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Using rainout shelters to evaluate climate change effects on the demography of *Cryptantha flava*

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Summary

1. Precipitation in arid regions is temporally variable with much of it arriving in discrete, unpredictable pulses. Climate change models predict an increase in the variation of precipitation, with longer droughts and larger rainfall events, in addition to increased temperatures.

2. A life table response experiment (LTRE) was conducted with the herbaceous arid-land perennial *Cryptantha flava* (Boraginaceae) from 1997 to 2000, in order to determine how variation in precipitation affects asymptotic population growth (λ) and vital rates. Variation in precipitation took two forms, through rainout shelters erected just before and during the 1999 spring growing season, and through naturally occurring variation over the 4 years.

3. An unexpected effect of rainout shelters on λ was observed that could not be attributed to drought. The λ value decreased greatly in control census plots in the 1998–99 transition but did not decrease in sheltered of plots. The 1999 spring, when shelters were in place, was unusually cold, resulting in frost damage to unsheltered plants. Plants under shelters experienced elevated nighttime temperatures and escaped frost damage. The greater value of λ in the sheltered plots is attributable almost entirely to greater contributions of survival, growth and stasis.

4. There were residual effects of the 1999 drought treatment in the 1999–2000 transition as λ decreased in the sheltered populations while λ increased in control populations. Compared to controls, there were large negative effects of survival, growth, and stasis and a large positive effect of retrogression in the droughted plots.

5. Natural variation in fecundity contributed considerably to inter-annual variation in λ in control plots. Annual variation in fecundity strongly paralleled annual variation in seedling establishment. The relative contributions of other vital rates varied greatly among the annual transitions.

6. *Synthesis.* The study illustrates the sensitivity of this arid-land species to early season frost events and to variation in precipitation. It suggests the importance of considering the seasonal timing of precipitation events when projecting the population-level consequences of global climate change, with particular attention given to precipitation that triggers germination and seedling establishment. Researchers using shelters to create drought treatments should consider their nighttime warming effects.

Key-words: *Cryptantha flava*, drought, frost, Great Basin desert, herbaceous perennial, life table response experiment (LTRE), plant demography, precipitation pulses

Introduction

Arid systems are expected to be particularly sensitive to the increase in climatic variability forecast by global climate change models (Holmgren *et al*. 2006). Precipitation in arid regions is already highly variable, with much of the moisture delivered in unpredictable pulses that can trigger rapid responses in the activity, growth or reproduction of organisms (Schwinning *et al*. 2004). Global climate models predict an increase in the magnitude and frequency of extreme precipitation events such as extended droughts and major storms (Easterling *et al*. 2000; Diffenbaugh *et al*. 2005) in addition to the expected increase in temperature (Trenberth *et al*. 2007).

In order to understand the ecological consequences of altered climate, it is necessary to understand how climatic

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variability impacts the demography of natural populations. The stochastic nature of environmental variation poses a particular challenge to understanding demographic responses of populations to changing climatic conditions or to building predictive demographic models (Boyce *et al.* 2005). Data from empirical studies are needed in order to improve the accuracy of the demographic models and to better understand the consequences of changing precipitation and temperature regimes.

One approach to assess how environmental variation impacts population growth is to employ life table response experiments (LTRE). A LTRE can integrate a variety of ecophysiological and reproductive responses to climatic variation into demographic responses by comparing population transition matrices between respective populations. The LTRE partitions the difference in overall annual asymptotic population growth (λ) into variation associated with matrix elements or vital rates such as survival, growth and fecundity distributed across individuals of different sizes, ages or developmental stages (Caswell 1989, 2000). Using this approach, it is possible to assess how existing and experimentally manipulated climatic variation impacts λ and to identify the vital rates that most contribute to the differences in λ.

In this study with the Great Basin (USA) cold desert perennial *Cryptantha flava* (Boraginaceae), we conducted a number of LTRE analyses to examine how inter-annual climatic variation and experimental drought alter λ and component vital rates, based on 4 years of demographic data. In order to create drought, we left rainout shelters in place over half the sampling plots for almost 3 months in the third year, beginning just before the start of the growing season. An unintended effect of the shelters was an increase in nighttime temperatures. Because elevated temperatures – especially nighttime temperatures – are also predicted by global climate change models (Karl *et al.* 1991; Trenberth *et al.* 2007), concurrent changes in water availability and temperature are realistic simulations of climate change. These concurrent changes may be particularly important in cold deserts, where the beginning of the growing season coincides with substantial probabilities of nighttime radiative frosts. Rosette-forming herbaceous perennials, like *C. flava*, are generally common in those systems (McLaughlin 1986).

Specifically we asked the following questions: To what extent does λ vary among years within a natural population of *C. flava*, and can we identify likely environmental causes of the variation? Is λ affected when plants are sheltered from precipitation immediately prior to and during the spring growing season? If so, does the variation in λ seem related to drought or elevated nighttime temperatures? How do population vital rates contribute to observed differences in λ?

Methods

THE STUDY SYSTEM

Cryptantha flava grows in sandy soils from central Wyoming, throughout eastern Utah, and into northern Arizona and New Mexico, USA. A plant consists of 1 to > 70 basal leaf rosettes, each with an apical meristem. All of the rosettes are connected to a single taproot by a branched woody underground stem (caudex). The narrow, nearly vertical, oblanceolate leaves (6.0–9.0 cm long) first appear in mid-April. New leaves are produced and old ones die throughout the spring and early summer growing season (Casper *et al.* 2001), and new rosettes arise from axillary buds. Most seedling emergence occurs in October, with seedlings overwintering as green plants, although a few emerge in spring.

