

Shading by shrubs in a desert system reduces the physiological and demographic performance of an associated herbaceous perennial

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Summary

1 A 2-year field study examined the demographic consequences of association with shrubs in an herbaceous perennial, *Cryptantha flava*. Physiological data were collected to evaluate whether shrub effects were mediated primarily through water, nutrient or light availability.

2 Microclimatic conditions under the north side of shrubs differed from open microhabitats, primarily in light availability. Due to little photosynthetic acclimation to light, daily photosynthesis for plants under shrubs was reduced proportionally to the light regime.

3 Shading did not reduce stomatal conductance proportionally to photosynthesis, which led to decreased water use efficiency for plants under shrubs. Few differences were found in leaf water potential between microhabitats, indicating that little competition for water was occurring.

4 There was little evidence for shrub-induced nutrient island effects. Soil nitrogen, phosphorus and organic content did not differ between open and shrub microhabitats. Leaf nitrogen content also differed little between plants in the two microhabitats.

5 Growth and flowering responses of individuals under shrubs were reduced relative to those in the open, even for plants located on the south side of shrubs.

6 Over this 2-year period of average to above-average rainfall, association of *C. flava* with shrubs was dominated by competition for light, rather than for water or nutrients. Future investigations will address whether this asymmetric competitive interaction changes during years with below-average rainfall to a facilitative interaction, or one of increased competition for water.

Key-words: competition, growth rates, microclimate, photosynthesis, water relations

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Introduction

The shrub species that dominate most sparsely vegetated arid lands are important components of the pronounced spatial habitat heterogeneity typical of these systems (Aguir & Sala 1999). Microhabitats under or near shrub canopies may vary dramatically from those in open, full sun locations, even when just a few centimetres away (Shreve 1931; Shmida & Whittaker 1981; Gutierrez *et al.* 1993). Also, where populations of co-occurring plant species are spread across both microhabitats, associations with shrubs are likely to contribute significantly to population level variation in plant growth and demographic traits (Tielbörger & Kadmon 1995, 2000).

Shrubs may have complex effects: in addition to providing shade, they may moderate air and soil temperatures, create nutrient islands as their litter decomposes, and alter the spatial distribution of soil water (Richards & Caldwell 1987; Gutierrez *et al.* 1993; Jackson & Caldwell 1993; Shumway 2000). Although many shrub species reduce the amount of soil water or nutrients present (Fonteyn & Mahall 1978; Caldwell *et al.* 1985), others, such as the cold desert shrub *Artemisia tridentata*, may increase water availability in upper soil layers via hydraulic lift (Richards & Caldwell 1987; Caldwell *et al.* 1998).

Interactions between shrubs, or between shrubs and plants of other growth forms range from competition to facilitation (Fowler 1986), and the strength and direction of these interactions can change with environmental conditions (Freeman & Emlen 1995; Callaway 1997;

Brooker & Callaghan 1998; Holzapfel & Mahall 1999). For example, Tielbörger & Kadmon (1997, 2000) found that both facilitative and inhibitory interactions between shrubs and annuals varied between years, species and life history stages. Shrubs may facilitate establishment of cacti through moderation of extreme temperatures, but the relationship may change to competition as seedlings grow (McAuliffe 1984; Franco & Nobel 1989). In a system where water and nutrients often limit plant growth, facilitation will occur if the benefits accrued from higher water or nutrient levels near shrubs outweigh the disadvantages of reduced light (Holmgren *et al.* 1997).

The nature of the interactions between shrubs and associated species has been investigated in several ways. Some studies have searched for non-random spatial relationships between individuals of different species that could reflect either competition or facilitation (Shmida & Whittaker 1981; Gutierrez *et al.* 1993; Freeman & Emlen 1995). Others have documented the consequences of these different microhabitats for plant size, seedling establishment or other demographic traits (Friedman & Orshan 1975; Tielbörger & Kadmon 1995; Casper 1996). Few have investigated the physiological bases for demographic responses to the shrub microhabitat (McAuliffe & Janzen 1986; Callaway 1992; Shumway 2000), although such information is clearly important to understanding why the responses occur. By examining both physiological and demographic responses, we may be able to understand the mechanistic bases of plant response to habitat heterogeneity imposed by shrubs (Caldwell & Pearcy 1994). For example, such studies could distinguish between the relative effects of nutrients, water availability and light on the carbon gain, growth and reproductive functions of shrub-associated species (Shumway 2000).

In this paper, we take a multifaceted approach to investigating the response of the herbaceous perennial *Cryptantha flava* (A. Nels.) Payson to shrub microhabitats in an arid system. We measure both shrub effects on microclimate, and physiological and demographic responses of naturally occurring individuals of *C. flava* to the resulting microhabitats. A previous long-term study with a cohort of *C. flava* at the same site documented higher growth rates and the production of more flowering stalks, but higher mortality in the open microhabitat (Casper 1994; Casper 1996). A major goal of the present study was to evaluate whether these performance differences were mediated through shrub effects on water, nutrients and/or light.

Specifically, our study addresses the following questions: (i) how do shrubs affect air and soil temperatures, light levels and soil water immediately surrounding them?, (ii) do rates of photosynthesis and seasonal carbon gain in *C. flava* respond to shrub-induced microhabitat changes?, (iii) how do individuals of *C. flava* respond to shrub-induced microhabitat changes in terms of water potential, stomatal conductance and water use efficiency?, (iv) do leaf nitrogen contents and/

or soil nutrient levels suggest that *C. flava* individuals under shrubs benefit from a shrub-induced nutrient island effect?, and (v) what are the demographic consequences of the shrub microhabitat, as expressed through plant size and size-specific flowering, mortality and growth?

Materials and methods

THE STUDY SYSTEM

Cryptantha flava grows in sandy soils throughout the semiarid Colorado Plateau, ranging from central Wyoming, through eastern Utah, and into northern Arizona and New Mexico. Its narrow, oblanceolate leaves (typically 6.0–9.0 mm long) first appear in mid-April and are organized in basal rosettes supported by a highly branched woody caudex. Due to the dense packing of rosettes and nearly vertical leaf orientation, the plant resembles a bunchgrass. Flowering begins in mid-May when some apical meristems convert from leaf to flower production; a rosette bolts to form an elongated stem, with evenly distributed leaves, and a terminal inflorescence, which may bear more than 70 flowers. Flowering rosettes die as seeds ripen in early July, and the remaining leaves on vegetative rosettes usually senesce a few weeks later. Some mortality also occurs among vegetative rosettes with plants losing many rosettes in unfavourable years (Casper 1996). Seeds either germinate with October rains and seedlings overwinter or germinate the following spring.

