Microhabitat dependent responses to resource pulses in the aridland perennial, *Cryptantha flava*

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Summary

1 A 3-year field study examined the physiological and demographic consequences of resource pulse use by an herbaceous, aridland perennial, *Cryptantha flava*, as well as potential competitive and facilitative interactions with larger shrubs.

2 We applied a pulse of urea and faecal pellets, simulating Mule deer excretions, to plants growing between and under Sagebrush and Rabbitbrush canopies.

3 We hypothesized that *C. flava* would show strong positive responses to N pulses in open microhabitats, and such plants had approximately 50% increases in leaf N concentrations within days of pulse application, accompanied by increased photosynthetic rates. Over the next year, higher rates of growth and reproduction were found in the plants receiving supplemental N.

4 We predicted that due to shading, plants would not respond to N pulses when growing under shrubs but supplemental N caused increases in leaf N similar to that in open growing plants. However, the response of both growth and reproduction was less than in the open, suggesting at least partial light limitation.

5 In 2000, a year of below average precipitation, all plants decreased in size, but survival was facilitated under shrubs (93%) relative to that of open plants (84%).

6 In the open, there was a trade-off between rapid growth in favourable years and survival in dry years. Supplemental N in years of average precipitation increased RGR from 0.42 to 1.16 rosettes rosette^{-1} year^{-1}, but reduced from −0.02 to −0.2 in dry years.

7 Plant performance in aridlands thus results from complex interactions between microhabitat, nutrient pulses and yearly precipitation patterns.

Key-words: competition, drought, facilitation, nitrogen pulses, trade-offs

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Introduction

Arid regions of the world are generally noted for their low primary productivity which is due to a combination of low, unpredictable water supply and low soil nutrient concentrations (Smith *et al*. 1997). The effects of low levels of precipitation (< 250 mm per year) are often compounded by the highly variable timing of its occurrence (Noy-Meir 1973). In addition to limiting biomass production, dry conditions lead to slow decomposition rates, and the combination of these factors leads to low levels of soil nitrogen and organic matter (Burke 1989).

The high spatial and temporal heterogeneity of soil minerals in arid systems complicates the effects of the low resources levels. Spatially, soil nitrogen may vary over a scale of cm (Jackson & Caldwell 1993). Litter accumulation and enhanced decomposition for example, leads to soil N levels usually being higher under the canopy of aridland shrub species (Garcia-Moya & McKell 1970; Hook *et al*. 1991) than in intershrub spaces. Another biotic factor that may affect local soil nutrient concentrations are large mammals such as pronghorn antelope (*Antilocapra americana*), elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) in the south-western United States. Urine and faeces create patches with high concentrations of available N (Stillwell & Woodmansee 1981), as does the decomposition of dead animals. However, the effects of large mammals on soil nutrient heterogeneity and, particularly, plant responses to mammal-generated nutrient patches are less well characterized in arid systems than in temperate grasslands and forests (McNaughton *et al*. 1988; Pastor *et al*. 1993; Steinauer & Collins 1995).

Temporal variability in aridland soil nutrient supply may be generated by snowmelt and unpredictable

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precipitation – factors that temporarily increase mineralization rates by soil microbes (Burke 1989; Bowman 1992; Gallardo & Schlesinger 1992). These relatively brief, localized nutrient pulses can be an important component of the total nutrient supply over the growing season for plants (Campbell & Grime 1989). Plants in habitats with high temporal and spatial heterogeneity in soil nutrient availability have several mechanisms to exploit ephemeral nutrient pulses. Morphologically, plants may rapidly increase fine root growth in areas of high nutrient concentrations (Jackson & Caldwell 1989; Caldwell *et al*. 1991). Physiologically, plants may increase root uptake kinetics to exploit microsite enrichment (Jackson *et al*. 1990). However, the ability of plant roots to respond to nutrient pulses often depends on overall plant demand for nutrients (Jackson & Caldwell 1989; Bilbrough & Caldwell 1997), the seasonal timing of nutrient pulses (Gebauer & Ehleringer 2000) and the availability of other resources (e.g. light, Bilbrough & Caldwell 1995).

Large shrubs in desert ecosystems have a large influence on community structure. For example, they may modify the surrounding microclimate by dampening temperature variation, raising humidity, decreasing wind speed and reducing irradiance under their canopies (Valiente-Banuet & Ezcurra 1991; Forseth *et al*. 2001). Shrubs may also increase the concentration of soil nutrients (Gutierrez *et al*. 1993) and modify soil moisture levels (Caldwell *et al*. 1998) in their immediate area. Because of the effects of shrubs on the surrounding microhabitat, interactions between shrubs and plants of other growth forms may range from competition to facilitation (Fowler 1986; Callaway 1997; Holzapfel & Mahall 1999). Tielbörger & Kadmon (1997, 2000) found both facilitation and asymmetric competition between shrubs and annual plants, depending upon the year, species and life history stage. Holmgren *et al*. (1997) hypothesized that facilitation between shrubs and associated plants will occur if the benefits from higher water or nutrient levels near shrubs outweigh the disadvantages of reduced light under their canopy. Thus, facilitation between shrubs and associated plants may occur during particularly dry years (Bertness & Callaway 1994) whereas, during times of higher resources, associated plants may experience competitive interactions resulting in decreased performance.

