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Variation in leaf level energy balance components of *Encelia canescens* along a precipitation gradient in north-central Chile.

Variación en los componentes del balance de energía a nivel foliar de *Encelia canescens* a lo largo de un gradiente de precipitación en el norte-centro de Chile.

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ABSTRACT

Leaf characteristics of several populations of *Encelia canescens,* located in north-central Chile, were studied in order to evaluate differences in energy balance components along an aridity gradient.

In the most arid regions, new vegetative growth and plant height were correlated in a 1:1 manner, while in regions where average rainfall is over 25 mm both variables were independent.

Leaf absorptance did not change with increasing aridity in the year of our studies. The mean value measured (70.8±1.1%) was between the values reported for desert and mediterranean vegetation types. Leaf angle increased with aridity along the entire gradient (i.e., from 50° at 30°S to 75° at 25°30'S), consequently the potential midday solar radiation incident on an *E. canescens* leaf changed from 64% to 26% along the transect. The changes in leaf angle observed would result in a reduction in transpiration of approximately 8% and of 1.2°C in leaf temperature.

No differences were found among populations in leaf carbon isotope ratios (-26.7±.27‰), leaf nitrogen content (2.35±0.15%) and carbon/nitrogen ratio (16.42±1.40). These results suggest similar water-use effiency among populations along the latitudinal gradient studied and might also indicate no differences in their potential rates of photosynthesis. Increases in leaf angle could be a strategy for optimization of productivity as well as a means of morphological adjustment to the onset of drought.

Key words: leaf angle, leaf pubescence, carbon isotope ratio, aridlands, rainfall.

RESUMEN

Las características foliares de varias poblaciones de *Encelia canescens,* localizadas en el norte-centro de Chile, fueron estudiadas para evaluar sus diferencias en los componentes del balance de energía a lo largo de un gradiente de aridez.

En las regiones más áridas, el crecimiento vegetativo del año estuvo correlacionado 1:1 con la altura de la planta, mientras que ambas variables fueron independientes en regiones donde el promedio anual de precipitación es sobre 25 mm.

El porcentaje de absorbancia foliar no cambió con el incremento en aridez en el año de estudio. El promedio medido (70,8±1,1%) está entre los valores reportados para las vegetaciones de desierto y mediterránea. El ángulo foliar incrementó con la aridez a lo largo del gradiente (i.e., desde 50° a los 30°S hasta 75° a los 25°30'S). Esto significa que la radiación solar incidente a mediodia en una hoja de *E. canescens* potencialmente cambiaría desde 64% hasta 26% a través del transecto. Un cambio en el ángulo foliar como el observado podría resultar en una reducción de la transpiración cercana al 8% y una reducción en la temperatura foliar de 1,2°C.

No se encontraron diferencias entre las poblaciones en la proporción de isótopos de carbono foliar (-26,7±0,27‰), contenido de nitrógeno foliar (2,35±0,15%) y proporción de carbono/nitrógeno (16,42±1,40). Estos resultados sugieren eficiencia similar en el uso del agua y también podrían indicar tasas similares de fotosíntesis potencial. Un incremento en el ángulo foliar puede ser interpretado como una estrategia para la optimización de la productividad tanto como un ajuste morfológico a la sequía.

Palabras claves: ángulo foliar, pubescencia foliar, proporción de isótopos de carbono, zonas áridas, precipitación.

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INTRODUCTION

Along gradients of decreasing precipitation in arid land ecosystems, plant species show variation of energy-balance related leaf characteristics (e.g.,leaf pubescence, leaf angle, leaf size) in association with the increase of aridity (Comstock & Mahall 1985, Ehleringer 1980, 1981, 1988a, Ehleringer & Comstock 1989, Ehleringer & Cook 1987, Shaver 1978, Smith 1978). We infer that these changes in leaf characteristics play a role in enhancing plant performance or survival.

Several studies have investigated the ecological and adaptative aspects of leaf pubescence in desert plants (Ehleringer 1981, 1982, Ehleringer et al. 1976, 1981, Ehleringer & Björkman 1978, Harrington & Clark 1988, Smith & Nobel 1977, 1978). In *Encelia*, a genus of suffrutescent, drought-deciduous shrub species, there is a progressive replacement of one species by another along a gradient of increasing aridity in both North and South America, such that species on drier sites possess more pubescent leaves (Ehleringer et al. 1981). According to these authors, leaf pubescence increase with aridity at the same rate in both continents. Ehleringer and Mooney (1978) demonstrated that leaf pubescence in *Encelia farinosa* was an effective means of reducing leaf temperature and it had three major effects: 1) reduced transpiration rate under water-limiting conditions, 2) increased rates of carbon gain because leaf temperature was closer to temperature optimum for photosynthesis, and 3) provided the leaf with a means of avoiding high lethal leaf temperatures. In common-garden studies, Ehleringer and Cook (1990) showed that the presence of pubescence resulted in higher plant growth rates than in *Encelia* lacking pubescence.

Similar to increases in leaf pubescence, increased leaf angle will result in a decrease in the amount of irradiance incident on a leaf. As a consequence, leaf angle also has a significant influence on leaf temperature and on the processes of photosynthesis and transpiration (Comstock & Mahall 1985, Ehleringer 1981, Ehleringer & Werk 1986).

