Oecologia (1991) 86:594–597

Oecologia

Short communications

Ecophysiological differences among juvenile and reproductive plants of several woody species

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Received April 10, 1990 / Accepted in revised form January 31, 1991

Summary. Photosynthetic and water relations characteristics of small juvenile and large reproductive plants were investigated during one growing season for four woody species native to Red Butte Canyon, Utah, USA: *Acer negundo*, *Artemisia tridentata*, *Chrysothamnus nauseosus*, and *Salix exigua*. For all species, juvenile plants differed from reproductive plants in at least one of the following characters: water potential, stomatal conductance, photosynthetic rate, or water-use efficiency. Late in the growing season, mortality occurred within juvenile plants (apparently due to a lack of water), but not within reproductive plants. The observed differences between juvenile and reproductive classes are discussed in terms of environment, development, and mortality selection.

Key words: Development – Ecophysiology – Environment – Mortality selection – Water-use efficiency

The juvenile phase of plants lasts from germination to the onset of reproduction, and for woody plants the transition to reproduction is often a function of plant size (Harper and White 1974). Because of potential size differences among plants (both above and belowground), characteristics of juvenile and reproductive plants may vary in response to microenvironmental differences (Frazer and Davis 1988). The ecophysiological characteristics favored in each life-history phase may be distinct since juveniles are potentially under different selective pressures than reproductive plants (Grubb 1977; Cook 1979). For example, in mesic habitats, the soil environment may be similar for juvenile and adult plants, yet juveniles are exposed to a very different aerial environment, and plants might be expected to differ in their photosynthetic characteristics. This is in contrast to arid habitats where soil moisture is the primary factor limiting growth, and juveniles by virtue of a shallower root may be exposed to greater spatial and temporal variation in soil water availability; therefore water use characteristics may be of particular interest.

The purpose of this investigation was to determine if smaller juvenile and larger reproductive plants of arid-land perennial species differed in water status, gas exchange characteristics and mortality rates. The study includes two species restricted to relatively mesic riparian habitats (*Acer negundo* and *Salix exigua*) and two species capable of occupying both riparian and xeric-slope habitats (*Artemisia tridentata* and *Chrysothamnus nauseosus*). Since juvenile and reproductive size classes of all four species are non-overlapping in the field, this study does not distinguish size and life history class effects.

Materials and methods

The study was conducted in the Red Butte Canyon Research Natural Area, approximately 1.5 km east of the University of Utah, Salt Lake City, UT, USA. The site receives an average of 580 mm precipitation annually, one fourth occurring in summer (Dina 1970). In 1988, when this study was conducted, rainfall was near average during winter and spring, but there was no summer precipitation. Two contrasting sites were selected for study. The first, hereafter referred to as "wet site", was a riparian habitat located along a stream just before it entered into a reservoir (1630 m elevation). The plants sampled on the wet site were *Chrysothamnus nauseosus* ssp. *hololeucus* (Gray) H. & C. [juvenile height: 19.6 ± 1.0 cm (mean ± sd), $n = 47$; adult height: 70.5 ± 5.8 cm, $n = 33$], *Acer negundo* L. [juvenile height: 20.1 ± 1.6 cm, $n = 40$; adult height: 330.0 ± 33.3 cm, $n = 20$], and *Salix exigua* Nutt. [juvenile height: 18.1 ± 0.8 cm, $n = 60$; adult height: 172.0 ± 7.1 cm, $n = 20$]. The second site, hereafter referred to as "dry site", was a scrub oak, xeric slope approximately 300 m from the wet site. The plants sampled on the dry site were *C. nauseosus* ssp. *hololeucus* [juvenile height: 14.1 cm ± 0.6 cm, $n = 60$; adult height: 100.1 ± 2.9 cm, $n = 20$] and *Artemisia tridentata* ssp. *vaseyana* (Rydb.) J Boivin [juvenile height: 13.4 ± 0.7 cm, $n = 60$; adult height: 76.1 ± 7.4 cm, $n = 10$]. Both sites were at early successional stages. At the wet site there was a major flooding event in 1984 and in the dry site there was disturbance associated with reservoir construction in 1929. The reproductive class for all species consisted of plants that flowered during the 1988 season or earlier, and the juvenile class consisted of smaller plants which exhibited no indication of ever having

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flowered. For *S. exigua*, juvenile plants were first-year seedlings; for all other species juveniles were greater than one-year old (as indicated by morphology).

