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Parallel Evolution of Leaf Pubescence in *Encelia* in Coastal Deserts of North and South America

James Ehleringer[1], Harold A. Mooney[2], Sherry L. Gulmon[2] and Philip W. Rundel[3]

[1] Department of Biology, University of Utah, Salt Lake City, UT 84112, USA
[2] Department of Biological Sciences, Stanford University, Stanford, CA 94305
[3] Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717, USA

Summary. Members of the shrub genus *Encelia* occur in the arid coastal regions of western North America and South America along gradients of precipitation extending from less than 50 mm annually to somewhat over 350 mm. At moist ends of the gradient species possess glabrate, green leaves. Proceeding to drier regions, the species possess progressively more pubescent, whiter leaves. Leaf absorptance to solar radiation decreases with precipitation in an identical pattern along gradients in both North and South America.

Indroduction

Along gradients of decreasing precipition in arid lands of southwestern North America, there are numerous species that increase in leaf pubescence (hairiness) or are replaced by more pubescent-leaved species in response to increased aridity (Ehleringer 1981 a). Recent studies of such species suggest that leaf pubescence results in increased reflectance to solar radiation, lower leaf temperatures and lower rates of water loss (Ehleringer et al. 1976; Ehleringer and Björkman 1978; Ehleringer 1981 b). The most studied examples of pubescence increase are found in the genus *Encelia*. For the pubescent-leaved shrub *Encelia farinosa*, the presence of hairs is apparently an important feature which enables this species to successfully occupy hot, desert habitats (Ehleringer and Mooney 1978).

Members of the genus *Encelia* are common in the arid regions of southwestern North America (Munz 1959; Shreve and Wiggins 1964). They also occur in the coastal, arid regions of northern Chile, Peru, and the Galapagos Islands in South America (Blake 1914; Wiggins and Porter 1971). The taxonomic descriptions of *Encelia* species suggest that as in North America both glabrate and pubescent leaved species occur in South America.

The purpose of this study was to compare the distributions of coastal *Encelia* species in North and South America to determine if parallel evolution of leaf pubescence and hence spectral properties was occurring within this genus. Specifically we wanted to know whether at points of homoclimate between North and South America were plants found with comparable degrees of leaf pubescence. If so, this would provide strong evidence for the role of climate, specifically aridity, in the selection of leaf morphological properties.

Methods

Encelia species were sampled along gradients of decreasing precipitation. In North America species were sampled along a coastal transect from Laguna Beach, California (33° 33′ N, 117° 47′ W) south to Magdalena Bay, Baja California Sur (24° 38′ N, 112° 09′ W) during August 1979. In Chile species were sampled along a coastal transect from Fray Jorge (30° 34′ S, 71° 11′ W) north to Antofagasta (23° 29′ S, 70° 26′ W). Climatic data for these regions are available from U.S. Weather Bureau Records, Hastings and Humphrey (1969), Almeyda and Saez (1958), and Hajek and di Castri (1975).

The species distributions were determined by examination of herbarium vouchers from the California Academy of Sciences, San Diego Natural History Museum, Stanford University, Univerity of California, Berkeley and the Universtity of Arizona Herbarium as well as by personal observations.

Leaf absorptance to solar radiation was measured using a 23 cm diameter Ulbricht integrating sphere. Light to the integrating sphere was either sunlight (via a heliostat) or monochromatic (Bausch and Laumb monochromator). The leaf absorptance is a percentage measurement and thus changes in leaf absorptance are changes in the percentage of light absorbed by the leaf. Further details of the theory and measurement of leaf absorptance using this technique are described in Ehleringer and Björkman (1978) and Ehleringer (1981 b).