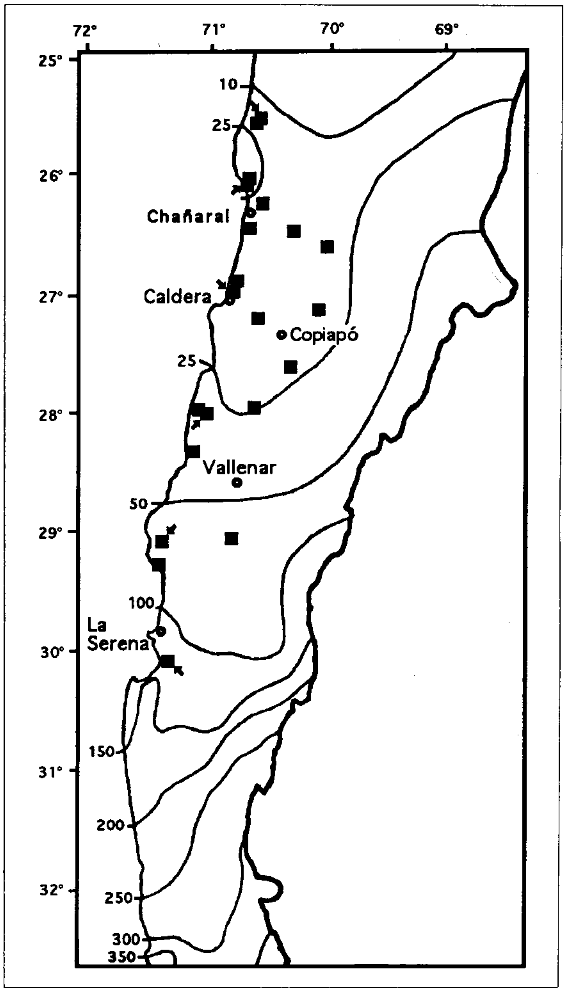

Fig. 1: Location of 21 *Encelia canescens* populations studied between latitude 25°23'S and 30°00'S in north-central Chile. The arrows show populations sampled for water potential, leaf angle, and growth form characteristics. Isohyets for mean annual rainfall from Borcosque & Zárate (1972) and Huber (1975).

Localización de 21 poblaciones de *Encelia canescens* estudiadas entre las latitudes 25°23'S y 30°00'S en el norte-centro de Chile. Las flechas indican las poblaciones muestreadas para potencial hídrico, ángulo foliar, y características de forma de crecimiento. Isohietas para precipitación media anual según Borcosque & Zárate (1972) y Huber (1975).

A reduction in the total amount of irradiance on a leaf as a consequence of increasing leaf angle and/or pubescence may also be an effective means of decreasing risk of photochemical damage for a supersaturating photon flux (i.e., photobleaching or photoinhibition) (Ludlow & Björkman 1984, Ludlow & Powles 1988).

Leaf size may also have an important functional role in the regulation of leaf temperature in desert plants (Smith 1978). Small leaf size is common among desert plants, and it has been suggested that a small leaf size prevents overheating and acts to increase water-use efficiency by reducing the amount of water transpired per amount of CO_2 fixed during photosynthesis (Smith 1978, Taylor 1975). In contrast, a large leaf size in combination with high transpiration rates, may also act to reduce leaf temperatures (Smith 1978).

Encelia species from North American deserts are well studied with respect to leaf characteristics along aridity gradients. Hence, the presence of *Encelia* in South American deserts provides a unique opportunity to compare there leaf-level patterns for a separate, but similar gradient. With this purpose, we evaluated leaf characteristics of *Encelia canescens* along an aridity transect in north-central Chile.

Marticorena & Quezada (1985) recognize 4 varieties of *Encelia canescens* (*E. canescens* Lam. var. *canescens*, *E. canescens* var. *oblongifolia* (DC) Blake, *E. canescens* var. *tomentosa* (Walp.) Ball, and *E. canescens* var. *lanuginosa* Johnston. These varieties occur from the matorral vegetation of Termas del Soco (30°43'S) to desert regions near Paposo (25°23'S), in Chile (Ehleringer et al. 1981). The four varieties differ with respect to plant height, degree of pubescence and leaf size: from short plants, with very thick cottony tomentum and small leaves in the northernmost *E. canescens* var. *lanuginosa,* to tall plants, with scarce pubescence and large leaves in the southernmost *E. canescens* var. *oblongifolia* (Ehleringer et al. 1981, Johnston 1929).

METHODS

Field observations and measurements were made on *Encelia canescens* shrubs growing under natural conditions between 25°23' and 30°00'S during late winter of 1991 (September 2 to 9) (Fig 1). The mean annual rainfall in north-central Chile is between 250 mm at 32° and less than 10 mm at 25°S (Borcosque & Zárate 1972, di Castri & Hajek 1976). Additionally, the predictability of precipitation decreases as mean annual rainfall declines (Rundel et al. 1991). However, in coastal mountains between 250 to 800 m, the fog contribution to the total precipitation can be as much as 661 mm in comparison with 184 mm by rainfall in Fray Jorge National Park (30°34'S) (Arévalo 1975) and 110 mm versus 2.2 mm near Antofagasta (23°40'S) (Muñoz 1967). The mean annual temperature is 14.8°C in La Serena (29°54'S) and 17.4°C in Taltal (25°25'S). The minimum and maximum mean temperature are 11.2° and 18.9° in La Serena, and 14.5°C and 22.0°C in Taltal (di Castri & Hajek 1976). Rainfall data for 1991 are available from Dirección General de Aeronáutica Civil (1991).

At intervals of approximately one degree of latitude, 6 *E. canescens* populations were sampled for midday leaf water potential, leaf angle, and characteristics of growth

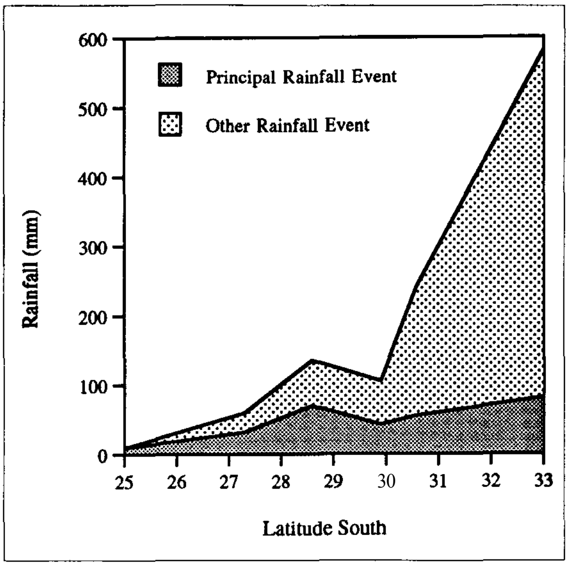

Fig. 2: Rainfall during 1991 between 25° and 33°S in north-central Chile. Principal rainfall event is the maximum precipitation in 24 h during 1991. Data from Dirección General de Aeronáutica Civil (1991) and CONAF IV-Región (unpublished data).