The field site is located in Uintah County in northeastern Utah at 1730 m elevation, where the vegetation is dominated by the shrubs *A. tridentata* Nutt. and *Chrysothamnus nauseosus* (Pallas) Britt., and the small tree *Juniperus osteosperma* (Torr.) Little, although only *A. tridentata* and *Ch. nauseosus* co-occurred with our study plants. Mean monthly temperatures range from -8.4°C in January to 21.3°C in July. Annual precipitation averages 215 mm, with most in the autumn and spring (Fig. 1). Many plants used in our study were

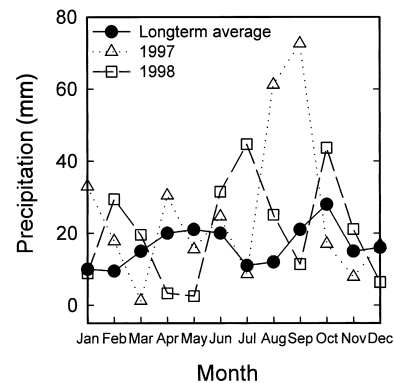


Fig. 1 Long-term, 15-year mean monthly precipitation (1982–97) recorded at the Vernal, Utah airport (USA), the nearest meteorological station to the Red Fleet research site. Also shown are the total monthly precipitation values for 1997 and 1998.

mapped individuals located within 12 plots, each 5×5 m and divided into 1 m^2 quadrats for spatial reference.

MICROCLIMATE

Microclimatic conditions under the north side of shrub canopies (compass direction $< 90^\circ$ or $\geq 270^\circ$) and in the open (> 0.50 m from the outer edge of any shrub canopy) were characterized from 30 April to 12 July in 1997 and in 1998, using four shrubs (two each of *A. tridentata* and *Ch. nauseosus*) adjacent to three of the study plots in each of the years. Photosynthetic photon flux (PPF), solar radiation from 0.4 to $0.7 \mu\text{m}$, was measured using quantum sensors (Biggs *et al.* 1971) placed in the open and under shrubs at 0, 0.15 and 0.35 m distances in from the outer edge of the shrub canopy. Temperatures at 0 and 0.10 m above the soil surface, as well as 0.01 m below the soil surface, were measured with shaded copper–constantan thermocouples placed in the open and at 0 and 0.30 m distances in from the outer edge of shrub canopies. Leaf temperatures of *C. flava* were measured by inserting fine-wire copper–constantan thermocouples into the abaxial surface of a single leaf on nine different plants, three located under the canopy of *A. tridentata* shrubs, three under *Ch. nauseosus* shrubs, and three in the open. Temperature and PPF sensors were logged every 60 s with CR 21 dataloggers (Campbell Scientific, Logan, UT, USA) with averages calculated every 30 min.

Soil water content (percentage mass) was measured approximately every 2–3 weeks from early May to late June in both years. Soil cores from both open and shrub microhabitats (directly under the canopy, on the north side) were removed by pounding a 0.05-m-diameter aluminium cylinder into the soil to a depth of 1–1.5 m. The soil core was then separated into different depth intervals, weighed, dried to constant mass in an 80° oven, and weighed again.

Soil samples for nutrient analyses were collected from the top 0.20 m of soil approximately every 2 weeks from 29 April to 7 July in 1999. Two to three cores were collected in each of three microhabitats, open and under the north side of *A. tridentata* and *Ch. nauseosus* shrubs each sampling period. After drying, soil samples were sent to the Utah State University Analytical Laboratories (Logan, UT, USA) for analysis of nitrate, ammonium, phosphorus and potassium concentrations, and organic content.

PHYSIOLOGICAL MEASUREMENTS

The following data were collected for individuals of *C. flava* in the open and under the north side of shrub canopies at various times during the 1997 and 1998 growing seasons: photosynthetic response to controlled levels of PPF, diurnal courses of photosynthesis and stomatal conductance under ambient conditions, leaf carbon isotope values, predawn and midday leaf

water potentials, leaf nitrogen content, and leaf specific weight.

Photosynthetic light response curves were constructed for 27 plants in the open microhabitat and 18 under shrubs in 1997 using a LiCor 6200 closed photosynthesis system (LiCor, Inc. Lincoln, NE, USA) equipped with a detachable LED light source (Quantum Devices Barneveld, WI, USA). One to three leaves from a vegetative rosette were enclosed in a 0.25-L chamber and first exposed to $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF and ambient air for a 5–10-min equilibration period after which the air was recirculated and CO_2 depletion over two consecutive 15-s periods was measured. The average of the two measurements was taken as the photosynthetic rate. Photosynthesis was similarly measured on the same leaves after decreasing PPF to 1800, 1500, 1200, 800, 400, 200 and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF.

Predawn and midday leaf water potentials were collected using a Scholander type pressure chamber (Plant Moisture Systems, Corvallis, OR, USA); measurements were taken approximately every 2 weeks beginning in May and ending in July when leaves became brittle and broke prior to the endpoint for water potential measurements. Sample sizes were small in order to minimize destructive sampling of plants within the plots.

Carbon isotope values were measured on leaves collected in July from both microhabitats in all 12 plots. With the exception of those that died, the same individuals were sampled in 1997 ($n = 162$) and 1998 ($n = 152$). Two to four leaves from each plant were dried and ground to a fine powder in liquid nitrogen. Carbon isotope ratios (δ , $^{13}\text{CO}_2/^{12}\text{CO}_2$) were determined relative to the Pee Dee Belemnite standard by mass spectrometry at the Stable Isotope Ratio Facility for Ecological Research (SIRFER) at the University of Utah (Salt Lake City, UT, USA). Carbon isotope ratio values were converted to discrimination values (Δ) by the equation (Farquhar *et al.* 1989):

$$\Delta = (\delta_a - \delta_p)/(1 + \delta_p/1000)$$

where δ_a is the carbon isotope ratio of CO_2 in the atmosphere (assumed to be -8 per mil, ‰), and δ_p is the measured carbon isotope ratio of the plant tissue.

Leaf nitrogen content was measured on a percentage dry weight basis. Three leaves from each of 4–10 plants in each microhabitat were collected from plants adjacent to the study plots on four sampling dates in 1997 (26 April, 28 May, 8 June, and 9 September) and six in 1998 (8 April, 24 April, 9 June, 10 July, 12 August and 11 September). Leaves were dried to constant mass, weighed and ground to a fine powder in liquid nitrogen. Nitrogen content was measured using a Perkin-Elmer model 2400 Series 2 (Norwalk, CT, USA) nitrogen analyser at the University of Maryland, or by the SIRFER. No instrumental bias was found for duplicate leaf samples analysed by both facilities. Leaf specific weights were determined for a single leaf from each of

12 plants located adjacent to the study plots in each microhabitat on 28 May 1997. Leaf areas were measured using a LiCor Model 3100 leaf area meter; leaves were then dried to constant mass before weighing.

