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Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs

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Abstract Plant species and functionally related species groups from arid and semi-arid habitats vary in their capacity to take up summer precipitation, acquire nitrogen quickly after summer precipitation, and subsequently respond with ecophysiological changes (e.g. water and nitrogen relations, gas exchange). For species that respond ecophysiological, the use of summer precipitation is generally assumed to affect long-term plant growth and thus alter competitive interactions that structure plant communities and determine potential responses to climate change. We assessed ecophysiological and growth responses to large short-term irrigation pulses over one to three growing seasons for several widespread Great Basin and northern Mojave Desert shrub species: *Chrysothamnus nauseosus*, *Sarcobatus vermiculatus*, *Atriplex confertifolia*, and *A. parryi*. We compared control and watered plants in nine case studies that encompassed adults of all four species, juveniles for three of the species, and two sites for two of the species. In every comparison, plants used summer water pulses to improve plant water status or increase rates of functioning as indicated by other ecophysiological characters. Species and life history stage responses of ecophysiological parameters (leaf N, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, gas exchange, sap flow) were consistent with several previous short-term studies. However, use of summer water pulses did not affect canopy growth in eight

out of nine comparisons, despite the range of species, growth stages, and site conditions. Summer water pulses affected canopy growth only for *C. nauseosus* adults. The general lack of growth effects for these species might be due to close proximity of groundwater at these sites, co-limitation by nutrients, or inability to respond due to phenological canalization. An understanding of the connections between short-term ecophysiological responses and growth, for different habitats and species, is critical for determining the significance of summer precipitation for desert community dynamics.

Keywords Carbon and nitrogen isotopes · Gas exchange and sap flow · Nutrient limitations · Pulse use · Water relations

Introduction

Resource pulses are thought to be important drivers of community dynamics in desert ecosystems (Beatley 1974; Noy-Meir 1973). Plants in arid and semi-arid systems are primarily limited by water but nutrients may be co-limiting. Summer precipitation pulses can affect ecophysiological parameters directly by increasing soil water availability and also by effects on nutrient availability. Many short-term isotopic and ecophysiological studies have demonstrated that plant species, functional groups, and life stages differ in the capacity to use summer resource pulses in the Great Basin, Mojave, and Colorado Plateau regions of western USA (Hodgkinson et al. 1978; Flanagan et al. 1992; Donovan and Ehleringer 1994; Phillips and Ehleringer 1995; Lin et al. 1996; BassiriRad et al. 1999; Hamerlynck et al. 2000; Gebauer and Ehleringer 2000; Williams and Ehleringer 2000; Gebauer et al. 2002; Schwinning et al. 2002; Ivans et al. 2003). Although there is a great deal of variation, annuals, shallow-rooted perennials and juvenile plants generally have the greatest proportion of summer precipitation in their transpiration stream. The proportional use of this

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potential resource decreases for species that are more deeply rooted or have fewer active shallow roots.

Global climate change models predict potential alterations in the distribution and seasonality of rainfall (Houghton et al. 1996; Mahlman 1997; Giorgi et al. 1998). Differential acquisition and ecophysiological responses to summer precipitation pulses by species or functional groups may alter competitive interactions under scenarios of changing precipitation patterns associated with global climate change (Ehleringer et al. 1999; Novoplansky and Goldberg 2001). However, there are relatively few tests of the assumption that acquisition of water from a particular source or flexibility in water source use confers an advantage to integrated plant performance, e.g. absolute use of resources, survival, growth, or fitness (but see Novoplansky and Goldberg 2001; Schwinning et al. 2002). For some desert shrubs, use of summer precipitation pulses does not necessarily lead to above-ground growth (Hodgkinson et al. 1978; Gebauer et al. 2002). In addition to evolutionary specialization related to root distribution and hydraulic constraints (Schwinning and Ehleringer 2001; Sperry and Hacke 2002), species may differ in other factors such as nutrient limitations and phenological potential to respond to summer resource pulses (Hodgkinson et al. 1978; Comstock and Ehleringer 1992; Reynolds et al. 1999). An understanding of growth responses to changing summer precipitation is critical for linking pulse use to community dynamics.

We present data from several studies of shrub growth responses to summer water pulses in lowland Great Basin and northern Mojave habitats where summer precipitation is typically very low. The objective was to determine the extent to which substantial simulated summer precipitation pulses affected ecophysiological processes and growth. We used large short-term irrigation pulses that generally exceed the amounts used by other short-term pulse studies, but similar large-scale irrigations have been used to assess the effect of changes in precipitation on community structure (Weltzin and McPherson 2000). Irrigation water was applied as large discrete pulses during the summer growing season. If large events produce substantial and consistent effects, then the role of smaller pulses will deserve further investigation. The studies included four widespread shrub species that vary in root depth distribution and salt tolerance, and also included adult and juvenile life stages for three of the species. We expected summer water pulses to have large impacts on the ecophysiology and growth of relatively shallow-rooted juvenile plants of all species, and adults of the less deeply rooted species [*Atriplex confertifolia* (shadscale, C₄) and *A. parryi* (Parry saltbush, C₄)], as compared to the more deeply rooted and phreatophytic adults of *Chrysothamnus nauseosus* (rabbitbrush, C₃) and *Sarcobatus vermiculatus* (greasewood, C₃).