Plants were randomly selected for water relations and gas exchange measurements. Diurnal courses of xylem pressure potential (ψ) were measured on branches with a pressure chamber (PMS Instruments, Corvallis, OR). Diurnal courses of stomatal conductance (g) and net photosynthesis (A) for *C. nauseosus*, *A. tridentata*, and *S. exigua* were measured on intact branches with a portable gas exchange system (LI-6200, Li-Cor Inc., Lincoln, NE). Leaf areas were determined with a Li-Cor 3100 area meter (Li-Cor Inc., Lincoln, NE). Instantaneous water-use efficiency (A/E), the molar ratio of carbon gain (A) to transpirational water loss (E), was calculated from maximum gas exchange rates, using leaf temperature inside chamber and absolute humidity of air outside chamber to calculate the leaf-to-air vapor pressure deficit. Stomatal conductance of *A. negundo* was measured on intact leaves with a steady state porometer (LI-1600, Li-Cor Inc., Lincoln, NE).

Measurements of ψ, g and A were conducted in early July, approximately one month into a drought which persisted throughout the summer. Also during early July, leaves were sampled from all plants on the dry site and from selected plants on the wet site, for carbon isotope discrimination (Δ). Leaf Δ is related to the long-term intercellular CO_2 concentration and has been correlated with long-term A/E (Farquhar et al. 1989). Carbon isotopic composition ratios was measured on dried, ground leaf samples using an in-vial combustion with cupric oxide and silver foil (Ehleringer and Osmond 1989). The isotopic composition was measured on an isotope ratio mass spectrometer (delta E, Finnigan MAT, San Jose, CA). Carbon isotope ratios (δ^{13} C) were calculated from isotope compositions, relative to the PDB standard. These isotope ratios were then converted to carbon isotope discrimination (Δ) values, using an atmospheric carbon dioxide value of -8‰ (Farquhar et al. 1989). After the physiological measurements and leaf collections for Δ, survival was monitored for all plants through the remainder of the growing season.

An approximate t-test was used for juvenile and reproductive class comparisons of ψ, g, A, and A/E, and a standard t-test was used for comparisons of Δ values (Sokal and Rohlf 1981). Comparisons are reported as significant when $p < 0.05$.

Results and discussion

Plants in both juvenile and reproductive classes had the least negative water potentials at predawn, and water potentials declined until midday and remained low throughout the afternoon. Significant differences between juvenile and reproductive classes that occurred at predawn were generally consistent throughout the day. As such, predawn values are presented for class comparisons (Fig. 1). Predawn ψ was significantly more negative for juveniles as compared to reproductive plants for *C. nauseosus* and *A. tridentata* at the dry site, and for *A. negundo* at the wet site. However, juveniles of *C. nauseosus* and *S. exigua* were not significantly different from reproductive plants at the wet site.

Maximum values of g and A were used to compare the juvenile and reproductive classes in each species (Fig. 1). For diurnal courses, we observed that maximum gas exchange activity occurred at mid morning and then activity declined through the remainder of the day (data not shown). The juveniles of both *A. tridentata* and *A. negundo* had lower g values than reproductive plants. Photosynthetic rates were also lower in juveniles of *A. tridentata* (photosynthetic data were not collected for *A. negundo*). On the dry site, juveniles of *C. nauseosus* had lower A values than reproductive plants, but g values were not significantly different. On the wet site, juvenile and reproductive plants of *C. nauseosus* had equivalent A values, but g values for juveniles were significantly higher. In *S. exigua*, there were no significant differences in A or g values between classes. The instantaneous A/E of juveniles was significantly lower than that of the reproductive class for *S. exigua* and *C. nauseosus* (wet site) (Table 1). Instantaneous A/E of the juvenile class of *A. tridentata* was significantly higher than that of the reproductive class.

