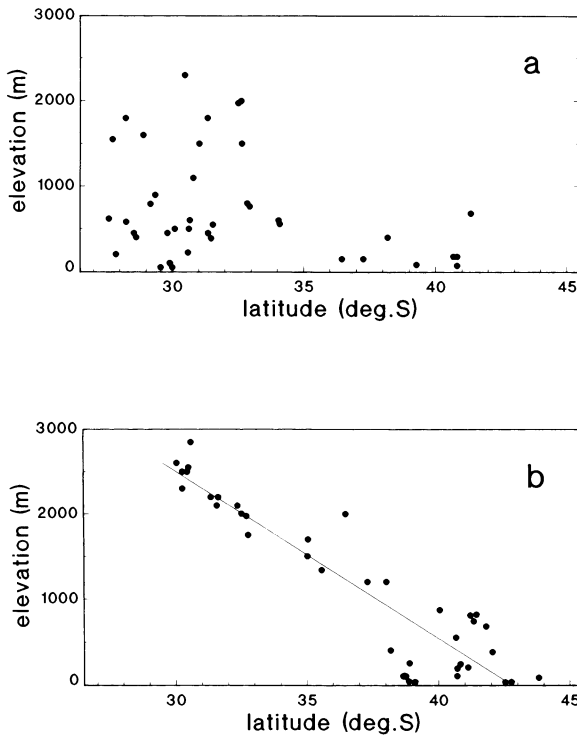
FIG. 4. Regression of altitude on latitude for collection sites of *L. cuneifolia* and *L. nitida*. Data were obtained from herbarium labels that included altitudinal information. *L. cuneifolia*: $r^2 = 0.09$, $n = 40$, NS, *L. nitida*: $r^2 = 0.85$, $n = 40$, $P < .001$. The regression equation for *L. nitida* is altitude = $8386 - 196.24$ latitude; standard error of the slope is 13.32.

belt, and is only found at lower elevations growing as a riparian species, on the southern aspects of hills, or in areas where water accumulates. *L. nitida* is also found at these latitudes, but occupying a third altitudinal range where colder and moister conditions prevail (Roig 1972, 1976), or in depressions at lower elevations, where both cold air and water tend to accumulate (Morello 1956). On the Atlantic side of the Patagonian Monte (40°–44° S), where rains are evenly distributed throughout the year, *L. divaricata* is the dominant species on the dry, gravelly Patagonian plateau (Bertiller et al. 1981), while *L. nitida* behaves as a riparian species, growing along washes and playas. Towards the Andes, however, where temperatures are lower and rainfall is more concentrated in winter, *L. divaricata* disappears and *L. nitida* becomes common in nonriparian habitats. The fourth species, *L. ameghinoi*, has a cushion-type growth form and is usually found on nonrocky, wind-erodable sites (mostly playas and loose sedimentary ridges) exposed to the strong Patagonian westerlies.

Leaf orientation and biogeographic distribution

Of the four *Larrea* species, *L. ameghinoi* shows a prostrate growth habit, while the other species develop erect branches from ground level, producing the polypodial growth form that gives *Larrea* scrub its typical physiognomy. Apart from their different growth habits, *L. ameghinoi* and *L. nitida* are similar in other aspects, such as the compound leaf morphology, the flower anatomy, and the merocarp texture and size (Hunziker et al. 1977, Simpson et al. 1977). These two species frequently hybridize under natural conditions, and the F_1 hybrids produce a large proportion of viable seed (Hunziker et al. 1969, 1977). *L. divaricata* shows divaricate leaves with two folioles partially joined at the base and forming a dihedral. *L. cuneifolia* is also bifoliate, but the folioles are joined along most of their internal edge and form a single plane.

Larrea leaves are opposite and stipulate, and successive pairs are arranged in the same plane. This type of phyllotaxis is common in the Zygophyllaceae. Axilar branches develop also along this plane, and the resulting arrangement of aerial modular parts generates planar leaf clusters, as new branch modules tend to reproduce the orientation of the parent branch. Many Zygophyllaceae (e.g., *Bulnesia* spp.) show secondary leaf and stem orientation, which allows leaves to intercept light without interfering with each other. In three of the South American *Larrea* species, however, both leaves and branches maintain their original planar arrangement. Thus, the plants acquire a fern-like architecture in which the whole branch forms a relatively flat light-intercepting structure.