Materials and methods

The studies were conducted at two sites: a Great Basin cold desert site and a northern Mojave warm desert site. The cold desert site is on the north shore of Mono Lake, California, USA (38°5'N, 118°58'W; 1,955±10 m elevation). The study species at Mono Lake are *Chrysothamnus nauseosus* (Pallas) Britton ssp. *consimilis* (E. Greene) H. M. Hall and Clements and *Sarcobatus vermiculatus* (Hook.) Torrey. The warm desert site is on the location of the historic (1900s) western shoreline of Owens Lake, California, USA, which is now a dry playa (36°3'N, 118°W; 1,095±10 m elevation; Dahlgren et al. 1997). The study species at Owens Lake are *A. confertifolia* (Torrey and Fremont) S. Watson, *A. parryi* S. Watson, and *S. vermiculatus*. Mean annual precipitation is 160 mm and 149 mm per year at the Mono Lake and Owens Lake sites, respectively. These sites are characterized by low (<20% of annual) summer precipitation (June–September, Comstock and Ehleringer 1992). The majority of precipitation falls during cooler winter months (November through March), creating relatively high levels of available soil moisture at all soil depths in the spring, but declining moisture in shallower soils throughout the typically dry summer months (Comstock and Ehleringer 1992; Donovan et al. 2003). Natural precipitation totals were substantially less than normal in 2000 and 2002, while 2001 precipitation was near average at both study sites. All of the study species except *C. nauseosus* are halophytes. The four study species are community dominants at our alkaline/saline basin study sites that represent a major community type in the Great Basin and Mojave (Shreve 1942; Benson and Darrow 1981; West 1983).

Mono Lake site and experimental design

Adult shrubs

Chrysothamnus nauseosus and *S. vermiculatus* were selected at a successional mature site with few juveniles (Diverse Dunes site, ~275 m on the N-S transect, Donovan and Richards 2000; Toft and Elliott-Fisk 2002, same shrub populations as in Donovan et al. 1996, 2003; see these references for soil and site characteristics). Roots of both species penetrate to the groundwater capillary fringe (Donovan et al. 1996). Depth to groundwater was ~3 m and fell 0.5 m from spring 2000 to fall 2002. Soils and groundwater [electrical conductivity (EC) ~1.5 dS m⁻¹] are only marginally saline (Donovan et al. 1996). Canopy dimensions for *C. nauseosus* and *S. vermiculatus* were ~130×170 cm (height, diameter) and 140×190 cm, respectively. Five species × irrigation treatment combinations, described below, were replicated once in each of 12 blocks (see Donovan et al. 2003 for more details). For both *C. nauseosus* and *S. vermiculatus*, treatments consisted of control plants that received natural rainfall (NA) and plants that received pulsed surface irrigation (IR). An additional treatment, pulsed deep irrigation (DP), was

established on *S. vermiculatus* using PVC tubing to increase soil water availability in deep (>1.25 m) soil layers only, leaving the surface layers dry. This treatment served as a type of control for response to pulses of water, without potential limitations of root embolism (Sperry and Hacke 2002) or water supply limitations, since roots in those layers did not experience substantial drying. Logistics of water delivery dictated that only one species could receive this treatment. Water was applied with pressure compensating drip emitters spread evenly over a 2 m radius circle around the IR shrubs of both species or distributed from emitters through four PVC tubes around each DP-treated *S. vermiculatus*. Drip irrigation was used because it reduces soil disturbance and avoids ponding and runoff. Irrigation pulses lasted 2–4 days per month from May through September. The amount of water added during these periods in 2000, 2001, and 2002 was 160, 148, and 19% of mean annual precipitation, respectively. Each irrigation pulse raised volumetric soil moisture (neutron probe, CPN, Martinez, Calif.) of the upper soil profiles in the IR treated plants to field capacity (18–21%) and the wetting front penetrated to ~150 cm depth, not deep enough to leach nutrients from the rooting zone (see Donovan et al. 1996). Soil moisture in the NA treatment was less than 10% throughout the 0–200 cm profile. For the DP treatment each pulse wetted the soil from 125 cm to >200 cm depth to field capacity. Between irrigation pulses no water was added and the soil was allowed to dry down.

Juvenile shrubs

Chrysothamnus nauseosus and *S. vermiculatus* juveniles were selected at a younger successional site (500 m on the N-S transect Donovan and Richards 2000; Toft and Elliott-Fisk 2002), ~225 m from the adult site. Depth to groundwater was approximately 4 m in spring 2001. Plants with canopy dimensions of ~15×15 cm were chosen based on the absence of reproductive structures from previous years and a spacing of at least 2 m apart. Four species × irrigation treatment combinations (2 species × 2 irrigations; NA, IR); were replicated once in each of 5 blocks. Each IR plant of both species received water 2–4 days each month from May to September 2001 with intervening dry periods. The amount of water added was 180% of mean annual precipitation.

Owens Lake site and experimental design

Adult and juvenile shrubs: Two field plots that varied in salinity were established at the Owens Lake site. At the low salinity site, groundwater (EC ~20 dS m⁻¹) was 1.1–1.8 m depth across the site in 2002. At this site, adults of *A. confertifolia*, *A. parryi* and *S. vermiculatus* were chosen with canopy dimensions of ~20×35 cm, 20×35 cm, and 100×140 cm, respectively. At the high salinity site, groundwater (EC ~50 dS m⁻¹) was less than 1 m depth

in 2002. At this site, *A. parryi* adults and *A. parryi* juveniles were chosen with canopy dimensions of ~20×35 cm and 8×5 cm, respectively. For further details on the low (LM3–4) and high salinity (LM7) Owens sites, see Dahlgren et al. (1997). Roots of all adults penetrate to the groundwater capillary fringe. Species × irrigation combinations were replicated once in each of 5 blocks at each site, as at the Mono Lake site. Each IR plant received irrigation water two to four times per week for a duration of 2–4 h from April through October. Soil surface layers were allowed to dry between pulses. Relative to mean annual precipitation, the added water was 90–190% for *A. confertifolia* adults, 90–160% for *A. parryi* adults, 90–130% for *S. vermiculatus* adults, and 80–140% for *A. parryi* juveniles, for 2001 and 2002 respectively.