Carbon isotope discrimination values for leaves of *C. nauseosus* and *S. exigua* at the wet site were significantly higher for juvenile than for reproductive plants. These results suggest that long term A/E was lower in juvenile than in reproductive plants for these species (Farquhar et al. 1989), and are consistent with the observed significant differences in instantaneous A/E (Table 1). There was a negative correlation between mean A/E and mean Δ for all classes and species (data from Table 1) ($r = -0.62$, $p = 0.10$, df$=6$).

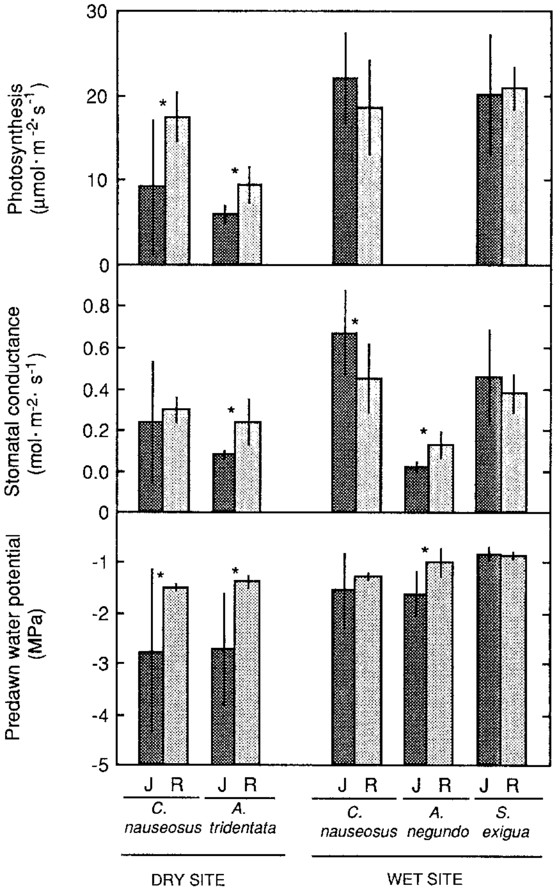

Fig. 1. Predawn water potentials (MPa), stomatal conductance (mol m^{-2} s^{-1}), and photosynthesis (µmol m^{-2} s^{-1}) of juvenile (J) and reproductive (R) classes of *Chrysothamnus nauseosus*, *Artemisia tridentata*, *Acer negundo* and *Salix exigua* at wet and dry sites. Bars indicate the average and standard errors for each variable, $n = 10$ for each bar. An * over a pair of bars indicates a comparison of J and R classes with an approximate t-test that was significant at $p < 0.05$

Table 1. Carbon isotope discrimination (Δ), A/E (photosynthesis/transpiration, mmol/mol) and percent mortality of juvenile (J) and reproductive (R) classes of *Chrysothamnus nauseosus*, *Artemisia tridentata*, *Acer negundo* and *Salix exigua* at wet and dry sites. Data for Δ and A/E are presented as mean ± 1 standard deviation (number of replicates). Mortality data are presented as percent mortality [total number censused]. The superscripts indicate a *t*-test comparison of J and R classes for Δ and A/E. * $=p<0.05$, ** $=p<0.01$, ns = non significant

		Δ (‰)	A/E (mmol/mol)	%mortality
Dry site				
Chrysothamnus nauseosus	J	20.59±1.33 (46) ns	1.12±0.78 (10) ns	47 [60]
	R	20.01±0.75 (10)	1.46±0.12 (10)	0 [20]
Artemisia tridentata	J	20.44±1.01 (58) ns	2.00±0.61 (9)*	10 [60]
	R	20.17±0.82 (10)	1.21±0.35 (5)	0 [20]
Wet site				
Chrysothamnus nauseosus	J	21.89±1.20 (16)**	0.94±0.37 (16)*	6 [47]
	R	20.13±1.74 (13)	1.39±0.52 (14)	0 [33]
Acer negundo	J	19.56±0.93 (37) ns		45 [40]
	R	19.15±1.45 (10)		0 [20]
Salix exigua	J	20.93±0.86 (9)**	1.41±0.28 (10)**	20 [60]
	R	19.73±0.41 (9)	2.10±0.28 (10)	0 [20]