Numerous studies have investigated interactions between large shrubs and associated plant species by examining spatial relationships (Eccles *et al*. 1999), seedling establishment and growth (Tielbörger & Kadmon 1995; Casper 1996). Fewer studies have examined the physiological mechanisms underlying the observed changes in plant performance (Shumway 2000; Forseth *et al*. 2001). Even fewer studies have combined a third factor in the investigation of shrub–smaller plant interactions – that of nutrient pulses. Due to the multiple factors (both biotic and abiotic) and the complex interactions that may result, integration of a variety of these

factors is important in complex systems in order to understand observed patterns in plant performance. The study reported here takes a manipulative approach to examine the effects of microhabitat location on N pulse use by a long-lived herbaceous perennial, *Cryptantha flava*. We experimentally manipulated soil N around selected study plants by mimicking a one-time pulse of urea-derived N, such as that generated by Mule deer excretions.

The specific hypotheses tested were as follows.

1. Plants in open microsites will respond positively to a pulse of N through rapid uptake and incorporation of N into leaf photosynthetic structures. This, in turn will lead to significantly greater growth and reproduction in these plants than in plants not receiving a pulse of N.

2. Due to asymmetric competition for light with larger shrubs, individuals of *C. flava* located under shrub canopies will not respond positively to soil N pulses. Due to high year-to-year variation in precipitation in this arid system, we designed the study to extend over 3 years to look at interactive effects of precipitation and nutrient supply. Below average precipitation between the 2nd and 3rd year of the study allowed us to test a further, *post hoc*, hypothesis.

3. The effects of N pulse use will be contingent upon seasonal precipitation, with low water availability limiting or eliminating the positive response of plants in the open to N. As a corollary to this, we were also able to test the predictions of Holmgren *et al*. (1997) and Bertness & Callaway (1994) that shrubs will ameliorate physical conditions for plants associated with them in drier years and act as competitors during average and above average soil moisture conditions.

Materials and methods

THE STUDY SYSTEM

Crypthantha flava (A. Nels.) Payson (Boraginaceae) grows in sandy soils in the Uintah Basin and Canyonlands regions of the Colorado Plateau. The growth habit of this herbaceous perennial consists of a woody caudex supporting densely packed rosettes of nearly vertical leaves. Above-ground vegetative growth begins in late March, flowering begins mid-May and seeds are set by mid-July. Flowering is initiated by bolting of vegetative rosettes that die after producing a single flowering stalk. Most vegetative rosettes senesce during the hot, dry summers that characterize the Colorado Plateau, followed by limited vegetative growth and some seedling germination in the fall when precipitation increases.

The study site was on land managed by the US Bureau of Land Management at a site in north-eastern Utah approximately 15 km N of Vernal, UT (1730 m elevation, 40°30′ N, 109°22′30″ E). Long-term annual precipitation averages 208 mm, with considerable monthly variation across years (Fig. 1). During the years in which this study was conducted, an extremely
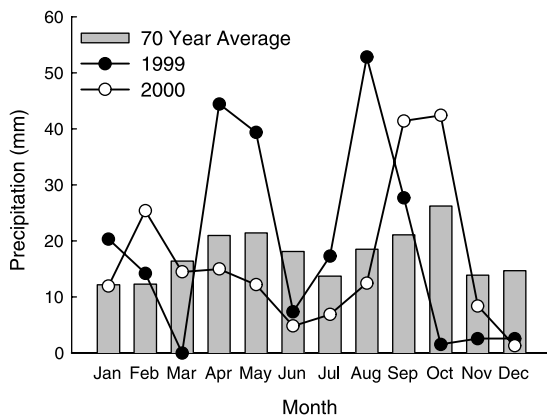
Fig. 1 Seventy-year mean monthly precipitation (1928–2000) recorded at the Vernal Airport, approximately 15 km south of the Red Fleet study site. Also shown are mean monthly precipitation values for 1999 and 2000.

dry autumn in 1999 was followed by average to above average snowfall in early 2000. Continued below average precipitation in March–June led to an extremely dry spring 2000 growing season. In this area, *C. flava* occurs at mid-level elevations of 1500–2300 m. Vegetation is dominated by large shrubs of sagebrush (*Artemisia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus*) and a small tree (*Juniperus osteosperma*). The study area has a high degree of environmental heterogeneity, including shrubs, rock outcrops, soil depth differences and variable drainage patterns (Forseth *et al*. 2001). Previous work on this population of *C. flava* showed that individuals growing under shrubs experienced asymmetric competition for light that reduced photosynthetic carbon gain, growth and reproduction compared to plants in the open (Forseth *et al*. 2001).

A large herd of migratory mule deer (*Odocoileus hemionus*) over-winters at the study site, resulting in a significant increase in the local recycling of N via urine and faeces. Excretion-generated patches are spatially heterogeneous, with densities ranging from 300 to 4900 ha^{-1}. Peek & Forseth (2003) calculated that an average of 2430 groups of pellet per hectare would amount to over 16 kg ha^{-1} year^{-1} of N. Although mule deer *do not* feed on *C. flava*, they do influence its microhabitat by redistributing N from other plants into concentrated patches. An associated study (Peek & Forseth 2003) showed that small non-reproductive plants responded to urea derived N from artificial urine deposits with rapid uptake and utilization of N for photosynthesis and growth.