Ecophysiological parameters

The effects of irrigation treatments on plant predawn water potentials (Ψ_{pd}) were measured following sunny days: 17 July 2001 for Mono Lake adults ($n = 6$ replicates), 8 September 2001 for Mono Lake juveniles ($n = 5$), and 9 August 2001 for Owens Lake adults and juveniles ($n = 5$). Measurements of Ψ_{pd} were made on terminal leafy stems with a Scholander type pressure chamber (PMS, Corvallis, Ore.), adhering to rigorous procedures to minimize errors (Turner 1988).

Leaf or shoot gas-exchange was measured at midmorning (period of maximum gas exchange) using a LI-6400 (Li-Cor, Neb., USA) on 17 July and 18 August 2001 for Mono Lake adults ($n = 6$), and on 1 July 2002 for *A. parryi* adults at the high salinity Owens Lake site ($n = 5$). Sample CO₂ was 360 $\mu\text{mol}\cdot\text{mol}^{-1}$, PPFD was maintained slightly above ambient (1600–1900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and cuvette temperature and relative humidity tracked ambient. Leaves within the cuvette were excised and scanned for leaf areas using a desktop scanner and image analyzing software (Scion Corp., 2000, Frederick, MD; and Win RHIZO v. 5.0A software, Regent Instruments, Canada).

Leaf samples for isotopic analysis and nitrogen content were collected at the time of plant Ψ_{pd} for all Mono Lake plants and early July 2002 for all Owens Lake plants. Leaves were sampled from apical sunlit branch tips, oven dried at 65°C for 48 h, and ground to a fine powder. For Mono Lake adults, leaf samples were analyzed for %N, leaf $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ on a dual inlet stable isotope ratio mass spectrometer (Delta C, Finnegan, Bremen Germany, interfaced with a Carlo Erba CN analyzer, Milan, Italy) at the University of Georgia Institute of Ecology Stable Isotope Laboratory. For Mono Lake juveniles and all Owens Lake plants, leaf $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were analyzed on a continuous flow isotope ratio mass spectrometer (Europa Scientific Hydra 20/20) and leaf tissue N concentrations were determined on a CN analyzer (Carlo Erba) at the University of California, Davis, Stable Isotope Facility. Isotope values are presented relative to PDB and atmospheric N₂ standards (Ehleringer and Rundel 1989).

Table 1 Mean values (± 1 SE) for ecophysiological characters of *Chrysothamnus nauseosus*, *Sarcobatus vermiculatus*, *Atriplex confertifolia*, and *A. parryi* in non-irrigated (NA natural rainfall), surface pulse irrigated (IR) and deep pulse irrigated (DP) treatments at Mono and Owens Lake sites, Calif., USA. Characters are pre-dawn plant water potential (Ψ_{pd}), leaf N, leaf $\delta^{15}\text{N}$, leaf $\delta^{13}\text{C}$, leaf photosynthetic rate (A), leaf transpiration rate (E), leaf stomatal conductance (g), and total daily sap flow standardized per unit sapwood area ($\text{kg H}_2\text{O m}^{-2}$ xylem area day^{-1}). Total daily sap flow is based on measurements of large basal stems (whole canopy sections). For all characters, species and life-stages $n = 5-6$, except for sap flow where $n = 3$. ND indicates not determined. Asterisks indicate significant differences between water treatments, ** $P < 0.01$, * $P < 0.05$