A vegetative meristem may continue to produce leaves for several growing seasons until it bolts, resulting in an erect stalk with evenly distributed leaves and a terminal inflorescence. Flowering stalks usually bear more than 30 flowers, and each flower normally produces a single nutlet, although occasionally two develop (Casper 1988). Flowering is initiated in spring, with the first flowers opening by mid-May. Rosettes that have produced flowering stalks die after seeds ripen in mid-June to early July. As the soil dries in late summer, the remaining leaves on vegetative rosettes senesce, and the meristems become quiescent, although late summer rainstorms can trigger new leaf production (Casper *et al.* 2001). The death of vegetative rosettes mostly takes place between growing seasons and is the main source of the size retrogression (shrinkage) described here. Retrogression is more common in older individuals (L.H. Spindler & B.B. Casper, unpublished data) and in dry years (Casper 1996). Plant life spans as long as 21 years have been documented at this site (Casper, unpublished data).

The study population is located adjacent to Red Fleet State Park in Uintah County in northeastern Utah at 1730 m elevation (40°30′N, 109°22′30″E), where vegetation is dominated by sagebrush, *Artemisia tridentata* Nutt., rabbitbrush, *Chrysothamnus nauseosus* (Pallas) Britt., and the small tree *Juniperus osteosperma* (Torr.) Little.

EXPERIMENTAL DESIGN

Eighteen 5 × 5 m study plots, spatially arranged in six blocks of three plots, were demarcated within the natural population in early spring 1997, ensuring at least 1.0 m spacing between plots and several meters between blocks (Casper *et al.* 2001, 2006). One plot per block was chosen at random to receive a drought treatment in 1998 and another in 1999. The remaining six plots served as controls. The 1998 drought treatment consisted of sheltering plots during precipitation events by drawing tarps over metal frames, while in 1999 polyethylene shelters were left in place continuously between 1 March and 23 May (Casper *et al.* 2001). The 1998 drought treatment was much less effective, as indicated by field measurements of pre-dawn and midday water potentials, stomatal conductance and photosynthesis (Casper *et al.* 2006), because the tarps were not in place during some precipitation events. We detected no differences in λ between the control plots and those sheltered in 1998 for any transition, so we excluded the plots sheltered in 1998 from all of the analyses presented here.

In 1999, the rainout shelters consisted of polyethylene roofing material attached to a 6 × 6-m metal frame (roofing material overhung plots by 0.5 m on each side to reduce edge effects), which was slanted from 1 to 2.5 m to allow runoff. Polyethylene was selected in an effort to minimize microclimate effects as it transmits both photosynthetically active (400–700 nm) and infrared radiation (Reynolds *et al.* 1999). Temperatures were monitored continuously under the shelters, and ambient temperatures and precipitation were measured at the field site during the growing season for each of the 4 years (Casper *et al.* 2006).

CLIMATIC DATA

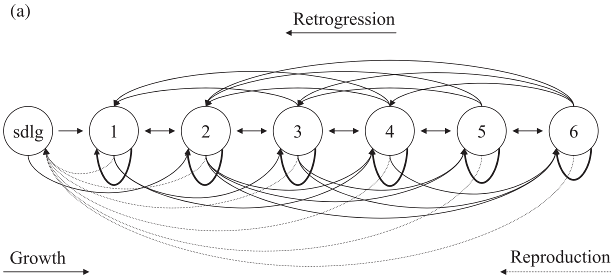
Precipitation and temperature during the study were compared to long-term climatic means (1971–2000) from data collected at the Maeser 9 weather station, located *c.* 18 km SW of the site, at 1950 m elevation (Western Regional Climate Center, http://www.wrcc.dri.edu).

CENSUSES

For the purpose of conducting annual plant censuses, we divided each plot into 25 1-m^2 quadrats guided by stakes placed at meter intervals around the plot perimeter. For plots in three of the six blocks, we mapped and followed every individual in 13 alternate quadrats using Cartesian coordinates. In the remaining three blocks, we mapped plants in seven quadrats randomly selected from among the 13. An annual census took place in late May with the 1999 census occurring while the shelters were still in place. We counted the total number of rosettes and the number of flowering stalks on each mapped plant, and measured plant height, defined as the length of the longest leaf. We counted, but did not map, the number of seedlings per quadrat, instead mapping the survivors the following year. For plants under or within 10 cm of a shrub, we recorded their distance from the outer edge of the shrub canopy and their compass direction (in degrees) with respect to the shrub. For this study, we controlled for light environment by only including plants > 0 cm from the edge of any shrub canopy on the south side ($90 < x < 270°$) and > 10 cm on the north.

MATRIX CONSTRUCTION

We classified plants into seven arbitrary size classes, chosen after several years of observing size transitions in this species. The size classes were: first-year seedlings, which are distinguishable by their persistent cotyledons, and six post-seedling sizes based on both height and numbers of rosettes (Fig. 1). In contrast to stage class models that classify plants based on life-history attributes (i.e. seedlings, juveniles, non-flowering adults, flowering adults), the large number of size classes we used allowed us more precision in describing growth or size retrogression, one of our main interests (Casper 1996). In the first post-seedling size class, plants had ≤ 5 rosettes and were ≤ 3.5 cm in height; plants in sizes 2–6 were all > 3.5 cm tall and were defined by plants having 1–5, 6–10, 11–20, 21–30 or > 30 rosettes, respectively (Fig. 1).



(b)

$$\mathbf{A} = \begin{bmatrix} 0 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\ G_{12} & S_2 & R_{32} & R_{42} & R_{52} & 0 & 0 \\ G_{13} & G_{23} & S_3 & R_{43} & R_{53} & R_{63} & R_{73} \\ 0 & G_{24} & G_{34} & S_4 & R_{54} & R_{64} & R_{74} \\ 0 & G_{25} & G_{35} & G_{45} & S_5 & R_{65} & R_{75} \\ 0 & 0 & G_{36} & G_{46} & G_{56} & S_6 & R_{76} \\ 0 & 0 & G_{37} & G_{47} & G_{57} & G_{67} & S_7 \end{bmatrix}$$

Fig. 1. (a) Life cycle graph for Cryptantha flava. Solid arrows pointing from left to right represent growth from one size class to another. Solid arrows from right to left represent retrogression (or shrinkage) from one size class to another. Dashed arrows represent fertility (reproduction). Arrows originating and ending at the same size class represent stasis. Size classes are defined in the text. (b) A population projection matrix corresponding to the life cycle graph. The elements of the matrix represent mean fertility per individual (F_i) for plants in size class *i*, the probability of survival and growth from size class *i* to size class *j*, (G_{ij}), the probability of surviving and remaining in the same size class (S_i), or the probability of retrogression from size class *i t*o size class *j* (R_{ij}). Zero entries represent transitions that were never observed.