The sampling trip along the Monte Desert showed that leaf orientation is a very constant character for each species (Table 1). *L. ameghinoi* shows mostly horizontal leaves with no azimuthal preference. *L. cuneifolia* shows erect leaves with a marked eastern azimuth. *L. divaricata* shows oblique folioles with no azimuthal preference, and *L. nitida* shows erect leaves with a north-northeast (NNE) azimuth. For three of the species, individual leaves have an orientation similar to that of the planar branches. The branches of *L. cuneifolia* face east (i.e., the adaxial face of the leaves forming the branch has an azimuth of ≈90°), while the branches of *L. nitida* chiefly face NNE, and those of *L. ameghinoi* face vertically upwards. In contrast, *L. divaricata* shows secondary orientation in both leaves and branches.

Plant architecture

The *G* test showed inclination and azimuth to be independent variables in all cases, with the exception of the unstressed plants of *L. ameghinoi*. Significant differences were found in either orientation or azimuth between the four species, and also between the unstressed and the stressed individuals of *L. ameghinoi* and *L. nitida* (Fig. 5). No significant differences were found for any species between individual plants within treatments.

The wind-exposed individuals of *L. ameghinoi* showed no clear azimuthal orientation, i.e., all leaves were nearly horizontal. The wind-protected plants

TABLE 1. Architecture and geographic distribution of the four *Larrea* species at different locations in arid regions of Argentina. Data are angular (circular) means and standard deviations, in degrees. $n = 40$ leaves for each mean. $\cdots$ = species absent from the site.

| | *Larrea* species | | | | | | | |
| | L. ameghinoi | | L. cuneifolia | | L. divaricata | | L. nitida | |
Locality	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
	Leaf azimuths							
Pipanaco (28°1′ S, 68°41′ W)	$\cdots$	$\cdots$	92	16	274	121	$\cdots$	$\cdots$
Chilecito (28°44′ S, 67°36′ W)	$\cdots$	$\cdots$	86	21	44	113	$\cdots$	$\cdots$
Jáchal (30°17′ S, 68°40′ W)	$\cdots$	$\cdots$	82	18	$\cdots$	$\cdots$	$\cdots$	$\cdots$
Papagayos (32°46′ S, 65°19′ W)	$\cdots$	$\cdots$	$\cdots$	$\cdots$	52	125	$\cdots$	$\cdots$
Mendoza (32°55′ S, 68°56′ W)	$\cdots$	$\cdots$	100	25	347	132	$\cdots$	$\cdots$
San Antonio (41°31′ S, 65°21′ W)	22	105	84	21	2	130	21	45
Madryn (42°49′ S, 65°7′ W)	279	133	$\cdots$	$\cdots$	264	130	29	31
	Leaf inclinations							
Pipanaco	$\cdots$	$\cdots$	87	13	67	26	$\cdots$	$\cdots$
Chilecito	$\cdots$	$\cdots$	85	15	78	17	$\cdots$	$\cdots$
Jáchal	$\cdots$	$\cdots$	92	11	$\cdots$	$\cdots$	$\cdots$	$\cdots$
Papagayos	$\cdots$	$\cdots$	$\cdots$	$\cdots$	73	30	$\cdots$	$\cdots$
Mendoza	$\cdots$	$\cdots$	86	18	65	26	$\cdots$	$\cdots$
San Antonio	19	13	94	12	73	27	89	11
Madryn	16	10	$\cdots$	$\cdots$	79	27	92	10

showed a significant difference in leaf orientation ($G = 70.6$, 7 df, $P < .001$), as more north-facing leaves were found, and these showed a higher inclination. In the wind-protected individuals of *L. ameghinoi* leaf inclination and azimuth were not independent; the north-facing leaves showed a higher inclination than the rest ($G = 18.0$, 7 df, $P < .02$).

The unstressed *L. nitida* individuals were significantly oriented to NNE azimuths. The stressed plants showed a similar mean value for azimuths, but a significantly higher angular variance, as indicated by a G test ($G = 60.4$, 5 df, $P < .001$) and by the differences in azimuthal standard deviations between both groups (Fig. 5). Additionally, the leaves of the unstressed individuals were mainly vertical ($\bar{X} = 95.3°$), while most of the stressed leaves showed significantly lower inclinations ($\bar{X} = 87.0°$; $G = 38.5$, 2 df, $P < .001$). The branches of the stressed plants showed an inward curving of the branch planes.