	Plant Ψ_{pd} (MPa)	Leaf N (%)	Leaf $\delta^{15}\text{N}$ (‰)	Leaf $\delta^{13}\text{C}$ (‰)	A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	E ($\text{mmol m}^{-2} \text{s}^{-1}$)	g ($\text{mmol m}^{-2} \text{s}^{-1}$)	Total sap flow ($\text{kg m}^{-2} \text{day}^{-1}$)	
								17 July 2001	17 July 2001
Mono Lake adults									
<i>C. nauseosus</i>									
NA	-0.6 (0.1)**	1.8 (0.1)	5.5 (0.3)	-27.3 (0.3)	14.6 (2.1)	5.1 (0.5)	185 (18)	13,140 (3,609)	13,280 (3,340)
IR	-0.4 (<0.1)**	1.9 (0.1)	4.9 (0.3)	-27.0 (0.2)	15.8 (2.1)	5.2 (0.8)	206 (37)	12,530 (1,880)	13,580 (1,660)
<i>S. vermiculatus</i>									
NA	-2.0 (0.2)*	1.0 (0.1)	9.3 (0.5)	-23.9 (0.3)	6.7 (0.7)	2.6 (0.3)	79 (11)	8,520 (2,930)	7,070 (3,000)
IR	-1.4 (0.1)*	1.0 (0.04)	11.8 (0.8)	-23.7 (0.2)	7.2 (1.2)	2.6 (0.4)	80 (15)	8,110 (1,230)	6,900 (1,370)
DP	-1.8 (0.1)*	0.9 (0.03)	9.9 (1.0)	-23.7 (0.2)	8.9 (3.1)	2.9 (0.5)	91 (21)	9,980 (2,900)	9,170 (3,650)
Mono Lake juveniles									
<i>C. nauseosus</i>									
NA	-2.2 (0.3)	2.4 (0.2)	2.4 (0.6)	-25.5 (0.3)**	ND	ND	ND	ND	ND
IR	-1.8 (0.2)	2.0 (0.1)	2.4 (0.5)	-28.6 (0.5)**	ND	ND	ND	ND	ND
<i>S. vermiculatus</i>									
NA	-3.3 (0.1)**	1.7 (0.1)	9.5 (0.2)	-24.0 (0.8)	ND	ND	ND	ND	ND
IR	-2.4 (0.1)**	1.7 (0.3)	8.1 (0.6)	-24.2 (0.3)	ND	ND	ND	ND	ND
Owens Lake adults									
<i>A. confertifolia</i> , low salinity									
NA	ND	1.5 (0.1)*	2.3 (0.4)	-14.4 (0.3)**	ND	ND	ND	ND	ND
IR	ND	1.8 (0.1)*	2.9 (0.5)	-13.4 (0.1)**	ND	ND	ND	ND	ND
<i>A. parryi</i> , low salinity									
NA	-2.9 (0.4)	1.1 (0.1)**	2.3 (0.5)*	-14.2 (0.2)*	ND	ND	ND	ND	ND
IR	-2.3 (0.2)	0.8 (0.03)**	3.9 (0.3)*	-13.4 (0.1)*	ND	ND	ND	ND	ND
<i>S. vermiculatus</i> , low salinity									
NA	-4.7 (0.2)*	1.7 (0.1)	7.5 (0.7)	-23.7 (0.2)	ND	ND	ND	ND	ND
IR	-4.3 (0.1)*	1.9 (0.1)	7.2 (0.9)	-23.7 (0.5)	ND	ND	ND	ND	ND
<i>A. parryi</i> , high salinity									
NA	-2.7 (0.2)**	1.0 (0.1)	3.2 (0.4)*	-13.7 (0.1)	5.3 (1.8)	4.3 (0.7)	191 (37)	ND	ND
IR	-1.4 (0.1)**	0.9 (0.6)	1.4 (0.4)*	-13.7 (0.1)	6.1 (1.3)	4.6 (0.6)	203 (24)	ND	ND
Owens Lake juveniles									
<i>A. parryi</i> , high salinity									
NA	-2.4 (0.1)**	0.96 (0.1)	-0.3 (0.2)*	-13.6 (0.2)	ND	ND	ND	ND	ND
IR	-1.6 (0.1)**	1.05 (0.1)	1.4 (0.6)*	-13.8 (0.3)	ND	ND	ND	ND	ND

Stem sap flow was measured using heat balance collars (Dynamax, Houston, Tex.) on each species-irrigation combination for adult shrubs at Mono Lake ($n = 3$). Stems with heat balance collars were harvested to determine zero flows. Active sapwood area was determined using a digital caliper on excised stems to measure the outer diameter of active sapwood and heartwood. Diameter was measured in two directions and averaged. Active sapwood area was calculated (using the area of a circle) as total xylem area minus heartwood area. Sap flow was standardized per unit sapwood area. To determine if differences in leaf area were related to differences in sap flow, leaf area of each instrumented stem was estimated from a relationship between measured leaf area and dry leaf biomass determined on a subsample of leaves. Differences in average sap flow rates were analyzed by averaging sap flow rates measured every 15 min over a several day period (4 days in July, 6 days in August, 2001) that included days of leaf gas exchange measurements. Total daily sap flow was calculated by summing hourly sap flow rates for each day and taking the average over the several day period.

Vegetative growth

The effects of irrigation treatment on vegetative growth were determined from non-destructive measurements of initial (before irrigation experiment) and final (post irrigation experiment) canopy dimensions. Mono Lake adults were measured in spring 2000 and fall 2002 ($n = 12$ replicates, encompassing three growing seasons). Mono Lake juveniles were measured in spring and fall 2001 ($n = 5$, one growing season). All species and life history stages at Owens Lake were measured in spring 2001 and fall 2002 ($n = 5$, two growing seasons). Canopy volume was calculated as an ellipsoid shape (Messina et al. 2002). Percent change in canopy volume was calculated as (final-initial)/initial. Canopy volume is closely related to canopy and leaf biomass for our study species (Drenovsky 2002; R. L. Tiller et al., unpublished data), and has been frequently used to document shrub growth responses. For example, it was used to determine *C. nauseosus* growth dynamics in response to fluctuating depth to ground water (Toft 1995) and sagebrush growth responses to simulated browsing (Messina et al. 2002).

Statistical analysis

For all measured variables, differences due to irrigation treatments ($\alpha = 0.05$) were determined using one-way ANOVA models (equivalent to t -tests in the case of only two treatments). Data were inspected to make sure the assumption of equal variances was met. In the case of unequal variances and only two treatments, the Welch Statistic was used. Canopy volume data consisted of repeated sampling on the same individuals. Therefore, multivariate ANOVA with repeated measures were used to

determine if there were significant effects ($\alpha = 0.05$) of irrigation pulses on canopy volume (SAS 1989). Natural log transforms were used to meet the assumptions of MANOVA.