Size-structured population projection matrices (**A**) were constructed from the between-year size transition probabilities and fertility values for each size class according to the methods outlined by Caswell (1996, 2001). Matrix elements representing survival and growth to a larger size (G_{ij}), survival and remaining the same size (S_i), and survival and retrogression to a smaller size (R_{ij}) were calculated from pooled data. Data were pooled over five plots receiving the drought treatment and for six control plots for each of the three yearly transitions (1997–98, 1998–99 and 1999–2000), yielding six summary projection matrices in total – two treatments × three transitions. One of the treatment plots was excluded from the analyses because in 1998 (i.e. prior to the drought treatment) it had an order of magnitude more seedlings than the other 11 plots. A summary matrix is preferred over averaging the matrices from each replicate plot so as to avoid disproportionate representation of plots with low plant densities or low sample sizes in some size classes (Horvitz & Schemske 1995; Bruna & Oli 2005). Size-specific fertility values (F_i) were estimated as follows:

$$F_i = \frac{fl_i \times S}{n_i} \qquad \text{eqn 1}$$

where fl_i is the proportion of all flowering stalks produced by individuals in size class *i* in year$_t$, n_i is the number of individuals in size class *i* in year$_t$, and *S* is the total number of seedlings in year$_{t+1}$. Past field experiments, in which large numbers of seeds were planted within natural populations (Casper 1988, 1994, 1996), indicated very little between-year seed banking; most seeds germinate the first year they are planted or not at all.

Matrix elements for size-based matrix models can often be expressed as combinations of two or more underlying vital rates (Franco & Silvertown 2004) such as survival in a given size class (σ_i), positive growth from one size class to another (γ_{ij}), retrogression to another smaller size class (ρ_{ij}), stasis or remaining in the same size class (τ_i), and individual fecundity (ϕ_i). *Cryptantha flava* reproduces seasonally, and thus we used the following birth-pulse formulae relating matrix elements and lower-level vital rates (Caswell 2001):

$$G_{ij} = \sigma_i \gamma_{ij} \qquad \text{eqn 2}$$

$$S_i = \sigma_i \tau_i \qquad \text{eqn 3}$$

$$R_{ij} = \sigma_i \rho_{ij} \qquad \text{eqn 4}$$

$$F_i = \sigma_i \phi_i \qquad \text{eqn 5}$$

where *i* represents one size class and *j* represents a different size class. Size class-specific survival was estimated by counting the total number of individuals in size class *i* in year *t* that lived to year *t* + 1 and stasis was estimated as the number of individuals in size class *i* in year *t* that remained in size class *i* in year *t* + 1.

The annual asymptotic population growth rate (λ) for each of the two treatment groups over each yearly transition was estimated as the dominant eigenvalue for each **A** matrix, and 95% confidence intervals were estimated from 10 000 resampling runs (Manly 1997) using a bias-corrected percentile interval bootstrap approach (Caswell 2001). Population-level demographic data do not meet the assumptions of classical statistical hypothesis testing, that is, data are not normally distributed (Caswell 2001). We therefore conducted permutation tests, without assumptions regarding normality or variance (Manly 1997), to determine significant differences between treatments.

SENSITIVITY AND LTRE ANALYSES

The demographic consequences of drought treatments and year were evaluated using a LTRE approach, in addition to sensitivity and elastivity analyses (Jongejans & de Kroon 2005). The LTRE analyses were used to determine how individual matrix elements – or in this case, vital rates – contributed to variation in population growth rate (Caswell 2001). We used a linear, two-factor, fixed effect LTRE model to examine how vital rates contributed to variation in λ:

$$\lambda^{mn} = \lambda^{\cdot\cdot} + \alpha^{m} + \beta^{n} + (\alpha\beta)^{mn} \qquad \text{eqn 6}$$

where $\lambda^{\cdot\cdot}$ represents the dominant eigenvalue for the overall mean matrix, $\mathbf{A}^{\cdot\cdot}$, of all treatments and years, α^{m}, β^{n} and $(\alpha\beta)^{mn}$ represent the main effects of treatment *m*, year *n*, and the interaction of treatment and year, respectively. The relative strengths of each of the effects are indicated by the absolute values of the differences from $\lambda^{\cdot\cdot}$.

We calculated the sensitivities of individual vital rates, x_p, rather than matrix elements, $a_{i,j}$, using the chain rule:

$$\frac{\partial\lambda}{\partial x_p} = \sum_{i,j} \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x_p} \qquad \text{eqn 7}$$

We calculated the contribution of the differences in vital rates to the overall effect on the population growth rate (Caswell 1996; Cooch *et al.* 2001), rather than the contribution of differences in the matrix elements (Levin *et al.* 1996; Caswell 2001). Because the **A** matrices are fully defined using combinations of the lower-level vital rates, we used an additive, linear approximation to decompose the contributions of each vital rate to the LTRE effect according to:

$$\alpha^{\sim m} = \sum_{p} \sum_{i,j} (x_p^{m\cdot} - x_p^{\cdot\cdot}) \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x_p}\bigg|_{\frac{1}{2}(\mathrm{A}^{m\cdot} + \mathrm{A}^{\cdot\cdot})} \qquad \text{eqn 8}$$

$$\beta^{\sim n} = \sum_{p} \sum_{i,j} (x_p^{\cdot n} - x_p^{\cdot\cdot}) \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x_p}\bigg|_{\frac{1}{2}(\mathrm{A}^{\cdot n} + \mathrm{A}^{\cdot\cdot})} \qquad \text{eqn 9}$$

