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Carbon isotope discrimination, water-use efficiency, growth, and mortality in a natural shrub population

Abstract In order to scale up from the ecophysiological characters of individual plants to population-level questions, we need to determine if character patterns in natural populations are stable through time, and if the characters are related to growth and survival. We investigated these questions in a 3-year study for one character, integrated water-use efficiency (WUE) as estimated by carbon isotope discrimination (Δ) in a population of the Great Basin shrub, *Chrysothamnus nauseosus*. WUE was a conservative character for a given plant within and across seasons, and a previously documented difference between two size classes (represented by juveniles and adults) was maintained; smaller juveniles had a lower WUE than larger adults. The lower WUE of juveniles was often accompanied by higher rates of photosynthesis and stomatal conductance as compared to adults even though juveniles generally had more negative xylem pressure potentials. Although many discussions of the role of WUE in natural populations have been based on the expectation that higher WUE (lower Δ) is generally associated with less growth, we found no such relationship for juvenile plants in this population (i.e. Δ was not positively correlated with height increase). In addition, juvenile plant mortality was not correlated with Δ. Although there were stable patterns of WUE for plants in this population, the positive correlation between WUE and size, and the lack of a negative correlation between WUE and height growth, make it unlikely that the WUE of an individual plant will be related in a simple manner to its growth and survival in the population.

Key words Carbon isotope discrimination · Growth mortality · Size · Water-use efficiency

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Introduction

Lack of water limits establishment and productivity of *Chrysothamnus nauseosus* (Pallas) Britt., a Great Basin shrub, and of many other arid and semi-arid plants (Noy-Meir 1973; Fisher and Turner 1978; MacMahon and Schimpf 1981; Caldwell 1985; Owens 1987; Donovan and Ehleringer 1991; Donovan et al. 1993; Donovan and Ehleringer 1994a). Variation in plant ecophysiological characters that relate to water use and water status may affect growth and survival. Within a population of *C. nauseosus*, variation in such characters has been documented by a comparison of plants from two size and life-history classes. Smaller shallow-rooted plants (non-reproductive, designated as juveniles) use summer rain when it is available, and experience large fluctuations in water availability through the growing season (Donovan and Ehleringer 1994b). In contrast, larger deeply rooted plants (reproductively mature, designated as adults) rely on soil moisture from winter recharge and do not experience large seasonal fluctuations in xylem pressure potentials (Branson et al. 1976; Flanagan and Ehleringer 1991; Flanagan et al. 1992; Donovan et al. 1993; Donovan and Ehleringer 1994b). During the growing season that marked the initiation of the present study, the two size classes of *C. nauseosus* also differed in rates of gas exchange, although not necessarily as expected: the smaller and more water stressed juveniles had the higher rates of photosynthetic carbon gain (A) and stomatal conductance to water vapor (g) and lower water-use efficiency (WUE). For this paper WUE refers to leaf level process on either instantaneous time scale (A/E, ratio of photosynthetic gain to transpirational water loss, determined by gas exchange measurements) or integrated time scale (integrated A/E estimated from leaf carbon isotope discrimination, Δ, where integrated WUE and Δ are inversely correlated: see Methods for theory relating Δ and A/E). Integrated WUE was positively correlated with plant size, and the differences in WUE for juveniles and adults were related to size and not reproductive status (Donovan and Ehleringer 1992). A lower WUE (either

instantaneous or integrated) has also been associated with smaller plant size in other water-limited plant communities (Knapp and Fahnestock 1990; Sandquist et al. 1993). In order to determine the importance of these relationships for plants in the natural populations, we need to determine if these patterns are stable through time on the scale of growing seasons.