Precipitación durante 1991 entre los 25° y 33°S en el norte-centro de Chile. El principal evento de precipitación se refiere al agua caída máxima en 24 h. Datos de la Dirección General de Aeronáutica Civil (1991) y CONAF IV-Región (datos no publicados).

form. Leaf angles of 10 plants per population (6 replicates per plant) were estimated using a hand-held clinometer (Suunto Instruments, model PM-5/360 PC). Additionally, a total of 21 populations along the transect were sampled for subsequent lab studies.

Water potentials were measured using a Scholander-type pressure chamber. Sample size was 10 shrubs per population.

Leaf absorptance of solar radiation was measured using a 23-cm diameter Ulbricht integrating sphere, that had been coated on the inside with a thin layer of magnesium oxide. Monochromatic 625 nm light to the integrating sphere was provided by a monochromator (Ehleringer 1981). Total leaf absorptance of solar radiation (400-3,000 nm waveband) was calculated from the leaf absorptance to the 400-700 nm waveband ($A_{400\text{-}700}$) as:

$$A_{400\text{-}3,000} = 0.73\ A_{400\text{-}700} - 11.9 \quad \text{(Eq. 1)}$$

Leaf area was measured using a leaf area meter (LICOR Instruments, Lincoln, Nebraska, USA).

Carbon isotope ratios ($\delta^{13}C$) were measured on dried, ground leaf tissues using an in-vial sealed combustion technique (Ehleringer & Osmond 1991). Isotope ratios were measured on a Finnigan MAT delta S isotope ratioing mass spectrometer. Results are expressed in parts per thousand (‰) relative to the PDB (Pee Dee Belemnite) standard. The repeatability error of each sample was 0.11‰.

Nitrogen and carbon content values of leaf tissues were measured on an elemental analyzer (2400 CHN Elemental Analyzer, Perkin-Elmer, Norwalk, Connecticut). The precision of each measurement is 0.3%.

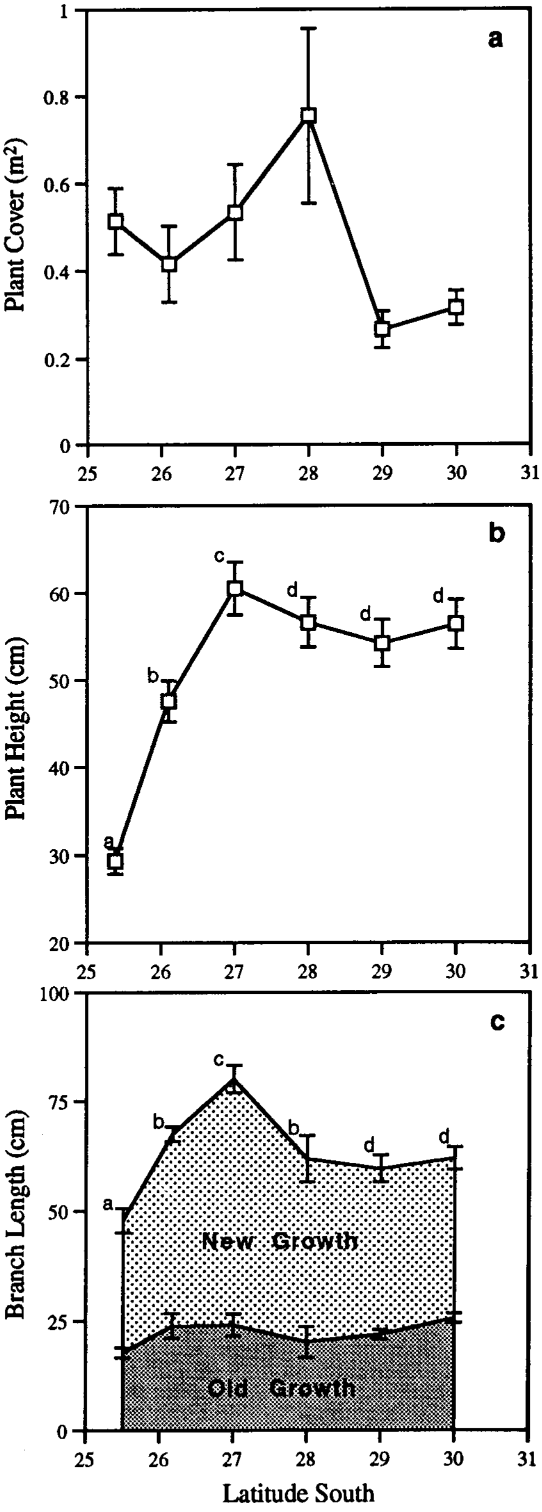

Fig 3: Plant cover (a), plant height (b) and branch length (c) of *Encelia canescens* in north-central Chile during September 1991. Vertical bars represent ±1 standard error. Same letters over points show no significant differences with Tukey test.

Cobertura (a), altura de la planta (b) y longitud de las ramas (c) de *Encelia canescens* en el norte-centro de Chile durante Septiembre 1991. Barras verticales representan ±1 error estándar. Las mismas letras sobre los puntos indican diferencias no significativas con el test de Tukey.

RESULTS

Climatic gradient

The total rainfall during 1991 (Rainfall_{1991}) was positively correlated with latitude (LS) (Fig. 2) as:

$$\text{Log}_{10}(\text{Rainfall}_{1991}) = 0.208 * \text{LS} - 4.046$$
$$R^2 = 0.93,\ P < 0.001 \quad \text{(Eq. 2)}$$

Because meteorological stations are limited along the transect studied, and do not permit a detailed analysis at the population level, we preferred to use latitude in subsequent analysis. During 1991, at latitudes lower (further North) than 29°, the principal rainfall event (i.e., maximum rainfall in 24 hours) constituted over 50% of total annual rainfall (Fig. 2). In north-central Chile, most of this rain fell during winter, and at latitudes lower than 31°, over 96% of total rainfall occurred between June and July.