Results

The distributions of coastal *Encelia* species in North America is essentially parapatric. The distribution boundaries are distinct and appear to be associated with changes in vegetation type. While the species or varieties typically do not occur together, there are rare regions of overlap, and in these zones hybrids between the two species are evident. As shown in Fig. 1 the distribution of *Encelia californica* Nutt. extends from Pt. Sal, California (34° 33′ N, 120° 36′ W) south to El Rosario, Baja California Norte (30° 03′ N, 115° 43′ W), where it is a dominant component of the coastal sage vegetation type. In the Valle El Rosario (30° 03′ N, 115° 43′ W) *Encelia asperifolia* (Blake) Clark and Kyhos first appears and extends south to the beginning of the Vizcaino Desert at Villa Jesus Maria, Baja California Norte (28° 18′ N, 114° 0′ W). *Encelia palmeri* Vasey and Rose is quite common throughout the low elevation Vizcaino Desert region from Villa Jesus Maria south to Punta Conejo, Baja California Sur (24° 04′ N, 111° 01′ W).

In Chile, the distributional boundaries of *Encelia* species are somewhat more difficult to establish because of the small number of collections which have been made. *Encelia canescens* var. *oblongifolia* (DC.) Blake occurs in the mattoral vegetation from Termas del Soco (30° 43′ S, 71° 38′ W) north to about Choros Bajos (29° 17′ S, 71° 44′ W) (Fig. 2). Farther north in more arid and open shrubland, *Encelia canescens* Lam. occurs from Cachiyuyo (29° 05′ S, 70° 54′ W) to Caldera (27° 03′ S, 70° 50′ W). *Encelia canescens* var. *lanuginosa* is found from just south of

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Offprint requests to: J. Ehleringer

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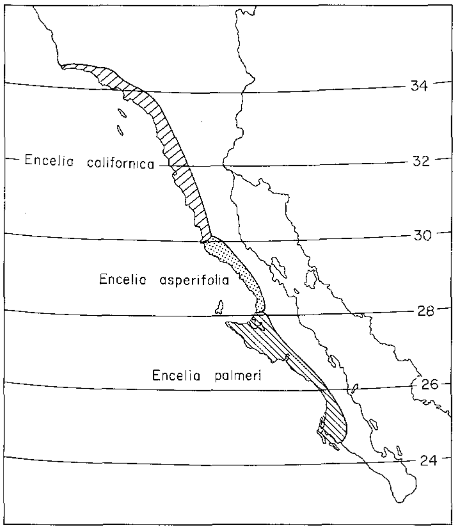

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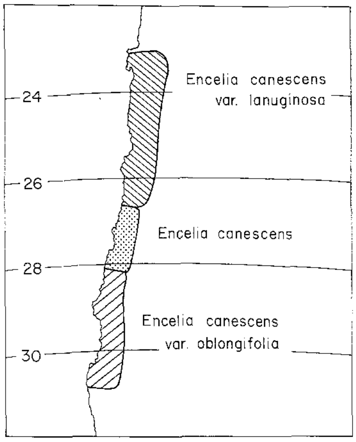

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Fig. 1. Distribution of coastal *Encelia* species in North America

Fig. 2. Distribution of coastal *Encelia* species in South America

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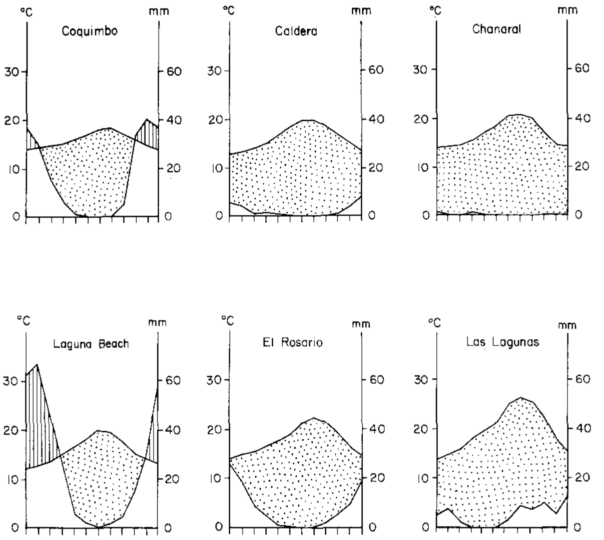

