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Contrasting water-use patterns among size and life-history classes of a semi-arid shrub

L. A. DONOVAN and J. R. EHLERINGER

Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA

Summary

1. Ecophysiological characteristics of plants from different size and life-history classes were investigated in a field population of *Chrysothamnus nauseosus*.
2. Juvenile plants (>1-year-old but pre-reproductive) had higher rates of photosynthesis, stomatal conductance and transpiration than reproductive adults, even though pre-dawn xylem pressure potentials of juveniles were slightly lower. Juveniles were also less water-use efficient than adults based on instantaneous gas exchange (photosynthesis/transpiration) and carbon isotope discrimination (Δ).
3. A comparison of Δ -values indicated a gradient of water-use efficiency that was correlated with size: Seedlings < Juveniles = Small Adults < Large Adults. Reproductive status did not account for any variation independent of size.
4. Small establishing plants may experience short-term environmental conditions and long-term selective pressures different from those of larger reproductive plants.
5. The pattern of smaller plants having higher rates of gas exchange and less efficient use of water in the absence of higher pre-dawn xylem pressure potentials suggests a developmental progression in ecophysiological parameters with increasing size, in addition to the environmentally induced variation that has been documented for these characters for many species.

Key-words: Carbon isotope discrimination, *Chrysothamnus nauseosus*, juveniles, photosynthesis, plant size, water-use efficiency

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Introduction

Variations in plant size and ecophysiological characters within populations are often attributed to differences in age and/or microenvironment (Harper 1977; Knapp & Fahnestock 1990). The microenvironment of a plant can be characterized by factors such as soil moisture, temperature, nutrients and light. Water is the factor most often limiting growth in semi-arid habitats, and soil water availability generally decreases with increased proximity to surface layers (Caldwell *et al.* 1977; Fowler 1986; Frazer & Davis 1988). In the Great Basin, this pattern results from soil moisture recharge during the winter, and subsequent loss both by surface evaporation and plant extraction during the summer when temperatures are higher (Caldwell *et al.* 1977). Plants that have shallow root systems, such as seedlings and juveniles, should therefore experience lower water availability during the growing season, compared to individuals rooted in deeper soil horizons.

Plant size not only affects the microenvironment experienced by the plant, but can also reflect different developmental or life-history stage. For

example, the shift from juvenile (non-reproductive) to reproductive status is often associated with size in woody plants (Harper & White 1974). Selection may produce different responses to water availability during the juvenile or establishment phase as compared to adults, i.e. a developmental shift as a character, since selection can vary in strength or direction over the lifetime of a plant. Many gas exchange and water relations characteristics exhibit genetic variation (Farris 1987; Farquhar, Ehleringer & Hubick 1989; Geber & Dawson 1990; Schuster *et al.* 1992) that could be subject to selection. Thus, the responses of small establishing plants may be inherently different from those of the adult, reflecting either developmental shifts favoured by selection or developmental constraints (Cook 1979; Brown & Archer 1990). The expression of characters in the field as a function of plant size incorporates both environment and life-history class effects; these are largely inseparable when observing natural populations.

Recent attention has focused on the ecophysiological characteristics of different size/life-history classes within a population (Frazer & Davis 1988; Brown &

Archer 1990; Knapp & Fahnestock 1990; Cui & Smith 1991; Donovan & Ehleringer 1991). In general, smaller plants in the juvenile life-history stage are more water stressed than larger adults, and this has been attributed to differences in rooting depth and soil moisture availability. Lower xylem pressure potentials are generally accompanied by lower rates of photosynthesis and conductance, as might be expected based on our general understanding of short-term responses to decreased water availability (Frazer & Davis 1988; Brown & Archer 1990; Knapp & Fahnestock 1990; Cui & Smith 1991; Donovan & Ehleringer 1991). However, several studies have found that lower xylem pressure potentials for juveniles are actually accompanied by less efficient use of water, which may be associated with successful establishment (Knapp & Fahnestock 1990; Donovan & Ehleringer 1991).