During 1991, the mean annual temperature was cooler than the long-term average along the latitudinal gradient studied. For instance, at La Serena (29°54'S), the values were 13.9°C for 1991 compared with a long-term mean of 14.8°C and, at Copiapó (27°18'S), 15.4°C (1991) versus 16.3°C (long-term). During the period of maximum growth for *Encelia canescens* (August - September, F.A. Squeo, unpublished data), mean temperatures were 11.7°C and 12.8°C in La Serena and Copiapó, respectively. The maximum mean temperatures during this same period were 15.4°C and 20.8°C for the two respective sites.

Growth form characteristics

Both plant cover ($F_{(5,9)}= 2.09$, P= 0.08) and old branch length (i.e., old growth) ($F_{(5,9)}=$ 1.92, P= 0.11) showed no significant differences among populations along the transect (Fig. 3a, c). On average, plant cover was 0.46 m^2 (SE=±0.05, n= 59) and old branch length was 22.2±0.89 cm (n= 59, range= 9.5 to 42.5 cm).

New growth as well as plant height showed significant latitudinal variation ($F_{(5,9)}= 10.43$ and 12.28, P < 0.001, respectively) (Fig. 3b, c). Both new growth and plant height increased with precipitation in the three most northern populations, but these trends were not significant in the other populations. These data suggest two distinct life forms of *E. canescens*. In one group, from regions of less than 25 mm mean annual precipitation (less than 50 mm in 1991), plant height was strongly dependent on new growth (Fig. 4). Plant height of the second group is independent of new growth and occupies regions over 25 mm of annual precipitation (ranges from 50 to 150 mm in 1991).

Leaf characteristics

Populations in the more arid latitudes exhibited significantly steeper leaf angles (Fig 5a). Leaf angles of the northernmost population (25°30'S) were nearly 75°, whereas leaf angles of the population at 30°S were less than 50°. These data suggest strong differences in the midday irradiance incident on a leaf. The cosine of the angle of incidence, a direct measure of the fraction

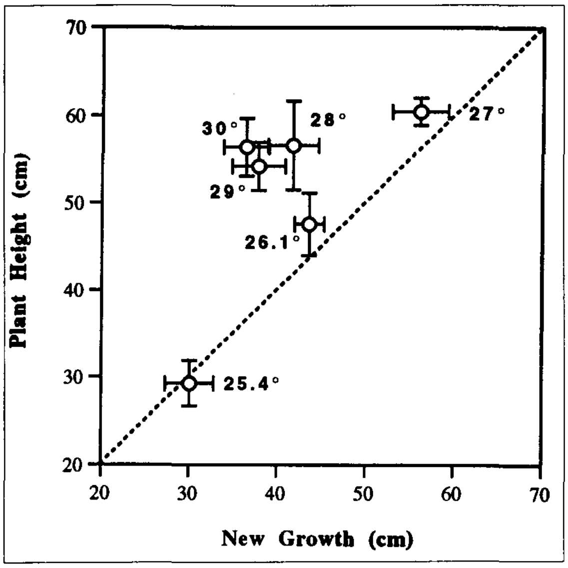

Fig 4: Plant height versus new growth of *Encelia canescens* in north-central Chile during September 1991. Vertical and horizontal bars represent ±1 standard error.

Altura de la planta versus crecimiento nuevo de *Encelia canescens* en el norte-centro de Chile durante Septiembre de 1991. Barras verticales y horizontales representan ±1 error estándar.

of solar radiation incident on a leaf, was 25.9% at 25°30' in contrast to 64.3% at 30°S.

No significant latitudinal correlation was observed with leaf absorptance (Fig. 5b). Leaf absorptance population means were between 60.2% and 78.6% over the latitudinal gradient. The overall average of leaf absorptance in *E. canescens* was 70.8±1.1% (n=20 populations). Both leaf angle and absorptance of populations at 28°S deviated most from the species average (Fig 5a,b). In this same region (i.e., «La Travesia»), rainfall in 1991 was close to 100 mm, which is 2-3 times higher than the long-term mean annual precipitation at this latitude. The population at 27°04'S showed the lowest absorptance values (60.2±6.8%), possibly because these plants were growing on a dry coastal dune.

Leaf area and leaf weight/area ratio were not significantly correlated with latitude (r= -0.32 and r=0.03, P > 0.05, respectively) (Fig 6). On average, individual leaf area was 4.73 ±0.40 cm^2 (n=20, range= 2.11 to 10.50) and leaf weight/area ratio was 12.52 ±0.63 mg cm^{-2} (n=20, range= 7.51 to 18.14). The population at Pan de Azúcar National Park (26°07'S, 70°35'W), growing close to a wash, showed the largest mean leaf area (10.5 cm^2).

Neither leaf nitrogen content nor carbon/nitrogen ratio showed significant correlations with latitude (r= 0.14 and r= 0.08, P