The leaves of *L. cuneifolia* showed a significant tendency toward eastern azimuths and vertical inclinations. No significant differences were found between stressed and unstressed plants, allowing the two data sets to be pooled for plotting and subsequent data analyses. Finally, the folioles of *L. divaricata* showed no specific azimuthal orientation and an oblique inclination ($\bar{X} = 73.5°$). For this species, stressed and unstressed plants were not significantly different, and data of both groups were pooled.

Light interception

The simulations of the light interception properties of unshaded leaves for the four species are shown in Fig. 6. In the cases of *L. ameghinoi* and *L. nitida*, where

stressed and unstressed individuals showed significant differences in their leaf orientations, the simulations were performed separately on the data sets describing the foliar orientation of each group of plants. In the cases of *L. cuneifolia* and *L. divaricata*, the two data sets were pooled.

L. ameghinoi showed a maximum interception of DSR at midday, and a higher efficiency in summer. The wind-protected (unstressed) individuals showed a better winter DSR interception compared to the wind-exposed individuals. *L. cuneifolia* showed maximum efficiencies in the early morning and late afternoon, and a minimum at midday. The simulation indicated that the adaxial faces of the leaves intercept DSR mainly in the morning, while interception in the afternoon is done mostly by the abaxial faces.

L. divaricata showed a relatively uniform pattern of DSR interception, reaching values of ≈ 400 W/m² in both winter and summer. In the early morning interception was equally distributed between adaxial and abaxial faces, but at midday it was mostly the adaxial faces that intercepted DSR. Total interception at midday in winter was slightly higher than in summer, but the interception by adaxial faces was comparable for both seasons.

The unstressed individual of *L. nitida*, which had leaves with predominantly NNE azimuths, showed for the winter simulation high light interception values in the morning, which reached > 600 W/m² and decreased gradually after 1100. In the summer simulation the behavior was different: the leaves did not intercept much DSR in the morning; the interception pattern was bimodal with a local minimum at midday and a peak of > 400 W/m² in the late afternoon. This after-
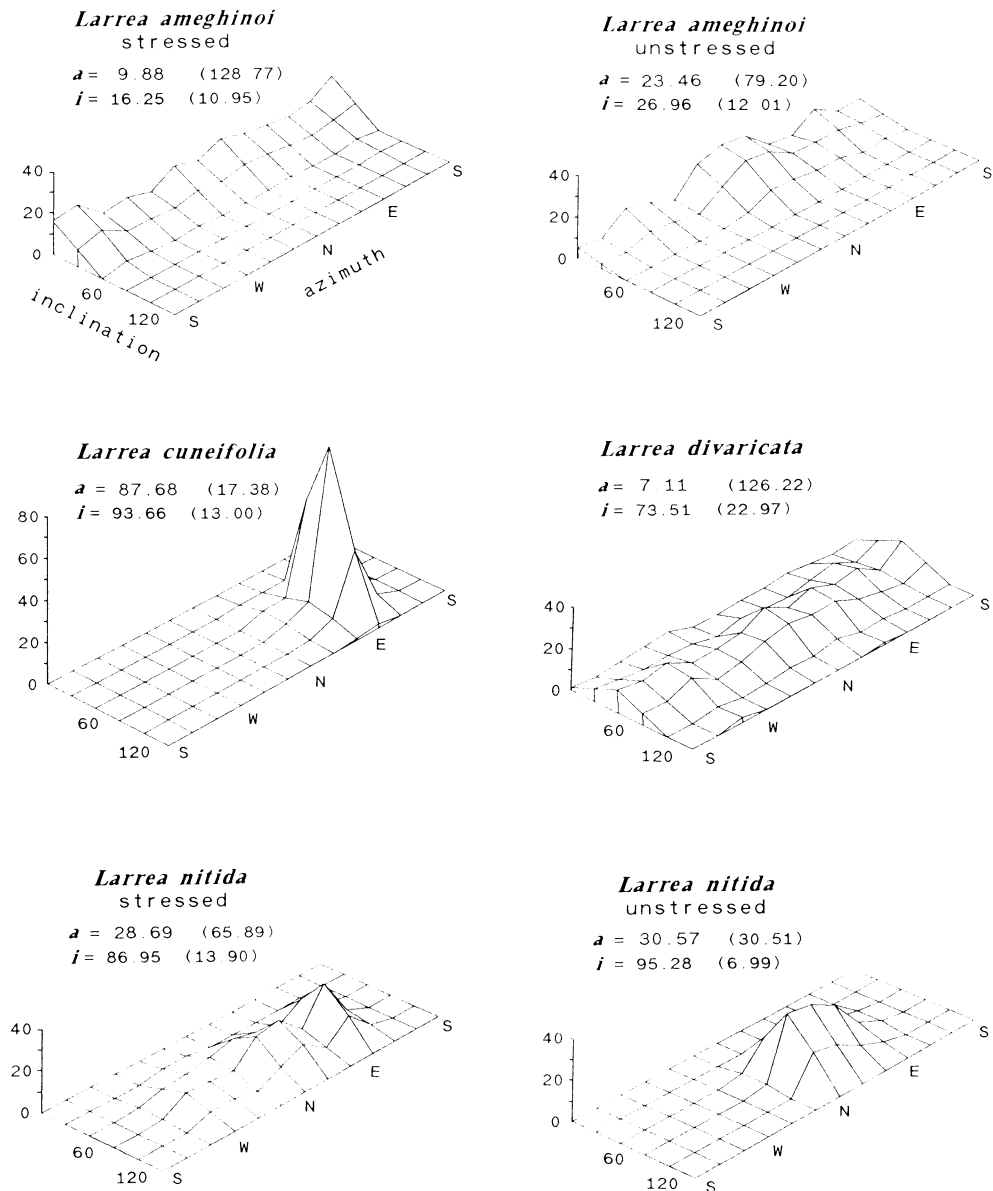
FIG. 5. Frequency distributions of leaf azimuths and inclinations for *L. ameghinoi*, *L. cuneifolia*, *L. divaricata*, and *L. nitida*. In the case of *L. ameghinoi* and *L. nitida*, which showed significant ($P < .01$) differences between the stressed and the unstressed groups, the two groups of leaves were plotted separately ($n = 100$ for each graph). The plots for *L. cuneifolia* and *L. divaricata* were obtained by pooling the information for all the sampled individuals, which did not differ significantly between groups ($n = 200$). The mean azimuth (a) and mean inclination (i) are indicated for each plot. Angular standard deviations are shown in parentheses.