DEMOGRAPHY

Demographic data were collected in all 12 plots but not necessarily from the same plants as those used for physiological measurements. Depending on plant densities, data were either collected in 13 alternate 1 m² quadrats within each plot or in seven quadrats selected randomly from among the 13. For this study, we further excluded quadrats where shrubs were absent, to restrict the data set to those plants under or near the same shrubs and control for larger-scale spatial variation in plant performance. All plants past seedling stage were classified in one of three microhabitat categories. Plants classified in the open category were located > 0.10 m from the outer canopy edge of a shrub. Plants directly under shrubs together with those in the open but ≤ 0.10 m from a shrub canopy were placed into a north or a south category. The north category included plants located < 90° or ≥ 270° while the south included plants ≥ 90° and < 270°. Plants in the three microhabitats were compared for size differences in 1997, size-specific growth and mortality between 1997 and 1998, and size-specific flower stalk production in both years.

STATISTICAL ANALYSES

Data were analysed using ANOVA. In analysis of microclimate and physiological variables, microhabitat and soil depth (in the case of soil water content) were treated as fixed effects and date (within a year) treated as random. In all analyses, data collected in association with the two shrub species were combined. For soil nutrients and percentage organic matter, a one-way ANOVA comparing the fixed effect of shrub vs. open microhabitats was conducted on pooled data from all sample dates. Only the carbon isotope discrimination (Δ) was measured for the same individuals in both 1997 and 1998, and in that case a repeated-measures ANOVA was employed. Otherwise, separate ANOVA models were used for measurements made in different years. Data were transformed when necessary to achieve assumptions of homogeneity of variance; predawn water potential values from 1997 were transformed using \tan^{-1} , soil phosphorus concentrations and percentage organic matter were log transformed, and Δ -values were \ln transformed.

Individual photosynthetic light response curves measured in the field were fit to a non-rectangular hyperbolic equation (Prioul & Chartier 1977), using the actual rates measured at 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF as estimates of dark respiration (R_d) and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF for estimates of light-saturated photosynthetic rate (A_{max}). Other parameters derived from these equations were the initial slope of the photosynthesis: PPF

relationship (apparent quantum efficiency, AQE), the light compensation point (PPF required to reach a value of 0 net photosynthesis) and the PPF required to achieve 90% of A_{max} (PPF @ A_{90}). This last parameter was used as an estimate of photosaturating PPF. The parameters A_{max} , AQE, R_d , light compensation point and PPF @ A_{90} were then compared between open and shrub microhabitats using MANOVA.

The demographic data were highly non-normal, so all analyses except for size-specific growth rates employed nonparametric statistical methods. Plant size in 1997 was compared among the three microhabitats using Kruskal–Wallis ANOVA. Percentage mortality as a function of microhabitat and plant size (< or ≥ median) was examined using log-linear methods. Likewise, log-linear methods were used to compare size-specific flowering among microhabitats after grouping plants by size categories, using intervals of four leaf rosettes, and by numbers of flowering stalks, 0, 1 or > 1 stalk.

Randomization procedures were used to obtain *P*-values for an ANCOVA to test the hypothesis that plants from different microhabitats exhibited different size-specific growth rates. Growth rate was calculated as [(number of rosettes in 1998) – (number of rosettes in 1997)]/(number of rosettes in 1997), and the number of rosettes in 1997 was used as the covariate. Type II sums of squares were used due to unequal sample sizes between microhabitats. Because the growth data violated the assumption of normality, a randomization test of the above hypothesis was carried out (Manly 1997). One thousand data sets in which individual observations were randomized among microhabitat classes, while retaining the original sample sizes, were created. Then, test statistics were recalculated with parametric ANCOVA to generate a distribution of possible outcomes (Petraitis, Beaupre & Dunham 2000).

Results

MICROCLIMATE

Microclimatic differences between open and shrub microhabitats were driven by differences in solar radiation, which on average was reduced by 45% under shrubs (Fig. 2). However, individual shrub canopies were highly heterogeneous, due to size differences among shrubs and branch death creating canopy gaps. This resulted in large differences in PPF under shrubs over short time and spatial scales. Soil temperatures were higher in the open, but air and leaf temperatures did not differ greatly between microhabitats. This was most likely due to the small size of shrubs and efficient convective and transpirational cooling of the narrow leaves of *C. flava* (Fig. 3).

Soil water content was lower under shrubs, particularly for the upper soil layers, and generally decreased over time, although larger rains recharged the upper soil layers (Fig. 4). Results are presented for 1998 only, as the pattern was similar in 1997. ANOVA results for

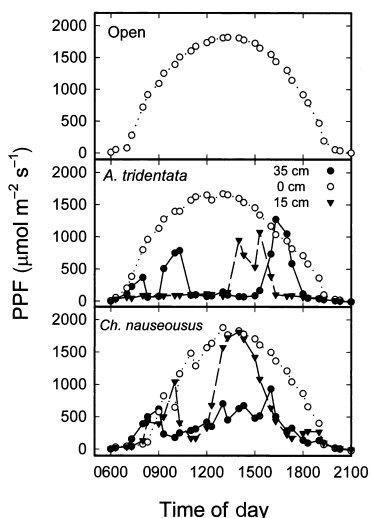


Fig. 2 Diurnal course of photosynthetic photon flux (PPF), on a horizontal surface measured on 31 May 1997 at Red Fleet (UT, USA). Data are presented for both open microhabitat, and different depths under the canopies of a selected *Artemisia tridentata* and *Chrysothamnus nauseosus* individual.

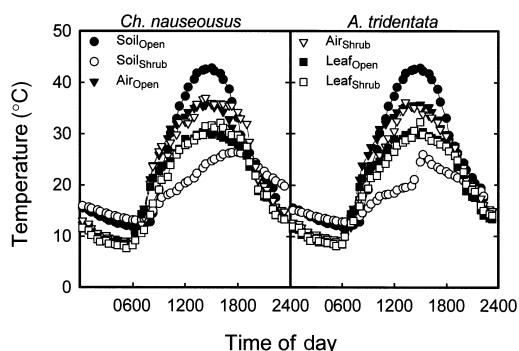


Fig. 3 A representative diurnal course of air, soil and *Cryptantha flava* leaf temperatures under the canopy of selected *Artemisia tridentata* and *Chrysothamnus nauseosus* individuals. Data presented were collected on 31 May 1997, but are qualitatively similar to data collected throughout the spring growing seasons of 1997 and 1998. Means \pm SE (symbols are larger than SE).