WUE (instantaneous A/E and integrated A/E estimated from Δ) and W (transpiration efficiency or ratio of biomass accumulation to total water consumption) are thought to be related to fitness and hence subject to selective pressure in natural populations (Cohen 1970; Cowan 1982; DeLucia and Heckathorn 1989; Farris and Lechowicz 1990; Ehleringer 1993). Although there is much interspecific variation, greater water-use efficiency is thought to be characteristic of, and advantageous for, plants from more arid habitats (Field et al. 1983; Smith and Nobel 1986; Schuster et al. 1992a; Ehleringer 1993; but see Yoshi 1986). Discussions of the role of WUE in natural populations are generally based on the potential for lower WUE (lower A/E and W, or higher Δ) to be associated with higher rates of A and biomass accumulation (Cohen 1970; Cowan 1982; Ehleringer and Cooper 1988; Donovan and Ehleringer 1992). This reasoning requires that higher rates of A and E and hence lower WUE (A/E) are predominantly due to decreases in stomatal limitation to A (Farquhar and Sharkey 1982), and that the plants have a similar photosynthetic capacity (which can be visualized as the initial slope of the functional relationship between A and internal CO_2 concentration, c_i). Based on this scenario, we previously suggested that plants with transient water sources (subject to competition or evaporative loss), such as juveniles of C. nauseosus, would benefit from having a lower WUE and gaining as much carbon as possible (Donovan and Ehleringer 1992). Within a population, however, individual plants can differ in photosynthetic capacity as well as the degree of stomatal limitation, and a lower WUE is not necessarily related to increased A or biomass accumulation (Field et al. 1983; Hubick et al. 1986; Virgona 1992). For C. nauseosus grown in controlled greenhouse and garden conditions, the relationship between WUE and growth has been shown to depend on the environment, and lower WUE can in fact be associated with greater biomass accumulation (Donovan and Ehleringer 1994a). Although a growing number of researcher are examining the relationship of WUE to growth and performance for non-agricultural plants under controlled conditions (e.g., Toft et al. 1989; DeLucia and Heckathorn 1989; Farris and Lechowicz 1990; Schuster et al. 1992b; Dawson and Ehleringer 1993; Donovan and Ehleringer 1994a), these relationships need to be explored in natural populations, including all of the variation in abiotic and biotic factors that are inherent to such systems.

This study explores the relationship of WUE to growth and survival in a natural population of C. nauseosus. The objectives were to determine if previously documented differences between juveniles and adults were stable through several seasons, and if WUE was re-lated to height growth and mortality for plants establishing in this population.

Methods

Site description

The study was conducted at the Tintic Range Experimental Station, Tintic, Utah (39°55' N, 122°03' W, elevation 1775 m), in an area dominated by C. nauseosus ssp. hololeucus (Asteraceae). C. nauseosus, commonly called rubber rabbitbrush, ranges from southwestern Canada to northwestern Mexico in sagebrush steppe and pinyon-juniper woodlands. It is a winter-deciduous 1–2 m tall shrub that produces leaves in spring and sets seed in fall. The study area receives an average of 374 mm precipitation annually (23-year mean) with 75% occurring from October through May, predominantly as snow (Owens 1987). Precipitation at the site was below average in 1989 and 1990, 215 mm and 222 mm, respectively, and 1991 was close to average in amount and monthly distribution of precipitation, with 276 mm received between January and September (Donovan et al. 1993).

The study was initiated in May 1989 (Donovan and Ehleringer 1992) and continued till August 1991. In 1989, all juveniles ($n=620$), and randomly selected small adults ($n=33$) and large adults ($n=45$) were tagged within a 1750-m² area. Plants were categorized on the basis of size and evidence of reproductive activity from previous years:

1. Juveniles: plants older than 1 year but prereproductive prior to 1989
2. Small adults: small reproductive plants that had flowered prior to 1989
3. Large adults: reproductive plants from the largest size classes in the population

Seedlings were numerous during all 3 years of the study and were marked and followed for survival within small subplots as a separate study (Donovan et al. 1993). Forty-one seedlings that germinated in spring 1990 and survived through that year were tagged as 1-year-olds in spring 1991, and analyzed as a separate group for size and mortality effects in this study.

Growth and mortality

During 1989, height and number of stems greater than 5 cm were measured for juveniles in May, June, July and August. During the following two years, all tagged plants were measured in June for height and number of stems greater than 5 cm length (up to 100 stems). Each fall plants were surveyed for survival and presence or absence of flowers. An assessment of deaths on any sample date was confirmed on subsequent sampling dates.

Carbon isotope discrimination theory

For C_3 plants, carbon isotope discrimination (Δ) is related to integrated A/E, because Δ and A/E are both in part determined by c_i/c_a. Farquhar et al. (1982) developed the theoretical relationship

$$\Delta = a + [(b-a)c_i/c_a]$$

where a is the carbon isotope fractionation occurring due to diffusion in air (4.4‰), and b is the net fractionation due to carboxylation (predominately by RuBP carboxylase, approximately 27‰). As carbon is assimilated over time, the Δ of the leaf tissue provides an integrated estimate of the c_i/c_a. A/E is also related to c_i/c_a as illustrated by the following equation:

$$A/E = [c_a(1-c_i/c_a)]/1.6v$$

where v is the difference in water vapor concentration between leaf and atmosphere divided by total atmospheric pressure. Thus, Δ can be used to estimate integrated A/E provided that plants being com-

