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# Ecomorphology and habitat utilization of *Echinocereus engelmannii* and *E. triglochidiatus* (Cactaceae) in southeastern California

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# ECOMORPHOLOGY AND HABITAT UTILIZATION OF
# *ECHINOCEREUS ENGELMANNII* AND *E. TRIGLOCHIDIATUS* (CACTACEAE)
# IN SOUTHEASTERN CALIFORNIA

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Abstract.— The relationship between form and habitat utilization of *Echinocereus engelmannii* and *E. triglochidiatus* was studied in southeastern California. The major difference in form is in the density of stems comprising the canopy. These differences in morphology create differences in the daily heat loads of each species. *Echinocereus triglochidiatus*, with its stems densely packed and in contact with each other over much of their lengths, continues to gain heat internally as the sun sets due to conductance between the stems. In contrast *E. engelmannii*, with a more open canopy, begins to lose heat as the sun goes down. As a result, *E. triglochidiatus* is successful in the juniper-pinyon zone where winter temperatures are cold for long periods and *E. engelmannii* is more successful in the lower desert regions where very hot, summer temperatures prevail. In the latter case, daytime buildup in heat load is reduced by convective cooling as air moves through the open canopy. Differences in microhabitat utilization occur that provide a second mechanism to reduce daily heat load buildup on hot summer days in the juniper-pinyon zone.

Plants in their natural habitats must cope with the environmental variations experienced in each microhabitat. A series of adaptive strategies, which involves gaining access to sufficient water, nutrients, and light for maintenance, growth and reproduction while at the same time avoiding the effects of desiccation and extreme temperatures that can lead to mortality, is used to achieve this (e.g., Gates 1962). Nowhere are these strategies more apparent than in plants occupying extreme environments. In particular, most morphological aspects of members of the Cactaceae have been suggested as representing ecological strategies for their successful adaptations to hot, dry environments (Gates 1962, Felger and Lowe 1967, Nobel 1978, 1980a, Yeaton et al. 1980).

The literature on problems of adaptations in form for Cactaceae involves two types of studies; one in which access to sufficient light for photosynthesis is considered (Rodriquez et al. 1976, Nobel 1980b, Yeaton et al. in review) and the other in which avoidance of extreme temperatures, particularly freezing temperatures, is emphasized (Felger and Lowe 1967, Gibbs and Patten 1970, Mozingo and Comanor 1975, Nobel 1978, 1980a). Two extremes in the form of Cactaceae parallel

this division. When access to light is discussed, platyopuntias, a group with flattened cladodes, are usually studied. In contrast, when temperature is a problem, the growth form of the species studied is usually some variant of a cylinder.

In this study, the relationship between heat load and habitat utilization is examined for two species of *Echinocereus* that are morphological variants of the cylindrical form. *Echinocereus engelmannii* (Parry) Lemaire is found on rocky slopes of elevations of 600–1500 m in the Mojave Desert of California (Benson 1969). It is caespitose with 5 to 60 stems forming an open mound. The second species, *Echinocereus triglochidiatus* Engelm., is found at somewhat higher elevations (1000–2500 m) above the deserts, usually in the juniper-pinyon woodland (Benson 1969). It also has a caespitose form with multiple stems forming a dense mound. The compactness of stems in the mounds is the most striking difference in form between the two species and results in a lower effective surface-to-volume ratio in *E. triglochidiatus*. I concentrated on this morphological dissimilarity (1) to determine what differences occur in the daily heat load experienced by individuals of each species and (2) to explain

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differences in habitat utilization by each species.

## STUDY AREAS AND METHODS

A population of *Echinocereus engelmannii* was studied at Hole-in-the-Wall at the base of the Providence Mountains in the Mojave Desert of southeastern California (latitude 35°3′ N, longitude 115°23′ W). For a description of this site, see Yeaton and Cody (1979). Populations of *E. engelmannii* and *E. triglochidiatus* were studied in the juniper-pinyon zone (latitude 35°4′ N, longitude 115°28′ W). Here rainfall is more abundant and average maximum daily temperatures are lower (Oosting 1956, Trombulak and Cody 1980). As a result, snow is common during the months of December, January, and February and persists for several days or weeks, in contrast to the lower desert site. At the upper site the dominant vegetation consists of *Artemisia tridentata*, *Juniperus monosperma*, and *Pinus monophylla*.