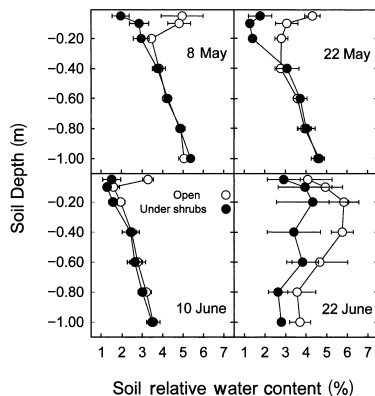


Fig. 4 Soil water content at different soil depths in open and shrub microhabitats for four different dates in 1998. Data presented are means of three replicate cores in each microhabitat \pm SE.

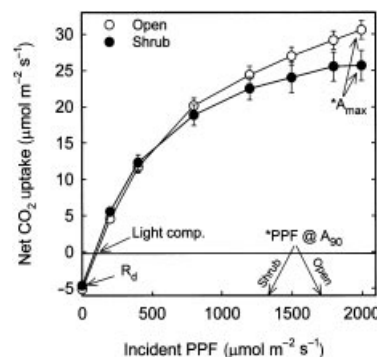


Fig. 5 Composite curves constructed from the response of photosynthesis to light for *Cryptantha flava* individuals in open and shrub microhabitats. Bars represent the means \pm SE. Asterisks indicate significant differences between light response parameters.

1998 revealed a significant effect of date ($F_{3,111} = 23.467$, $P < 0.001$), microhabitat ($F_{1,111} = 26.423$, $P < 0.001$), soil depth ($F_{6,111} = 4.807$, $P < 0.001$), and significant Date \times Depth ($F_{18,111} = 3.237$, $P < 0.001$) and Microhabitat \times Depth ($F_{6,111} = 2.828$, $P = 0.0134$) interactions.

No significant differences between shrub and open microhabitats were found for soil nitrate, ammonium, phosphorus or percentage soil organic matter (data not shown). Soil potassium levels were, however, significantly higher under shrubs (mean \pm SE $126.5 \pm 13.0 \mu\text{g g}^{-1}$) than in open microhabitats ($79.1 \pm 8.6 \mu\text{g g}^{-1}$) ($F_{1,11} = 9.24$, $P < 0.02$). Total soil nitrogen (nitrate plus ammonium) ranged between 0.97 and $27.48 \mu\text{g g}^{-1}$ in the open, and from 2.00 to $11.51 \mu\text{g g}^{-1}$ under shrubs. Mean total soil nitrogen did not differ between microhabitats, with mean \pm SE values of 5.22 ± 1.05 in open ($n = 26$) and $5.79 \pm 0.63 \mu\text{g g}^{-1}$ for shrub ($n = 17$) microhabitats.

PHYSIOLOGICAL MEASUREMENTS

Photosynthetic light response curves differed only slightly between microhabitats (Fig. 5), but with significantly higher A_{max} ($F_{1,43} = 4.475$, $P = 0.040$) and PPF @ A_{90} levels ($F_{1,43} = 7.890$, $P = 0.007$) found for plants in the open. Consequently, shading by shrub canopies limited diurnal rates of photosynthesis for plants under shrubs (Fig. 6a). On average, *C. flava* individuals located beneath shrubs fixed only 59% of the total daily carbon as plants in the open.

Stomatal conductances were not reduced to the same extent as photosynthesis by shading from shrubs (Fig. 6b). This, combined with similar leaf temperatures in open and shrub microhabitats, resulted in transpirational water loss being reduced by only approximately 20% under shrubs (Fig. 6c) compared with open microhabitats. The fact that the shrub microhabitat reduced photosynthesis in *C. flava* more than conductance caused plants in open microhabitats to have higher intrinsic rates of water use efficiency (Fig. 6d).

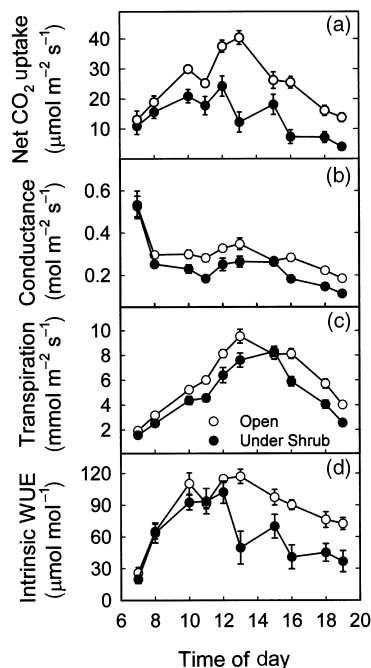


Fig. 6 Diurnal courses of photosynthesis (a) measured on *Cryptantha flava* plants in the open or under shrubs. Plants were exposed to ambient light levels and temperatures. (b) Measured stomatal conductances on the same plants. (c) Transpiration rates, calculated using ambient air speeds, calculated leaf boundary layer conductances and ambient vapour pressure deficits. (d) The ratio of photosynthesis to stomatal conductance, a measure of intrinsic water use efficiency (WUE). Data are means \pm SE. Data presented are from 31 May 1997, but were qualitatively similar on all other days of measurement throughout the 1997 and 1998 growing seasons.

Differences between microhabitats in photosynthetic gas exchange responses were reflected in leaf carbon isotopes. Carbon isotope discrimination (Δ) was consistently higher for plants under shrubs (Table 1, $F_{1,163} = 125.123$, $P < 0.001$). Values in 1998 were significantly higher than in 1997 ($F_{1,163} = 339.978$, $P < 0.001$), but the Microhabitat \times Year interaction was not significant, indicating consistent differences between microhabitats. There was considerable intrapopulation variation in Δ , with a range of 3.8‰ in 1997 and 4.3‰ in 1998 (Table 1).