This study investigates variation in ecophysiological characters of *Chrysothamnus nauseosus* (Pallas) Britt., a common shrub in the semi-arid Great Basin where rates of drought mortality are often high for seedlings and juveniles (Owens 1987; Donovan & Ehleringer 1991). The study objectives are: (1) to compare two distinct size/life-history classes, juveniles and adults, to determine whether juveniles that have lower xylem pressure potentials and lower rates of gas exchange are less conservative in their water-use efficiency; (2) to explore the intrapopulation relationship between water-use efficiency and size; and (3) to determine whether shifts in water-use efficiency are associated with the switch from non-flowering to flowering life-history stage.

Materials and methods

The study was conducted at the Tintic Range Experimental Station, Tintic, Utah (39° 55'N, 122° 03'W, elevation 1775 m). The site was dominated by *Artemisia tridentata* Nutt. and *Juniperus osteosperma* (Torr.) Little, until it was cleared and disc-ploughed in the early 1950s. Since then the site has recovered, with grazing limited to approximately 2 weeks each spring except for the study year, 1989, during which grazing was excluded. The site is currently occupied by *A. tridentata*, *C. nauseosus* ssp. *hololeucus*, *C. viscidifloris* (Hook.) Nutt., *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, and perennial and annual grasses. Soils are sandy loams (Jensen 1983), and the area receives an average of 374 mm precipitation annually (23-year mean) with 281 mm (75%) occurring from October through May, predominately as snow (Owens 1987). Precipitation during the 12 months preceding the June 1989 sampling was 218 mm, with 176 mm (81%) occurring from October through May (G. Bartells, personal communication).

C. nauseosus (rubber rabbitbrush) is a winter deciduous 1–2 m tall shrub that produces leaves in spring and sets seed in autumn. Plants were tagged in

April 1989 within a 1750-m² area. Plants were assigned to the following categories, based on size and evidence of reproductive activity from previous years:

1. Seedlings: plants which germinated in 1989.
2. Juveniles: plants older than 1 year but pre-reproductive.
3. First-Year Adults: plants which flowered for the first time in 1989.
4. Small Adults: small reproductive plants that had flowered prior to 1989.
5. Large Adults: reproductive plants from the largest size classes in the population.

Within the study area, all Juveniles ($n = 530$) and First-Year Adults ($n = 90$) were tagged. Small Adults ($n = 33$) and Large Adults ($n = 45$) were randomly selected and tagged. Randomly selected Seedlings ($n = 9$) were harvested, and hence were not part of the permanently marked population.

JUVENILE AND LARGE ADULT COMPARISON

Xylem pressure potentials (ψ) and gas-exchange rates were compared between Juveniles ($n = 20$) and Large Adults ($n = 20$) in June of 1989. Diurnal courses of ψ were measured on randomly selected branches with a pressure chamber (PMS Instruments, Corvallis, Oregon, USA). Diurnal courses of stomatal conductance (g) and net photosynthesis (A) were measured on intact branches with a portable gas-exchange system (LI-6200, Li-Cor Inc., Lincoln, Nebraska, USA). All gas-exchange measurements were made at photon flux densities exceeding 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Leaf areas were determined with a Li-Cor 3100 area meter (Li-Cor Inc.). Instantaneous water-use efficiency (A/E), the molar ratio of carbon gain to transpirational water loss was calculated from maximum gas-exchange rates, using leaf and air temperature inside the chamber and absolute humidity of air outside of the chamber to calculate the leaf-to-air vapour pressure deficit (v). E was then calculated from g and v . To determine leaf length, two leaves per stem were measured for each stem from the xylem pressure potential or gas-exchange measurements.

Juvenile and Large Adult classes were also compared for long-term, integrated measures of physiological performance. Leaf samples were collected in June 1989 for analysis of carbon isotope discrimination (Δ) and leaf carbon and nitrogen content. Leaf nitrogen and carbon concentrations were measured with a CHN analyzer (2400 Elemental Analyzer, Perkin-Elmer, Norwalk, Connecticut). Leaf-specific weights, from leaves used for gas exchange, were used to convert the nitrogen concentration to an area basis. Photosynthetic nitrogen-use efficiency (PPNUE) was calculated as photosynthesis/nitrogen concentration (*sensu* Field & Mooney 1986), for