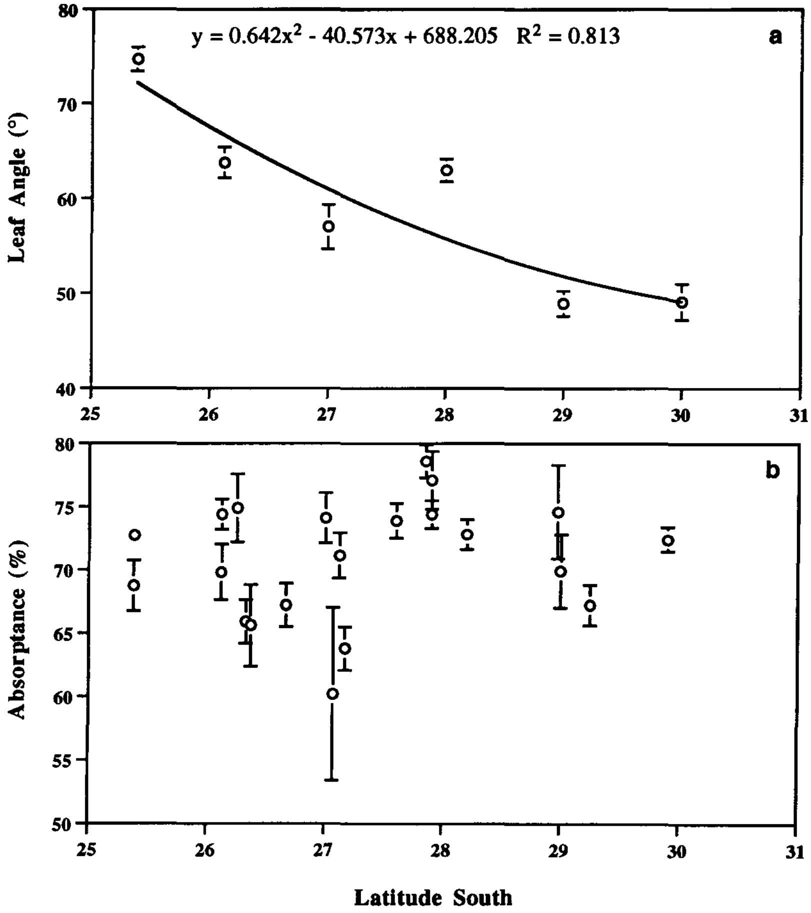

Fig. 5: Leaf angle (a) and leaf absorptance at 400-700 nm (b) of *Encelia canescens* in north-central Chile during September 1991. Vertical bars represent ±1 standard error.

Angulo foliar (a) y porcentaje de absorbancia foliar a 400-700 nm (b) de *Encelia canescens* en el norte-centro de Chile durante Septiembre de 1991. Barras verticales representan ±1 error estándar.

> 0.05, respectively) (Fig. 7a, b). On average, leaf nitrogen content was 2.35 ±0.15% (n= 21, range= 0.87 to 3.55) and the carbon/nitrogen ratio was 16.42 ±1.40 (n=21, range= 10.12 to 38.89)

Leaf carbon isotope ratios ($\delta^{13}C$) were not correlated with latitude (r= -0.12, P > 0.05) (Fig. 7c). *Encelia canescens* $\delta^{13}C$ values were less than -26 ‰, except in four populations located between 26°-27°S. Three of these populations were located in the more arid interior desert (i.e., between 650 to 1780 m) and the last population was growing on a dry coastal dune (the same population with the lowest leaf absorptance in Fig. 5b).

Leaf water potential at midday showed significant differences between populations in the transect ($F_{(4,9)}$= 37.10, P < 0.001) (Fig. 8). The two northern *Encelia canescens* populations showed extremes values. The population at Pan de Azúcar National Park (i.e., 26°07'S) had the highest water potential (-1.15 ±0.15 MPa, n=10) while the Taltal population (25°23'S) exhibited the lowest water potential (-3.14 ±0.38 MPa, n=10). These values suggest different local water supplies and/or a different potential evapotranspiration rate. However, fog was dense in Pan de Azúcar National Park, in contrast with the drier habitat for Taltal's populations.

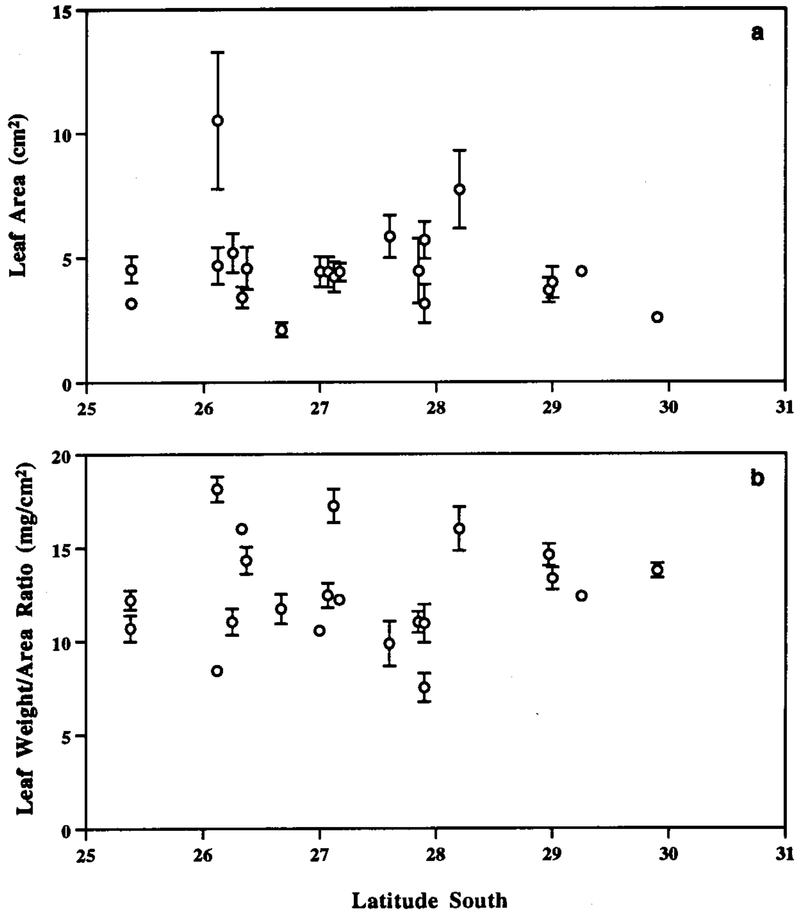

Fig. 6: Leaf area (a) and leaf weight/area ratio (b) of *Encelia canescens* in north-central Chile during September 1991. Vertical bars represent ±1 standard error.

Area foliar (a) y relación peso/area foliar (b) de *Encelia canescens* en el norte-centro de Chile durante Septiembre de 1991. Barras verticales representan ±1 error estándar.

Leaf temperature

Leaf energy budget models, as originally developed by Rashke (1960) and Gates (1962, 1980), can be used to explore the interactions between various modes of energy exchange and leaf temperature. Leaf energy exchange equations were used to calculate energy budget relationships between leaf temperature, leaf absorptance and leaf angle (Fig. 9). The wavelengths important for heat-balance studies are those between 400 and 3,000 nm, whereas the 400-700 nm waveband is important in photosynthesis. We used equation 1 to convert between $A_{400\text{-}3{,}000}$ and $A_{400\text{-}700}$.

