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DIFFERENCES IN CARBON ISOTOPE DISCRIMINATION BETWEEN SEEDLINGS AND ADULTS OF SOUTHWESTERN DESERT PERENNIAL PLANTS

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ABSTRACT—Carbon isotope discrimination (Δ) is associated with long-term water-use efficiency (ratio of photosynthesis to transpiration), and varies within and among desert plant species. The variation of Δ within aridland perennial plants may be related to life-history class attributes, while differences in Δ between long- and shorter-lived species may be based on life-form dependent tradeoffs of growth and survival. We examined these patterns in two desert environments and asked if life-history class and life-form related differences in Δ occurred in *Coleogyne ramosissima*, *Larrea tridentata*, *Encelia farinosa*, *Ambrosia dumosa* and *Gutierrezia microcephala*. The mean Δ values of seedlings were greater than those of adults for all species except *G. microcephala*. The difference between life-history classes may represent a shift from low water-use efficiency (high Δ) during establishment to high water-use efficiency (low Δ) as an adult. Our results suggest that this shift is based on genetically- and/or environmentally-induced ontogenetic changes in plant metabolism. Such changes may be beneficial if a high Δ and low Δ are favored at different developmental stages. Interspecific comparisons showed that adult long-lived plants had lower Δ values than adults of shorter-lived species in the same community, but for seedlings the same pattern was found for only one pair of species. Thus the previously shown trend for long-lived species to have lower Δ values than shorter-lived species may depend on the stage of development.

In desert environments where water availability is the most limiting resource to plant productivity and reproduction (Fischer and Turner, 1978), plant water use traits may be strongly influenced by selection (Cohen, 1970). The natural variability of these traits may provide information with respect to differences in selective processes both within and among species. For C$_3$ plants carbon isotope discrimination (Δ) is related to long-term water-use efficiency (Farquhar et al., 1989), and studies have found this trait to be quite variable in aridland species (Ehleringer and Cooper, 1988; Smedley et al., 1991).

Although the use of stable carbon isotopes in plant research has primarily focused on leaf level applications, this technology can also allow the pursuit of broader ecological and evolutionary questions. Recently, a number of studies have addressed the significance of variation in stable carbon isotope composition within and between native plant species (Ehleringer and Cooper, 1988; Toft et al., 1989; Geber and Dawson, 1990; Medina et al., 1991; Smedley et al., 1991). These investigations suggest that the variation in Δ within aridland perennial plants may be related to distinct life-history attributes, such as differences in developmental stage (Donovan and Ehleringer, 1991) and life expectancy (Ehleringer and Cooper, 1988; Smedley et al., 1991).

Donovan and Ehleringer (1991) reported that Δ for two Great Basin species, *Chrysothamnus nauseosus* and *Salix exigua*, was significantly greater for juvenile plants than for adult plants growing in the same habitat. Despite having a similar water status, the difference in Δ values between classes indicated that juvenile individuals

were less water-use efficient (corroborated by gas exchange measurements) and were operating at a higher internal CO_2 concentration relative to mature plants. Donovan and Ehleringer (1991) suggested that the difference in mean Δ values between life-history classes may have resulted from physiological changes during development (which can be genetic and/or environmental in origin). A lower Δ for the adult classes could also result via mortality selection eliminating the highest Δ juveniles prior to maturity. However, to the contrary, Donovan and Ehleringer (1991) found that juveniles with lower Δ were less likely to survive in a dry microenvironment.

Physiological changes during the life-span of an individual might be expected to result in such patterns if these shifts are related to fitness differences and/or environmental influences. It has been shown that competition may favor low water use efficiency (high Δ individuals) in early development while individuals with greater water use efficiency (low Δ) may have an advantage after maturity (Cohen, 1970; Donovan and Ehleringer, 1991; Donovan and Ehleringer, 1992).

Differences in Δ values between long- and shorter-lived species of a community may be based on differing requirements for growth and survival between species. For example, annuals may show low water-use efficiency (high Δ) and rapid growth versus greater water-use efficiency (low Δ) and persistence through drought for perennials (Cohen, 1970). Indeed, studies have shown that longer-lived species have lower values of Δ than shorter-lived plants of the same community (Ehleringer and Cooper, 1988; Smedley et al., 1991). These differences however, have only been tested using mature individuals of each life form.