Table 1. Comparison of Juvenile and Large Adults classes of *Chrysothamnus nauseosus* for the Tintic, Utah population, June 1989, presented as mean \pm SD: pre-dawn xylem pressure potential (ψ_{pd}), midday xylem pressure potential (ψ_{md}), photosynthesis (A_{max}), stomatal conductance to water vapour (g_{max}), instantaneous ratio of internal to ambient CO₂ concentration (c_i/c_a), transpiration (E), instantaneous A/E , carbon isotope discrimination (Δ), integrated c_i/c_a estimated from Δ , integrated A/E estimated from Δ and the leaf-to-air vapour pressure deficit, leaf nitrogen, potential photosynthetic nitrogen-use efficiency (PPNUE), and plant height. All differences between Juvenile and Large Adult classes were significantly different ($P < 0.05$) based on a two-tailed Student's t -test comparison of juveniles and adults, with the exception of the instantaneous c_i/c_a which was based on a one-tailed Student's t -test since the direction of the difference was predicted. Sample sizes ranged from 18 to 20 for the Juvenile class, and from 19 to 20 for the Large Adult class

	Juveniles	Large Adults
ψ_{pd} (MPa)	-0.86 ± 0.23	-0.63 ± 0.09
ψ_{md} (MPa)	-1.72 ± 0.20	-1.60 ± 0.16
A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	21.5 ± 3.0	19.2 ± 3.7
g_{max} ($\text{mol m}^{-2} \text{s}^{-1}$)	0.32 ± 0.08	0.26 ± 0.08
Instantaneous c_i/c_a	0.68 ± 0.06	0.64 ± 0.08
E ($\text{mmol m}^{-2} \text{s}^{-1}$)	6.91 ± 2.25	4.77 ± 1.22
Instantaneous A/E (mmol mol^{-1})	3.30 ± 0.73	4.31 ± 1.22
Δ (‰)	19.88 ± 0.73	18.48 ± 1.02
Integrated c_i/c_a	0.69 ± 0.03	0.63 ± 0.05
Integrated A/E (mmol mol^{-1})	3.16 ± 0.67	4.46 ± 0.95
Leaf nitrogen (mmol g^{-1})	1.53 ± 0.12	1.86 ± 0.21
PPNUE (mmol mol^{-1})	86.8 ± 17.5	58.3 ± 13.1
Plant height (m)	0.21 ± 0.07	1.24 ± 0.07

plants that were used for instantaneous gas exchange and xylem pressure potential measurements. Carbon isotopic composition was measured on dried, ground leaf samples (Ehleringer & Osmond 1989), using an isotope ratio mass spectrometer (delta S, Finnigan MAT, San Jose, California). Carbon isotope ratios ($\delta^{13}\text{C}$) were calculated from isotope compositions, relative to the PeeDee Belamite (PDB) standard, and converted to carbon isotope discrimination (Δ , ‰) values, using an atmospheric carbon dioxide value of -8‰ (Farquhar *et al.* 1989). Integrated estimates of c_i/c_a were calculated from leaf Δ , and integrated estimates of A/E were calculated using these integrated c_i/c_a values and estimates of v from the field gas exchange (Farquhar *et al.* 1989).

Measures of instantaneous and integrated characters for the Juvenile and Large Adult classes were compared with two-tailed Student's t -tests, with the exception of the instantaneous c_i/c_a which was compared with a one-tailed Student's t -test since the direction of that difference was predicted (Donovan & Ehleringer 1991).

POPULATION ANALYSIS

Concurrent with the June collection of leaf samples from the 40 plants used in the Juvenile and Large Adult comparison, leaves were collected from all the remaining plants in the study. The leaf samples were analysed for carbon isotopic composition as described in the previous section. Leaves collected in June were approximately the same age for all plants and hence were appropriate for comparisons of carbon isotope values, whereas collections later in

the season might have incorporated different cohorts of leaves. The distribution of Δ -values for the population was tested for deviation from normality using a Kolmogorov–Smirnov test. An F_{max} test for equality of variances for Δ indicated that variances were not significantly different among the size/life-history classes (Sokal & Rohlf 1981). An analysis of variance and a Duncan–Waller multiple range test were used to test for differences in mean Δ among the size/life-history classes. At the time of leaf collection, Seedlings, Juveniles, and First-Year Adults were measured for plant height and number of stems greater than 5 cm length. Small Adults and Large Adults were measured for plant height in June 1990. Correlation analyses were used to test for relationships between size and the ecophysiological characters of ψ_{pd} (pre-dawn), ψ_{md} (midday), A , g , A/E and Δ (Sokal & Rohlf 1981). The effects of size and reproductive status on Δ were separated using an analysis of covariance and included only values from the overlapping Juvenile and First-Year Adult size classes.