The energy-balance simulations showed that both leaf angle and total leaf absorptance significantly influence leaf temperature (Fig 9a) and leaf transpiration rate (Fig. 9b). However, a change in leaf angle from 50° to 75° at an $A_{400\text{-}700}$ of 50% ($A_{400\text{-}3{,}000}$= 24.6%) decreased leaf temperature by only 0.7°C, compared with a 1.3°C change with an $A_{400\text{-}700}$ of 80% ($A_{400\text{-}3{,}000}$= 46.5%). A similar pattern was observed for transpiration, whereby transpiration rates decreased 5.4% and 9.0%, respectively.

DISCUSSION

Growth form

Over the latitudinal gradient studied, two distinct growth forms are associated with variations in rainfall patterns. In the most arid regions, new vegetative growth and plant height are correlated in approximately a 1:1 manner, while in regions where a relatively greater amount of rainfall occurs each year the plant height is independent of new growth. This results in plants becoming more herbaceous as rainfall becomes less predictable, yet, plant height has been included as a character to distinguish among *Encelia canescens* varieties (Johnston 1929).

Leaf characteristics

In contrast with North American *Encelia* species (Ehleringer et al. 1981), our data show that leaf absorptance in *E. canescens* was not associated with aridity in the year our studies were conducted. Ehleringer et al. (1981) showed that leaf absorptance in the 400-700 nm waveband for *Encelia* species (including *E. canescens*) was not correlated with mean annual precipitation at locations with rainfall greater than 90 mm (mean absorptance was close to 85%). However, in regions with mean annual precipitation less than 50 mm, leaf absorptance decreased with decreasing precipitation to a value as low as 44%. In this same work, Ehleringer et al. showed that *E. canescens* from northern populations of South America (26°S), when grown under well-watered conditions in a greenhouse, have sparse leaf pubescence and a high absorptance of 80%. In contrast, under droughted greenhouse conditions, the leaf pubescence became dense and absorptance decreased to 53%. We observed no correlation between leaf absorptance and precipitation at our sites. We suspect that the rainfall during 1991 was sufficiently high that the patterns proposed by Ehleringer et al. (1981) were not exhibited. However, leaf absorptances in *E. canescens* (this study) were very close to means reported by Ehleringer & Comstock (1989) for the Chilean (81%, range from 75 to 84%) and the California coastal scrub (82%) vegetation types, and for the Chilean (82%) and the California evergreen sclerophyllous (78%) vegetation types. Comparing these community-level means as well as those for plants along the Wasatch Front of Utah (Ehleringer 1988b), Ehleringer & Comstock (1989) proposed that no large changes in leaf absorptance should occur in a major fraction of the flora until seasonal drought effects become severe.

Reduction in the amount of solar radiation on the leaf can be accomplished by means other than reduced leaf absorptance. Changes in leaf angle may result in effects similar to changes in leaf pubescence. Along a precipitation gradient in the Wasatch Mountains of Utah, leaves of shrub and herb species at the most arid sites have steeper leaf angles than those from mesic