$$\alpha\beta^{\sim mn} = \sum_{p} \sum_{i,j} (x_p^{mn} - x_p^{\cdot\cdot}) \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x_p}\bigg|_{\frac{1}{2}(\mathrm{A}^{mn} + \mathrm{A}^{\cdot\cdot})} - \alpha^{m} - \beta^{n} \qquad \text{eqn 10}$$

where $x_p^{m\cdot}$ denotes the mean vital rate *P* in the mean matrix of drought and control treatments, $x_p^{\cdot\cdot}$ denotes the vital rate *P* in the overall mean matrix, and $x_p^{\cdot n}$ denotes the mean vital rate *P* in the mean matrix of all year treatments. The sensitivities of the vital rates were evaluated at the midpoint between the two **A** matrices (Cooch *et al.* 2001).

We present vital rate elasticities for both the drought and control treatments in each of the three yearly transitions and the LTRE main effects of drought treatment and transition year. Instead of presenting the overall interactions between drought treatment and year, we used the LTRE approach to make specific comparisons of vital rates between particular matrices of interest, comparable to planned comparisons. (i) We compared the drought and control treatments for the 1998–1999 transition and again for the 1999–2000 transition. This is because we were specifically interested in the demographic consequences of the drought treatment, and we reasoned that some residual effects of the drought treatment might still be apparent in the 1999–2000 transition. Similar comparisons were not made for the 1997–98 transition, when λ values for drought and control treatments did not differ and elasticities of vital rates were very similar in the two treatments. (ii) To explore demographic consequences of natural climatic variation in the control treatment only, we used the 1997–98 transition as a baseline and compared the 1998–99 transition and the 1999–2000 transition to it.

Finally, we wanted to understand how temporal variation in flower stalk production might have contributed to variation in seedling emergence and, therefore, to variation in the vital rate of fecundity that we observed among transition years. Both the number of flower stalks (seed production) in year *t* and the successful germination of those seeds can affect the number of seedlings emerging in year *t* + 1. On a per plot basis, we tallied the number of flowering stalks and the number of seedlings per m^2 for control plots only and used ANOVA to examine differences among years. Tukey's least significant difference was used for post-hoc comparisons.

Results

CLIMATE PATTERNS

At the Maeser 9 NW climate station, annual precipitation averaged 357 mm from 1971 to 2003, and mean monthly temperature ranged from –6.2 °C in January to 20.4 °C in July. The greatest annual monthly precipitation occurs in September and October, and the lowest in November–January (Fig. 2).

During the growing seasons encompassed by this study, there were several periods with exceptionally high or exceptionally low precipitation (Fig. 2). Both the 1998 and 1999 growing seasons were wetter than normal. In 1998, precipitation was about 60% of the long-term mean during April and May, but this was followed by a wet June, when precipitation was 3.5 times the mean. In 1999, above normal precipitation occurred during the growing season and extended into late summer with roughly twice the long-term mean precipitation falling from May through August. The growing season in 2000 was dry as precipitation was below normal beginning in the winter of 1999–2000 and again in April–August 2000.

There were other notable precipitation extremes that fell outside the spring and early summer growing season. Large rainfall events occurred in late summer and early autumn in 1997, resulting in 2.2 times the long-term mean from August

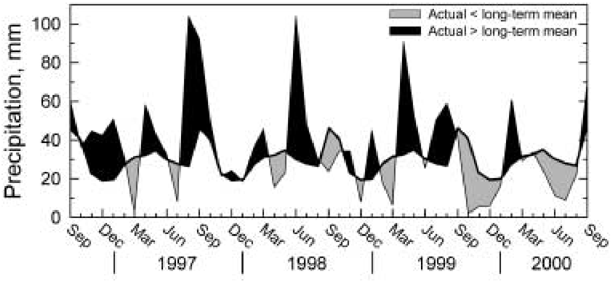


Fig. 2. Monthly precipitation totals at the Maeser 9 weather station during the 4 years of the study in comparison to the long-term mean monthly totals (1971–2000). Figure is from Casper *et al.* (2006).

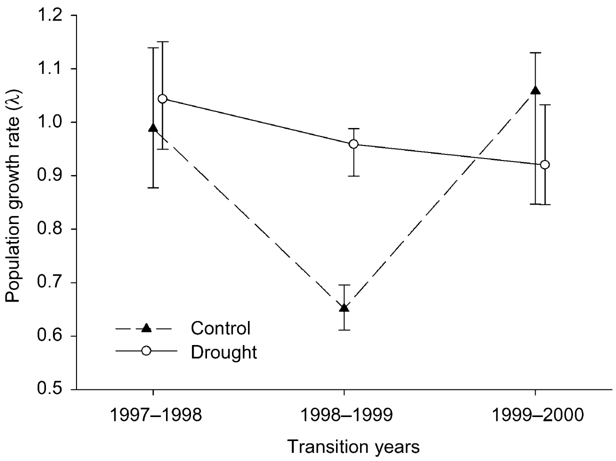


Fig. 3. Asymptotic population growth rate (λ) ± 95% confidence intervals for droughted and control populations of *Cryptantha flava* in each of the 3 yearly transitions.

through October. Weather station data (Fig. 2) show precipitation well above the long-term mean during June and July 1998, but in this particular case, the weather station data differ substantially from that at the field site, where no more than 8.0 mm fell during any 1 week (Casper *et al.* 2001). Precipitation data taken on-site during the 1998 and 1999 growing seasons were otherwise consistent with weather station data taken at the Maeser 9 NW climate station.

Growing season temperatures deviated from the long-term mean most noticeably between April and June 1999, when unusually cold temperatures coincided with the period shelters were in place. At the study site, there were 13 dates between 1 April and 15 May 1999 when ambient nighttime air temperatures dropped below 0 °C (Casper *et al.* 2006).