Results

Plant ecophysiological responses

For all species and growth stages, irrigation pulses significantly affected at least one of the ecophysiological parameters related to plant water or nutrient relations (Table 1). As expected, summer water pulses increased plant Ψ_{pd} . This increase was significant for all comparisons except for *C. nauseosus* juveniles at Mono Lake and *A. parryi* adults at the Owens Lake low salinity site. The irrigation-induced increases in Ψ_{pd} were modest, 0.2–0.9 MPa, except for *A. parryi* adults at the Owens Lake high salinity site, where irrigation increased Ψ_{pd} by 1.3 MPa. *A. confertifolia* Ψ_{pd} was not measured. Irrigation pulses generally did not affect leaf N concentration, except for inconsistent effects on the *Atriplex* species at the Owens Lake low salinity site where there was an increase in leaf N for *A. confertifolia* and a decrease for *A. parryi*.

Stable isotopic ratios of leaves were used as indicators of pulsed summer irrigation effects on nitrogen cycling/assimilation processes and on time-integrated carbon assimilation (Högberg 1997; Farquhar et al. 1988). $\delta^{15}\text{N}$ values of all species were not significantly affected by irrigation, except for *A. parryi*, where irrigation pulses resulted in either an increased or decreased leaf $\delta^{15}\text{N}$ depending on the site and life history stage (Table 1). Although irrigation did not affect $\delta^{15}\text{N}$ of *S. vermiculatus*, $\delta^{15}\text{N}$ of this species was consistently $\sim 5\%$ higher than in co-occurring species. Additionally, $\delta^{13}\text{C}$ values were generally not affected by irrigation, with three exceptions. Irrigated *C. nauseosus* juveniles at the Mono Lake site had more negative $\delta^{13}\text{C}$ values than control plants, indicating (in combination with unchanged leaf N concentration) that irrigation increased stomatal conductance (Farquhar et al. 1988). Irrigated *A. parryi* and *A. confertifolia* had less negative $\delta^{13}\text{C}$ values than control plants, but these differences could be due to changes in stomatal conductance or bundle sheath leakiness because both these species possess the C_4 photosynthetic pathway (Bowman et al. 1989; Sandquist and Ehleringer 1995).

Daytime rates of leaf-level gas exchange (A , E , and g) for adults of both *S. vermiculatus* and *C. nauseosus* at Mono Lake were unaffected by irrigation treatments in July (Table 1) and August (data not shown). Similarly daytime rates of A , E , and g of *A. parryi* at the high salinity site were not affected by irrigation. Sap flow of major basal branches (whole canopy sections) was also assessed for *S. vermiculatus* and *C. nauseosus* adults at Mono Lake. Total daily sap flow (Table 1) and average sap flow rates (data not shown) standardized per unit sapwood area were not affected by irrigation treatment ($P > 0.70$). Total sap flow per unit leaf area was also not affected by irrigation

treatment for either sampling period ($P > 0.41$, data not shown).

Plant growth responses

With only one exception, there were no significant interactive effects of time and irrigation treatment on canopy volume for any of the species or growth stages. This indicates that net growth of the shrubs was not affected by additional summer water pulses (i.e. plants in control and irrigated treatments experienced similar changes in canopy volumes through time). The one exception was for *C. nauseosus* adults at Mono Lake, where control plant canopy volumes decreased by 28% over three growing seasons, while irrigated plants decreased in canopy volume by only 2% (Fig. 1; Table 2, time \times treatment interaction $F_{1,11}=10.03$, $P=0.009$).

Although there were generally no effects of irrigation treatment on canopy growth during the experimental periods, there were some differences among the species and life history stages in canopy growth over time (see column for time, within-subject effect, in Table 2). The adult plants at Mono Lake, *S. vermiculatus* in all treatments and non-irrigated *C. nauseosus*, experienced 25–30% reduction in total canopy volume over the three

growing seasons from 2000 to 2002, likely associated with 2 years of low precipitation and the ~50 cm decline in groundwater. Mono Lake juveniles increased in canopy volume over one season (2001). At Owens Lake, over two growing seasons (2001–2002), *A. parryi* juveniles tended to increase canopy volume through time ($P=0.06$), similar to the juvenile shrubs at Mono Lake. Adult shrubs at Owens Lake exhibited relatively small changes in canopy volume with the canopies either shrinking or expanding slightly, with the exception of adult *A. confertifolia* which had a significant increase in canopy volume through time (Table 2, Fig. 1).

Discussion

Plant growth in arid and semi-arid environments is thought to be most limited by water availability (Noy-Meir 1973). Thus, it is not surprising that in every comparison, plant use of pulsed summer irrigation resulted in more favorable water status or a response in other ecophysiological characters. Species and life history stages differed in responses of ecophysiological parameters (leaf N, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$) consistent with many previous short-term studies. Although we did not use stable isotopic labeling to trace water sources, changes in plant water potentials and other ecophysiological parameters indicate that the