Results

JUVENILE AND LARGE ADULT COMPARISON

Juveniles had significantly lower pre-dawn (ψ_{pd}) and midday (ψ_{md}) xylem pressure potentials than Large Adults in early June (Table 1). Diurnal patterns indicated that xylem pressure potentials declined from ψ_{pd} values until early afternoon when ψ_{md} were measured, and recovery of less than 0.2 MPa was

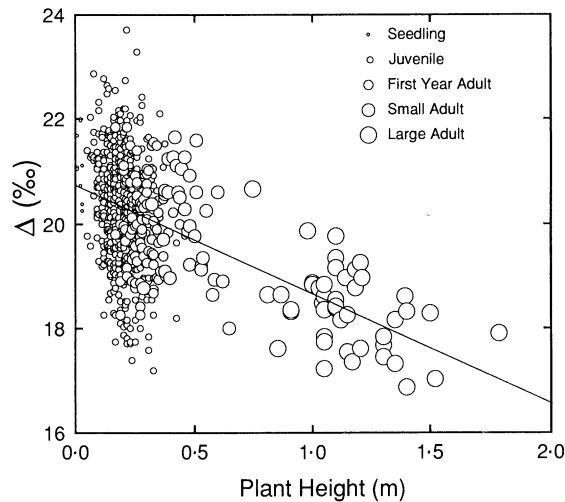


Fig. 1. The relationship between plant height (m) and carbon isotope discrimination (Δ , ‰) for Seedlings ($n = 9$), Juveniles ($n = 530$), First-Year Adults ($n = 87$), Small Adults ($n = 33$) and Large Adults ($n = 45$). $y = 20.71 - 2.05x$, $r = 0.452$, $P < 0.001$.

observed during the remaining portion of the day (data not shown). There was no significant correlation between ψ_{pd} or ψ_{md} and size within each life-history class.

In June, maximum rates of A , g and E occurred at mid-morning for both classes, and Juveniles had significantly higher rates of A , g , and E than Large Adults (Table 1). Juveniles were also operating at higher internal CO_2 concentration values (c_i) than Large Adults. Instantaneous water-use efficiency (A/E) of Juveniles was therefore less than that of Large Adults due to differences in A , g and v . The integrated estimates of instantaneous ratio of internal to ambient CO_2 concentration (c_i/c_a) calculated from Δ were in close agreement with the c_i/c_a calculated from the instantaneous gas-exchange measurements (Table 1).

In order to interpret Δ -values as estimates of A/E , the v experienced by the plant tissues must be taken into consideration. For gas-exchange measurements, the v for Juvenile leaves (21.8 mPa/Pa) was slightly higher than that for leaves of Large Adults (18.6 mPa/Pa) due to both higher air and leaf temperatures for juveniles (22.4 and 24.1°C, respectively) as compared to adults (21.5 and 22.5°C). The air

temperature differences reflected the expected temperature gradient above the ground surface. However, Juveniles and Large Adults differed in c_i as well as v . Estimates of integrated A/E calculated from leaf Δ and v agreed with the instantaneous A/E calculated from gas-exchange measurements (Table 1). Thus, observed differences in Δ can be interpreted as differences in c_i and v , which in turn are represented as differences in A/E . Both instantaneous and integrated estimates indicated that Juveniles were operating at a higher c_i value and lower A/E values than Large Adults. A , E and A/E values were not significantly correlated with size or ψ_{pd} within these two size/life-history classes.

Juvenile leaves had lower nitrogen content and lower PPNUE than those of Large Adults (Table 1). Leaf lengths of Juveniles (3.0 ± 0.7 cm) were also significantly shorter than those of Large Adults (4.1 ± 0.6 cm). Leaf specific weight was not significantly different between the classes (168 ± 27 and 182 ± 33 g m^{-2} for Juveniles and Large Adults, respectively).