CLIMATE EFFECTS OF SHELTERS

The shelters eliminated all precipitation between 1 March and 23 May 1999, a total of 11.3 cm; details of excluded precipitation can be found elsewhere (Casper *et al.* 2001). An unintended effect of the shelters was to elevate nighttime air temperatures above ambient by 2.6 + 0.1 °C (mean ± SE), presumably due to re-radiation of infrared radiation from the structure itself (Casper *et al.* 2006). When nighttime temperatures under the shelter dropped below freezing it was for shorter periods than in areas outside the shelters. During the early spring, flowering stalks on unsheltered plants were noticeably frostbitten; many open flowers and mature flower buds were killed. This damage did not occur on sheltered plants. In contrast to the difference in nighttime air temperatures, daytime temperatures under shelters were always within 0.5 °C of ambient.

VARIATION IN λ

For the 1997–98 transition, the values of λ for controls and the plots that were to receive the 1999 drought treatment were not significantly different from each other or from 1.0, indicating relatively stable population sizes (Fig. 3). Between the 1997–98 and the 1998–99 transitions, there was no significant change in λ for the droughted plots, but λ in the control plots dropped sharply (λ = 0.66) in 1998–99 (Fig. 3). This change in the control plots resulted in a large difference in λ between the control plots and the droughted plots for the 1998–99 transition ($P < 0.001$). There was a large increase in λ for the control plots between the 1998–99 and 1999–2000 transitions so that λ for controls was slightly greater than for the droughted plots, but not significantly so ($P < 0.09$).

ELASTICITIES AND CONTRIBUTIONS OF VITAL RATES

In 1998–99, the first transition encompassing the 1999 drought treatment, the droughted plots had higher elasticities for survival, growth, stasis and fecundity than the control plots (Fig. 4). This indicates that the contributions of these vital rates to λ were particularly important in the droughted plots during the 1998–99 transition. There were also notable differences in elasticities between the droughted plots and the

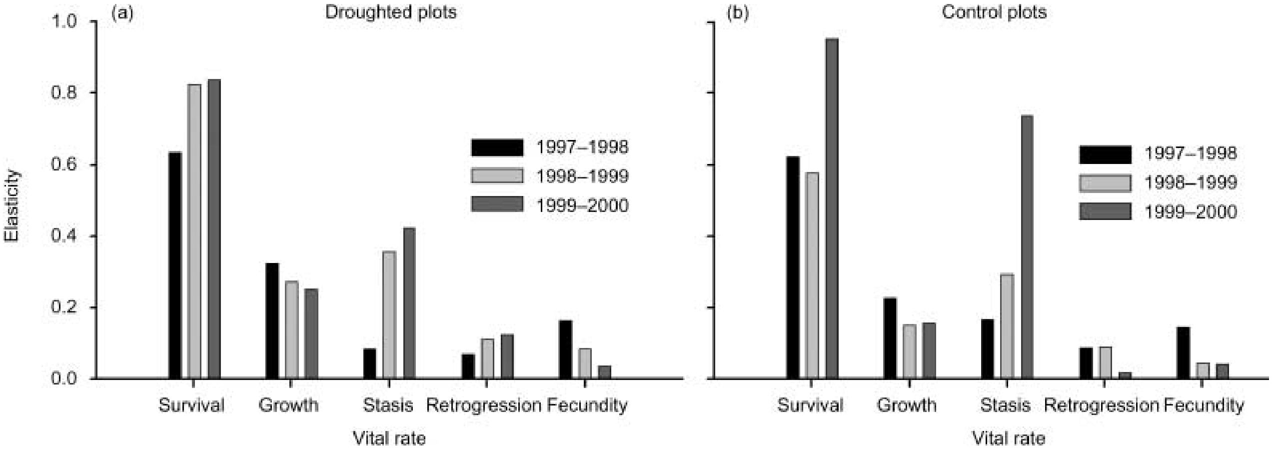


Fig. 4. Elasticities for vital rates of *C. flava*. (a) Elasticity values in droughted populations and (b) in control populations for each of the yearly transitions.