At each study site, all individuals of *E. engelmannii* and *E. triglochidiatus* were categorized according to the kind of microhabitat utilized. The characteristics of these microhabitats were quantified from the perspective of the plant. Three general microhabitats may be distinguished at the juniper-pinyon site: rocky slope, composed of a mosaic of boulders and gravel and found at slope angles greater than 8 degrees; under juniper and pinyon, generally at slope angles less than 8 degrees; and washes, disturbed areas with *Artemisia tridentata* dominating the plant community. At the desert study site, only the rocky slope microhabitat is utilized extensively, washes are rarely colonized by *Echinocereus* (possibly due to greater effects of erosion), and no counterpart to juniper-pinyon canopy exists. The following microhabitat characteristics were recorded for each *Echinocereus* individual whenever possible: slope aspect (either north-facing [270–90 degrees] or south-facing [90–270 degrees]), shaded or unshaded by adjacent rocks or plants. These data were organized into contingency tables with row headings consisting of the two species of *Echinocereus* and column headings describing the contrasting characteristics of each microhabitat. Entries into the tables were the numbers of individuals encountered in each situation. Totals from table to table were not necessarily equivalent because some individuals could not be assigned to a particular category. Either Chi-square or Fisher Exact Probability tests were employed to determine differences in microhabitat utilization between the two species (Siegel 1956).

The sizes of the 10 largest individuals of each species in each microhabitat were measured. Because both species form mounds that are roughly hemispherical in shape, one approximation of size is the diameter of the mound. A second measure of size is the number of stems comprising each mound. To describe the degree of openness of the canopy of each individual, a ratio of the number of stems divided by the mound diameter was calculated and compared by means of a Student's t-test (Steel and Torrie 1960). In addition, the diameters of one stem from 25 individuals of each species were measured and tested similarly.

Daily temperature regimes were measured for a large (0.5 m diameter) individual of each species that had been transplanted into a shallow clay pot and removed to an open site where the plant would not be shaded over the course of a day. The two species were set side-by-side and a Yellowsprings Instrument Tele-thermometer and probes were used to simultaneously record hourly ambient air temperature, cactus surface temperatures (on the east-facing side of the center stem), and internal stem temperatures (at 6 cm and 10 cm depths in the center stem of each individual). These temperatures are plotted for 15 September 1980 and are used to illustrate the differences in daily heat loads due to degree of openness of the canopy. Graphs were made of the daily course of the ambient air

TABLE 1. Habitat utilization by individuals of *Echinocereus triglochidiatus* and *E. engelmannii* in the juniper-pinyon zone of the Providence Mountains, California.

| Species | Rocky slopes | Pinyon pine or wash |
|---|---|---|
| *E. triglochidiatus* | 65 | 39 |
| *E. engelmannii* | 38 | 0 |

Fisher Exact Probability Test, p < 0.001.

temperatures and the differences between ambient temperatures and surface and internal temperatures for each species.

## RESULTS

At the desert site, only individuals of *Echinocereus engelmannii*, utilizing rocky slope microhabitats, are found. At the juniper-pinyon site, individuals of both species occur. At this site *E. engelmannii* is found only in the rocky slope microhabitat, but *E. triglochidiatus* is found in all three microhabitats (Table 1). At the juniper-pinyon site, *E. engelmannii* is located on south-facing slopes only, but individuals of *E. triglochidiatus* are equally divided between north- and south-facing slopes (Table 2). *Echinocereus engelmannii* apparently requires open, sunny microhabitats for successful establishment, but *E. triglochidiatus* is favored by more shaded, northern exposures. This distinction is further illustrated by the characteristics of microhabitat involving shading. *E. engelmannii* is almost always found in unshaded microhabitats, but *E. triglochidiatus* is found in shaded situations, whether it occurs on north- or south-facing slopes (Table 3).

The means and standard errors for size measurements of the 10 largest individuals of each species in each microhabitat are given in Table 4. Comparison of the mean values for mound diameters and number of stems between the two species on the rocky slope at the juniper-pinyon site shows that *E. triglochidiatus* is much larger than *E. engelmannii* (for diameter t = 6.54, d.f. = 18, p < 0.001; for number of stems t = 10.23, d.f. = 18, p < 0.001). These differences combine to give significantly lower mean values for the ratio of stem number/mound diameter for *E. engelmannii*, indicating that the spacing between stems is relatively large (t = 12.58, d.f. = 18, p < 0.001). This is not due to differences in stem diameter because no significant difference was found between the two species (for *E. engelmannii* stem diameter x̄ ± S.E. = 5.18 cm ± 0.16; for *E. triglochidiatus* x̄ ± S.E. = 4.82 cm ± 0.15; t = 1.63, d.f. = 48, 0.2 < p < 0.1). No difference in the stem number/mound diameter ratio exists between the upper and lower

