Brenda B. Casper

Demographic consequences of drought in the herbaceous perennial *Cryptantha flava*: effects of density, associations with shrubs, and plant size

Abstract The demographic consequences of a severe drought year were examined for two experimental plantings of the herbaceous desert perennial *Cryptantha flava*(Boraginaceae) in northeastern Utah, United States. A total of 6680 nutlets were planted individually or in clusters of four both under shrubs and in open microhabitats within two natural populations. Survival, growth, and flowering as a function of density and microhabitat were followed for 7 years, including 1 year when precipitation just before and during the growing season was 74.5% below normal. The design permitted assessment of how intraspecific density and shrub cover affect demographic response to drought. Mortality increased and flowering decreased dramatically during drought but neither varied with density or between shrub and open microhabitats. For plants growing under shrubs, survival (at Site 1) and growth (at Site 2) varied with shrub species. Average aboveground plant size also decreased during drought. Population size hierarchies were rearranged because larger plants lost leaf rosettes while many smaller plants grew. Density and microhabitat affected plant performance in non-drought years but more often at Site 1 than at Site 2. Individuals growing alone often were more likely to flower and/or produced more inflorescences when they did flower than did individuals growing with at least one other plant. However, for 2 years, survival rates at Site 1 were higher for plants growing in clumps than for single individuals. Shrubs also had mixed effects on plant performance. In some years, survival was higher under shrubs, but at Site 1 plants in the open often were more likely to flower and/or produced more inflorescences. Thus despite severe demographic consequences of drought, the study provided no evidence that intraspecific competition, interference by shrubs, or facilitation by shrubs increases under limited soil water.

Introduction

Despite extensive information on the anatomical and physiological bases of drought tolerance in plants (Hsaio 1973; Turner and Kramer 1980), surprisingly few studies have quantified demographic responses of natural populations to drought conditions. Reports of increased mortality, especially among seedlings (Newman 1967; Klemow and Raynal 1985; Barden 1988; Ehleringer 1993), or decreased plant cover (Fowler 1986a; Bauder 1989; Tilman and Downing 1994) are fairly common, but less is known about how individuals vary in their ability to survive, grow, or reproduce during drought and whether drought alters demographic consequences of plant interactions (but see Ehleringer 1993).

This study examines demographic responses to a year-long drought in even-aged populations of the herbaceous desert perennial *Cryptantha flava* (Boraginaceae) at two sites in eastern Utah. Annual variation in survival, plant size, and inflorescence production was measured from seedling emergence in the autumn of 1983 through the flowering season in the spring of 1990. The area experienced a severe drought during 1988 and 1989 that extended over much of the western United States (Ehleringer 1993; Tilman and Downing 1994), and the study focuses on how demographic traits differed in 1989 from those seen in other years.

The system potentially involves both competitive and facilitative plant interactions. Because seeds were planted individually or in clumps of four, both under the canopy of shrubs and in the open, the design permits evaluation of whether drought affected either the expression of intraspecific competition or the relative performance of individuals growing under shrubs compared with those in the open. Competition, especially below ground, is now well-documented in desert systems, but facilitative interactions occur as well (Fowler 1986a). Desert shrubs

B.B. Casper
Department of Biology, University of Pennsylvania,
Philadelphia, PA 19104-6018, USA
E-mail: bcasper@sas.upenn.edu; fax: (215) 898-8780

can moderate temperatures and improve soil water and nutrient levels (Turner et al. 1966; Charley and West 1975; Jordan and Nobel 1979; Nobel 1989). By doing so, shrubs often facilitate the establishment or growth of annuals, cacti, or woody seedlings (Went 1942; Muller 1953; Turner et al. 1966; Steenbergh and Lowe 1969; Halvorson and Patten 1975; McAuliffe 1988), although suppression of associated plants may occur as well (Friedman and Orshan 1975).