noon peak, however, is mostly due to interception by the abaxial faces. The most important feature shown by the simulation is that *L. nitida* maximizes DSR interception in winter, and performs poorly in summer. The simulation for the stressed individual showed a similar, but less marked, trend in winter DSR interception, and a more pronounced midday minimum in summer. The infolding of the branch plane due to water stress affects the daily pattern of interception, which,

particularly in summer, presents low DSR interception values at midday, approximating the behavior of *L. cuneifolia*.

DISCUSSION

There is a remarkable correlation between plant architecture and the biogeographic distribution of South American *Larrea* species. *L. ameghinoi* presents horizontal leaves and prostrate growth, which allow its
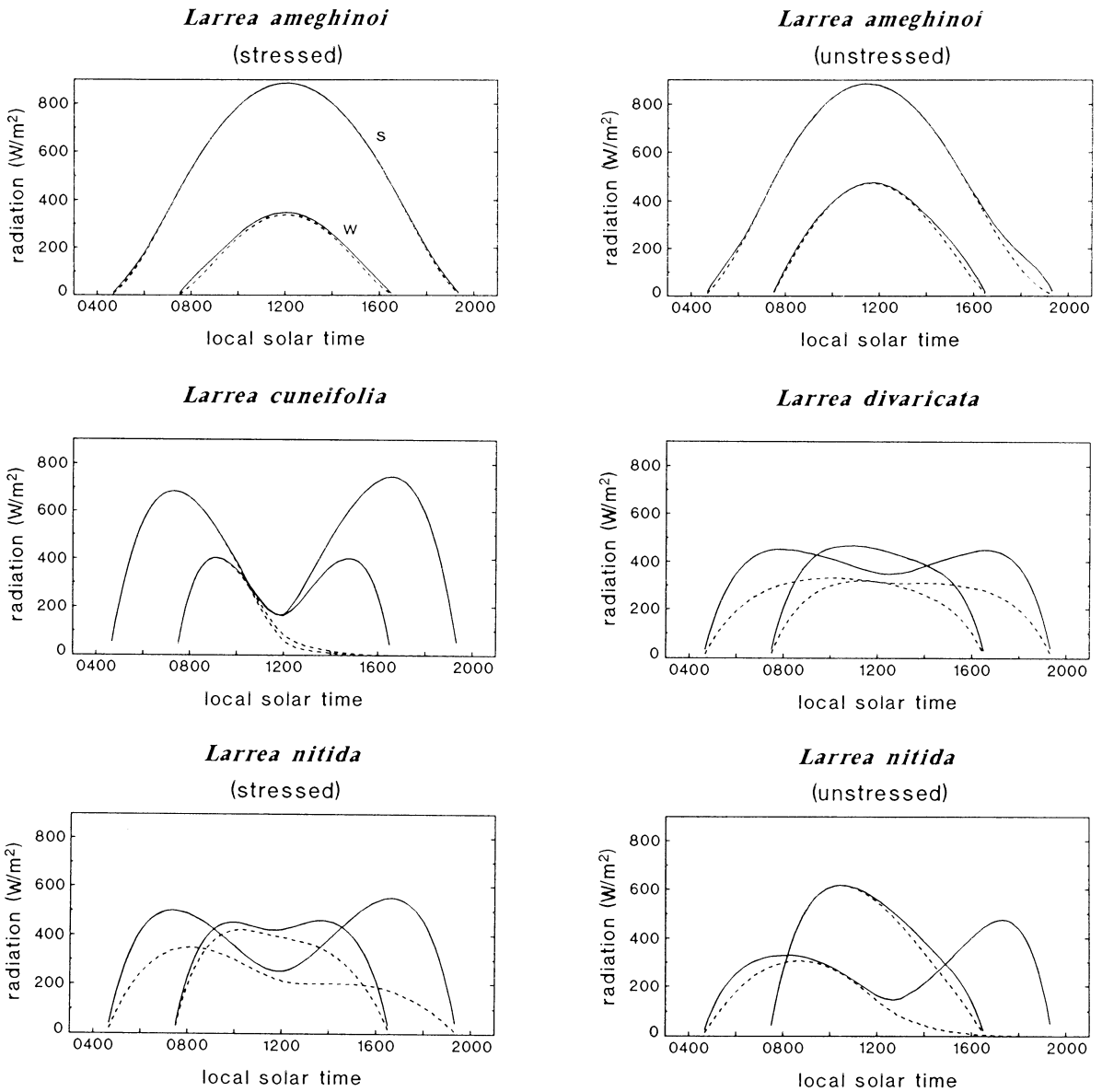
FIG. 6. Mean interception of direct solar radiation (watts per square metre) for unshaded leaves of *L. ameghinoi, L. cuneifolia, L. divaricata,* and *L. nitida* as a function of local solar time. Broken lines indicate adaxial interception, continuous lines indicate total interception. The simulation was done for 42° S latitude and for the summer solstice (*s*), and the winter solstice (*w*). Separate simulations were performed on leaf orientation data from the stressed and unstressed individuals of *L. ameghinoi* and *L. nitida*; in these cases angular information from 100 leaves was used in each simulation. The simulations for *L. cuneifolia* and *L. divaricata* were performed on the pooled leaf orientation data sets (*n* = 200 leaves for each species).

development on sites that are exposed to the Patagonian westerlies. Its growth form is inadequate from the point of view of DSR interception. The species is an inefficient interceptor in winter and early spring, when moisture conditions are adequate in Patagonia, and maximizes interception in the dry summer. This apparently contradictory architecture is the result of selection for