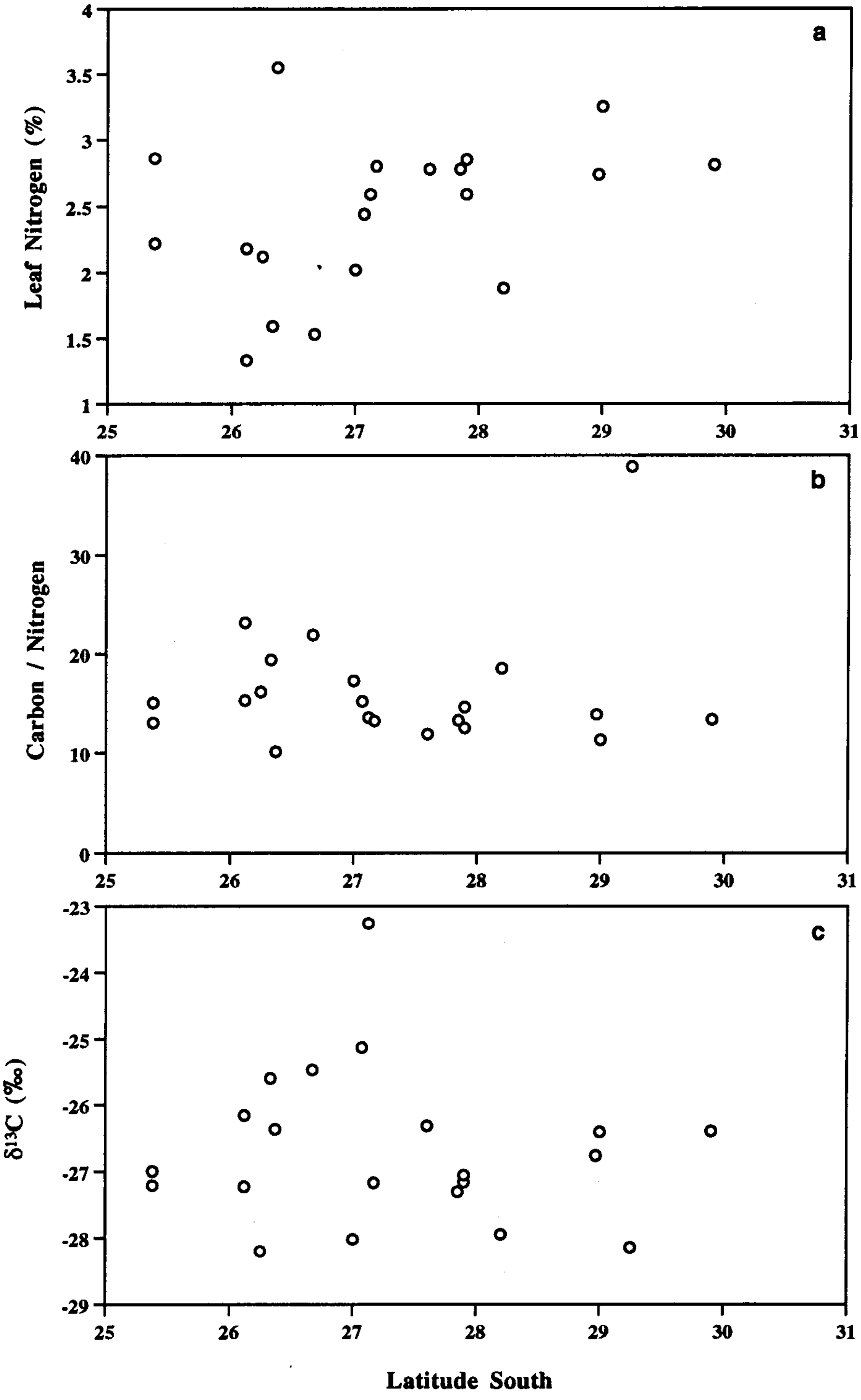

Fig. 7: Leaf nitrogen content (a), carbon/nitrogen ratio (b) and leaf carbon isotope ratios (c) of *Encelia canescens* in north-central Chile during September 1991.

Contenido de nitrógeno foliar (a), proporción de carbono/nitrógeno (b) y proporción de isótopos de carbono (c) de *Encelia canescens* en el norte-centro de Chile durante Septiembre de 1991.

sites (Ehleringer 1988b). In the warmer Mojave and Sonoran Deserts, leaf angles for evergreen-leaved perennials tend to be more steeply inclined (49.2±10.3°, n=3 species) than those for deciduous-leaved perennials (29.7±2.4°, n=6) (Ehleringer & Werk 1986).

In *E. canescens*, leaf angle increased with aridity along the entire gradient. These leaf angles (49° - 75°) are steeper than those reported by Ehleringer (1988a) for *E. farinosa* (27°) and *E. frutescens* (25°) from Death Valley, California (35°45'N - 116°20'W, 300 m). The potential midday solar radiation incident on a *E. canescens* leaf changed from 64% to 26% along the transect. These values are lower than the impact of leaf angle on *E. farinosa* (89%) and *E. frutescens* (91%). Our results suggest that *E. canescens* is using an alternative energy-budget variation than the North American *Encelia* species. In addition to increased leaf pubescence under drought conditions (Ehleringer et al. 1981), *E. canescens* may further reduce the incoming solar radiation incident through steeper leaf angles. Ehleringer (1988a) used leaf energy budget modelling to show two patterns in *Encelia* species: in *E. farinosa*, the amount of energy absorbed is decreased by a reduction in leaf absorptance, while in *E. frutescens*, the amount of energy dissipated is increased by transpiration. Using a similar modelling effort, *E. canescens* is predicted to show similar patterns as *E. farinosa* but in this case the amount of energy absorbed is decreased through an increase in leaf angle.

Comstock & Mahall (1985) calculated that a transpirational saving, resulting from increasing leaf angle under water-stress, could be important in improving the probability of plant survival during extreme water stress periods. In E. *canescens* with a leaf absorptance of 71%, we calculated that a change in leaf angle from 50° to 75° would result in a transpiration reduction of close to 8% and a reduction of leaf temperature by 1.2°C. Reductions in the amount of absorbed solar radiation by a leaf may result in: 1) a higher intercellular CO_2 concentration and 2) an increased water-use efficiency via decreased transpiration. Similar to the adaptive significance of leaf hairs proposed by Ehleringer & Mooney (1978) an increase in leaf angle may be an effective means of reducing transpiration rate under water-limiting conditions and prolonging photosynthetic activity into the drought period.

Under similar external partial pressures of CO_2, carbon isotope ratio analysis may be used for long-term estimates of intercellular CO_2 concentration (c_i) and water-use efficiency (Farquhar et al. 1989). A 1‰ change in carbon isotope ratio is equivalent to approximately a 15 $\mu l\ l^{-1}$ difference in c_i (Ehleringer et al. 1992) and a decrease in the operational c_i value indicates an increase in the stomatal diffusion limitation to photosynthesis and also an increase in leaf water-use efficiency (unless offset by a substantial rise in leaf temperature).

The mean carbon isotope ratio of *Encelia canescens* in this study (i.e. -26.70±0.27‰, n=20) was similar to those values reported by Ehleringer (1988a) for southwestern North American desert *E. frutescens* (-28.3) and *E. farinosa* (-26.7‰), and close to the average for lowland C_3 species (-27‰)

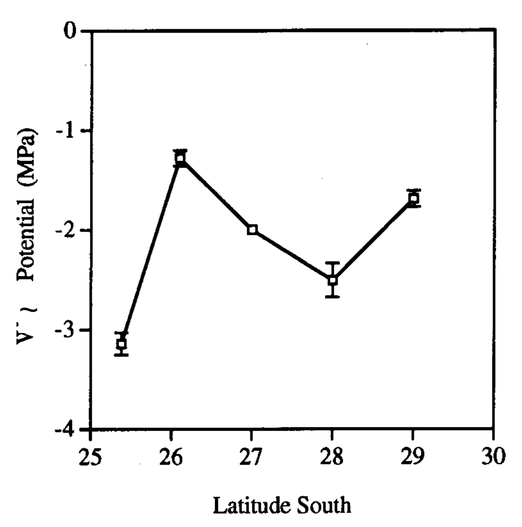

Fig. 8: Water potential at noon of *Encelia canescens* in north-central Chile during September 1991. Vertical bars represent ±1 standard error.

Potencial hídrico al mediodía de *Encelia canescens* en el norte-centro de Chile durante Septiembre de 1991. Barras verticales representan ±1 error estándar.