The potential for temporal environmental heterogeneity to affect biotic interactions is widely recognized (Antonovics and Levin 1980; Diamond and Case 1986; Fowler 1988), but there is no agreement on whether competition should increase or decrease with drought. Some workers suggest that competition should be most intense where resources are most limiting (Newman 1973; Antonovics and Levin 1980; Tilman 1988; Taylor et al. 1990). This view has been expressed regarding both plant and animal systems and is apparently the basis for the prediction of Fowler (1988) that drought should result in a brief but intense period of increased competition in plant communities. Consistent with this explanation is the expectation that under conditions of limited soil resources competition should mostly occur through belowground interactions (Tilman 1988). The alternative perspective is that competition should be most intense where soil resources produce the greatest plant biomass or productivity (Grime 1977; Keddy 1989) and plants compete strongly for light. This line of thinking led early workers to predict that competition should be unimportant in deserts in general (Fowler 1986b). If the latter view is correct, competition may decrease in importance in years of low rainfall.

The question of how temporal environmental variation affects relationships of facilitation has received less attention. Bertness and Calloway (1994) hypothesize that the frequency of positive interactions should increase with greater abiotic stress and call for more studies of plant interactions within the framework of the physical environment. By resulting in increased environmental stress, drought could exaggerate differences in the relative performance of plants growing under shrubs compared with those in the open. If so, facilitation should be most pronounced in drought years.

Given these possible responses to drought, the specific goals of this paper are to (1) contrast mortality and plant size during the drought year with mortality and size in non-drought years, and (2) examine mortality, plant size, and inflorescence production as a function of intraspecific density and shrub cover in all years. For the subset of plants growing under shrubs, growth and mortality during drought were also compared among canopy shrub species.

Methods

Description of species

Cryptantha flava (A. Nels.) Payson grows in sandy soils throughout the semi-arid Colorado Plateau of eastern Utah and adjoining states. The woody, often branched caudex – a shortened, mostly underground stem – bears densely packed rosettes of nearly vertical, narrow oblanceolate leaves that initiate in early spring and largely senesce by late summer. A leaf rosette dies after producing a single inflorescence which, on average, bears 45–55 flowers. Peak flowering varies from early May to early June, depending on the location and year. Nutlets ripen about a month later. Although all four ovules may be fertilized, abortion usually results in only one (or two) mature nutlet(s) per flower (Casper 1984). The nutlet(s) remains enclosed within the large pubescent calyx that serves as the dispersal unit. Most seedlings emerge following rains in October and remain green throughout the winter, although a few additional seedlings may appear in early spring (B.B. Casper, personal observation.) At the sites studied here, natural seedling densities are higher away from shrubs than under them, but adult densities do not differ between the two microhabitats (B.B. Casper, unpublished work). Herbivory is almost exclusively confined to inflorescences.

Description of sites

The experiment was conducted in two natural populations, about 12 km apart, in Uintah Co. in northeastern Utah, United States. The vegetation at both sites is dominated by the juniper *Juniperus osteosperma* (Torr.) Little and shrubs, but there are also large areas of bare soil. Although the shrub community is slightly more diverse at Site 2 than at Site 1, *Artemesia tridentata* Nutt. and *Chrysothamnus nauseosus* Nutt. are the most common species at both sites. Site 1 is located on rangeland managed by the United States Bureau of Land Management while Site 2 is protected from grazing by cattle within the boundaries of Steinaker State Park. Cattle may rarely damage the plants by trampling, but they do not normally forage on them. The experiment largely avoids areas of Site 1 where junipers had been felled but not removed several years prior to the study. The two sites apparently differ in their ability to support the growth of *C. flava*. Densities are higher and mean plant size is larger at Site 1 (B.B. Casper, unpublished work). On average, plants at Site 1 have more than twice the number of flowering stalks than those at Site 2.

Climatic data

Monthly summaries of precipitation and temperature were obtained from the National Climatic Data Center, NOAA, Asheville, North Carolina. Data were collected daily at the Vernal airport located about 11 km S of Site 2 and 19 km SSW of Site 1. Total precipitation from October (year *t*), usually the month with greatest precipitation, to September (year *t* + 1) was calculated for each year, beginning in 1983. Monthly precipitation and mean monthly temperatures were also examined for October 1987 to September 1990, which encompasses the year just before the drought, the drought year itself, and the subsequent year. Comparisons were made with normal precipitation and temperatures which are mean values calculated for the 30-year period 1961–1990.