EXPERIMENTAL DESIGN

Experimental plants were chosen from a natural population based upon their size, reproductive status and spatial location. A total of 240 plants in the open and 120 plants under the canopy of either *A. tridentata* or *Ch. nauseosus* were marked and followed from 1999 to 2001. In 1999, two thirds of the open and shrub plants received a 1-L application of simulated mule deer urine (5.3 g urea N based on Stillwell 1983) and fresh faecal pellets (UF). A fresh faecal pellet group from a nearby natural excretion event was collected and transferred to experimental plants. In 2000, half of the treated plants received an additional application of urine and faeces (2xUF), while the other half were left alone (1xUF). The remaining one third of these plants served as controls (CO), with no manipulation in any of the 3 years of the study. A subset of these controls were treated with deionized water to identify whether any of the effects of adding 1 L of urine were due to water addition. However, no such effects were detected (Peek & Forseth 2003) and these treatments are combined with the controls in the results presented here.

Microclimatic conditions in the open and under shrubs were measured at various times during the 1999 and 2000 growing seasons. We measured relative soil water content gravimetrically by taking soil cores with a 0.05-m diameter aluminium cylinder to depths of 5, 10, 20, 40, 60, 80 and 100 cm. We also extracted ammonium (NH_4^+) and nitrate (NO_3^-) from soil cores taken from the upper 20 cm at approximately 10-day intervals. We extracted ions from the soil using an equilibrium reaction by shaking soils in 2 M KCl for 1 hour. Extracts were then analysed colourimetrically (Lachat QC 8000 Flow Injection, Zellweger Analytics, UK). In addition, we estimated mineralization rates per kg soil per day using Dowex® HCR-S cation (20–50 mesh) and Dowex® 1 × 8-50 anion (20–50 mesh) exchange resins (Lajtha 1988). To load resins with exchangeable H$^+$ and OH$^-$ ions, resins were placed in separately labelled anion and cation nylon bags and washed in 2 M HCl for 1 hour, followed by rinsing with deionized water. Anion and cation bags were then placed in the field in the bottom of 4 × 20 cm vertically aligned aluminium cylinders in the open and under shrubs for 100 days. The aluminium cylinders were pounded into the ground, removed, and replaced in the original hole, flush with the surrounding soil, with the respective washed anion or cation resin at the bottom of the cylinder. This was done to effectively capture all ions per unit weight of soil. Resins were extracted with 50 mL of 2 M KCl and analysed colourimetrically.

Physiological measurements were taken on a subset of experimental plants throughout the 1999 and 2000 growing seasons. We examined net photosynthetic rates, stomatal conductances and internal CO$_2$ concentrations on open plants only. Little information can be gained from instantaneous measurements of plants under shrubs due to the variability in photosynthetic photon flux (PPF) from full sun levels of 2000 μmol m^{-2} s^{-1} to full shade levels of 200 μmol m^{-2} s^{-1} within seconds (M.S. Peek, unpublished data). Forseth *et al*. (2001), however, did show that shrub plants are light limited for photosynthesis in years of average to above average precipitation. Gas exchange measurements

were taken using a LiCor 6200 closed photosynthesis system (LiCor, Inc. Lincoln, NE, USA) during the hours of 0900–1400 MST to ensure saturating light levels and to restrict the range of ambient temperature and vapour pressure deficit. From these data, the ratio of photosynthesis to stomatal conductance was calculated as an estimate of instantaneous intrinsic water use efficiency (WUE).

Leaf tissue was collected for measurement of nitrogen concentrations at various times during the 1999 and 2000 seasons, using different subsets of plants to minimize destructive harvesting. Leaf tissue was dried to a constant mass in an 80 °C oven, and ground in liquid N2 to a fine powder with a mortar and pestle. Nitrogen concentration was measured on a percentage dry weight basis via combustion in a Perkin-Elmer 2400 Series CHN analyser (Norwalk, CT).

Demographic measurements were collected on all treatment plants for the 3 years of the study. We counted the total number of rosettes, which is positively correlated with above-ground biomass, and number of flowering stalks on each individual. We then compared size specific growth as ([Rosette number$_t$ – Rosette number$_{t-1}$]/Rosette number$_{t-1}$) and size specific reproductive effort across all treatments in 1999, 2000 and 2001. Size specific reproductive effort was defined as RE = [no. flowering rosettes/total rosettes] × 100, and split into reproductive efforts of 0; $0 < RE \leq 25$; $25 < RE \leq 50$; and $RE > 50$. We also noted survival and compared treatment and location effects on mortality rates in 2000 and 2001.

STATISTICAL ANALYSES

Data were analysed using mixed models analysis of variance techniques. For microclimate data, physiological measurements, rosette number and size specific growth rates, we used microhabitat location (open or under shrub canopy) and N pulse treatment (control [CO], urine + faeces [2xUF] and urine + faeces in 1999 only [1xUF]) as fixed effects. Different sampling dates within years were treated as random effects separately because subsets of experimental units were sampled at each date. Leaf N concentrations were analysed with a two factor fixed effect model for main effects of treatment and microhabitat location as well as any significant interactions. Any pair-wise comparisons were adjusted for experiment-wise error using Tukey's adjustment. All data met the assumptions of the ANOVA model, with the exception of soil mineral N concentrations, which were log transformed to meet homogeneity of residuals. Reproductive effort and mortality were analysed using loglinear techniques. Chi square values from the original data were compared to a distribution of 1000 generated values from randomization procedures, preserving original sample sizes in each treatment category, to obtain *P*-values for the probability of obtaining the observed results by chance (Manley 1991).

Results

SOIL RESOURCE LEVELS

Soil relative water contents were similar between open and shrub locations, particularly for the upper soil layers (Fig. 2). Only during 1999 did soil moisture diverge between microhabitats, where open habitats remained wetter at deeper soil depths than under shrubs. A significant sampling date effect was found ($F_{5,278} = 4.87$, $P < 0.03$), which resulted in significantly drier soils later in the season, particularly for the upper soil layers. In 2000, soils were significantly drier than in 1999 ($F_{1,278} = 4.87$, $P < 0.03$).