Water potential did not differ consistently between plants in the two microhabitats. In 1997, predawn leaf water potentials (Fig. 7) were lower for plants under shrubs ($F_{1,101} = 8.745$, $P < 0.004$) and declined over the sampling dates ($F_{3,101} = 57.6$, $P < 0.001$), while the Microhabitat \times Date interaction was not significant. Midday leaf water potentials also declined over time in

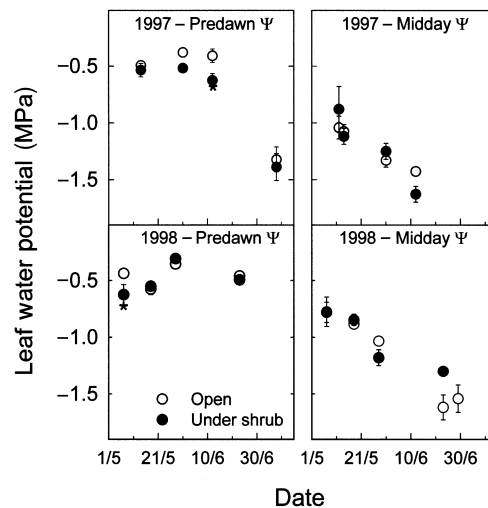


Fig. 7 Predawn and midday measurements of leaf water potential collected in 1997 and 1998 on individuals of *Cryptantha flava* in two different microhabitats. Data are means \pm SE. Asterisks represent differences at $P \leq 0.05$ for individual measurement periods.

1997 ($F_{3,66} = 18.342$, $P < 0.001$), but neither microhabitat nor the Microhabitat \times Date interaction term was significant. In 1998, predawn leaf water potentials (Fig. 7) did not differ between microhabitats, but a significant Microhabitat \times Date interaction term ($F_{3,60} = 3.332$, $P = 0.025$) reflects lower water potentials for plants under shrubs on the first sampling date; date also proved significant ($F_{3,60} = 17.307$, $P < 0.001$). Midday leaf water potentials in 1998 were significantly lower in open microhabitats ($F_{1,47} = 4.231$, $P = 0.0453$) and declined over time ($F_{4,47} = 19.814$, $P < 0.001$), but the Microhabitat \times Date interaction was not significant.

Leaf nitrogen content was higher for plants under shrubs in 1998 ($F_{1,101} = 4.332$, $P = 0.040$), but not in 1997 (Fig. 8). The Date \times Microhabitat interaction was also significant in 1998 ($F_{5,101} = 2.429$, $P = 0.040$), but not in 1997. Leaf nitrogen content declined over sampling dates both in 1997 ($F_{3,97} = 46.54$, $P < 0.001$) and in 1998 ($F_{5,101} = 42.143$, $P < 0.001$).

Leaf specific weight was significantly higher in open (11.12 ± 0.60 mg cm $^{-2}$) compared with shrub microhabitats (8.71 ± 0.47 mg cm $^{-2}$; $F = 38.56$, $P < 0.001$).

DEMOGRAPHY

Plant size differed among microhabitats in 1997 (Kruskal–Wallis $H = 14.18$, $P < 0.001$) when disproportionately more plants on the north side of shrubs had fewer than

Table 1 Stable carbon isotope discrimination values for plants in open and shrub microhabitats. Data are presented as means \pm SE

Microhabitat	1997		1998	
	Δ (‰)	Range	Δ (‰)	Range
Open	19.366 \pm 0.039	18.000–20.800	20.376 \pm 0.054	18.100–21.700
Shrub	20.265 \pm 0.060	18.600–21.800	21.134 \pm 0.080	19.300–22.400

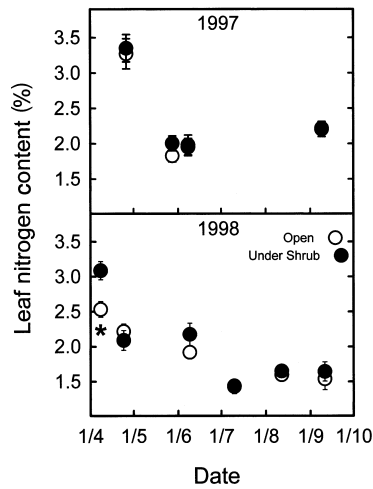


Fig. 8 Leaf nitrogen contents measured during the 1997 and 1998 growing seasons on *Cryptantha flava* individuals in two different microhabitats, open or under shrubs. Data are means \pm SE.

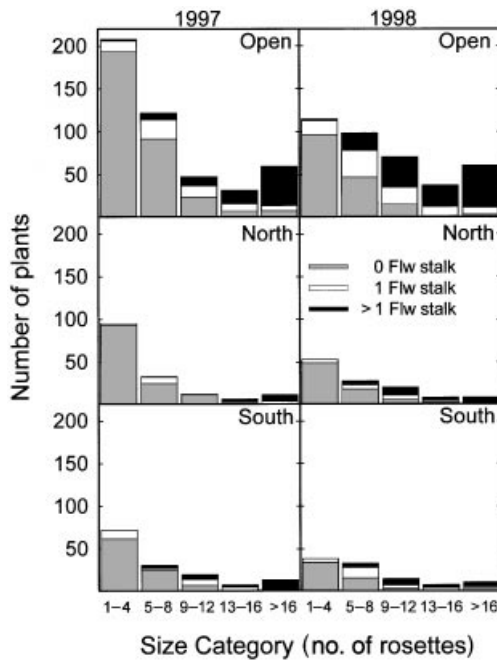


Fig. 9 Frequency of plants in different size categories for three different microhabitats, open, north side of shrubs and south side of shrubs. Also shown is their flowering status, 0, 1 or > 1 flowering stalk(s) in 1997 and 1998.

four leaf rosettes (Fig. 9a). Size distributions did not differ between the south and open microhabitats. Of the 763 plants surveyed in 1997, 26.0% died before the 1998 census. Plants smaller than the median were more likely to die (partial association $\chi^2 = 36.6$, d.f. = 1, $P < 0.001$), but mortality did not differ among microhabitats, independent of size (best-fit maximum likelihood model $\chi^2 = 7.78$, d.f. = 6, $P = 0.255$). The best-fit maximum likelihood model explaining flower stalk production included both size and microhabitat in 1997 (model $\chi^2 = 25.65$, d.f. = 24, $P = 0.371$) and 1998 (model $\chi^2 = 16.731$, d.f. = 24, $P = 0.8598$). Size was a

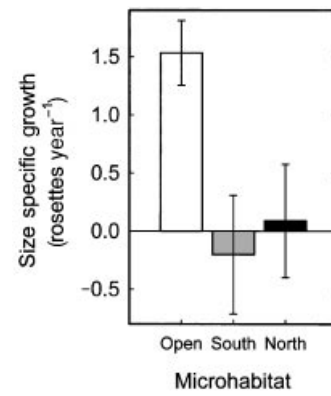


Fig. 10 Size-specific growth rates between 1997 and 1998 (means \pm SE) for plants of *Cryptantha flava* in three different microhabitats. For this graph, size-specific growth is defined as [(size in 1998 – size in 1997)/size in 1997].

significant factor in both models ($P < 0.001$), with larger plants more likely to flower (Fig. 9). Based on partial association χ^2 values, microhabitat contributed more importantly to the model in 1998 ($\chi^2 = 10.35$, d.f. = 4, $P < 0.04$) than in 1997 ($\chi^2 = 5.47$, d.f. = 4, $P < 0.25$). Plants on the north side of shrubs were less likely to flower than plants in the other two microhabitats (Fig. 9).