Planting design

Nutlets were collected from 40 maternal parents at Site 1 in July 1983 and planted in late August. The experiment was designed to assess the importance of post-dispersal seedling competition as selection pressure in the evolution of single-seededness (Casper 1994). Accordingly, nutlets were either planted individually or in clusters of four, in order to simulate the maturation of all four

ovules within the dispersal unit. Individual nutlets and clusters of nutlets were planted in two microhabitats, under shrubs and in the open, at least 0.5 m from the same shrubs. Plantings under shrubs were usually less than 20.0 cm from the edge of the shrub canopy. At each planting location, the topsoil was removed to a depth of approximately 10.0 cm and screened to remove any nutlets dispersed naturally. The screened soil was replaced in bottomless paper cups, about 7.0–8.0 cm in diameter. Because the cups extended about 2.0 cm above the soil surface, they prevented the sandy soil from shifting and defined the exact planting locations. The four cups placed under each shrub and the four placed nearby in the open were spaced at least 0.4 m apart and were alternately planted with one or a cluster of four nutlets. A cluster was created by placing four nutlets together on the soil surface and depressing them into the soil as a group. All four nutlets within a cluster, and in most cases all nutlets planted in association with a particular shrub, were from the same maternal parent. Therefore, plants growing in clusters were at least half-sibs as they would be if all four ovules matured within the same dispersal unit. Shrubs were selected arbitrarily without regard to species. The planting design was replicated at 190 shrubs at Site 1 and 144 shrubs at Site 2 for a total of 6680 planted nutlets.

Censuses

Seedlings were first counted in November 1983. Additional emergence and survivorship were determined through censuses conducted three times during the growing seasons of 1984 and 1985 and once, usually in late May, each year thereafter. Dead plants often remained until the next census, and missing plants were scored as dead unless there was evidence of disturbance. Plants were individually tagged in 1985 with colored plastic-coated wire placed around the caudex. These wires were replaced with large color-coded twist ties as the plants grew. Beginning with 1985, plant size, measured as the number of rosettes having at least three leaves, was recorded annually along with the number and condition of any infloresences. The numbers of inflorescences used in analyses included those damaged or removed by herbivores.

Some plants from the natural population at Site 1 were harvested and used to determine the extent that rosette number serves as an estimate of aboveground vegetative biomass. Plants were collected in the drought year of 1989 and again in 1990. Individuals were chosen to represent a range of rosette numbers. Whole vegetative rosettes were removed from the caudex, dried to constant biomass in a 70°C oven, and weighed. Regression analysis was used to examine the relationship between the number of leaf rosettes and dry vegetative biomass in each of the 2 years. The slopes of the two regression equations were compared statistically in order to determine whether the relationship between rosette number and vegetative biomass differed between the drought year and 1990.

Analyses

Because plants in the two populations differed greatly in most components of plant performance, data from the two sites were analyzed separately. Few clusters of plants were composed of more than two individuals after the second growing season, so plants growing in clusters of two or more were combined in a single density category and compared with those growing alone. General linear model ANOVA for unbalanced design (SAS 1985) was used to examine the number of rosettes and the number of inflorescences per plant as a function of density category the previous year and microhabitat (under a shrub or in the open). Since size measurements were made in the middle of the growing season, density the previous year is likely to influence plant size at least as much as current-year density. Probability levels for ANOVA were determined by randomization procedures (Manly 1991) because log-transformation failed to normalize the data. Microhabitat and density were both considered fixed effects in the ana-

lyses. Survival from the last census of the previous year and the percentage of plants flowering were analyzed as a function of density category the previous year and microhabitat using CATMOD log-linear analysis (SAS 1985). Maternal seed source was never used as an independent variable because there had been no attempt to randomize seeds from different parents among shrubs; variation resulting from maternal parentage and spatial habitat heterogeneity could not be separated.