The intent of this study was to expand on earlier observations of intra- and interspecific variation in Δ, and to test the generality of those hypotheses which suggest that there are life-history class related changes in Δ and life-form dependent differences in Δ. We asked if the age-class differences in Δ occurred in additional desert perennial species from a broader range of desert environments including the Sonoran and Colorado Plateau deserts. We also compared Δ values of seedling classes for long-lived and shorter-lived species as an extension of the previously reported differences between mature individuals. Finally, we tested for microsite effects by examining correlations between seedlings and their nearest adult neighbor of the same species.

MATERIALS AND METHODS—Plant material was collected from a Colorado Plateau site (11.5 km N Lee's Ferry, Coconino Co., Arizona, 1,340 m) and a locality in the northwestern Sonoran Desert (4 km W, 14.5 km S Oatman, Mohave Co., Arizona, 425 m). The mean annual precipitation is similar for both sites (144 mm and 111 mm respectively), but mean annual temperature and average number of sub-freezing days differ greatly between sites (14.5°C, 100 days and 22.7°C, 7 days respectively). At each site the two dominant shrubs were sampled, each representing either a long-lived or shorter-lived component of the perennial vegetation (see Schuster et al., 1992). For the Colorado Plateau site these species were *Coleogyne ramosissima* Torr. (long-lived, >100 years) and *Gutierrezia microcephala* (DC.) Gray (shorter-lived, 20–30 years maximum). *Larrea tridentata* (DC.) Cov. represented the long-lived component of the Sonoran Desert (>700 years), and *Encelia farinosa* Gray the shorter-lived species (30 to 50 years maximum). Also included in our survey was *Ambrosia dumosa* (Gray) Payne, a shorter-lived perennial (25 to 35 years) from a Mojave Desert region (Death Valley, California; 19.3 km W, 6.5 km N Shoshone, Inyo Co., California, 907 m) with predominantly winter precipitation (annual means: rainfall 51 mm; temperature 24.9°C; 14 sub-freezing days).

Leaf samples from seedlings and their nearest adult plant of the same species ($n = 15$ to 30 per class) were collected on the same date with the exception of *A. dumosa* for which seedling and adult samples were chosen randomly within the population. Within a site each species was sampled at different dates due to variation in the timing of seedling emergence (Table 1). The term seedling refers to plants less than one year of age, with the exception of *C. ramosissima*. The "seedlings" of this species were the youngest plants of the populations and only a few centimeters tall, but they could not unequivocally be declared first-year plants. These individuals were not reproductively mature, and ring counts from other *C. ramosissima* of this size suggested that these individuals were no more than three years old. The term seedling is used here only for simplicity.

Leaf samples were oven dried, ground with mortar and pestle, and analyzed for carbon isotope ratio on a Delta-S mass spectrometer (Ehleringer and Osmond, 1989). The value for carbon isotope composition of a plant leaf (δ_p) is the molar abundance ratio of the plant leaf (R_p) relative to that of a standard (R_s), the PDB carbonate,

$$\delta_p = R_p/R_s - 1$$

Here, we have transformed δ_p to the notation of carbon isotope discrimination (Δ; Farquhar and Richards, 1984) by the equation

$$\Delta = (\delta_a - \delta_p)/(1 + \delta_p)$$

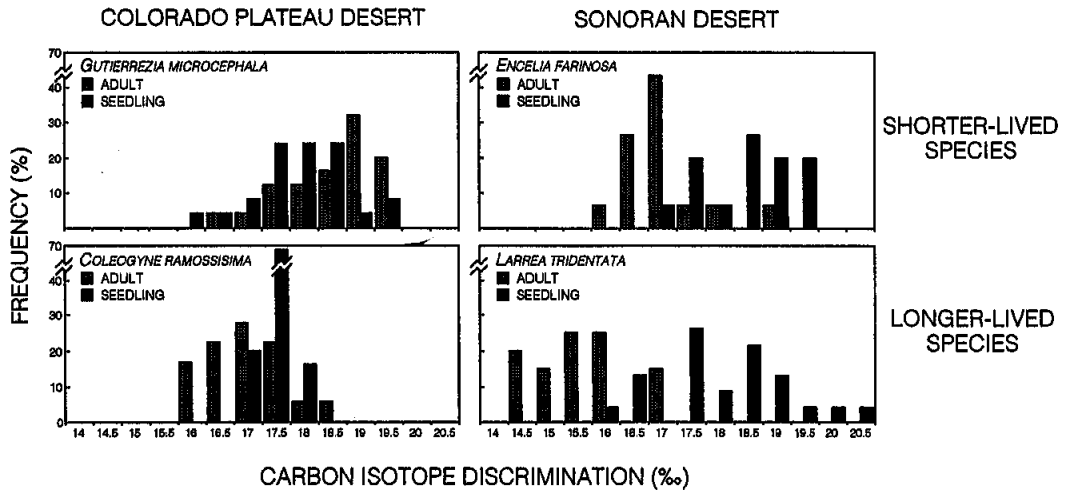In short, Δ is the difference of carbon isotope compo-