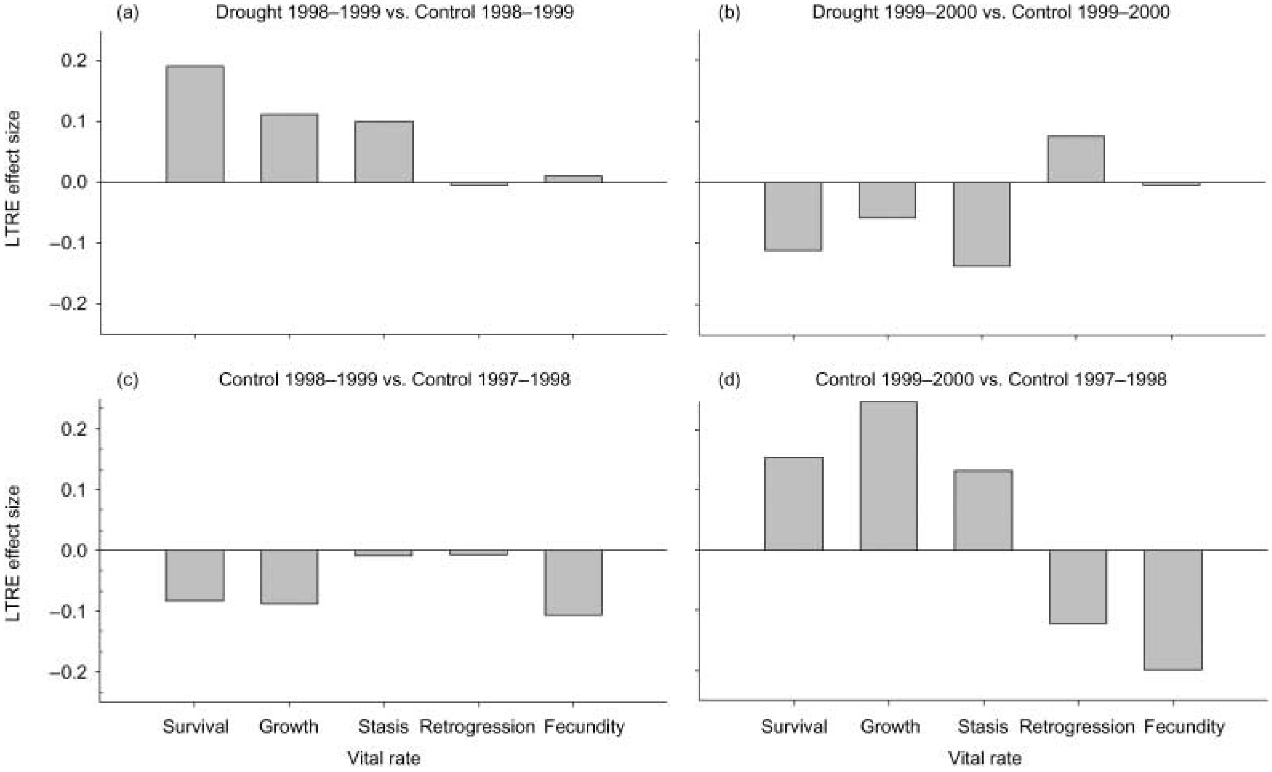


Fig. 5. LTRE analyses that decompose the contributions of vital rates to the differences in λ between (a) drought and control plots during the 1998–99 transition; (b) drought and control plots during the 1999–2000 transition; (c) the 1998–99 and 1997–98 transitions for the control plots only; (d) the 1999–2000 and 1997–98 transitions for the control plots only.

control plots during the 1999–2000 transition despite their similar λ values. While the elasticities for growth and retrogression were slightly higher in the droughted plots (Fig. 4a), the elasticities of survival and stasis were higher in the control plots (Fig. 4b). The elasticity for fecundity was similarly low in the two treatments. For the control plots, in particular, the elasticities for survival and stasis were higher in 1999–2000 than in other transition years.

The two-way LTRE analysis showed that across all three transitions, more variation in the contributions of the various vital rates to the differences in λ occurred among years than between the two treatments. In addition, the maximum year effects were greater than the maximum effects of the drought treatment by a factor of three (results not shown). There were also treatment × year interactions for the different vital rates, which were particularly evident in the 1998–99 and the 1999–2000 transitions, consistent with the application of the drought treatment in the 1999 growing season.

Specific planned comparisons using the LTRE approach indicated that the large difference in λ between the drought and control plots during the 1998–99 transition is attributable almost entirely to *greater* survival, growth, and stasis in the drought treatment (Fig. 5a). In contrast, for the 1999–2000 transition, the droughted plots showed large *negative* effects of survival, growth, and stasis and a large positive effect of retrogression, in comparison to controls (Fig. 5b). An examination of the contributions of particular vital rates to differences in λ across yearly transitions in the control plots revealed negative effects of survival, growth and fecundity during the 1998–99 transition in comparison to the 1997–98 transition (Fig. 5c). When the 1999–2000 transition was compared with the 1997–98 transition for the controls, there were positive effects of survival, growth, and stasis and negative effects of retrogression and fecundity (Fig. 5d). Thus, even for yearly transitions when λ values were similar, the component vital rates differed.

Variation in fecundity among the inter-annual transitions in control plots reflects variation in the numbers of seedlings, which is largely independent of flower stalk production. There were more seedlings in 1998 (Fig. 6) than in other years ($F_{3,20} = 8.62$; $P < 0.01$), and this shows up as greater fecundity in the 1997–98 transition. The large number of seedlings in 1998 must have been due to an increase in emergence (which would have occurred mostly in Autumn 1997) because the number of flowering stalks, an estimate of seed production, was not greater in 1997 than in other years. For the 1999–2000 transition, flower stalk production in 1999 and the number of seedlings present in 2000 were both low. In fact, flower stalk production was lower in 1999 than in other years ($F_{3,20} = 3.09$; $P < 0.05$, Fig. 6).

Discussion

We draw four main conclusions from this LTRE study of *C. flava*: (i) There is considerable natural, annual variation in λ. (ii) In the 1998–99 transition, the unexpectedly larger value of

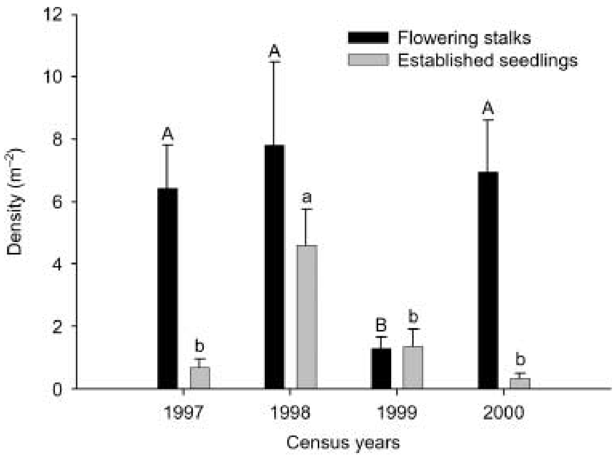


Fig. 6. Seedling and flowering stalk densities (per m^{-2}) in control plots only (± SE). Data were collected at the spring census, but most of the seedlings would have emerged the preceding autumn. Significant differences ($P < 0.05$) are indicated by different upper case or lower case letters for flowering stalks and seedlings, respectively.

λ for droughted plots and the positive contributions of survival, growth and stasis, when compared to controls, suggest that shelters rescued plants from the abnormally cold nighttime temperatures that occurred in early spring 1999. (iii) Adverse effects of the rainfall reduction by the 1999 drought treatment were apparent in the 1999–2000 transition as reflected in a decrease in λ from the 1998–99 transition, a decrease in λ relative to the control populations, and by large negative effects of survival, growth, and stasis and a positive effect of retrogression, compared to controls. (iv) Autumn rains that trigger seedling emergence can have a large impact on fecundity as a vital rate.