pared are similar for (1) evaporative demand (v), which is a function of leaf temperature and absolute humidity of the atmosphere, and (2) the proportions of non-stomatal water loss and respiratory carbon loss. Although these conditions are unlikely to be entirely met for this or any other field study, errors were minimized by making intraspecific comparisons at a single location and for similar periods of time. Measurements of leaf temperatures were also used to evaluate potential differences in v (Ehleringer et al. 1992). In this study, leaf temperatures for juveniles and adults did not differ by more than 1.5° C, supporting the interpretation of Δ as integrated A/E. The use of Δ as an integrated estimate of c_i/c_a for *C. nauseosus* has also been supported by experimental data (Donovan and Ehleringer 1994a) and evaluation of on-line discrimination (S. Phillips, personal communication). For this study, WUE is measured on either an instantaneous time scale (by A/E) or an integrated time scale (by Δ, where Δ and WUE are inversely correlated).

Carbon isotope discrimination measurements

For determination of carbon isotope composition, leaves were collected from all tagged plants in June 1989, and from a subset of approximately 60 plants in August 1989, June 1990, and June 1991. In addition, the 1-year-old cohort plants that had leaves were sampled in June 1991. June samples represent the same age leaf cohort for the whole population, whereas the August samples may have included leaves of different ages: large plants continued to produce new leaves throughout the summer growing season while smaller plants generally did not produce new leaves after late-spring. Carbon isotope composition was measured on dried, ground leaf samples (Ehleringer and Osmond 1989) using a isotope ratio mass spectrometer (delta S, Finnigan MAT, San Jose, Calif., USA). Carbon isotope ratios ($\delta^{13}C$) were calculated from isotope compositions, relative to the PeeDee Belemnite standard, and converted to carbon isotope discrimination (Δ, ‰) values, using an atmospheric carbon dioxide value of -8‰ (Farquhar et al. 1989).

Xylem pressure potential and gas exchange measurements

Measurements of xylem pressure potentials (ψ) were made on randomly selected branches with a pressure chamber (PMS Instruments, Corvallis, Ore., USA). In June and August of 1989 (1 day

each month, 20 juvenile and 20 adult plants), ψ was measured every 2 h from 1 h before sunrise (designated as predawn or ψ_{pd}) to dusk, and early afternoon minima were designated as ψ_{md} (midday). For June 1990 (25 juveniles and 17 adults) and June 1991 (6 juveniles and 6 adults) sampling dates, ψ_{pd} and ψ_{md} were measured; in August 1990 (17 juveniles and 16 adults) and 1991 (7 juveniles and 6 adults), ψ_{pd} was measured. Stomatal conductance (g) and net photosynthesis (A) were measured on intact stems (same plants sampled for ψ) with a portable gas exchange system (LI-6200, Li-Cor Inc., Lincoln, Neb., USA). Leaf areas were measured with a LI-3100 (Li-Cor Inc.). In June and August 1989, 1 day after ψ measurements, gas exchange measurements were taken every 2 h to determine the diurnal courses. Maximum rates for all sampling dates occurred at mid-morning, and these rates are designated as A_{max} and g_{max}. Light intensities for gas exchange measurements were greater than 1200 μmol m^{-2} s^{-1} for June 1989 and greater than 1600 μmol m^{-2} s^{-1} for subsequent sampling dates. The leaf-to-air vapor pressure deficit (v) was calculated from leaf and air temperature inside the chamber and absolute humidity of air outside of the chamber. Transpiration rate (E) was then calculated from g and v. For June 1991, measurements of g (and hence E and c_i/c_a) were not available due to a problem with the humidity sensor.

Data analysis

Ecophysiological characters for juvenile and adult size classes were compared with either t-tests, or approximate t-tests in case where the variances differed (Sokal and Rohlf 1981). Relationships among characters (among and across size classes) were tested with Pearson's product-moment correlations.

Results

Comparison of juvenile and adult size classes

Juveniles differed from large adults in several ecophysiological characters at each June (early growing season) and August (late growing season) sampling date (Table 1). Juvenile ψ_{pd} values were more negative than those of

Table 1 Comparison of juvenile (J) and large adult (A) classes of *Chrysothamnus nauseosus* for a population at Tintic, Utah, for June and August 1989–1991 (ψ_{pd}, MPa predawn xylem pressure potential, ψ_{md} MPa midday xylem pressure potential, A_{max} μmol m^{-2} s^{-1} maximum photosynthetic rate, g_{max} mol m^{-2} s^{-1} maximum stomatal conductance to water vapor, E transpiration rate, c_i/c_a ratio of internal to ambient leaf CO_2, A/E instantaneous water-use efficiency, T_{air} °C air temperature, T_{leaf} °C leaf temperature, v mmol/mol air leaf-to-air vapor pressure deficit, Δ ‰ carbon isotope discrimination, *height* m, and n sample size, *na* not available due to equipment failure, – not measured)