Size-specific growth rates were highly variable, even within a microhabitat, especially for plants under shrubs (Fig. 10). In the analysis of size-specific growth rate, none of the 1000 random data sets exhibited $F_{1,559}$ values as extreme as the value of 6.27 observed in the parametric analysis. These results indicate that size-specific growth rates differed significantly among microhabitats ($P \leq 0.002$) and that the violation of the assumption of normality did not affect the results of the parametric ANCOVA. The data in the three microhabitat classes did not violate the assumption of homogeneity of slopes ($F_{2,559} = 13.665$, $P \geq 0.5986$). There was also a significant effect of plant size ($F_{1,559} = 116.67$, $P \leq 0.001$), as well as significant differences among microhabitats in size-specific growth rates. Smaller plants grew relatively more than large plants. Multiple comparison tests for planned comparisons among the microhabitat classes revealed that size-specific growth rates were significantly higher in the open microhabitat class than in either the north ($P \leq 0.011$) or the south ($P \leq 0.003$) under shrubs. Size-specific growth rates of the north and south microhabitat classes were not significantly different from each other or from zero.

Discussion

Our study shows that shrubs negatively impact the physiological and demographic performance of *C. flava* primarily by reducing light availability. We base this conclusion on several findings: (i) both light levels and photosynthesis were greatly reduced under shrubs, and plants exhibited little photosynthetic acclimation; (ii) transpiration was not reduced as much in plants

under shrubs as was photosynthesis; (iii) midday leaf water potentials were rarely different between microhabitats; (iv) leaf N content and soil nutrient levels differed little between microhabitats; (v) the demographic data were consistent with light being primarily important, as demographic characteristics on the south side of shrubs were more similar to those in the open microhabitat than were those on the north.

The possibility that shading may limit plant performance in desert habitats has received little attention. Most studies in these high light environments have focused on water, nutrients and temperature as limiting factors (MacMahon & Schimpf 1981; Caldwell 1985; Smith & Nobel 1986; Comstock & Ehleringer 1992). Shrubs often improve these environmental factors, especially under stressful conditions, thereby facilitating species associated with them (Franco & Nobel 1989; Gutierrez *et al.* 1993; Callaway 1997; Caldwell *et al.* 1998). Literature addressing the physiological, morphological and growth responses of plants to reduced light has largely developed from research in tropical and temperate forests, in ecosystems with large temporal and spatial variation in light regimes (Boardman 1977; Evans *et al.* 1988). Only a limited number of studies have recognized that shading from trees or shrubs may suppress the growth of associated smaller plants in deserts as well (Franco & Nobel 1989; Zhang *et al.* 1995; Holmgren *et al.* 1997).

The fact that shrubs do not change soil water availability in a way that impacts either positively or negatively the performance of *C. flava* is suggested by several pieces of evidence. Stomatal conductance and transpiration declined less in the shrub microhabitat than did photosynthesis. If water deficits due to competition with shrubs were occurring, we would have expected stomatal conductances in *C. flava* to decrease at least proportionately to photosynthesis. Because they did not, plants under shrubs experienced an increase in intercellular CO₂ concentration (data not presented) and a reduction in intrinsic water use efficiency (WUE). Similar responses to shade are found typically in species from more mesic habitats (Boardman 1977; Farquhar & Sharkey 1982; Evans *et al.* 1988). Excess water loss due to higher conductance is usually not a problem where shade lowers temperatures, vapour pressure deficits and transpiration rates. However, in our study, leaf temperatures and vapour pressure deficits differed little between the two microhabitats. The fact that a high stomatal conductance still occurred suggests that competition for water is not as strong as the effect of reduced light, and that the ability to respond rapidly to increasing light levels is important.

Our conclusion from gas exchange measurements that plants under shrubs exhibit reduced WUE is corroborated by the carbon isotopic composition of leaf tissue. Leaf tissue carbon isotope discrimination is a long-term, integrated measure of the balance between stomatal conductance and photosynthesis (Ehleringer 1993; Farquhar *et al.* 1989). Therefore, Δ is inversely

related to WUE, given equal respiratory losses and vapour pressure deficits (Farquhar *et al.* 1989; Toft *et al.* 1989). Increases in Δ have often been associated with lower light conditions in forest habitats (Farquhar *et al.* 1989; Berry *et al.* 1997), but such responses to shading are rarely examined in arid land plants. One study (Vora *et al.* 1989) did report a 1‰ increase in Δ with shading in *Achyranthes aspera*, similar to results found here.

Although competition with shrubs for water was not as important as shading effects, upper soil layers were drier under shrubs (Fig. 4). Lower soil water content was found only in the upper layers where cold desert shrubs typically have many fine roots (Campbell & Harris 1977; Caldwell 1985). Shrubs may draw down this water source and intercept precipitation from smaller rainfall events, leading to the microhabitat differences observed. Canopy interception of rainfall was invoked as the mechanism behind negative effects of shrubs on annuals during dry years in a Negev desert system (Tielbörger & Kadmon 2000). If hydraulic lift (Richards & Caldwell 1987; Dawson 1993; Caldwell *et al.* 1998) occurred, it was not of sufficient magnitude to restore soil water content to levels equal to those in the open. Microhabitat differences in soil water were reflected in predawn water potentials but not at midday when plants were actively transpiring, again suggesting that plants under shrubs were no more water stressed than those in the open. The taproot of *C. flava* may reach 0.5 m in depth, so mature plants may not be totally dependent upon water in shallow soils. Additionally, lateral root development in *C. flava* may enable some individuals under shrubs to access water in the open microhabitat.