Soil mineral N concentrations were highly variable throughout both growing seasons with a significant date by microhabitat location interaction ($F_{18,253} = 1.80$, $P < 0.03$, Fig. 3a,b). For most sampling dates, no significant differences were evident between open and shrub habitats. However, two dates in 1999, 29 April and 1 June, and two dates in 2000, 12 February and 1 July, showed significantly higher mineral N concentrations for soils under shrub canopies. Seasonal mineralization rates, estimated using ion exchange resins, yielded significantly higher means for microhabitats under shrubs during fall 1999 and spring 2000 (Fig. 3c). Fall 2000 values were almost 10 times as great as all other dates, but with no significant difference between microhabitats.

PHYSIOLOGICAL RESPONSE TO N

In 1999, plants exposed to a N pulse (UF) maintained higher photosynthetic rates (Ps) and water use efficiencies (WUE) for most of the season after the pulse was applied (Fig. 4). In 2000, however, few significant differences between treatments existed for Ps, despite a second N application to one third of the plants (2xUF) (Fig. 4). Photosynthetic rates were significantly higher in 1999 than 2000 ($F_{1,741} = 373.24$, $P < 0.0001$). In contrast, WUE for 2xUF treated plants were significantly higher than controls for most of the 2000 season, although this was not seen for the 1xUF treated plants.

Leaf N (% by weight) concentrations were correlated with instantaneous Ps measurements, with higher N contents in 1999 than 2000 ($F_{1,1519} = 164.54$ $P < 0.0001$, Fig. 5). In 1999, UF treated plants maintained significantly higher percentage N by weight for both microhabitat locations for all sampling dates ($F_{3,1519} = 49.26$, $P < 0.0001$). The 2000 growing season also produced significant treatment effects, with 2xUF treated plants having the greatest percentage N concentrations followed by 1xUF treated plants and finally control plants.

DEMOGRAPHIC RESPONSES TO N

Initial size and reproductive effort were not statistically different in the plants chosen for different treatments
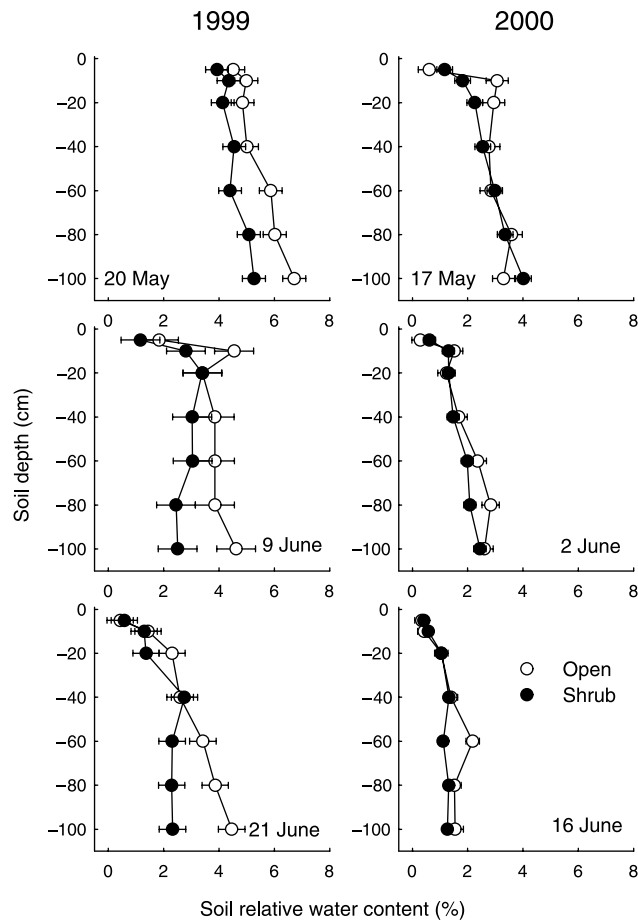
Fig. 2 Soil relative water contents at three different dates in 1999 and 2000 for open and under shrub microhabitats. Data are means of three to six replicate cores per microhabitat ± 1 SE.

within each microhabitat location (Fig. 6, $F_{1,400} = 0.5$ $P = 0.5$, Fig. 7, $\chi^2_{df=1} = 0.5$, $P = 0.62$). However, there was a significant location by reproduction interaction ($\chi^2_{df=3} = 29.3$, $P < 0.0001$), driven by the presence of fewer reproductive individuals and reproductive individuals showing lower efforts in the shrub relative to the open microhabitats (Fig. 7). The increase in size from 1999 to 2000 was significantly greater for UF treated plants than for controls in both open and shrub microhabitats (Fig. 6, $F_{1,396} = 16.4$, $P < 0.0001$). In addition, relative growth rates (RGR) were significantly different between treatments, but not for microhabitat, with control plants having rates of 0.42 ± 0.085 and 0.48 ± 0.119 rosettes rosette^{-1} year^{-1} for open and shrub microhabitats, respectively. N-treated plants had 2–4 times higher rates, 1.16 ± 0.094 and 0.86 ± 0.118 rosettes rosette^{-1} year^{-1}, than controls for open and shrub microhabitats, respectively.