ANNUAL VARIATION IN λ

Natural, annual variation in λ played an important role in this study. The level of annual variation of λ in control plots is large compared to that found in many other plant species in the absence of major disturbance (García 2003; Fröborg & Eriksson 2003; Jacquemyn *et al.* 2005) but similar to that reported for the monocarpic perennial *Centaura corymbosa*, a rare, narrow habitat endemic (Fréville *et al.* 2004).

For *C. flava*, survival and growth made large contributions, both positive and negative, to annual differences in λ. The change in direction from negative to positive contributions may be explained by the combination of inter-annual variation in both precipitation and growing season temperatures in this cold desert system. Survival consistently had the highest elasticity values for all three transitions, implying that changes to survival have a relatively greater impact on the population growth rate than changes to other vital rates.

Large differences in λ are also partially attributable to the annual variation in fecundity. Even though fecundity has a relatively low elasticity, which might be expected for a long-lived perennial (Franco & Silvertown 2004), it likely made large LTRE contributions due to the level of variation reflected in annual seedling establishment, an important component of fecundity.

DEMOGRAPHIC CONSEQUENCES OF SHELTERS

The greatest difference in λ between the drought and control plots occurred in the 1998–99 transition, but the difference was in the opposite direction predicted. Our expectation was that rainfall reduction caused by the shelters would adversely affect plant performance and cause a decrease in λ. Instead, λ changed little in the droughted plots from the previous transition, while λ for the control plots dropped dramatically. In comparison to control plots for the same (1998–99) transition, the difference in λ was primarily due to greater positive contributions of plant growth, survival and fecundity in the droughted plots. We think that the freezing nighttime temperatures in the spring of 1999 adversely affected λ in control plots and that the temperature elevation provided by the shelters rescued plants from the freezing effect. The fact that only plants outside the shelters were visibly frostbitten supports this interpretation. Researchers who use these shelters to create drought need to be aware of their effects on nighttime temperature and its potential biological importance.

Demographic consequences of the rainout shelters in 1999 continued into the 1999–2000 transition year, with negative consequences for λ; in comparison to control plots, there were large negative contributions of survival, growth, and stasis and a positive contribution of retrogression for the 1999–2000 transition. The greater contribution of retrogression is consistent with the increase in retrogression in response to natural drought observed for *C. flava* in a previous study (Casper 1996). Negative demographic repercussions from the 1999 drought would be expected in the 1999–2000 transition because we measured lower pre-dawn and midday leaf water potentials, lower stomatal conductance, and a 30% reduction in photosynthesis in the droughted plots, compared to controls, at the height of the 1999 growing season (Casper *et al.* 2006). The reduced photosynthesis could have made less carbon available to the perennial root system of *C. flava*, reducing over-winter survival and growth the following spring.

However, the drought effects on the 1999–2000 transition might have been ameliorated somewhat by additional factors: (i) After early May and for most of the summer, sheltered plants showed a longer leaf life span and a greater standing number of leaves per vegetative rosette than did control plants (Casper *et al.* 2001). Together with a smaller leaf size and greater specific leaf mass (Casper *et al.* 2001), these changes in leaf demography may have helped conserve carbon. (ii) Unusually heavy rains in August and very early September 1999 caused the production of some new leaves in both the drought and control plants (Casper *et al.* 2001) at a time when plants would be dormant in drier years. The combination of these factors may have partially compensated for the reduced leaf level carbon gain observed at the height of the spring growing season, thereby diminishing the overall imprint of the drought treatment on population demography.

RESPONSE TO PRECIPITATION OUTSIDE THE SPRING GROWING SEASON

Because variation in seedling emergence explained variation in fecundity independent of variation in flower stalk production, our study suggests that October rains have important consequences for the contribution of fecundity to λ, although inter-annual variation in granivory would also contribute to variation in seedling establishment. Seedlings were most abundant in 1998, after a particular wet October 1997. Episodic seedling establishment in response to large rainfall events is a common phenomenon in desert plants (Wiegand *et al.* 2004), and λ values could fluctuate greatly as a consequence. For *C. flava*, the contribution of fecundity to λ differed little between drought and control plots in either the 1998–99 or the 1999–2000 transition, providing further evidence that fecundity is more strongly affected by autumn precipitation than by climatic conditions during the spring growing season. In particular, any difference in seed set between the drought and control plots was probably obscured by overall poor seedling emergence in the dry autumn of 1999.

Because of our initial interest in changing precipitation patterns, we are also broadly interested in how major rainfall events outside the April–June growing season may affect population demography. We know that rains in late summer can renew leaf construction (Casper *et al.* 2001), and we can detect the isotopic signature of autumn carbon assimilation in leaf tissue the following spring (Casper *et al.* 2005). We would expect the lengthened growing season to increase plant growth and potentially increase λ, but we cannot point to such an effect during our study. Large late summer rains occurred in 1997 and 1999, but it is difficult to evaluate their specific contributions to the annual variation in λ because the intervening transition (1998–99) encompassed the unusually cold spring.

RELEVANCE TO CLIMATE CHANGE PREDICTIONS

In order to understand future climate effects on the demography of Great Basin desert perennials, we must consider two major predictions of the climate change models: the 1.0–2.5° increase in regional temperature (Leung *et al.* 2004) and increased variability in precipitation (Easterling *et al.* 2000). How the overall amount of precipitation will change is less clear (Leung *et al.* 2004). It is likely that soils will warm earlier in the year so that spring perennials will initiate growth earlier, resulting in a longer growing season (Walther *et al.* 2002). But the advanced phenology may also allow even more exposure to early season freezes that can have damaging consequences for floral meristems or overall plant performance (Inouye 2000; Stenseth & Mysterud 2002) as we found here. On the other hand, increased temperatures are also predicted to cause earlier termination of the growing season in summer due to earlier drying of soils and increasing water limitation (Karl & Trenberth 2003; Bell *et al.* 2004). How precipitation pulses will affect demography depend on their timing relative to the spring and summer growing season and autumn seed germination.