cushion-type, wind-resistant forms, at the expense of having a suboptimal light interception. The data from the wind-protected individual show that the plant has some phenotypic plasticity and, if wind conditions are less severe, it will tend to produce north-oriented leaves, which improve its interceptive function in winter. In accordance with its architectural features, *L. ameghinoi* is restricted to windy, open areas of the Patagonian steppe.

L. cuneifolia shows erect, east-facing leaves and branches, which maximize adaxial interception in the early morning and abaxial interception in the late afternoon, keeping noon interception at a minimum. This

species can tolerate very hot environments by physically evading the midday sun and intercepting DSR in early morning and late afternoon. The strong east orientation of adaxial surfaces suggests that light interception is different on the two sides of the leaves. Pyykkö (1966) and Ragonese (1960), however, have reported *L. cuneifolia* leaves to be perfectly isolateral, with similar palisade tissue and stomatal densities on both faces. If isolaterality confers similar photosynthetic capacities to both sides, it could be that the adaxial orientation to eastern azimuths is the nonadaptive result of a hormonal response to light. We have occasionally observed plants of *L. cuneifolia* with the adaxial side of leaves in the western branches facing west, a fact demonstrating that leaves that are shaded in the morning hours can reorient and face towards the sun at sunset. *L. cuneifolia* colonizes the hotter and drier parts of the Monte Desert, as could be expected from its distinct architectural features. It is particularly abundant in the more eastern and northern parts of the Monte, where rainfall events are of monsoon-type, Atlantic origin, and occur in summer. By intercepting DSR at dawn and dusk, this species manages to survive in the driest and hottest parts of the Monte Desert, where *L. divaricata* can only grow as a riparian species.