populations of *E. engelmannii*; however individuals of the upper population are significantly smaller in diameter (t = 6.06; d.f. = 18, p < 0.001) and in stem number (t = 6.38, d.f. = 18, p < 0.001) than are individuals measured at the desert site. For *E. triglochidiatus* a gradual reduction in diameter and stem number and an increase in the openness of the canopy occurs from the rocky slope through the juniper-pinyon to the washes (Table 4). The only significant differences occur between the rocky slope and wash microhabitats for this species (for mound diameter t = 2.47, p < 0.05; for stem number t = 4.48, p < 0.001; for the ratio t = 3.53, p < 0.01; d.f. = 18 in all cases).

The daily temperature regimes are shown in Figure 1. Ambient air temperature increases from early morning until late afternoon and decreases as the sun sets (Fig. 1a). For the relatively open-canopied *E. engelmannii*, surface temperatures are much greater during the early part of the day and decrease rapidly as the east-facing side of the stem is shaded in the later daylight hours (Fig. 1b). At the 6 cm depth, temperatures appear buffered and fluctuate around the ambient temperature during the day, heating up as the sun goes down (Fig. 1b). At the 10 cm depth, temperatures start below ambient in the morning, increase rapidly during the day, and gradually decrease in the evening (Fig. 1b). In contrast, the closed-canopied *E. triglochidiatus* maintains surface and internal stem temperatures below those of ambient during the daylight hours and gradually increase as the sun sets. By midnight, temperatures in *E. triglochidiatus* stems are greater than those for *E. engelmannii* under the same conditions (Fig. 1c).

TABLE 2. Slope aspect utilization for individual of *Echinocereus triglochidiatus* and *E. engelmannii* in the juniper-pinyon zone of the Providence Mountains, California.

| Species | North-facing (270–90 degrees) | South-facing (90–270 degrees) |
|---|---|---|
| E. triglochidiatus | 23 | 24 |
| E. engelmannii | 2 | 33 |

Fisher Exact Probability Test, p < 0.001.

## DISCUSSION

Felger and Lowe (1967) described changes in the form of *Lophocereus schottii* over a latitudinal gradient, with a tendency for larger diameter and a reduced number of stem ribs toward the colder, northern edges of its distribution. Also Niering, Whittaker, and Lowe (1963) demonstrated an increase in the diameter of *Carnegica gigantea* at the northern limits of its distribution. These changes have the effect of reducing the surface-to-volume ratio and increasing the time lag before the tissues suffer damages from freezing temperatures, as has been simulated by Lewis and Nobel (1977) and Nobel (1978). These changes occur within species, but the results may be extrapolated to those observed for the two species of *Echinocereus*. In form, *E. triglochidiatus* has a more closed canopy than does *E. engelmannii*, because its stems grow in contact with one another. Hence its surface-to-volume ratio is reduced, and the species approximates in form a solid cylinder or "barrel." *Echinocereus triglochidiatus* is found only at the juniper-pinyon site where exposure to freezing temperatures at night can be a severe problem. The time lag, in which the internal stem temperatures are still increasing because of conductance between stems after the sun sets, may enable *E. triglochidiatus* to survive low night temperatures. In contrast, *E. engelmannii* may be unable to survive low night temperatures due to its more open growth form. As a result, it is only established at the colder juniper-pinyon site on unshaded, south-facing rocky slopes. Here it can warm up rapidly in the morning, minimizing the time during which its tissues are exposed to freezing temperatures. Its growth form at the juniper-pinyon site, rather than approximating the compactness of *E. triglochidiatus*, is open due to the hot summer temperatures experienced in this microhabitat. The smaller maximum size, attained by *E. engelmannii* at the juniper-pinyon site, is probably the result of its establishment at the extreme upper limits of its elevational range, where its growth rate is slower and less constant and its probability of survival to the maximum sizes attained at the desert site is very low. At the desert site, freezing temperatures are less of a problem. High summer temperatures appear to be more critical there. One way of reducing the heat load of an individual is to open the canopy, permitting convective cooling as air moves through the canopy.