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References

Bell, J.L., Sloan, L.C. & Snyder, M.A. (2004) Regional changes in extreme climatic events: a future climate scenario. *Journal of Climate*, **17**, 81–87.

Boyce, M.S., Haridas, C.V., Lee, C.T. & NCEAS Stochastic Demography Working Group (2005) Demography in an increasingly variable world. *Trends in Ecology and Evolution*, **21**, 141–148.

Bruna, E.M. & Oli, M.K. (2005) Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. *Ecology*, **86**, 1816–1824.

Casper, B.B. (1988) Evidence for selective embryo abortion in *Cryptantha flava*. *American Naturalist*, **132**, 318–326.

Casper, B.B. (1994) Postdispersal 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.

Casper, B.B., Forseth, I.N. & Wait, D.A. (2005) Variation in carbon isotope discrimination in relation to plant performance in a natural population of *Cryptantha flava*. *Oecologia*, **145**, 541–548.

Casper, B.B., Forseth, I.N. & Wait, D.A. (2006) A stage-based study of drought response in *Cryptantha flava* (Boraginaceae): gas exchange, water use efficiency, and whole plant performance. *American Journal of Botany*, **93**, 978–987.

Casper, B.B., Forseth, I.N., Kempenich, H., Seltzer, S. & Xavier, K. (2001) Drought prolongs leaf life span in the herbaceous desert perennial *Cryptantha flava*. *Functional Ecology*, **15**, 740–747.

Caswell, H. (1989) Analysis of life table response experiments I. Decomposition of effects of effects on population growth rate. *Ecological Modelling*, **46**, 221–237.

Caswell, H. (1996) Analysis of life table response experiments II. Alternative parameterizations for size- and stage-structured models. *Ecological Modelling*, **88**, 73–82.

Caswell, H. (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, **81**, 619–627.

Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, MA.

Cooch, E., Rockwell, R.F. & Brault, S. (2001) Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. *Ecological Monographs*, **71**, 377–400.

Diffenbaugh, N.S., Pal, J.S., Trapp, R.J. & Giorgi, F. (2005) Fine-scale processes regulate the response of extreme events to global climate change. *Proceedings of the National Academy of Sciences USA*, **102**, 15774–15778.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.

Franco, M. & Silvertown, J. (2004) A comparative demography of plants based upon elasticities of vital rates. *Ecology*, **85**, 531–538.

Fréville, H., Colas, B., Riba, M., Caswell, H., Mignot, A., Imbert, E. & Olivieri, I. (2004) Spatial and temporal demographic variability in the endemic plant species *Centaurea corymbosa* (Asteraceae). *Ecology*, **85**, 694–703.

Fröborg, H. & Eriksson, O. (2003) Predispersal seed predation and population dynamics in the perennial understorey herb *Actaea spicata*. *Canadian Journal of Botany*, **81**, 1058–1069.

García, M.B. (2003) Demographic viability of a relict population of the critically endangered plant *Borderea chouardii*. *Conservation Biology*, **17**, 1672–1680.

Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R., Hice, C., Jaksic, F., Kelt, D.A., Letnic, M., Lima, M., López, B.C., Meserve, P.L., Milstead, W.B., Polis, G.A., Previtali, M.A., Richter, M., Sabaté, S. & Squeo, F.A. (2006) Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, **2**, 87–95.

Horvitz, C.C. & Schemske, D.W. (1995) Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecological Monographs*, **65**, 155–192.

Inouye, D.W. (2000) The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters*, **3**, 457–463.

Jacquemyn, H., Brys, R. & Neubert, M.G. (2005) Fire increases invasive spread of *Molina caerulea* mainly through changes in demographic parameters. *Ecological Applications*, **15**, 2097–2108.

Jongejans, E. & de Kroon, H. (2005) Space versus time variation in the population dynamics of three co-occurring perennial herbs. *Journal of Ecology*, **93**, 681–692.

Karl, T.R. & Trenberth, K.E. (2003) Modern global climate change. *Science*, **302**, 1719–1723.

Karl, T.R., Kukla, G., Razuvayev, V.N., Changery, M.J., Quayle, R.G., Heim, R.R. & Easterling, D.R. (1991) Global warming – evidence for asymmetric diurnal temperature change. *Geophysical Research Letters*, **18**, 2253–2256.

Leung, L.R., Qian, Y., Bian, X., Washington, W.M., Han, J. & Roads, J.O. (2004) Mid-century ensemble regional climate change scenarios for the western United States. *Climatic Change*, **62**, 75–113.

Levin, L.A., Caswell, H., Bridges, T., Cabera, D., Plaia, G. & DiBacco, C. (1996) Demographic responses of estuarine polychaetes to pollutants: life table response experiments. *Ecological Applications*, **6**, 1295–1313.

Manly, B.F.J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd edn. Chapman and Hall, London, UK.

McLaughlin, S.P. (1986) Floristic analysis of the southwestern United States. *Great Basin Naturalist*, **46**, 46–65.

Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G. & Tremmel, D.C. (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs*, **69**, 69–106.

Schwinning, S., Sala, O.E., Loik, M.E. & Ehleringer, J.R. (2004) Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia*, **141**, 191–193.

Stenseth, N.C. & Mysterud, A. (2002) Climate, changing phenology, and other life history traits: nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences USA*, **99**, 13379–13381.

Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., Soden, B. & Zhai, P. (2007) 2007: observations: surface and atmospheric climate change. *Climate Change 2007: The Physical Science Basis (Contribution of the Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, H.L. Miller). Cambridge University Press, Cambridge, UK.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wiegand, K., Jeltsch, F. & Ward, D. (2004) Minimum recruitment frequency in plants with episodic recruitment. *Oecologia*, **141**, 363–372.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com:

Appendix S1 Size-based population projection matrices for years 1997–2000.

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