Reproductive effort showed a treatment effect in 2000, as indicated by a significant treatment by reproduction interaction ($\chi^2_{df=3} = 47.3$, $P < 0.0001$). The 2xUF treatment had a higher proportion of reproductive plants, with greater reproductive efforts than controls (Fig. 7). Mortality differed between microhabitats ($\chi^2_{df=2} = 4.4$, $P < 0.05$), with higher mortality in open compared to shrub microhabitats, 5.0% and

4.2%, respectively. Mortality in 2000 was not affected significantly by N treatment ($\chi^2_{df=1} = 0.01$, $P = 0.9$).

In 2001, all plants shrank in size regardless of treatment or location (Fig. 7), resulting in no size differences among treatments in 2001 (Fig. 7, $F_{2,366} = 0.7$, $P = 0.8$). Since UF treated plants were larger than controls in 2000, equal sizes in 2001 translated into significantly lower RGRs for the 2xUF (-0.2 ± 0.09 and -0.2 ± 0.1 rosettes rosette^{-1} year^{-1} for open and shrub microhabitats, respectively) and 1xUF (-0.2 ± 0.07 and -0.2 ± 0.1 rosettes rosette^{-1} year^{-1} for open and shrub microhabitats, respectively) treated plants than in controls (-0.02 ± 0.04 and -0.09 ± 0.06 rosettes rosette^{-1} year^{-1} for open and shrub microhabitats, respectively). Plants were also significantly smaller under shrubs than in the open (Fig. 6, $F_{1,366} = 10.6$, $P < 0.001$). No significant interactions of reproduction with either microhabitat or treatment were found ($\chi^2_{df=3} = 5.0$, $P = 0.2$, $\chi^2_{df=6} = 9.0$, $P = 0.3$, respectively). Mortality in 2001 was higher than in 2000 (Fig. 7, hatched bars), with significant main effects of treatment and location ($\chi^2_{df=2} = 2.9, P < 0.05$, $\chi^2_{df=1} = 17.8, P < 0.0001$, respectively). Highest mortality occurred in the 2xUF treatment for both open and shrub microhabitats. Mortality was also higher in open microhabitats, 16% compared to 7% in the shrub microhabitat (Fig. 7).
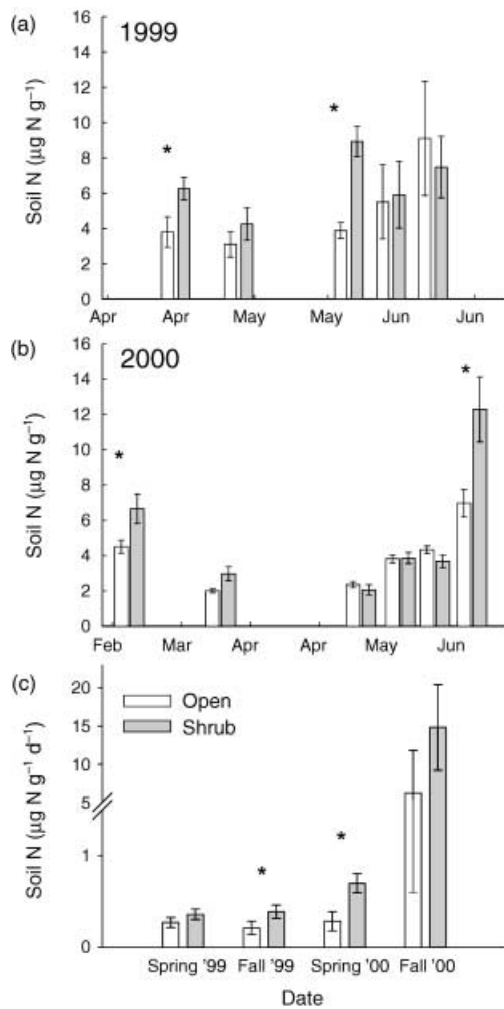
Fig. 3 Soil mineral nitrogen concentrations during the 1999 and 2000 growing seasons in open and under shrub microhabitats. Panels a and b represent instantaneous measurements of soil nitrogen means ± SE, asterisk denotes significantly different means (*n* = 10 per treatment per date). Panel c is an integrated measure of soil N for fall and spring seasons in 1999 and 2000 using ion exchange resin bags (*n* = 5 per treatment per date).

Discussion

Both water and nutrients have been found to limit plant growth in aridland ecosystems (Ettershank *et al*. 1978; Gutierrez & Whitford 1987). Our results are consistent with this, however, we have extended previous findings by illustrating the interactions between microhabitat, water and soil N. In particular, water availability determined the responses of *C. flava* to nitrogen pulses. A pulse of N increased photosynthesis, growth, and reproduction for plants in both open and shrub habitats in 1999, a year with adequate soil moisture, but actually decreased growth and survival in open microhabitats in years of below average precipitation (2000 and 2001).

PHYSIOLOGICAL RESPONSES

Most studies on aridland plant response to soil resource pulses have focused on either the roots (Jackson

& Caldwell 1989; Jackson *et al*. 1990; Caldwell *et al*. 1991; Bilbrough & Caldwell 1997) or the community (Steinauer & Collins 1995). Less attention has been placed on leaf physiology and population-level responses. Our results provided support for our first and third hypotheses (N promotes growth in open habitats and response depends on water supply), but not for the second hypothesis (N has little effect under shrubs). Higher soil N supply actually led to rapid plant uptake of N regardless of microhabitat. It is possible that *C. flava* has developed a luxury uptake pattern for N, taking up excess N when available, and then storing it for later use. Certainly, the light environment under shrubs did not permit as great a growth rate response to a N pulse as seen in open microhabitats, but stored N may sustain long-term growth under shrub canopies, which would not be detected in this short study.