FIG. 1—The relative frequencies of carbon isotope discrimination values for seedling and adult life-history classes in four of the five perennial species examined in this study. *Ambrosia dumosa* is excluded, but shows a similar pattern to *Encelia farinosa* (see Table 1). Each species represents either a long- or shorter-lived component of their respective Colorado Plateau or Sonoran desert habitat.

sition between CO_2 in the ambient environment (δ_a) and that fixed into organic matter. Thus Δ represents discrimination against the heavy isotope during the process of photosynthesis; higher Δ values correspond to greater discrimination.

The distribution of Δ values for all groups did not differ from normality. Comparisons of the mean discrimination between groups were made using t-tests, except in cases where *C. ramosissima* seedlings represented a single group. Due to the inequality of variances between this group and all others, a test of means with unequal variances was used (Sokal and Rohlf, 1981). The significance of differences in variance were tested with a ratio test of the coefficient of variation (CV) for each group. This test eliminates biases based on differences in means (Sokal and Rohlf, 1981). Correlations (Pearson's product-moment) were calculated between the paired adult and seedling samples for each species with the exception of *A. dumosa* (see above).

RESULTS AND DISCUSSION—The intraspecific comparisons of mean Δ values showed significant differences between adult and seedling plants for all species. For *C. ramosissima*, *L. tridentata*, *E. farinosa*, and *A. dumosa*, the mean seedling discrimination was greater than the adult mean (Fig. 1; Table 1). A significant, but opposite pattern was found for *G. microcephala* (Fig. 1; Table 1). The CV of Δ for all species, except *C. ramosissima*, did not differ among seedling and adult components of the population. In the *C. ramosissima* population, adult plants had a significantly great-

er CV than the seedlings ($F = 2.68$; $P < 0.05$). The Δ values of paired adult and seedling plants growing in the same microsite were not statistically correlated for any species.

The interspecific comparison of long- and shorter-lived species must be interpreted with caution due to differences in the sampling dates between species. However, we found adult long-lived plants to have significantly lower Δ values than adults of shorter-lived species (Table 1), a pattern similar to that found in an interspecific comparison of these same four species in which adult plants were sampled on the same date (Schuster et al., 1992). Our data for seedlings is presented only as an initial estimate of differences between early growth stages of long- and shorter-lived species.

Mean Δ values differed between seedling classes of the Colorado Plateau species, but not of the Sonoran species. In the Colorado Plateau desert, seedlings of *G. microcephala* had a significantly higher mean Δ than the seedlings of *C. ramosissima* plants (Fig. 1; Table 1). *C. ramosissima* seedlings, however, had much less variation in Δ values than those of *G. microcephala* seedlings ($F = 2.87$; $P < 0.01$). In the Sonoran desert community, *E. farinosa* seedlings were not significantly different in mean or variance of Δ values compared to seedlings of *L. tridentata*. These values represent Δ at the period of earliest growth for

TABLE 1—Comparison of the mean Δ values (coefficient of variation in parentheses) for seedling and adjacent adult individuals (except *A. dumosa,* see text) of each species. Level of significance for seedling versus adult means are reported below each species column, and that for long-lived versus shorter-lived components of each community are reported to the side (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

	Long-lived species	Shorter-lived species	
	Coleogyne ramosissima (October)	*Gutierrezia microcephala* (July)	
Colorado Plateau			
Seedlings	17.72 (1.46)	18.15 (4.19)	*
Adults	17.26 (3.92) *	18.75 (4.87) **	***
	Larrea tridentata (October)	*Encelia farinosa* (March)	
Sonoran Desert			
Seedlings	18.35 (6.12)	18.77 (4.17)	NS
Adults	15.86 (5.02) ***	17.25 (4.28) ***	***
		Ambrosia dumosa (September)	
Mojave Desert			
Seedlings		19.95 (3.17)	
Adults		19.30 (3.90) *	

individuals, however, interspecific differences may reflect temporal variation in the growing environment resulting from differences in the timing of seedling emergence.