Additional analyses were conducted using only plants under shrubs in order to determine whether demographic response to drought varied with the identity of the canopy shrub species. Plants growing under *Artemesia tridentata* were compared with those growing under any other species. *A. tridentata* was singled out because it is common at both sites and because of its known ability to improve soil water content through hydraulic lift (Richards and Caldwell 1987). In analyzing effects of shrub identity on growth during drought, the change in the number of leaf rosettes between 1988 and 1989 served as the dependent variable, and density and shrub identity were fixed independent variables. Plant size before drought was controlled for statistically by using the number of rosettes in 1988 as a covariate. Number of rosettes in 1988, which represents total growth before drought, was also analyzed as a function of density and shrub identity in order to determine whether shrub species affected growth in non-drought years. Number of rosettes in 1988 and the change in number of rosettes were log-transformed before analyses. Percentage survival during drought, from 1988 to 1989, was examined as a function of shrub identity but with density categories pooled since density did not affect survival that year.

Results

Climatic data

The period from October 1988 to September 1989 was by far the driest year during this study. Only 10.5 cm of precipitation, 49.5% below the normal of 20.8 cm, fell during that time. Precipitation during and just before the 1989 growing season was especially low; the 2.08 cm reported for January through May 1989 was 74.5% below normal (Fig. 1). In contrast, annual precipitation from October 1983 to September 1987 ranged from 18.1% to 48.9% above normal. Precipitation was still 28.0% below normal for the year October 1989 to September 1990 but more variable among months. Precipitation for January through May 1990 was 21.5% below normal, but above normal levels occurred in both February and April (Fig. 1).

Mean monthly temperatures during the last three years of the study were near normal except that January 1988 and January and February 1989 were colder by 3.1, 2.4, and 4.7°C, respectively, and December 1989 and January 1990 were 2.4 and 5.2°C warmer than normal.

Site differences

Differences between experimental populations in plant size and flowering paralleled performance differences in natural populations. By 1987, the fourth growing season, plants at Site 1 had roughly twice the number of leaf rosettes as plants at Site 2 (Fig. 2). Flowering was also much higher at Site 1 than at Site 2, where the proportion of individuals flowering never exceeded 13% in any
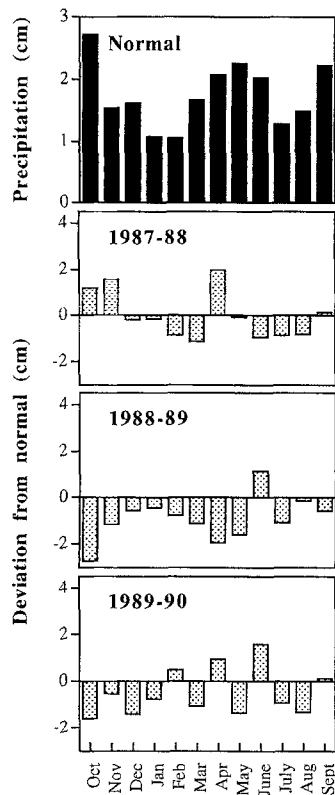
Fig. 1 Normal monthly precipitation for October 1987 through September 1990 (the mean for 1961 to 1990) and the monthly deviation from normal for the 3 years just before, during, and after the drought

Fig. 2 Annual mean number of leaf rosettes (± SD) separated by microhabitat and density. The 1989 census was during the drought year. Note the different size scales for the two sites

Fig. 3 Annual percentage mortality for both sites. All density and microhabitat categories are combined. Note the large increase in mortality between the 1988 and 1989 censuses

year. Despite overall differences in plant size and inflorescence production, the two populations responded very similarly to drought. However, in non-drought years, intraspecific density and microhabitat (shrub versus open) affected plant performance much more strongly at Site 1 than at Site 2. The specific effects of drought, intraspecific density, and shrub cover are considered below for each site separately.

General drought effects

During the drought year of 1988–1989, mortality increased and mean plant size decreased at both sites. The 30.4% and 38.2% mortality levels observed at Sites 1 and 2, respectively, were only surpassed by high seedling mortality the first year after emergence (Fig. 3). Mortality during drought was roughly three times mortality in most non-drought years. Mortality remained high (27.1%) at Site 2 between the 1989 and 1990 censuses, but dropped to 13.5% at Site 1.