	June 1989		August 1989		June 1990		August 1990		June 1991		August 1991	
	J	A	J	A	J	A	J	A	J	A	J	A
ψ_{pd}	−0.86	−0.63*	−1.39	−0.93*	−1.03	−0.90*	−2.37	−0.96*	−0.65	−0.63 ns	−1.59	−0.76*
ψ_{md}	−1.72	−1.60*	−2.42	−2.16*	−1.85	−1.82 ns	–	–	−1.76	−1.73 ns	–	–
A_{max}	21.5	19.2*	26.7	24.3 ns	19.6	13.1*	–	–	19.4	18.7 ns	–	–
g_{max}	0.32	0.26*	0.54	0.44 ns	0.36	0.18*	–	–	na	–	–	–
E	6.91	4.77*	15.55	11.76*	10.88	5.17*	–	–	na	–	–	–
c_i/c_a	0.68	0.64*	0.66	0.62*	0.67	0.59*	–	–	na	–	–	–
A/E	3.30	4.31*	1.88	2.11 ns	1.90	2.63*	–	–	na	–	–	–
T_{air}	22.4	21.5*	29.1	27.9*	26.8	25.5 ns	–	–	27.8	26.3 ns	–	–
T_{leaf}	24.1	22.5*	30.2	28.9 ns	28.5	26.8*	–	–	27.8	26.3 ns	–	–
v	21.8	18.6*	29.02	27.79	31.98	29.93 ns	–	–	na	–	–	–
Δ	19.88	18.48*	–	–	20.78	18.80*	–	–	na	–	–	–
Height	0.21	1.22*	0.19	1.21*	0.26	1.23*	0.26	1.23*	0.24	1.17*	0.24	1.17*
n	20	20	20	20	25	15	17	16	6	6	7	6

ns not statistically significant, * $P \leq 0.05$

Table 2 Correlation coefficients (r), sample size (n) and statistical significance of relationship among characters for a *C. nauseosus* population at Tintic, Utah (same plants as in Table 1) (A_{max} μmol m^{-2} s^{-1} photosynthetic rate, g_{max} mol m^{-2} s^{-1} stomatal conductance to water vapor, c_i/c_a ratio of internal to ambient CO_2 concentration, ψ_{pd} MPa pre-dawn pressure potential, ψ_{md} MPa mid day xylem pressure potential, Δ ‰ carbon isotope discrimination, *na* data not available)

	June 1989	August 1989	June 1990	June 1991
A_{max} and g_{max}	0.71 (n=39, P<0.001)	0.85 (n=40, P<0.001)	0.81 (n=42, P<0.001)	na
A_{max} and c_i/c_a	0.12 (n=39, P<0.474)	0.09 (n=40, P<0.568)	0.45 (n=42, P<0.003)	na
g and c_i/c_a	0.76 (n=39, P<0.001)	0.51 (n=40, P<0.001)	0.80 (n=42, P<0.001)	na
ψ_{pd} and A_{max}	−0.19 (n=39, P<0.128)	−0.11 (n=40, P=0.497)	−0.32 (n=42, P<0.045)	0.15 (n=19, P=0.535)
ψ_{pd} and g_{max}	−0.30 (n=39, P=0.066)	−0.07 (n=40, P=0.692)	−0.19 (n=42, P=0.128)	na
ψ_{pd} and c_i/c_a	−0.27 (n=39, P=0.086)	−0.14 (n=39, P=0.382)	−0.09 (n=42, P=0.584)	na
ψ_{pd} and ψ_{md}	0.52 (n=39, P=0.001)	0.68 (n=39, P=0.001)	−0.06 (n=42, P=0.693)	0.001 (n=19, P=0.952)
c_i/c_a and Δ	0.26 (n=39, P=0.089)	0.47 (n=21, P=0.034)	0.66 (n=31, P<0.001)	na

adults in June and August of each year (1989, 1990, and 1991) with the exception of June 1991. Juvenile ψ_{md} values were also more negative than those of adults in June and August of 1989, but not in June of 1990 and 1991. The lowest measured ψ_{md} values occurred in for both juvenile and adult classes. The difference between ψ_{pd} and ψ_{md} ranged from 0.7 to 1.5 MPa, and varied with class and sampling date.