These patterns in the distribution of carbon isotope discrimination have been ascribed to differences in developmental stage (intraspecific), and life-form (interspecific). It has been suggested that these patterns may result from variation of the selection processes during the life-span of a species and between plant members of a community (Ehleringer and Cooper, 1988; Donovan and Ehleringer, 1991; Smedley et al., 1991; Donovan and Ehleringer, 1992). We have extended these investigations to comparisons within the Colorado Plateau and Sonoran desert regions, and for both long and shorter-lived species within these regions.

A number of studies have demonstrated that there is a negative relationship between Δ and the ratio of carbon assimilation to transpiration, (A/E or water-use efficiency; Farquhar and Richards, 1984; Hubick et al., 1986; Geber and Dawson, 1990; Johnson and Bassett, 1991). A positive association of Δ with development rate and growth has also been found (Condon et al., 1987; Geber and Dawson, 1990). As such, the higher Δ values of seedling plants for four of five species examined in this study suggest that A/E is lower and growth more rapid during the establishment stage of a plant's life than as an adult. Indeed, it has been proposed that a lower A/E may confer a selective advantage to arid-land plants when in competition and/or where rooting depths are shallow, such as found in early life stages (Cohen, 1970). At maturity, however, greater water use efficiency (low Δ) may be advantageous for survival through droughts and/or persistence of activity into a drought period (Cohen, 1970; Ehleringer and Cooper, 1988). We

have found a pattern of Δ variation consistent with these hypotheses in all but one species examined in this study. The opposite pattern, found in *G. microcephala,* remains unexplained and demonstrates the necessity for more detailed physiological and ecological investigations into these observations.

Donovan and Ehleringer (1991) proposed that the mechanisms for Δ differences between life-history classes may stem from environmentally induced changes and/or genetically induced ontogenetic shifts in physiology. An additional possibility is mortality selection, but in their study, mortality selection alone could not account for the changes in Δ between seedling and adult groups.

Determination of the mechanisms responsible for Δ differences between adult and seedling classes is beyond the scope of this study, but our results do provide some insights. In mortality selection the changes in mean Δ values between adult and seedling classes should be accompanied by a reduction in variance (Endler, 1986). However, a reduction in variance was not found for any of the species in this study (Fig. 1). Furthermore, for four of the five species, adult Δ values were outside the range of seedling Δ values (Fig. 1), and we did not find similarities between the adult and seedling plants growing in the same microenvironment. These results suggest that the Δ differences are due to genetically- and/or environmentally-induced ontogenetic changes in plant metabolic processes as opposed to changes based solely on mortality selection. Mortality selection, however, may be included as part of a multiple interaction as suggested by Donovan and Ehleringer (1991).

Without repeated sampling of life-history classes, it is difficult to determine the causes of variation in Δ between seedling and adult groups. However, the pattern of a greater mean Δ value for seedling plants found in four of five species in this study suggests the presence of some common mechanism which decreases mean Δ between seedling and adult phases of development. These shifts may be advantageous to plants that experience environments in which both high and low Δ are favored at different developmental stages of life.

Analogous to the differences in selection over the life-span of an individual are those which may occur between short- and long-lived species of a community. In two aridland communities Smedley et al. (1991) and Ehleringer and Cooper (1988) found that species Δ values varied based on life-form. These studies only examined mature plants of these communities, but our results suggest that differences at maturity may not reflect differences for all life-stages (Table 1). The seedlings of the long-lived *Coleogyne ramosissima* did have a lower mean Δ value than seedlings of the shorter-lived *Gutierrezia microcephala,* however, in the Sonoran desert habitat, this pattern was not found between the long-lived *Larrea tridentata* and the shorter-lived *Encelia farinosa.* These disparities beg further investigation.

The results presented here demonstrate age-class specific differences in Δ for a number of species and desert regions. They suggest that the intraspecific pattern of lower Δ values in seedling age-classes may be a wide-spread phenomenon among desert perennial plants. Our data also suggest that the trend for long-lived species of a plant community to have lower Δ values than the shorter-lived species may depend on the stage of development. Each pattern deserves more detailed studies to decipher the mechanisms responsible for these patterns and studies utilizing a larger number of species and a broader range of environments will help to determine if these trends are common in desert perennial species.

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