C. nauseosus at the dry site exhibited no difference in either Δ or A/E between juvenile and reproductive classes (Table 1). However, there was a large range of Δ values (15.5 to 23.7‰) especially when compared to field values published for other species (Farquhar et al. 1989). Individuals of this species also had the highest juvenile mortality rate (Table 1). When juvenile plants were grouped by whether or not they survived the summer drought, the surviving juveniles had significantly higher Δ values (21.04 ± 1.20, $n=21$) than non-surviving juveniles (20.01 ± 1.20, $n=23$). The Δ value for surviving juveniles was also significantly higher than the Δ observed in reproductive plants (20.01 ± 0.75, $n=10$). There were no significant differences in Δ between surviving and non-surviving juveniles for the other species.

Up to 47% mortality occurred in the juvenile class of each species in late July and August (Table 1). Juvenile mortality was attributed to lack of water because plants desiccated without visible signs of herbivory or nutrient deficiency. There was no mortality in the reproductive class of any species (Table 1). In general, species that exhibited the highest juvenile mortality were those in which the juveniles had lower water potentials than the reproductive plants at mid season, and species that exhibited the lowest juvenile mortality were those in which there had been no difference in water potential between classes.

Since size was a main feature defining the two life-history classes, it is important to consider whether variation in size was related to the patterns for characteristics within and between classes. Surprisingly, for those comparisons where classes were significantly different for ψ, A, g, A/E, and/or Δ (Fig. 1 & Table 1), there were no significant correlations between plant height and the particular character within each of the classes. However, differences between classes were probably related to differences in size and hence microenvironment, especially soil moisture. Previous investigations have shown that plants adjust water potential, conductance, and water-use efficiency in response to soil moisture availability (Passioura 1982, Toft et al. 1989). Frazer and Davis (1988) found differences in seedling and adult water potentials as a function of rooting depth and soil moisture. In our study soil moisture content for both sites was highest in the spring from the winter recharge and declined as moisture was lost from the shallower layers by transpiration and evaporation. As such, differences in rooting depths of juvenile and reproductive plants may be sufficient to explain the observed differences in water potentials and related parameters.

Recent studies indicate that in addition to environmental variance, there are developmental and genetic variance components to water use characters (Parker and Pallardy 1985; Davis and Mooney 1986; Farris 1988; Hubick et al. 1988; Martin et al. 1989; Monson and Grant 1989). It is important to consider whether or not developmental shifts and/or mortality selection could contribute to the variation observed in this study. Developmental differences would occur when juvenile and reproductive plants have different water relations even when experiencing the same external environment. In this study, developmental variation in A/E was suggested by patterns for *C. nauseosus* (wet site) and *S. exigua* (wet site); juveniles had the same water potential as reproductive plants, but a lower A/E and a higher Δ. Mortality selection occurs when a character of an individual is correlated with its survival probability (Endler 1986), and in this study mortality paralleled differences in long-term A/E (as estimated by Δ) for *C. nauseosus* juveniles at the dry site. Early season Δ values were significantly higher for survivors as compared to those that died. If the variation in Δ was entirely due to environment, e.g. plants responded to drier microsites by becoming more water-use efficient, then the observed mortality would be random with respect to genotype. However, there may also be genetic variance for Δ (Farquhar et al. 1989), in which case the observed mortality could be differentially removing genotypes during the juvenile phase and contributing to differences between juvenile and reproductive classes.

In habitats where water can be limiting, a lower A/E is expected in plants that experience short-term droughts and/or competitive situations, whereas a higher A/E is thought to be favored in plants that experience long-term droughts and/or the absence of competition for water (Cohen 1970; Passioura 1982; Cowan 1982). To extend this hypothesis, a higher A/E may be beneficial to reproductive plants with deeper root systems, and hence a more stable water source which is less susceptible to competition. However, a lower A/E may be favored during establishment if decreased A/E is accompanied by increased growth and proportional allocation to root biomass. Increased allocation to roots will increase the probability of reaching deeper water stores necessary for survival through a drought period.

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