Nitrogen treatments led to increased instantaneous water use efficiency (i.e. the ratio of photosynthesis to stomatal conductance) of plants in the open (Fig. 4). This occurred in both years, with 2xUF treated plants having greater WUE than controls and 1xUF plants. Nevertheless, increased WUE did not translate to higher growth rates, greater reproductive efforts or increased survival in dry years. This result is somewhat surprising, given that many authors have argued that higher WUE may be of selective advantage in desert plants (Schuster *et al*. 1992; Arntz & Delph 2001). It is possible that in a highly opportunistic herbaceous perennial such as *C. flava*, WUE is not an important selective factor and other traits, such as growth rate, root architecture, carbon storage and phenological plasticity may be more important. Water use efficiency incorporates both water transport and photosynthetic traits. In order to support greater growth rates and water demands accompanying higher photosynthesis, the water transport system developed in new tissues may have had wider xylem elements with thinner walls. These traits maximize rate of transport, but also lower resistance to cavitation and embolism under low soil water potentials. Thus, opposing selection on the different components may have led to the positive relationship we found between mortality and WUE (Arntz & Delph 2001).

DEMOGRAPHIC RESPONSES

Higher photosynthetic rates in UF-treated plants formed the basis for greater size-specific growth rates between 1999 and 2000 compared to controls, consistent with our first hypothesis. However, reduced soil moisture levels during the spring 2000 growing season (Fig. 2) reduced photosynthesis in all treatments, supporting our *post hoc* hypothesis. Consequently, all plants had zero or negative growth rates between 2000 and 2001. N-pulse treated plants showed the greatest reductions; hence the benefits gained in one year from increased growth and reproduction were at least
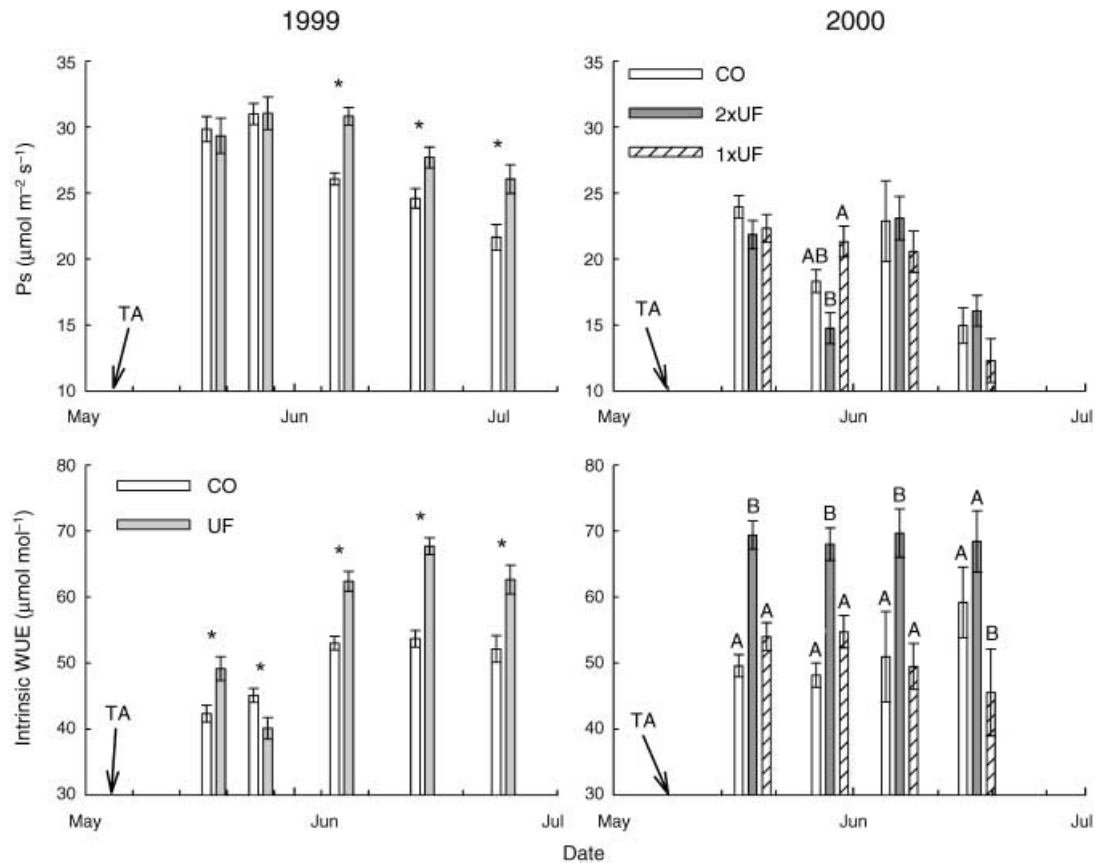
Fig. 4 Instantaneous photosynthetic rates and intrinsic water use efficiency (WUE) for *Cryptantha flava* plants growing in the open. Treatments in 1999 are control (CO) and urine and faeces treated (UF), 2000 treatments are control (CO) and urine and faeces treated in 1999 only (1xUF) and urine and faeces treated in 1999 and 2000 (2xUF). Data presented are means ± SE with asterisks representing significant differences of means in 1999. In 2000, common letters within sampling dates indicate means are not significantly different at $P < 0.05$ ($n = 30$ per treatment per sampling date). Arrows indicate N pulse application (TA).