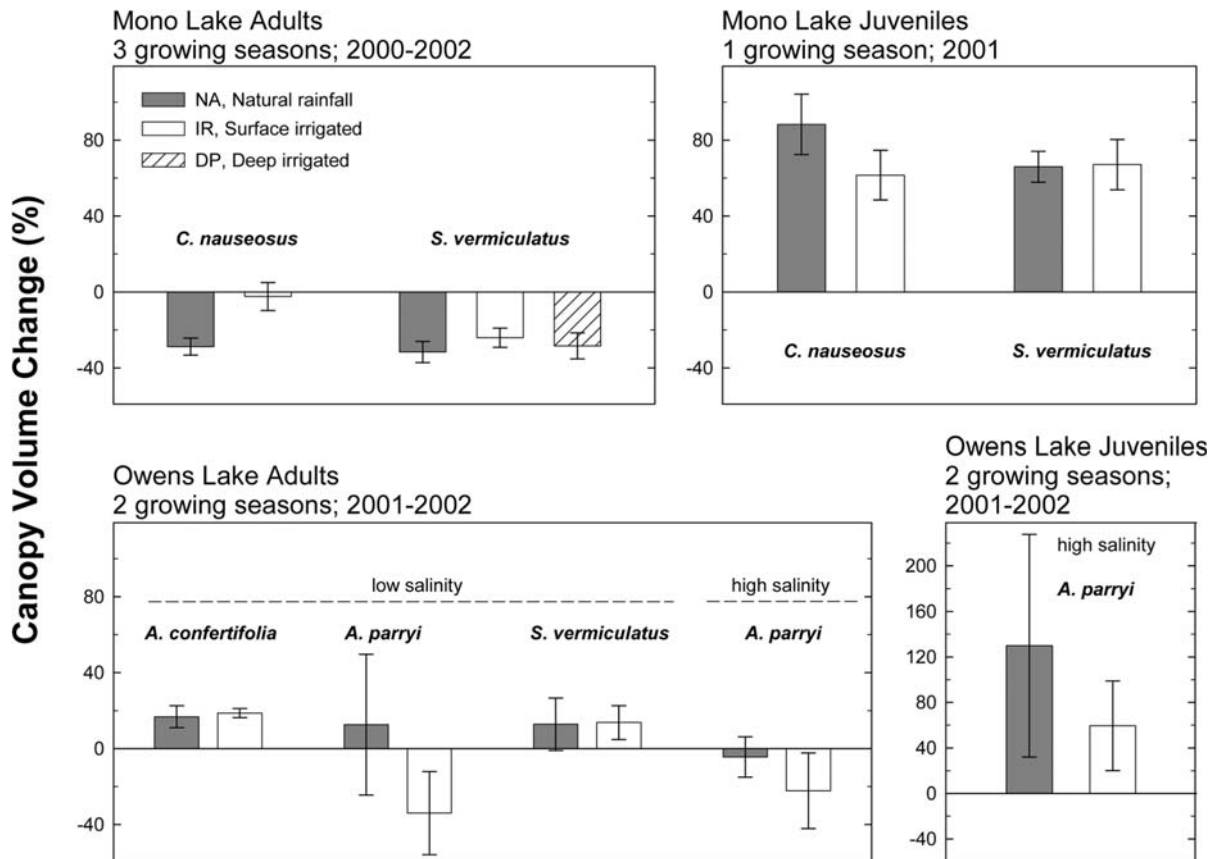


Fig. 1 The change in canopy volume expressed as a percentage of initial volume for *Chrysothamnus nauseosus*, *Sarcobatus vermiculatus*, *Atriplex confertifolia* and *A. parryi*. Statistics for the nine comparisons are presented in Table 2

Table 2 Results of repeated-measures analysis of variance for canopy volume measured at the beginning and end of irrigation experiments (encompassing 1–3 growing seasons; see Fig. 1). Study species were *C. nauseosus*, *S. vermiculatus*, *A. confertifolia* and *A. parryi* located at Mono Lake and Owens Lake, Calif., USA. Each MANOVA compared *NA* (native rainfall) and *IR* (surface pulse irrigated) treatment, except for *S. vermiculatus* adults at Mono Lake, which additionally had a *DP* (deep pulse irrigated) treatment, within

site, species and growth stage. Between subjects effect is treatment and within-subject effects are time and time \times treatment. Presented for each effect are an *F* statistic, significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns $P > 0.05$), and degrees of freedom for numerator (*dfn*) and denominator (*dfd*). A significant time \times treatment interaction indicates an irrigation effect on canopy growth. Canopy volumes are presented as % change in initial canopy volume in Fig. 1

	No. of seasons (years)	Between subjects		Within-subjects			
		Treatment		Time	Time \times treatment		
		<i>F</i>	dfn, dfd	<i>F</i>	dfn, dfd	<i>F</i>	dfn, dfd
Mono Lake adults							
<i>C. nauseosus</i>	3 (2000–2002)	0.27 ^{ns}	1, 11	18.89 ^{***}	1, 11	10.03 ^{**}	1, 11
<i>S. vermiculatus</i>	3 (2000–2002)	3.74 [*]	1, 11	65.76 ^{***}	1, 11	0.57 ^{ns}	1, 11
Mono Lake juveniles							
<i>C. nauseosus</i>	1 (2001)	2.14 ^{ns}	1, 4	126.32 ^{***}	1, 4	2.5 ^{ns}	1, 4
<i>S. vermiculatus</i>	1 (2001)	0.03 ^{ns}	1, 4	91.57 ^{***}	1, 4	0.00 ^{ns}	1, 4
Owens Lake adults							
<i>A. confertifolia</i> , low salinity	2 (2001–2002)	0.01 ^{ns}	1, 4	44.92 ^{**}	1, 4	0.19 ^{ns}	1, 4
<i>A. parryi</i> , low salinity	2 (2001–2002)	0.34 ^{ns}	1, 4	1.83 ^{ns}	1, 4	1.03 ^{ns}	1, 4
<i>S. vermiculatus</i> , low salinity	2 (2001–2002)	0.48 ^{ns}	1, 4	2.00 ^{ns}	1, 4	1.19 ^{ns}	1, 4
<i>A. parryi</i> , high salinity	2 (2001–2002)	0.26 ^{ns}	1, 4	2.99 ^{ns}	1, 4	0.03 ^{ns}	1, 4
Owens Lake juveniles							
<i>A. parryi</i> , high salinity	2 (2001–2002)	0.24 ^{ns}	1, 4	6.58 ^{ns}	1, 4	0.13 ^{ns}	1, 4