POPULATION ANALYSIS

Analysis of variance indicated a gradient in Δ , and hence in estimated c_i and A/E among size/life-history classes: Seedlings < Juveniles = First-Year Adults = Small Adults < Large Adults (Table 2). The Δ -values for individuals within the population ranged from 16.9 to 24.7‰, and were approximately normally distributed. For the population as a whole, plant size and Δ -values exhibited a significant negative correlation ($P < 0.001$) (Fig. 1). However, within each of the size/life-history classes there was no significant correlation between Δ and plant size. Juvenile and First-Year Adult classes overlapped in size (Table 2). An analysis of covariance for size and reproductive status (non-flowering or flowering) indicated that reproductive status did not account for a significant portion of the variance beyond that accounted for by variation in size.

Discussion

In this study, the juvenile and large adult classes of *C. nauseosus* differ in both water-use and photosynthetic nitrogen-use characteristics. These two

Table 2. Plant height (mean \pm SD) and carbon isotope discrimination (Δ) for Seedlings, Juveniles, First-Year Adults, Small Adults and Large Adults of *Chrysothamnus nauseosus* at Tintic, Utah, June 1989

	n	Height (m)	Δ (‰)
Seedlings	9	0.02 \pm 0.01	21.13 \pm 0.65 ^a
Juveniles	530	0.20 \pm 0.07	20.30 \pm 1.06 ^b
First-Year Adults	90	0.28 \pm 0.06	19.97 \pm 0.83 ^b
Small Adults	33	0.47 \pm 0.09	20.02 \pm 1.00 ^b
Large Adults	45	1.14 \pm 0.20	18.34 \pm 0.80 ^c

Small letters indicate the results of an analysis of variance and a Duncan-Waller multiple range test for Δ ; different letters indicate statistically significantly different Δ -values ($P < 0.05$).

classes also differ in plant size, and characteristics of plant populations that vary as a function of size are often attributed to variation in microenvironment. However, plant size incorporates both variation in microenvironment and life-history class effects. Immediate environmental effects are those where variation in microenvironment, such as available soil moisture, induces variation in a character for a particular genotype irrespective of developmental stage. Life-history class effects are those associated with developmental stages for a particular genotype, and result from either past selection regimes acting on characters, or developmental constraints. For life-history effects, the expression of a character would be a function of developmental stage, or size since it is often related to developmental stage, even in the absence of any variation in microenvironment. The field population data presented in this study incorporate both microenvironment and life-history class effects, since size is related to both factors.

In general, soil moisture in the Great Basin is recharged during winter and early spring, and then lost through surface evaporation and transpiration of shallow-rooted plants as the season progresses (Caldwell *et al.* 1977). In June when most growth occurred, however, the xylem pressure potentials of small non-reproductive *C. nauseosus* plants were only 0.2 MPa more negative than Large Adults, implying no substantial differences in water availability for the two classes. The lack of a more substantial difference in xylem pressure potential between juveniles and adults may be due to sampling in June, which was still early in the seasonal surface drydown cycle. Though large differences were not found in this study, the pattern of smaller plants having lower xylem pressure potentials has been found for other shrubs in the Great Basin (Caldwell *et al.* 1977; Donovan & Ehleringer 1991), as well as for other woody plants (Frazer & Davis 1988; Brown & Archer 1990; Cui & Smith 1991) and herbaceous perennials (Knapp & Fahnestock 1990).

Juveniles of *C. nauseosus* maintained higher rates of *A*, *g* and *E*, and had a lower *A/E* than adults, despite the lack of a large difference in xylem pressure potentials. This is consistent with a previous study of *C. nauseosus* in which rates of gas exchange were higher for juveniles than for adults in a stream-side population in which xylem pressure potentials did not differ (Donovan & Ehleringer 1991). However, this is contrary to other studies where the differences in xylem pressure potential as a function of size were greater, and lower gas-exchange rates accompanied the lower xylem pressure potentials (Brown & Archer 1990; Cui & Smith 1991).

Leaf nitrogen was lower for juveniles than adults. Since leaf nitrogen is often correlated with RuBPCase activity and hence the initial slope of photosynthetic response curves to carbon dioxide concentration (Field & Mooney 1986), our data suggest that the

initial slope of the response curve may be lower for juveniles. In addition, the higher maximum photosynthetic and conductance rate of juveniles suggests that the plateau or RuBP regeneration limited region of the response curve is greater for juveniles than for adults. Hence the data are consistent with the suggestion that juveniles and adults differ in photosynthetic response capacity.