L. divaricata has a generalized DSR interception pattern. Physiologically, it performs relatively well in all seasons and at all hours of the day. Expectedly, its distribution is wide, not only in the arid parts of Argentina, but reaching also a significant part of the Chaco woodlands, plus the Atacama and the Peruvian coastal deserts. Being a nonspecialist, it fulfills different ecological roles in different parts of the South American deserts. In the subtropical Monte it grows as a riparian species, while in the Chaco forest it colonizes the drier slopes and towards the south it survives on the open plains of the eastern Patagonian plateau. The species, however, tends to be more abundant in semiarid than in strictly arid environments. In this sense, it behaves differently from the North American creosote bush, the xerophytic *L. tridentata*, a fact noted and discussed by García et al. (1960) and Barbour et al. (1974).

L. nitida shows the type of leaf-orientation distribution that could be expected in a species that grows in cold environments. Its north-facing leaves and branches allow the gradual warming of the leaf surfaces during the morning, with a maximum light interception near noon, when the air temperatures are warmer. This species grows abundantly in the Patagonian Monte and also in the slopes of the Andes. Its general affinity with the more western side of the Patagonian and Monte Deserts links its distribution with winter-type rains of Pacific origin. The simulation showed that *L. nitida* intercepts a maximum of DSR during the winter months when the midday elevation of the sun is low. Its vertical leaves minimize DSR interception at noon during summer, when the environment is drier, rainfall is more scarce, and high temperatures can be limiting. This plant is successful in the cooler parts of the Andes, and in the cold, winter-moist parts of the Patagonian plateau. In some of the warmer parts of Patagonia it colonizes closed clayey playas where cold air and winter moisture tend to concentrate. The open parts of the plateau, receiving less moisture in winter but also less frost, are covered by the more generalist *L. divaricata*, while the areas more exposed to the Patagonian winds are colonized by *L. ameghinoi*.

In a series of studies, Barbour and collaborators analyzed the physiological behavior of South and North American *Larrea* species (Barbour and Díaz 1973, Barbour et al. 1974, 1977a, b). The different species showed similar anatomical and physiological characteristics, although it was obvious in the field that the habitat preferences of the South American species studied (*L. cuneifolia* and *L. divaricata*) were different. One of their conclusions was that "in view of the rather minimal differences found between the mesophytic *Larrea divaricata*, and the xerophytic *Larrea cuneifolia* and *Larrea tridentata*, we suggest that critical differences between the taxa might be due to shrub architecture rather than shrub physiology or leaf anatomy" (Barbour et al. 1974). Our results reinforce that conclusion. It seems that form, rather than physiology, is the main feature defining habitat preferences in the South American *Larrea* species.

Nobel (1981, 1982, 1988) reports a similar pattern of orientation in the cladodes of platyopuntias. In *Opuntia*, however, a species may show different orientations according to the environment it grows on, while in *Larrea* the behavior is relatively fixed at the species level. The results presented in this paper suggest that the branch architectures of the four South American *Larrea* species reflect the prevalent selective conditions endured under long periods in isolation, possibly during the Pleistocene glaciations when the Monte Desert shrank to a fraction of its present range. At some time during the Wisconsin glaciation, *L. divaricata* migrated to North America and evolved into the present *L. tridentata*. This species, however, is much more drought tolerant than its South American ancestor (García et al. 1960, Barbour and Díaz 1973), and there is evidence that it has developed some of the frondlike branching features that characterize *L. cuneifolia* and *L. nitida*. Neufeld et al. (1988) have shown that foliage clusters in *L. tridentata* are oriented predominantly towards the southeast, and that the inclination of these planar clusters becomes steeper in hotter and drier environments. This poses a set of interesting evolutionary questions: How does *L. tridentata* survive in extremely hot and dry environments that are not tolerated by its direct ancestor *L. divaricata*? Is *L. tridentata* converging towards the architecture of *L. cu-*

neifolia, or is it developing new architectural variants in the different deserts of North America? These questions remain to be investigated.

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