Leaf and soil nutrient contents provided no evidence that shrubs created nutrient islands for *C. flava*. In 1998, leaf N content differed significantly between shrub and open microhabitats early in the season only. This early-season difference could reflect a more rapid uptake of N in shrub-associated plants, perhaps due to earlier initiation of growth in response to moderation of cold night-time temperatures or earlier snow melt under shrubs. This difference rapidly disappeared, probably because leaf expansion caused dilution of initially high N contents. Evans & Ehleringer (1993) likewise reported no differences in soil N between intercanopy sites and soils under *A. tridentata* shrubs. Leaf N in *C. flava* is high for C₃ plants in general (Evans 1989), but is consistent with the high photosynthetic rates we measured (Field & Mooney 1986) and with values from other cold desert perennials (Caldwell 1985). The sandy soils at Red Fleet are very low in nitrogen, as is common in the Colorado Plateau (Evans & Ehleringer 1993), implying that *C. flava* has a strong ability to accumulate N in plant tissues. Nitrogen does limit growth in *C. flava*, as plants in the open respond rapidly to N fertilization (M. Peek & I. Forseth, unpublished data), and differences among populations in plant size and growth rate appear related to soil fertility levels (Casper 1996).

Plant sizes, growth rates and flowering in the different microhabitats reinforce the physiological data in pointing to light as being the limiting resource under shrubs. In general, these demographic traits were similar for plants in the open and under the south side of shrubs. On the north side, plants were smaller, grew at a slower rate and, in 1998, produced fewer flowering stalks for a given vegetative size than did plants in the open. In contrast, plants on the south side differed from those in the open only by having a smaller size-specific growth rate. These results are consistent with plants on the south sides receiving more light during the growing season than those on the north, as they should at this latitude. If there were a significant nutrient island effect, we would have expected plants on the south side of shrubs to perform even better than those in the open, at least in some capacities.

There may be several reasons why the demographic characteristics of south-side populations were not identical to those in the open. The 'south side' encompassed a broad spatial category, including all plants under and within 0.10 m of the shrub canopy in a 180° arc, from west to east, and many plants were deep enough under the canopy to have been shaded at midday. Thus, on average, total daily irradiance in the south microhabitat was still likely to be less than in the open. Because we only measured microclimate and physiological parameters on the north sides of shrubs, due to time and sampling constraints, we do not have a full picture of the south microhabitat. For example, perhaps the drier soils under shrubs proved more of a problem for plants on the south side, where evaporation from soils and transpiration should have also been greater.

The short-term demographic differences among microhabitats for *C. flava* suggest longer-term ramifications in life history traits. Plants located under the north side of shrubs may never achieve the size of individuals in the open and may have lower lifetime reproductive output. Given the slower growth rates of plants on the south side of shrubs, it must take longer for them to reach the same maximum size as plants in the open. Data from another study with *C. flava* suggest that, on average, plants do live longer under shrubs (Casper 1994, 1996). However, the results of our study do not suggest that shrubs facilitate the performance of *C. flava*, as they do for many associated species in arid habitats (Went 1942; Dawson 1993; Freeman & Emlen 1995; Tielbörger & Kadmon 1995; Aguiar & Sala 1999; Holzapfel & Mahall 1999); mean positive growth for *C. flava* plants under shrubs must only occur in some years.

Finally, we realize that plant performance differences between shrub and open microhabitats may well depend on large-scale environmental factors, such as overall soil fertility and rainfall. Tielbörger & Kadmon (1997, 2000) found that effects of desert shrubs on annual species varied among years with different rainfall. Several authors have proposed that the balance between

competition and facilitation will vary with life stage, physiology, indirect interactions and the degree of abiotic stress (Bertness & Callaway 1994; Callaway & Walker 1997; Goldberg & Novoplansky 1997). For example, Holmgren *et al.* (1997) developed a model based on the premise that plant canopies simultaneously positively affect the water balance of plants below them, and negatively affect light availability. Facilitation then occurs when the improvement of water relations exceeds the costs of light limitation. This may happen under dry conditions, but under less dry conditions, competition for light may be paramount. However, Tielbörger & Kadmon (2000) found no evidence for light limitation by shrubs of annuals, and contrary to expectation found that positive effects on reproduction increased with yearly precipitation. Because our study spanned 2 years with average to above-average precipitation, we did not explore how different precipitation amounts might have affected the plants' responses to shrubs. Based on current plant size distributions, shrubs must, over the long-term, suppress the performance of *C. flava*. However, another study with this system showed reduced plant performance differences between shrub and open microhabitats in a dry year (Casper 1996). It is unclear to what extent these results were caused by shrubs reducing the severity of drought, and to what extent they reflect a highly size-dependent response to drought (Casper 1996), with larger plants in the open microhabitat being affected more severely.

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References

- Aguiar, M.R. & Sala, O.E. (1999) Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution*, **14**, 273–277.
- Berry, S.C., Varney, G.T. & Flanagan, L.B. (1997) Leaf $\delta^{13}\text{C}$ in *Pinus resinosa* trees and understory plants: variation associated with light and CO_2 gradients. *Oecologia*, **109**, 499–506.
- Bertness, M.D. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.
- Biggs, W.W., Edison, A.R., Easton, J.D., Brown, K.W., Maranville, J.W. & Clegg, M.D. (1971) Photosynthesis light sensor and meter. *Ecology*, **52**, 125–131.
- Boardman, N.K. (1977) Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology*, **28**, 355–377.
- Brooker, R.W. & Callaghan, T.V. (1998) The balance between positive and negative plant interactions and its relationship