Although morphology appears to be an adaptation to the extremes in temperature that *Echinocereus* experiences, each species must cope with problems posed when the opposite climatic conditions occur. For example, hot summer days do occur at the juniper-pinyon site and freezing winter nights do occur at the desert site, although at a reduced frequency in comparison with their opposite extremes. Microhabitat differences become important in moderating the heat load and exposure to freezing temperatures. During the hot summer months, when the sun is directly overhead at midday, *E. triglochidiatus* is usually in the shade. Its daily heat load is reduced, because ambient temperatures in the shade are lower (Bannister 1976, Yeaton et al., in review). Conversely, in the winter months, when the sun is at a lower angle, *E. triglochidiatus* may be in direct sunlight during part of the day. At the desert site, *E. engelmannii* may avoid the effects of freezing temperatures by using unshaded microhabitats in which individual stems can heat rapidly in the early morning as the sunlight strikes them.

One comment should be made about the temperature measurements made. The great difference in surface temperature, recorded in the morning hours, is the direct result of differences in the canopy structure for the two species. As a result of its more open canopy, the stems of *E. engelmannii* are exposed at times to direct sunlight and heat more rapidly than do the stem surfaces of the closed-canopied *E. trigiochidiatus*, which are always shaded. For this reason surface and internal temperatures of *E. triglochidiatus* fluctuate similarly over the course of the day, and

TABLE 3. Shade utilization by individuals of *Echinocereus triglochidiatus* and *E. engelmannii* in the juniper-pinyon zone of the Providence Mountains, California.

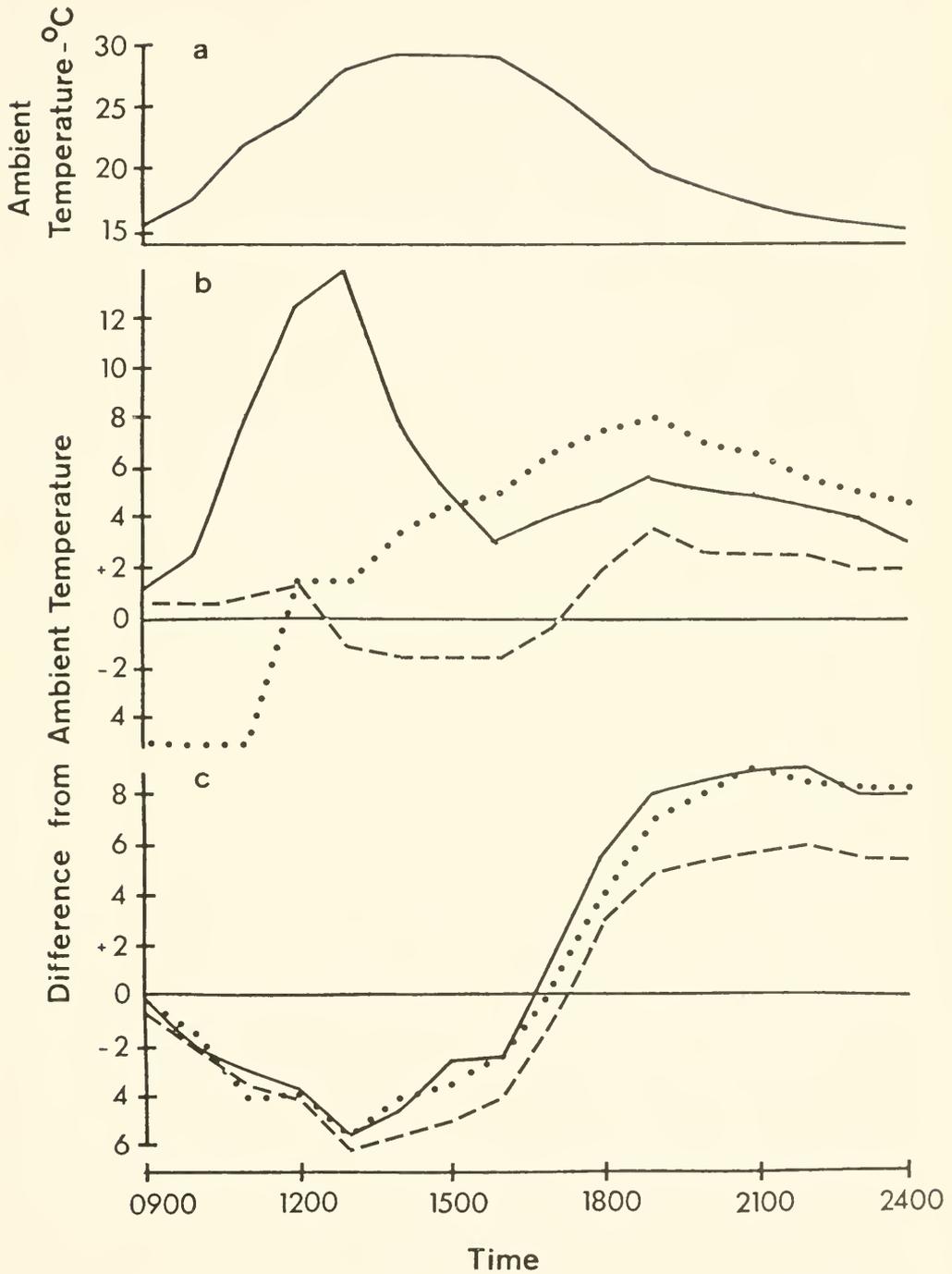| Species | Shade | No shade |
| --- | --- | --- |
| E. triglochidiatus | 67 | 5 |
| E. engelmannii | 5 | 38 |