plants did take up the irrigation water. However, improved water status did not result in higher rates of leaf gas exchange (*A*, *E* or *g*) for the three species on which gas exchange was measured, *S. vermiculatus*, *C. nauseosus*, and *A. parryi*. Use of summer irrigation pulses is consistent with previous reports of water uptake following simulated summer precipitation for two of our comparisons, adults of *A. confertifolia* (Gebauer et al. 2002) and juveniles of *C. nauseosus* (Donovan and Ehleringer 1994), but contrary to other previous reports for adult *C. nauseosus* (see below). However, uptake of added summer water pulses did not translate into a growth advantage for eight out of nine comparisons that encompassed a broad range of conditions and species. This challenges the common assumption that exploitation of pulses of water confers a direct growth response and competitive advantage in desert environments.

The differences in overall growth trends across sites may be due to differences in time intervals assessed, successional status of the communities, and depth to groundwater. The juveniles grew at both sites. Adult plants did not grow much or shrank at both sites. These differences between adults and juveniles reflect the successional status of the community. The Mono Lake adult site is a mature site with little recruitment that may have reached steady state. Juvenile sites are more open sites that appear to be in an early successional growth state. Differences in time intervals may also explain the dramatic canopy reduction of the Mono Lake adults relative to the other species and life stages. The Mono Lake adults were measured over three growing seasons that encompassed the extremely dry year of 2000; plants

may have reduced canopy volume considerably during this drought. All other canopy growth measures do not encompass this dry year. Groundwater is also deeper at the Mono Lake site and dropped over the three-year period, which likely contributed to reductions in plant canopy volume and may also explain why summer irrigation pulses translated into less canopy reduction for *C. nauseosus*.

We did not expect *C. nauseosus* adults at Mono Lake to have ecophysiological or growth responses to pulsed summer irrigation for two reasons. First, previous studies indicated no summer precipitation uptake for adults of *C. nauseosus* at other Great Basin and Colorado Plateau sites (Flanagan et al. 1992; Donovan and Ehleringer 1994; Gebauer et al. 2002). Second, it is a phreatophyte, with adult root systems accessing nearly fresh groundwater at 3–4 m depth at the Mono Lake site (Donovan et al. 1996). However, *C. nauseosus* adults did take up pulsed summer irrigation in our study. This discrepancy is possibly due to the greater amount of irrigation supplied in our study (wetting the soil to 1.5 m depth) as compared to previous studies. Additionally, adult *C. nauseosus* at our study site are apparently different from those in previous studies in that they had active shallow roots (30 cm) associated with hydraulic lift and daytime soil moisture uptake (Donovan et al. 2003; K.A. Snyder et al., unpublished data). One other difference is that *C. nauseosus* at our site is subspecies *consimilis*, which is likely different than the subspecies in previous studies [subspecies *hololeucus* (A. Gray) H.M. Hall & Clements in Donovan and Ehleringer 1994; subspecies not reported in other studies]. *C. nauseosus* ssp. *consimilis* is somewhat salt tolerant and

occurs mainly in alkaline soils of basin habitats and may have a different rooting ecology than subspecies more common on uplands [Baldwin et al. 2002; see also Cronquist 1994 whose taxonomic treatment gives this subspecies the name var. *oreophilus* (A. Nelson) H.M. Hall]. Although the uptake of added summer water pulses was a surprise, the more important point is that use of this water translated to beneficial effects on canopy volume changes, compared with controls, for adults of this species (Fig. 1, Table 2). Schwinning et al. (2002) observed that another shrub species (*Artemisia filifolia*) used pulse water but did not exhibit a gas exchange response, similar to our results with *C. nauseosus*. They hypothesized that the shallow water substituted for other water sources, saving other (deeper) water sources for later use. The hypothesis of substitution is consistent with effect of pulsed irrigation on *C. nauseosus* adult canopy volume but no effect of irrigation on branch sap flow or gas exchange. For *C. nauseosus*, the “saved” deeper water source apparently relieved limitations to canopy maintenance over time.

How then do we interpret the majority (eight of nine) of our comparisons, where use of pulsed summer irrigation did not result in any canopy growth responses? These plants are water limited. We know that year-year variation in winter/spring precipitation, fluctuations in depth to groundwater, and summer irrigation significant enough to recharge deep dry soil moisture layers affects long-term plant growth of these species (Fetcher and Trlica 1980; Johnson and Norton 1980; Toft 1995; Drenovsky 2002). Winter precipitation which penetrates to deeper depths may explain plant community distribution better than the distribution of summer rainfall (Brown et al. 1997; Reynolds et al. 1999). We consider a number of alternative possibilities that are not mutually exclusive.

One possibility is that roots were severely embolized and did not take up significant amounts of water from the irrigation pulses. This has been observed in several shrubs of the Great Basin (Kolb and Sperry 1999; Sperry and Hacke 2002), but is not likely to be the case in the current study. All watered plants were able to take up water as evidenced by improved predawn plant water status. Additionally, the response of adult *S. vermiculatus* to the DP treatment was the same as the IR treatment and roots in DP treatments were never subject to excessive soil drying that would cause embolism. Sap flow on shallow lateral roots showed significant fluxes of water through lateral roots on adult *S. vermiculatus* at the Mono Lake site (K.A. Snyder, unpublished data). Hydraulic lift, indicating shallow roots that are functional for water transport, was detected at 30 cm depth for adults of both *C. nauseosus* and *S. vermiculatus* at the Mono Lake site (Donovan et al. 2003). It is clear that the roots in our plants were not severely embolized.