- to environmental gradients: a model. *Oikos*, **81**, 196–207.
- Caldwell, M. (1985) Cold desert. *Physiological Ecology of North American Plant Communities* (eds B.F. Chabot & H.A. Mooney), pp. 198–212. Chapman & Hall, London.
- Caldwell, M.M., Dawson, T.E. & Richards, J.H. (1998) Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia*, **113**, 151–161.
- Caldwell, M.M., Eissenstat, D.M., Richards, J.H. & Allen, M.F. (1985) Competition for phosphorus: Differential uptake from dual-isotope-labeled soil interspaces between shrub and grass. *Science*, **229**, 384–386.
- Caldwell, M.M. & Pearcy, R.W. (1994) *Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Belowground*. Academic Press, New York, NY.
- Callaway, R.M. (1992) Morphological and physiological responses of three California oak species to shade. *International Journal of Plant Science*, **153**, 434–441.
- Callaway, R.M. (1997) Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia*, **112**, 143–149.
- Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.
- Campbell, G.S. & Harris, G.A. (1977) Water relations and water use patterns for *Artemisia tridentata* Nutt. in wet and dry years. *Ecology*, **58**, 652–659.
- Casper, B.B. (1994) Post-dispersal sibling competition and the evolution of single-seededness in *Cryptantha flava*. *Evolution*, **48**, 1377–1382.
- Casper, B.B. (1996) Demographic consequences of drought in the herbaceous perennial *Cryptantha flava*: effects of density, associations with shrubs, and plant size. *Oecologia*, **106**, 144–152.
- Comstock, J.P. & Ehleringer, J.R. (1992) Plant adaptation in the Great Basin and Colorado plateau. *Great Basin Naturalist*, **52**, 195–215.
- Dawson, T.E. (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant–plant interactions. *Oecologia*, **95**, 565–574.
- Ehleringer, J.R. (1993) Carbon and water relations in desert plants: An isotopic perspective. *Perspectives of Plant Carbon and Water Relations from Stable Isotopes* (eds J.R. Ehleringer, A.E. Hall & G.D. Farquhar), pp. 155–172. Academic Press, San Diego, CA.
- Evans, J.R. (1989) Photosynthesis and nitrogen relationships in leaves of C₃ plants. *Oecologia*, **78**, 9–19.
- Evans, R.D. & Ehleringer, J.R. (1993) A break in the nitrogen cycle in aridlands? Evidence from $\delta^{15}\text{N}$ of soils. *Oecologia*, **94**, 314–317.
- Evans, J.R., von Caemmerer, S. & Adams, W.W. III (1988) *Ecology of Photosynthesis in Sun and Shade*. CSIRO, Melbourne, Australia.
- Farquhar, G.D., Ehleringer, J.R. & Hubick, K.T. (1989) Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 503–537.
- Farquhar, G.D. & Sharkey, T.D. (1982) Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology*, **33**, 317–346.
- Field, C. & Mooney, H.A. (1986) The photosynthesis-nitrogen relationship in wild plants. *On the Economy of Form and Function* (ed. T.J. Givnish), pp. 25–55. Cambridge University Press, Cambridge, Cambridgeshire.
- Fonteyn, P.J. & Mahall, B.E. (1978) Competition among desert perennials. *Nature*, **275**, 544–545.
- Fowler, N. (1986) The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**, 89–110.
- Franco, A.C. & Nobel, P.S. (1989) Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology*, **77**, 870–886.
- Freeman, D.C. & Emlen, J.M. (1995) Assessment of inter-specific interactions in plant communities: an illustration from the cold desert saltbush grasslands of North America. *Journal of Arid Environments*, **31**, 179–198.
- Friedman, J. & Orshan, G. (1975) The distribution, emergence and survival of seedlings of *Artemisia herba-alba* Asso in the Negev Desert of Israel in relation to distance from the adult plant. *Journal of Ecology*, **63**, 627–632.
- Goldberg, D. & Novoplansky, A. (1997) On the relative importance of competition in unproductive environments. *Journal of Ecology*, **85**, 409–418.
- Gutierrez, J.R., Meserve, P.L., Contreras, L.C., Vasques, H. & Jaksic, F.M. (1993) Spatial distribution of soil nutrients and ephemeral plants underneath and outside *Porlieria chilensis* (Zygophyllaceae) in arid coastal Chile. *Oecologia*, **95**, 347–352.
- Holmgren, M., Scheffer, M. & Huston, M.A. (1997) The interplay of facilitation and competition in plant communities. *Ecology*, **78**, 1966–1975.
- Holzapfel, C. & Mahall, B.E. (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology*, **80**, 1747–1761.
- Jackson, R.B. & Caldwell, M.M. (1993) Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology*, **81**, 683–692.
- MacMahon, J.A. & Schimpf, D.J. (1981) Water as a factor in the biology of North American desert plants. *Water in Desert Ecosystems* (eds D.D. Evans & J.L. Thames), pp. 114–171. Dowden, Hutchinson and Ross Inc., Stroudsburg, PA.
- Manly, B.J.F. (1997) *Randomization, Bootstrap, and Monte Carlo Methods in Biology*. Chapman & Hall, New York, NY.
- McAuliffe, J.R. (1984) Sahuaro–nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia*, **64**, 319–321.
- McAuliffe, J.R. & Janzen, F.J. (1986) Effects of intraspecific crowding on water uptake, water storage, apical growth, and reproductive potential in the sahuaro cactus, *Carnegiea gigantea*. *Botanical Gazette*, **147**, 334–341.
- Petraitis, P.S., Beaupre, S.J. & Dunham, A.E. (2000) ANCOVA: Nonparametric and randomization approaches. *The Design and Analysis of Ecological Experiments*, 2nd edn (eds S. Scheiner & G. Gurevitch) CRC Press, Boca Raton, FL, in press.
- Prioul, J.L. & Chartier, P. (1977) Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO₂ fixation: a critical analysis of the methods used. *Annals of Botany*, **41**, 789–800.
- Richards, J.H. & Caldwell, M.M. (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia*, **73**, 486–489.
- Shmida, A. & Whittaker, R.H. (1981) Pattern and biological microsite effects in two shrub communities, southern California. *Ecology*, **62**, 234–251.
- Shreve, F. (1931) Physical conditions in sun and shade. *Ecology*, **12**, 96–104.
- Shumway, S.W. (2000) Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. *Oecologia*, **124**, 138–148.
- Smith, S.D. & Nobel, P.S. (1986) Deserts. *Photosynthesis in Contrasting Environments* (eds N.R. Baker & S.P. Long), pp. 13–62. Elsevier, Amsterdam, the Netherlands.
- Tielbörger, K. & Kadmon, R. (1995) Effect of shrubs on emergence, survival and fecundity of four coexisting annual species in a sandy desert ecosystem. *Ecoscience*, **2**, 141–147.
- Tielbörger, K. & Kadmon, R. (1997) Relationships between shrubs and annual communities in a sandy desert ecosystem: a three year study. *Plant Ecology*, **130**, 191–201.
- Tielbörger, K. & Kadmon, R. (2000) Temporal environmental

- variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–1553.
- Toft, N.L., Anderson, J.E. & Nowak, R.S. (1989) Water use efficiency and carbon isotope composition of plants in a cold desert environment. *Oecologia*, **80**, 11–18.
- Vora, A.B., Patel, J.A. & Punjani, B.L. (1989) Comparative photosynthesis and levels of metabolites in leaves and chloroplasts of sun-adapted and shade-adapted plants of *Achyranthes aspera* Lin. *Journal of Environmental Biology*, **10**, 159–164.
- Went, F.W. (1942) The dependence of certain annual plants on shrubs in southern California deserts. *Bulletin of the Torrey Botanical Club*, **69**, 100–114.
- Zhang, H., Sharifi, M.R. & Nobel, P.S. (1995) Photosynthetic characteristics of sun versus shade plants of *Encelia farinosa* as affected by photosynthetic photon flux density, intercellular CO₂ concentration, leaf water potential, and leaf temperature. *Australian Journal of Plant Physiology*, **22**, 833–841.

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