$x^2 = 72.8$ $p < 0.01$.

Fig. 1. The relationship between ambient temperature and surface and internal stem temperatures for transplanted *Echinocereus engelmannii* and *E. triglochidiatus* in an open site over a 15-hour period on 15 September 1980. (a), Ambient air temperatures; (b), The differences from ambient temperature for surface (_____), 6 cm deep (------), and 10 cm deep (......) probes in or on the central stem of *E. engelmannii*; (c), the same as b. but for *E. triglochidiatus*.

TABLE 4. Means and standard errors for size measurements of the 10 largest individuals of *Echinocereus triglochidiatus* and *E. engelmannii* found in each habitat utilized in the juniper-pinyon and desert zones of Providence Mountains, California.

| Habitat | Diameter (em) | No. Stems | No. Stems/Diameter | Individual Stem Diameter (mm) |
|---|---|---|---|---|
| Juniper-pinyon | | | | |
| *E. triglochidiatus*—Rocky | 45.20 ± 3.60 | 86.40 ± 7.44 | 1.93 ± 0.10 | 5.18 ± 0.16 |
| —Pinyon | 39.50 ± 4.50 | 76.40 ± 11.55 | 1.77 ± 0.17 | |
| —Wash | 34.50 ± 2.41 | 47.60 ± 4.43 | 1.41 ± 0.11 | |
| *E. engelmannii* —Rocky | 19.20 ± 1.69 | 10.00 ± 0.67 | 0.55 ± 0.05 | |
| Desert | | | | |
| *E. engelmannii* —Rocky | 47.20 ± 4.30 | 30.30 ± 3.11 | 0.67 ± 0.07 | 4.82 ± 0.15 |

widely divergent temperatures are recorded in the same period for *E. engelmannii*. The difference in surface temperature is further exacerbated by the differential movement of air through the canopies of the two species, resulting in different rates of convective cooling. Thus, surface temperatures may not be compared with the internal stem temperatures except as general trends. This is because the temperatures recorded on the surface are a direct response to environmental conditions, but the internal stem temperatures represent various degrees of integration of these same environmental conditions. The internal stem temperatures may be compared between the 6 cm and 10 cm depths and, as would be expected, the 10 cm depth becomes warmer than the 6 cm depth as the day progresses.

I have concentrated in this study on the differences in form of two species of *Echinocereus*. Other differences such as spine coverage, spine color, apical pubescence, and tissue thermal properties have been demonstrated as being important in the regulation of heat load in Cactaceae (Nobel 1978). Differences between the two species do exist for some of these characteristics (Benson 1969). *Echinocereus engelmannii* is more heavily spined and its spines are lighter colored than those of *E. triglochidiatus*. Also, the central spines of *E. engelmannii* are flattened in contrast to those of *E. triglochidiatus*. These factors contribute to its adaptation to unshaded microhabitats by increasing its albedo (Gibbs and Patten 1970, Nobel 1978). Additionally, *E. triglochidiatus* has permanent apical pubescence on mature stems, but *E. engelmannii* loses its pub-

escence after 2–3 years. Apical pubescence may have an insulative effect (Nobel 1978), which may be important in survival of stems of *E. triglochidiatus* in cold habitats. I have no information on the thermal properties of stem tissues.

Thus, the differences in morphology observed in *Echinocereus engelmannii* and *E. triglochidiatus* appear to be adaptations for avoidance of extreme climatic conditions in their preferred habitats, and differences in microhabitats enable the individual to avoid the opposite extremes should they occur. In other words, the constraints imposed by morphology are ameliorated by differences in microhabitat use.

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