In June of 1989 and 1990, juveniles had higher rates of A, g, and E than adult plants (Table 1), but not in August 1989. Juveniles generally had a higher c_i/c_a and Δ and a lower A/E than adults on each sampling date. Juveniles also had slightly higher leaf and air temperatures for each June sampling, and although v was significantly higher for one of the dates, v values for juveniles and adults did not differ by more than 3.2 mmol/mol air on these sampling dates.

Correlations among ecophysiological characters and Δ

ψ_{pd} was strongly correlated with ψ_{md} in June and August of 1989, but not on subsequent June sampling dates (Table 2). There were generally no significant correlations between ψ_{pd} and A, g or c_i/c_a. There were positive correlations between A and g, and between c_i/c_a and g on each sampling date, but c_i/c_a and A were positively correlated only in June 1990. There was a significant positive correlation between c_i/c_a and Δ in August of 1989 and June of 1990, but not in June 1989 (P=0.09).

Δ, size, and growth

For a set of 60 plants (including juveniles, small adults, and large adult) height and leaf Δ were negatively correlated at each sampling date (Fig. 1, June 1991, r=−0.84, P<0.001, and other sampling dates not shown: June 1989, r=−0.78, P<0.001; August 1989, r=−0.40, P=0.002; June 1990, r=−0.72, P<0.001). The Δ value was a seasonally and annually stable character for individual plants, based on high correlations between June and mid-August 1989, and between June 1989 and June 1991 (Fig. 2, r=0.69, n=60, P<0.001, and r=0.88, n=55, P<0.001, respective-
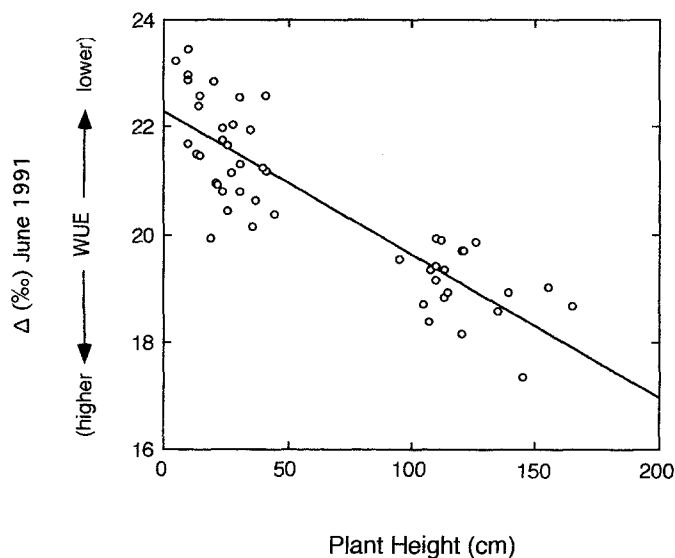

Fig. 1 Relationship between plant height (m) and leaf carbon isotope discrimination (Δ, ‰) or integrated water-use efficiency (WUE) for *Chrysothamnus nauseosus* population at Tintic, Utah, sampled in June 1991

ly), as well as for the correlation between June 1989 and 1990, and between June 1990 and 1991 (r=0.85, n=56, P<0.001, and r=0.83, n=55, P<0.001, respectively). However, the relationships did not fall on a one-to-one line, and a closer look at Δ values for plants initially designated as juveniles and adults indicated that they responded differently. From June to August of 1989 juvenile Δ values decreased by a average of 0.39‰, which was significantly different from the adult increase of 0.81‰ (t=6.41, n=54, P<0.001). In addition, from June 1989 to June 1991, juveniles' Δ values decreased by an average of 1.44‰, which was significantly more than the adult decrease of 0.93‰ (t=−2.78, n=49, P=0.008).