It is interesting to note that the PPNUE of juveniles was higher than that of adults, whereas *A/E* of juveniles was lower than that of adults. This supports the concept of trade-offs for instantaneous PPNUE and *A/E* at the leaf level (Field & Mooney 1986; Field, Merino & Mooney 1983). If the lower leaf nitrogen concentrations of juveniles indicate lower nitrogen availability in the juvenile microenvironment (Chapin 1989), then nitrogen may also be limiting for shallow-rooted plants.

Despite differences in instantaneous gas-exchange rates among juveniles and adults, there were no significant relationships between gas-exchange rates and size within these classes, which are similar to the results from a previous study of several woody species (Donovan & Ehleringer 1991). We suspect our failure to detect such relationships is due to (1) smaller range of size within classes and (2) small sample sizes used for these destructive measurements. The use of an integrated non-destructive estimate of *A/E* (Δ) facilitates the use of larger sample sizes and hence permits a more thorough evaluation of the relationship of at least this one parameter (*A/E*) to plant size. When the whole population is examined, there is a significant negative relationship between Δ and plant height, indicating that increasing plant size is associated with increasing water-use efficiency.

Much of the variation in Δ within the size and life-history classes of *C. nauseosus* (as seen in Fig. 1) is probably environmentally induced variation as a result of patchiness in water and nitrogen availability (Passioura 1982; Toft, Anderson & Nowak 1989; Johnson *et al.* 1990). However, a lack of substantial difference in soil moisture availability between classes indicates that interclass differences in gas exchange and water use are probably not a result of a gradient in moisture availability. In the absence of a large gradient in water availability, we might not expect any relationship between plant size and *A/E* as estimated by Δ . However, there is a strong negative relationship between size and Δ , suggesting a developmental or life-history class component of the observed variation, i.e. smaller plants may be intrinsically different from large plants in their responses to water availability. Since reproductive status (non-flowering or flowering) did not account for any significant variation in Δ beyond that accounted for by size, reproductive status itself is not the main character producing developmental differences in Δ .

Differences in water-use patterns among size/life-

history stages may be quite important. Small woody plants are relatively more dependent on water from brief unpredictable summer rain events that does not penetrate to deeper layers and is subject to loss through competition and evapotranspiration (Caldwell *et al.* 1977; Sala & Lauenroth 1982). Water is a transient resource for the small establishing plant, and theory predicts relatively less conservative use of water, basically a 'use it or lose it strategy' (Cohen 1970; Cowan 1982). By having a relatively lower A/E and potentially gaining more carbon, more biomass and deeper roots, a juvenile plant may be more likely to survive through summer drought. In contrast, mature *Chrysothamnus* are among the more deeply rooted shrubs in the cold desert communities (Branson, Miller & McQueen 1976) with tap-root lengths that often exceed 2 m (Klepper *et al.* 1978; Groenvelde 1989). Flanagan & Ehleringer (1991) and Ehleringer *et al.* (1991) found that mature *C. nauseosus* did not take up summer precipitation after a major summer storm, apparently remaining dependent on deeper ground water sources. For adults with a more stable water source that is less subject to competition, theory predicts that relatively more conservative water use would be favoured by selection, essentially partitioning out the available water through the season (Cohen 1970; Cowan 1982). This is consistent with the observed pattern for *C. nauseosus* over the range of plant sizes in the population; a progression in the operational c_i and A/E with seedlings having the highest c_i and lower A/E , and the large adults having the lowest c_i and higher A/E . For the comparison of seedlings and large adults, the observed difference of 2.79% in Δ corresponds to an estimated difference in integrated c_i of greater than 40 ppm, which would result in substantial differences in carbon gain and A/E . This is consistent with other studies indicating that smaller plants are less water-use efficient and operating at a higher c_i , despite lower xylem pressure potentials (Knapp & Fahnestock 1990). In addition to having a more stable water source, adults support far more leaf area than juveniles and transpire more water overall on a per plant basis. More conservative use of water on a unit leaf area basis by larger plants may also be related to the need for maintaining a large canopy through the summer in order to reproduce in the autumn.

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