Another possibility is that our study species all substituted surface water for deep water, potentially “saving” that deep water for later use (Schwinning et al. 2002). For example, sap flow measurements on lateral roots (experimentally severed at 1.2 m depth to prevent access to groundwater) of *S. vermiculatus* adults con-

firmed uptake of shallow soil water (K. A. Snyder et al. unpublished data) and irrigated plants used (based on stem sap flow measurements) the same amount of water as non-irrigated plants, supporting the idea that water was substituted. However, the close proximity of groundwater available to non-irrigated plants at our sites may have negated the substitution benefit of “saved” deep water for later use. There are issues of scaling that may also explain why “saved” water may not produce a net benefit in terms of individual plant growth. If the saved water is groundwater (as opposed to deep unsaturated soil water), any groundwater savings, from a small scale manipulation, would be averaged over a much larger area relatively rapidly because groundwater moves fast laterally due to high saturated hydraulic conductivity. Investigations of species-specific responses at sites that differ in depth to groundwater and the magnitude of summer rainfall are needed to assess the role of substitution in lack of growth responses.

The most probable explanation for no growth responses is suggested by a general lack of leaf N increases in our study. Plant growth was likely co-limited by N (or other nutrients). Leaf N concentrations in the study species are low (Table 1) and nutrient addition experiments at or near the study plots strongly support the potential for nutrient co-limitation of growth. Based on growth, leaf nutrient responses, and resorption, one experiment using factorial additions of N, P and water demonstrated that *S. vermiculatus* juveniles at Mono Lake were N-limited, while *C. nauseosus* was N and P co-limited (Drenovsky 2002; Drenovsky and Richards 2003). That study also documented water limitations in addition to the nutrient constraints to growth. Further evidence for nutrient limitations (N, P, and/or Mg) to canopy growth, leaf production, seed production and seed quality come from fertilization experiments with or without irrigation at both the Mono and Owens Lake sites (Drenovsky and Richards 2001; James et al. 2002). In all of these studies, fertilization was in late fall, winter, or early spring so that nutrient availability was increased during spring when growth rates of these shrubs are highest (see Comstock and Ehleringer 1992; Donovan et al. 1997).

Inorganic N availability increases very rapidly after rewetting of most soils due to increased microbial activity and turnover (Birch 1960; Gallardo and Schlesinger 1992; Stark and Firestone 1995; Paul and Clark 1996; Cui and Caldwell 1997; Lundquist et al. 1999; Burger 2002). Nutrient mobility also increases (Tinker and Nye 2000). Despite extremely low total soil N ($\leq 0.03\%$; Dahlgren et al. 1997; Donovan and Richards 2000) and the potential for ammonia volatilization (soil pH ≥ 9.3 ; Schlesinger and Peterjohn 1991; Schlesinger and Hartley 1992) at our study sites, summer irrigation pulses should have improved the nutrient status and potential growth of the nutrient co-limited shrubs. However, the lack of growth responses was generally associated with no changes in leaf N following summer irrigation, with the single exception of *A. confertifolia* at Owens Lake (Table 1).

The lack of N uptake, despite N availability and low leaf concentrations, was likely due to low plant N demand because growth rates are low during summer (Schenk 1996; Gastal and Lemaire 2002; Jeuffroy et al. 2002). Nitrogen uptake by woody plants is reduced as vegetative growth or reproductive sink activity declines, and if uptake does occur N is preferentially allocated to roots and stored (Weinbaum et al. 1978; Sanchez et al. 1992; Rosecrance et al. 1996; Quartieri et al. 2002). In fact, pulse experiments with labeled N (with and without water) at the Owens and Mono Lake sites indicate that the N uptake capacity of all of our study species declines by over 80% from spring when growth rates are high to summer when growth slows (J.J. James and J.H. Richards, unpublished data). Phenological canalization that sets these seasonal growth rate and plant nutrient demand patterns is strong in our Great Basin and Mojave study species (Hodgkinson et al. 1978; Comstock and Ehleringer 1992; Bilbrough and Caldwell 1997). This canalization limits plasticity to use summer resource pulses for growth. In contrast, *Larrea tridentata* is less constrained phenologically and can shift its major growth period to match the timing of seasonal moisture availability (BassiriRad et al. 1999; Reynolds et al. 1999).

Integration of multiple factors, such as nutrient additions in conjunction with precipitation manipulations and plant nutrient demand studies, appears necessary to fully assess the importance of summer resource pulses across scales from ecophysiological responses to growth and competitive interactions. It is essential that the magnitude of plant ecophysiological and growth responses be compared following pulses supplied at different times relative to the growth rate of the plants (i.e. comparing spring versus summer responses). In much of the Great Basin and Mojave, the predictable large magnitude pulse of mineralization and available soil moisture is in the spring, associated with warming soils and maximal plant growth periods. Further canopy growth in response to later pulses (i.e. summer) is not usually observed, although there may be other benefits such as survival, seed filling, root growth or acclimation processes to use of summer pulses (Hodgkinson et al. 1978; Comstock and Ehleringer 1992).

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