For *C. nauseosus*, canopy height for juvenile plants is strongly correlated with canopy width (r=0.79, n=106, P<0.001), and the shape of the canopy is spherical. We used changes in canopy height and number of stems (>5 cm) to non-destructively estimate aboveground growth for all juvenile plants. Canopy height and number of stems were positively correlated throughout the study
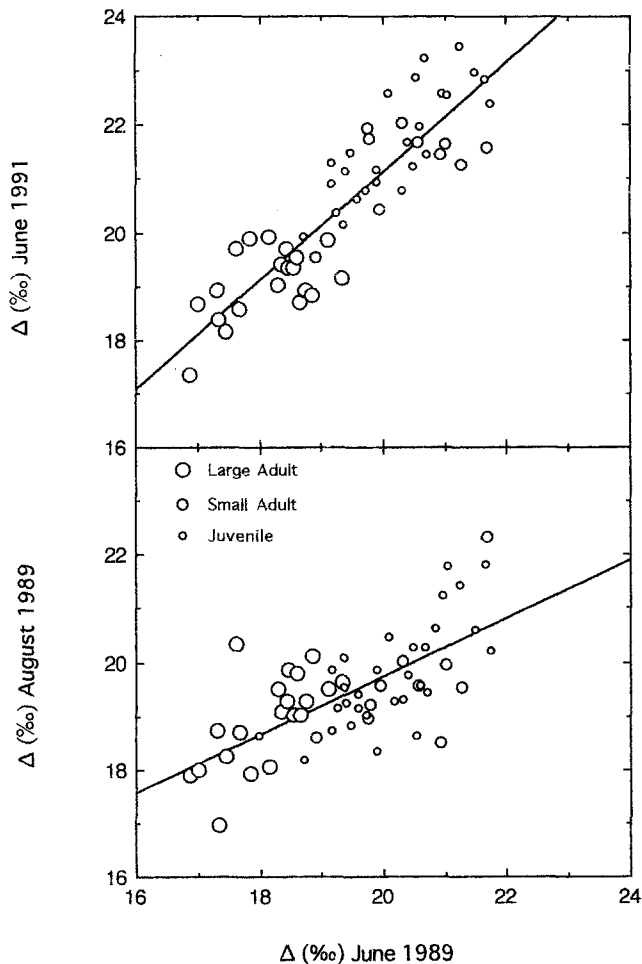
Fig. 2 Leaf carbon isotope discrimination (Δ, ‰) for *Chrysothamnus nauseosus* plants for a population at Tintic, Utah (same plants as in Fig. 1), sampled on June 1989, August 1989, and June 1991
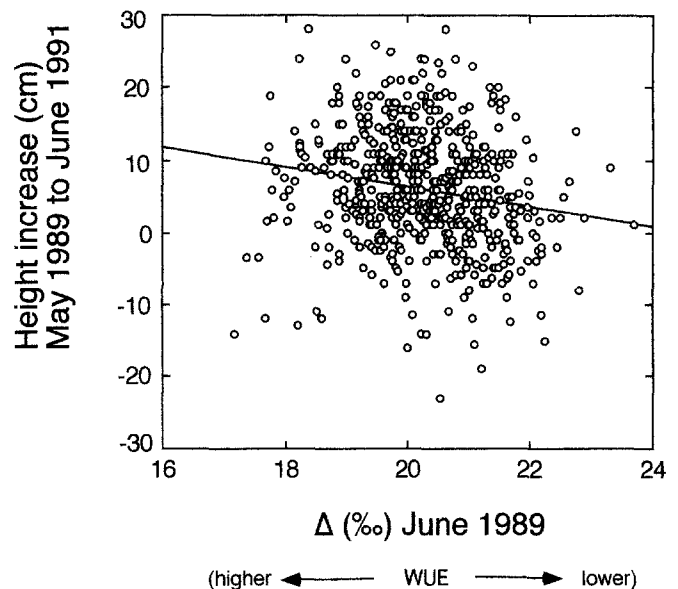

Fig. 3 Relationship between increase in plant height (May 1989 to June 1991) and leaf carbon isotope discrimination (Δ) or integrated water-use efficiency (WUE) sampled in June 1991, for *Chrysothamnus nauseosus* plants from the population at Tintic, Utah, that were juveniles in May 1989. Note that water-use efficiency (WUE) is inversely correlated with Δ

(e.g., for June 1989 $r=0.64$, $F=143$, $P>0.001$, $df=620$; and July 1989 $r=0.73$, $P<0.001$, $F=233$, $df=632$). Plants that were juveniles in 1989 increased in height by an average of 5.5 ± 4.3 cm ($\pm$ SD) during that growing season (May-August 1989), and increased in height an average of 6.1 ± 8.1 cm over the three growing seasons of the study (May 1989 until mid-June 1991), indicating relatively less growth in the latter two seasons. Estimates of growth using number of stems parallel those for height increases, and also indicated less net growth in the latter 2 years of the study. During 1990 and 1991, many plants actually decreased in canopy height due to dieback (dead stems still present) and to grazing from deer and rabbits. Seasonal height increase (from May 1989 to August 1989) and total height increase (from May 1989 to June 1991) were weakly positively correlated with initial height in May 1989 (seasonal, $r=0.11$, $n=591$, $P=0.007$; total, $r=0.19$, $n=585$, $P<0.001$). Seasonal height growth (from May 1989 to August 1989) was not correlated with Δ sampled in June 1989 ($r=-0.02$, $n=591$, $P=0.69$), but total height growth (from May 1989 to June 1991)

was weakly negatively correlated with Δ sampled in June 1989 (Fig. 3; $r=-0.18$, $n=589$, $P<0.001$). Of the plants initially marked as juveniles, 24% flowered during the next three growing seasons.