partially offset by negative growth in the following year. As a resource unit allocated to one function is then not available for other functions (Bloom *et al.* 1985), trade-offs exist among competing processes. We hypothesize that the increased growth and reproduction seen in N-treated plants resulted in a demographic cost of reduced growth and survival in years with low precipitation. This short-term trade-off does not necessarily result in a trade-off in lifetime fitness – we would need longer measurements to see if the benefits gained in higher resource years (higher seed set) outweighed the costs incurred in low resource years (low seed set and lost future reproduction). However, at least some of the plants receiving N were relatively young when they died between 2000 and 2001, suggesting the potential for a reduction of lifetime fitness. Casper (1996) found a similar result for *C. flava* in response to a severe drought. A cohort of plants that Casper had planted in 1983 had a size-based response to drought in 1988–89, with large plants being disproportionately affected. Because the plants were of an even age, rapid growth leading to larger sizes was apparently a disadvantage during severe drought conditions.

There are at least three different, non-exclusive mechanisms that might lead to size and growth biased responses to reduced precipitation. First, the higher availability of soil N may have led to increased allocation to above-ground tissues relative to root structures. High root/shoot ratios are advantageous to desert plants under water stress because greater root absorptive tissue can sustain transpirational water supply (Donovan & Ehleringer 1994). Second, higher N supplies may have led to higher allocation to growth and flowering, with reduced allocation to maintenance and storage. In this species, maintenance may be a function of building stronger and/or more xylem vessels in the perennating caudex. Lower soil water supplies might then lead to increased cavitation of xylem elements in larger plants, disrupting the water supply and leading to greater dieback under drought (Kolb & Sperry 1999). Third, larger plants may have greater respiratory costs than smaller plants. Water stress that caused lower photosynthetic rates due to stomatal closure would lead to greater reductions in growth due to the necessity of supporting this greater respiratory demand. This trade-off is commonly seen in large woody perennials such as trees, but it may also be seen in other perennial lifeforms (Yoda *et al.* 1965; Whittaker & Woodwell 1967).
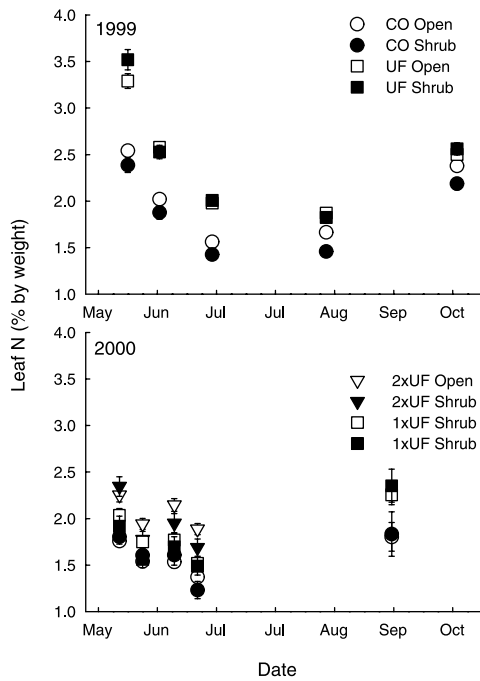
Fig. 5 Leaf nitrogen concentrations of *Cryptantha flava* (% by weight) measured during the 1999 and 2000 growing seasons in open and shrub microhabitats for control (CO) plants, urine and faeces treated (UF) plants. Data are means ± 1 SE (*n* = 25 per treatment per sampling date).
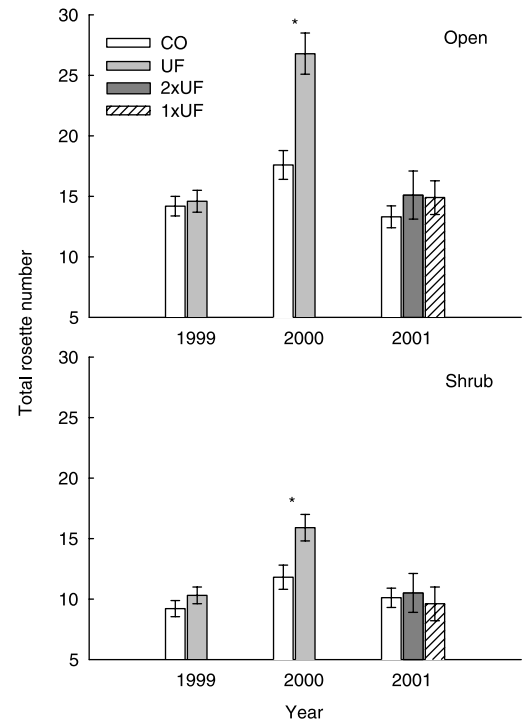

Fig. 6 Total rosette number for *Cryptantha flava* in different microhabitats for all N treatments. Bars are means ± 1 SE with an asterisk denoting significantly different means.

SHRUB MEDIATED EFFECTS

Large shrubs in deserts often act to ameliorate microclimatic conditions and facilitate survival and growth of plants under their canopies (Franco & Nobel 1989; Gutierrez *et al.* 1993). However, shrubs may also act in a competitive manner by decreasing soil water content and light levels below their canopy (Fowler 1986; Bilbrough & Caldwell 1995; Forseth *et al.* 2001). We were able to demonstrate the presence of fertile islands associated

with large shrubs, similar to that seen in many other deserts dominated by shrubs (Garcia-Moya & McKell 1970; Hook *et al.* 1991; Pugnaire *et al.* 1996; Moro *et al.* 1997). Nevertheless, the biological importance of shrub fertile islands in this system is unclear. Leaf nitrogen concentrations were reduced under shrubs in both years relative to leaves on plants in open microsites (Fig. 5). Plants were smaller, grew more slowly, and had lower reproductive efforts under shrubs than those in the open.