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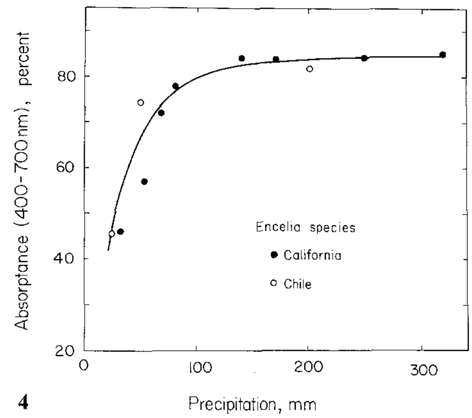


Fig. 3. Climate diagrams for habitats of *Encelia* species pairs in South America (*top*) and North America (*bottom*) proceeding from wettest habitats (*left*) to the driest (*right*)

Fig. 4. Leaf absorptance (400–700 nm) to solar radiation for coastal *Encelia* species as a function of the mean annual precipitation in mm

Chañaral (26° 23′ S, 70° 37′ W) extending north into the driest regions of the Atacama Desert.

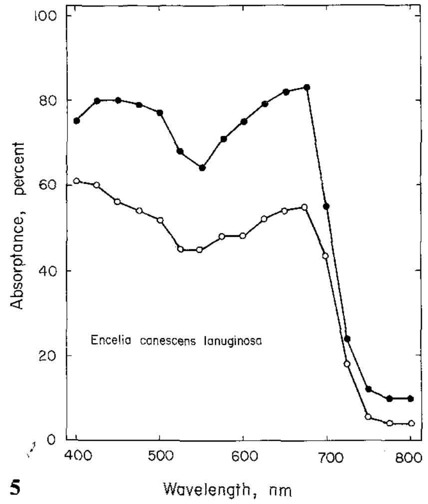
Along the coastal transects in both North and South America *Encelia* taxa are replaced by increasingly more pubescent-leaved forms as precipitation levels decrease. *Encelia californica* and *E. canescens* var. *oblongifolia* have glabrate leaves and occur in the wettest regions (100–350 mm annually). When annual precipitation decreases to 50–100 mm, these taxa are replaced by the moderately pubescent leaved species *E. asperifolia* and *E. canescens,* respectively. On the driest sites where precipitation levels are below 50 mm annually, the heavily pubescent leaved species *E. palmeri* and *E. canescens* var. *lanuginosa* are found.

Climate diagrams were constructed for representative locations within the distributions of the six *Encelia* taxa to determine if there was homology in the macroclimates where they occurred. Figure 3 illustrates the climates for the three matched pairs, the South American climate diagrams being offset by six months. There is a strong similarity in macroclimates of morphologically matched pairs in North and South America, but not between adjacent taxa in the same continent, indicating that *Encelia* species with similar pubescence morphologies are found in similar climates.

The extent to which there is a functional parallel evolution of leaf pubescence in these *Encelia* species is indicated by the leaf absorptance to solar radiation. Changes in pubescence density should change the leaf absorptance and reflectance characteristics.

On both continents leaf absorptance over the visible wavelengths was measured on samples of all taxa in the field at the end of the growing season. In both the North and South American *Encelia* taxa, the leaf absorptance was high (84–85%) at the wet end of the aridity gradient (Fig. 4). Proceeding to drier sites in both continents, leaf absorptances decreased. The decreases in leaf absorptance were greatest at the driest sites where absorptances were 46 and 44% in North and South America, respectively. The changes in leaf absorptance with precipitation were identical for North and South American *Encelia* species.

The spectral characteristics of pubescent leaved species change with the extent of drought imposed upon the plant. Figure 5 shows the variations in spectral characteristics seen for leaves of *E. canescens* var. *lanuginosa*, a species from extremely arid lands, grown under well-watered and droughted conditions in the greenhouse. Unter non-droughted conditions leaf pubescence is sparse, percent absorptance at all visible wavelengths is high, and the integrated 400–700 nm absorptance is 80%.