Δ, size, and survival

During the three growing seasons of the study, all of the plants originally marked as large adults ($n=45$) or small adults ($n=33$) survived. Of the plants tagged as juveniles at the initiation of the study ($n=625$), 95% survived during the three growing seasons. The initial mean height of the juvenile survivors (21.5 ± 7.0 cm) was significantly greater than the mean height of those that died (14.1 ± 6.0, $t=5.52$, $P<0.001$). For these same classes, the June 1989 mean Δ of the juvenile survivors (20.24 ± 1.04‰) was not significantly different from the mean Δ of those that died (20.56 ± 1.06‰, $t=1.62$, $P=0.105$). This lack of a relationship between Δ and survival was also found for the separate cohort of 41 one-year-old juveniles marked in spring 1991, 83% of which survived through the season. The mean Δ values (sampled early June 1991) for the survivors (23.44 ± 0.89‰) and those that died (23.25 ± 1.48‰) were not significantly different ($t=0.43$, $df=34$, $P=0.67$).

Discussion

We explored the role of leaf-level WUE for plants in a natural population of *C. nauseosus* by examining the re-

lationships among WUE, size (height), and ecophysiological characters at several sampling dates, and the relationship of integrated WUE to growth and survival. The use of Δ to estimate integrated WUE, supported by the gas exchange data in this field study and in common garden experiments (Donovan and Ehleringer 1994a), allowed us to look at a large number of plants in a natural population.

The ecophysiological differences between smaller juvenile plants and larger adult plants that were described earlier for just one sampling date (Donovan and Ehleringer 1992), have been found to be a more general phenomenon. In this study, we found that *C. nauseosus* juveniles had more negative xylem pressure potentials than did the larger adult plants, as expected given their shallower root distributions and the progressive decline in soil moisture for the Great Basin (Caldwell 1985; Donovan et al. 1993). This is consistent with the findings for other semiarid and arid systems (Frazer and Davis 1988; Brown and Archer 1990; Knapp and Fahnestock 1990; DeLucia and Schlesinger 1990; Cui and Smith 1991). Although juveniles had more negative xylem pressure potentials than adults, they occasionally had higher rates of A and g, and generally had a higher c_i/c_a and a lower A/E than adults. Thus both instantaneous (A/E) and integrated (Δ) WUE measurements indicated that WUE was positively correlated with canopy height, and that this relationship was stable through the growing season and over the 3 years of this study.

We proposed (Donovan and Ehleringer 1991) that mortality selection might contribute to differences between juveniles and adults and to the positive relationship between WUE and height. For a different population of *C. nauseosus*, we had found that juveniles with higher Δ values (i.e., least like the adults) early in the season were more likely to survive through the season. Mortality of juveniles that were phenotypically more similar to the adults would then necessitate a shift (developmental or environmental) back to values of adults. In this study, however, we found no phenotypic mortality selection relative to WUE for either the group of juveniles more than 1 year old, or for the cohort of 1-year-old seedlings. The low rate of juvenile mortality in this study, which did limit the power of the test for differences, was much lower than the rate of mortality documented in the severe drought year of the previous study (Donovan and Ehleringer 1991), and the effect of mortality rate on differential selection with respect to WUE is unknown.

The positive relationship between canopy height and WUE seems counterintuitive because smaller juvenile plants were more water-stressed than larger adult plants, and water stress usually increases WUE (Passioura 1982; Toft et al. 1989; Johnson et al. 1990; Donovan and Ehleringer 1994a). These differences in WUE for juveniles and adults have been attributed to size, and not reproductive status (Donovan and Ehleringer 1992), although photosynthetic rates for reproductive shoots and non-reproductive shoots have been reported to differ (Davis et

al. 1985). Thus, the positive relationship between canopy height and WUE suggests that as plants become larger, they may be responding to environmental gradients in resources other than just water, such as nitrogen (Field et al. 1983; Field and Mooney 1986; Toft et al. 1989). Juvenile plants did have lower leaf nitrogen levels than adults in the first year of this study, which could indicate a change in photosynthetic capacity with size (Donovan and Ehleringer 1992). Alternatively, we previously hypothesized that a developmental shift in WUE might be associated with successful establishment, where developmental shift referred to a change in the intrinsic physiology of the plant irrespective of environment (Donovan and Ehleringer 1991, 1992). However, we now feel that this term is confusing and the phenomenon can be adequately assessed as phenotypic plasticity, the definition of which includes variations in phenotype due to both environmental and developmental factors (Schlichting 1986; Sultan 1992). Controlled-environment studies with *C. nauseosus* have indicated that there is a great deal of phenotypic plasticity for WUE as a function of water availability and possibly age or size (Donovan and Ehleringer 1994a). The explanation for the positive correlation between WUE and plant size, and a further understanding of the role of WUE in natural populations, will require more rigorous assessments of phenotypic plasticity.