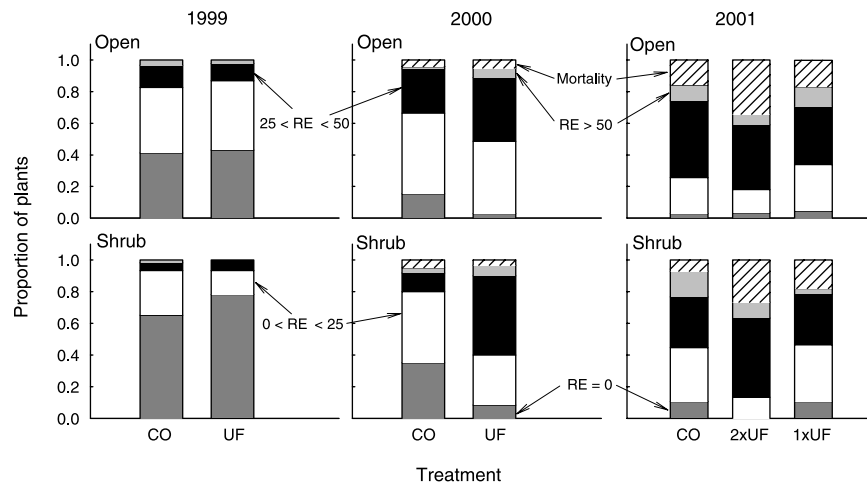Despite the presence of fertile islands, *C. flava* plants

Fig. 7 Proportion of *Cryptantha flava* plants in 1999, 2000 and 2001 in the open and under shrub canopies in four different reproductive effort categories for control (CO) and urine and faeces treatments (UF, 1xUF and 2xUF). Also shown in 2000 and 2001 is mortality (hatched portion) for plants in each treatment category and microhabitat location, there was no mortality in 1999 when plants were chosen.

located under shrubs that received supplemental N increased growth and reproduction in 1999, indicating that they were at least partially N-limited. Bilbrough & Caldwell (1995) found the opposite results in the perennial grass, *Agropyron desertorum*. This species exhibited a reduction in its root response to enriched soil when shaded. We hypothesize that our results stem from a combination of two factors; the weakly developed fertile island discussed above, and the heterogeneous canopies of shrubs in this habitat. Plants under shrubs show little photosynthetic shade acclimation (Forseth *et al*. 2001). *C. flava* is capable of responding rapidly to changes in photosynthetic photon flux with changes in photosynthetic rate (M. S. Peek, unpublished data). The lack of photosynthetic acclimation and the ability to rapidly respond to light allow *C. flava* to exploit gaps in the shrub canopy for photosynthetic carbon gain. Rabbitbrush and particularly sagebrush typically have uneven canopies due to branch death, growth patterns, and disturbances. This leads to direct penetration of the sun's rays to the soil surface, providing brief periods (several seconds to several minutes) of high light to plants located under shrubs. Higher soil N levels would allow *C. flava* to increase photosynthesis in these shrub microhabitats similarly to its response in open habitats. However, plants under shrubs remained smaller than open plants in terms of absolute size (Fig. 6). This is most likely due to the reduction in total light under shrubs, irrespective of sunflecks, that leads to reduced photosynthesis integrated over the entire growing season (Forseth *et al*. 2001).

Reduced soil water contents in 2000 resulted in a reduction in plant size and growth rates in the shrub microhabitat as it did in the open microhabitat. Shrubs did not exert any facilitative affects on the growth and reproduction of *C. flava* during this period. Shrubs did, however, facilitate survival of *C. flava* between 2000 and 2001. This supports the predictions of Holmgren *et al*. (1997) that competitive interactions are more important in years of high water supply, and facilitation may occur during periods of drought. Data from other studies on *C. flava* suggest that plants do live longer under shrubs (Casper 1994, 1996). However, whether this longer lifespan leads to greater fitness in terms of seed set is not known. The facilitation that occurs under shrubs may lessen fitness differences between microhabitats, but the higher growth rates and reproduction by individuals in open microhabitats in most years would far outstrip the survival benefits gained under shrubs in dry years. This interpretation is supported by the observation that distribution patterns in *C. flava* show no affiliation for shrubs in our population (M. S. Peek, unpublished data). Other studies have shown that strong facilitation leads to clumped distributions under shrubs for some annual species (Tielbörger & Kadmon 1997; Eccles *et al*. 1999).

In summary, this study confirms that aridland plant performance is mediated through multiple biotic and abiotic interactions. N addition experiments showed that *C. flava* is N-limited in both open and shrub microhabitats. However, exploitation of N pulses is regulated by precipitation such that reduced soil moisture may eliminate growth and photosynthetic effects altogether. A trade-off between rapid growth in favourable years and performance in dry years is evident, in that plants receiving supplemental N in years of average precipitation had the greatest positive response, but also the greatest negative response in reduced growth and mortality during dry years. Plants in shrub microhabitats are smaller, and have reduced reproductive efforts, relative to plants in open sites, but show increased survival during dry years, supporting the hypothesis that interactions between desert shrubs and other plant growth forms are mediated by temporal variability in precipitation (Callaway 1997; Tielbörger & Kadmon 2000).

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