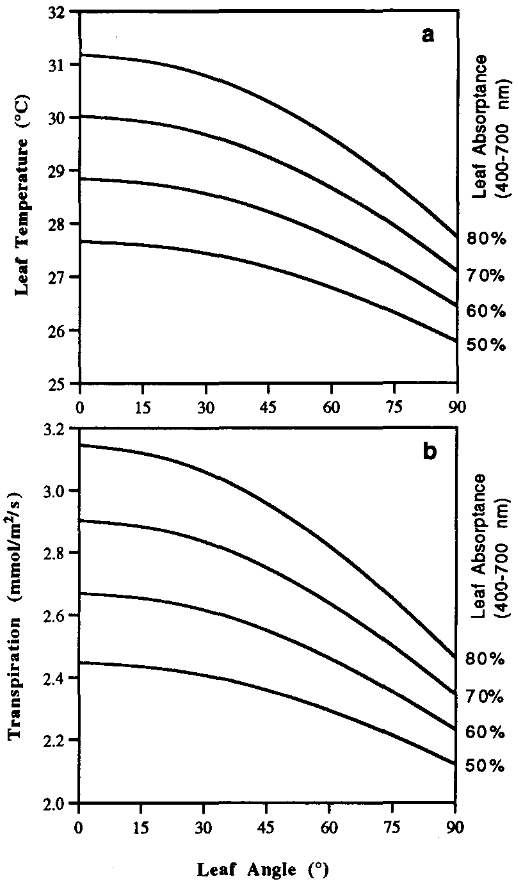

Fig. 9: Leaf temperature (a) and transpiration (b) of a hypothetical leaf of *Encelia canescens*. Conditions used in the simulation were: total solar radiation= 1,000 W m^{-2}, surface reflected solar radiation= 15% of total solar radiation, air temperature at 20 m= 10°C, air temperature at leaf height= 25°C, soil surface temperature= 50°C, relative humidity= 30%, wind speed= 1 m s^{-1}, leaf width= 2 cm and total leaf conductance= 0.1 mol m^{-2} s^{-1}.

Temperatura foliar (a) y transpiración (b) de una hoja hipotética de *Encelia canescens*. Las condiciones usadas en las simulaciones fueron: radiación solar total= 1.000 W m^{-2}, radiación solar reflejada en el suelo= 15% de la radiación solar total, temperatura del aire a 20 m= 10°C, temperature del aire a la altura de la hoja= 25°C, temperatura en la superficie del suelo= 50°C, humidad relativa= 30%, velocidad del viento= 1 m s^{-1}, ancho de la hoja= 2 cm y conductancia foliar total= 0,1 mol m^{-2} s^{-1}.

reported by O'Leary (1988). The predicted intercellular CO_2 concentration (c_i) for *E. canescens* based on equations from Farquhar et al. (1989) and an actual ambient CO_2 concentration (c_a) of 350 µl l^{-1} was 225 µl l^{-1}. This compares with the c_i values, reported by Ehleringer (1988a) using c_a of 340 µl l^{-1}, of 218 and 242 µl l^{-1} for *E. farinosa* and *E. frutescens*, respectively. No differences in carbon isotope ratios among *E. canescens* populations suggest similar water-use efficiency along the latitudinal gradient studied if we can assume similar vapor pressure deficit gradients. In contrast, more positive carbon isotope ratios were observed in plants from the interior desert (-24.8±0.76‰, n=3 populations) when compared to coastal populations (-27.2±0.34‰, n=6) at 26-27°S. This difference suggests long-term lower c_i and possibly lower conductance and transpiration rates in interior desert populations. Similar differences and conclusions were reached by Ehleringer & Cooper (1988) working on Mojave/Sonoran desert vegetation in Arizona (34°57'S, 114°25'W, 657 m). These authors found that species growing in a wash microhabit had a mean value of -26.6‰ in comparison with -24.2‰ for the slope microhabitat. That is, c_i values decreased with decreasing soil water availability between wash and slope microhabitats. They concluded that both the stomatal limitations and water-use efficiency of a species increased as soil water availability decreased.

For a diverse group of plants from Pan de Azúcar National Park (26°10'S, 70°35'W, 70 m), J.R. Ehleringer (unpublished data) measured a mean carbon isotope ratio of C_3 species at -22.64±0.45‰ (n=17 species, range: -20.14 to -25.27‰) in July 1989, and -24.71±0.98‰ (n=3) in December 1990. Excluding likely C_3/CAM species (sensu Griffiths 1991), the mean carbon isotope ratio for July 1989 was -24.39±0.72‰ (n= 8). We found lower carbon isotope ratio values (i.e., -26.16‰ and -27.22‰) for plants from this same area in September 1991. These data suggest plants were exposed to less drought during our sampling period. In comparison with other carbon isotope ratio data from Chile, *Encelia canescens* showed lower mean values than C_3 Portulacaceae from Cordillera de Los Andes at 18°S and 28°S, and over 3300 masl (i.e. -25.1±1.0 ‰, n= 10) (Arroyo et al. 1990). Higher carbon isotope ratio values were expected in high-elevation species (Körner et al. 1991).

Because Rubisco is between 40-80% of total soluble leaf protein in C_3 plants (Huffaker 1982), changes in rates of photosynthesis may reflect changes in leaf nitrogen contents (Friend et al. 1989). However, we found no latitudinal differences in leaf nitrogen contents. Our average values for leaf nitrogen content (2.35±0.15%) and carbon/nitrogen ratio (16.42±1.40) are close to values for deciduous species from chaparral shrubs of California (Williams et al. 1987). These authors reported leaf nitrogen contents between 1.65 and 2.63% and carbon/nitrogen ratios of between 17.5 and 29.8 for deciduous species when compared to 46.58% and 35.02 for evergreen species. Körner et al. (1991) found a positive correlation for lowland species between leaf nitrogen content and carbon isotope ratio; decreased carbon isotope ratio was correlated with low nitrogen content. The lack of significant latitudinal differences in nitrogen content and carbon isotope ratios for *Encelia canescens* could be interpreted as indicating no differences in potential rates of photosynthesis.

In conclusion, increases in leaf angle, in contrast with leaf pubescence, could be interpreted as a strategy for optimization of productivity of E. *canescens* and not only as a means of morphologically adjusting to the onset of drought.

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