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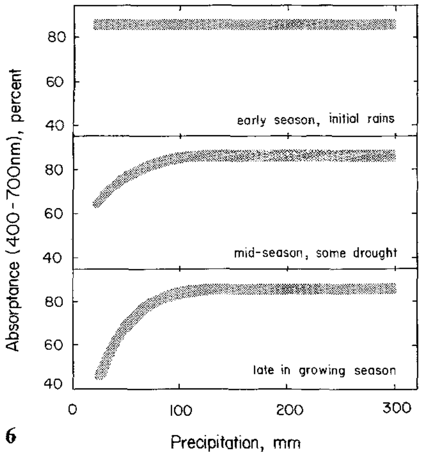

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Fig. 5. Leaf absorptance between 400 and 800 nm for leaves of *Encelia canescens* var. *lanuginosa* grown under well-watered (*closed circles*) and droughted conditions (*open circles*) in a greenhouse

Fig. 6. Proposed phenology of changes in leaf spectral characteristics of coastal *Encelia* species along a precipitation gradient. See text for further explanation

In contrast, under droughted greenhouse conditions the leaf pubescence becomes dense, the percent absorptance is decreased at all wavelenghts, and the integrated 400–700 nm absorptance is 52%.

Discussion

Parallel and convergent evolution has been described extensively in the mediterranean-type climate plant communities of California (North America) and Chile (South America) by di Castri and Mooney (1973), Mooney (1977), and Thrower and Bradbury (1977). Additionally, Mooney et al. (1974) have been able to demonstrate a similar convergence at the community level in the coastal desert regions which border the mediterranean-type climate communities. At a finer level of resolution in the mediterranean type climates, Mooney et al. (1974) and Mooney (1977) have been able to show a strong degree of convergence in the morphology, phenology, and physiology of ecological pairs from the two continents. The current study extends these findings (at least for morphology) to species pairs in these desert regions.

What is the adaptive value of pubescence to these species? Recent studies suggest that pubescence or other reflectance increasing structures (such as waxes or salt glands) 1) reduce water loss and 2) are a necessary component of photosynthetic adaptation to arid habitats (Mooney et al. 1978; Ehleringer and Mooney 1978; Ehleringer 1981a; Ehleringer 1981c). For photosynthetic adaptation, it appears that perennial desert plants either physiologically acclimate or morphologically acclimate to changes in the thermal environment (Ehleringer 1981c). Physiological acclimation involves a biochemical/physiological change in the photosynthetic system such that the leaf photosynthetic capacity is enhanced at the new temperature. Morphological acclimation occurs in those species which apparently do not physiologically acclimate. In morphological acclimation, there is a change in the leaf absorptance characteristics such that as air temperatures increase there is a decrease in leaf absorptance, and as a consequence leaf temperatures remain either constant or close to a fixed thermal optimum for photosynthesis. Morphological acclimation has been shown to occur in *Encelia farinosa*, an interior desert species (Ehleringer and Mooney 1978). The pubescence in the coastal desert *Encelia* may also prevent damaging high leaf temperatures. However, no data are available regarding the photosynthetic capacities of any of the coastal, pubescent species.

The leaf absorptance-precipitation response curve shown in Fig. 4 infers that coastal *Encelia* cannot physiologically acclimate their photosynthetic apparatus and therefore must morphologically acclimate. This morphological acclimation probably occurs with the onset of drought (Fig. 6). Thus, early in the growing season, after initial rains have fallen, the pubescence is minimal on all leaves along the precipitation gradient, resulting in high leaf absorptances and high photosynthetic potentials by all leaves. As drought develops and air temperatures increase, the plants at the driest end of the aridity transect respond first and produce lightly pubescent leaves with lowered leaf absorptances. This allows the leaves to remain close to the optimum temperature for photosynthesis. As the drought develops further and air temperatures increase more, the leaves produced are more pubescent and have progressively lower absorptances until at the end of the growing season the pattern observed in Fig. 4 is obtained.

The similarity in the extent of leaf pubescence development in *Encelia* in similar climates of North and South America and other California-Chile convergence studies supports the concept of a strong, selective role of macroclimate in determining plant form and function. That there are not an inordinately large number of adaptive possibilities within a growth form type to similar environmental regimes suggests that by understanding how plants have adapted to the environment in one location it may allow us to a priori predict the adaptive modes expected to be found in similar environments elsewhere in the world.

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