For this 3-year study, integrated WUE was a fairly conservative character for individual plants, and differences between individuals were maintained. We feel that the differences between individuals were probably due to stable microsites in the belowground environment, and not genetic differences. This is supported by the observation that juvenile WUE values did change more than adult values (both seasonally and annually), as expected since water availability in the juvenile root environment varies on a seasonal basis, and yearly root growth is more likely to change their belowground environment. The relative importance of environment can also be inferred from common garden experiments, although the quantitative genetic estimates of environmental and genetic variance components from the garden cannot be directly applied to the natural population. In common garden experiments with *C. nauseosus*, less than 20% of variation in WUE (Δ) could be attributed to family or genetic effects, and there were no significant interactions between family (genotype) and environment (Donovan and Ehleringer 1994a). Because variation in water availability (i.e., environment) in the field exceeded that in the controlled environment garden (based on xylem pressure potentials) the genetic variation in the field would probably account for an even smaller portion of the total phenotypic variance. Thus, the bulk of the variation in WUE (Δ) for plants in this population can probably be attributed to environment.

Many discussions of the role of WUE for plants in natural populations, including our own (Donovan and Ehleringer 1991, 1992), have been based on the potential for higher WUE to be associated with lower photosyn-

thetic carbon gain and lower growth or biomass accumulation (e.g., Cohen 1970; Cowan 1982). However, this relationship only holds true if stomatal limitation is the primary source of variation in WUE. For plants in a population, where photosynthetic capacity can also vary among individuals, higher WUE can be associated with higher rates of carbon gain and growth (Hubick et al. 1986; DeLucia and Heckathorn 1989; Virgona 1992). For experimentally grown *C. nauseosus* plants, higher WUE (estimated by Δ) was associated with greater biomass accumulation under irrigated conditions, and not associated under water-limited conditions (Donovan and Ehleringer 1994a). For *C. nauseosus*, the relative contributions in stomatal limitation and photosynthetic capacity, and hence the relationship of WUE to growth and performance in a particular population, appear to vary as a function of the environment. In this study of juvenile plants in a natural population we found that a lower WUE was not associated with a greater increase in height growth, and in fact there was a weak ($r=0.18$) but highly significant ($P<0.001$) relationship in the other direction (i.e. a negative correlation between Δ and height growth over the 3-year study). Although the mechanisms for variation in WUE are not determined and other factors potentially affecting growth were not eliminated, the pattern remains that greater WUE was not associated with reduced growth and fitness for plants in this population.

One critique of our study may be the use of changes in canopy height as an indicator of growth for *C. nauseosus*. We feel that canopy height was a reasonable indicator of aboveground size and growth since it was tightly correlated with numbers of stems and canopy width in this population. In controlled environment studies, canopy height had also been shown to be tightly correlated with numbers of stems, aboveground biomass and total biomass (Donovan et al. 1993; Donovan and Ehleringer 1994a). The use of changes in height as a measure of growth did exclude the belowground component and variation in WUE may be associated with differential partitioning to belowground biomass (Hubick et al. 1986; Virgona 1992). Another potential criticism of our study is that we did not attempt to control grazing by deer and/or rabbits, which would obviously affect our estimates of growth. This was intentional: a parallel study (Donovan and Ehleringer 1994a) looked at the relationship between WUE and growth under controlled conditions, and this study looked at this relationship in a natural population where many abiotic and biotic factors interact. Although herbivory and other biotic factors may be important intermediaries in the relationship between WUE and growth, the magnitude of these effects remain to be investigated.

In the context of this naturally established population, WUE (Δ) is a stable character for an individual plant, but it is unlikely that the WUE of will be related in a simple manner to its growth and survival. Rather than examining WUE as an isolated character, it may be productive to consider WUE as just one of a suite of characters that

relate as a group to growth and survival (e.g., DeLucia and Heckathorn 1989; Farris and Lechowicz 1990; Geber and Dawson 1990).

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