The drought year was the only year in which mean plant size, as measured by the number of leaf rosettes, decreased (Fig. 2). The greatest increase in plant size occurred between 1989 and 1990 (Fig. 2), just after the severe drought. At Site 1, flowering differed among years in the same way as plant size. The proportion of plants flowering decreased during the drought year but sharply
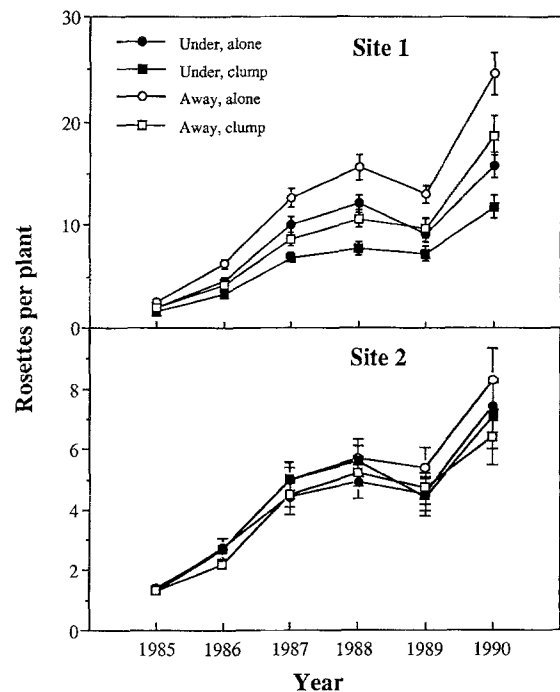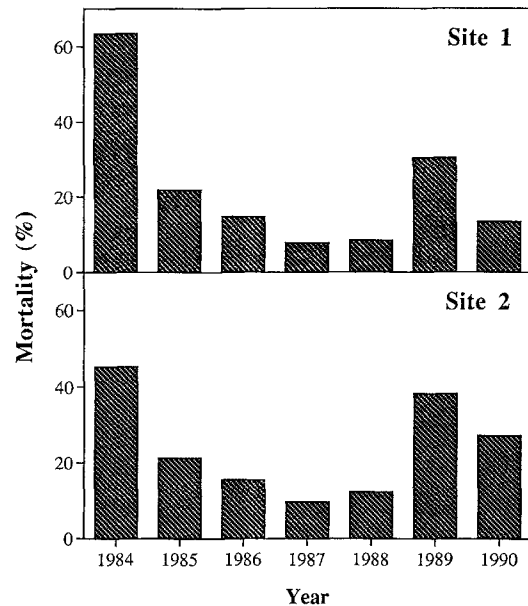
increased in the subsequent year (Fig. 4). At Site 1, the number of inflorescences per flowering individual also increased greatly the year after drought, especially for single individuals in the open microhabitat (Fig. 5). At Site 2, drought effects on flowering were expressed as reduced numbers of inflorescences per plant (Fig. 5), and flowering did not increase dramatically at that site the year after drought.
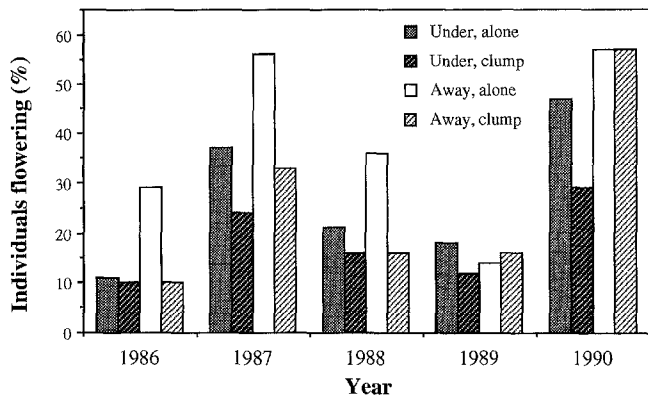
Fig. 4 Annual percentage of plants flowering as a function of density and microhabitat at Site 1 only. The percentage of plants flowering at Site 2 was never greater than 13% and never differed between density or microhabitat categories
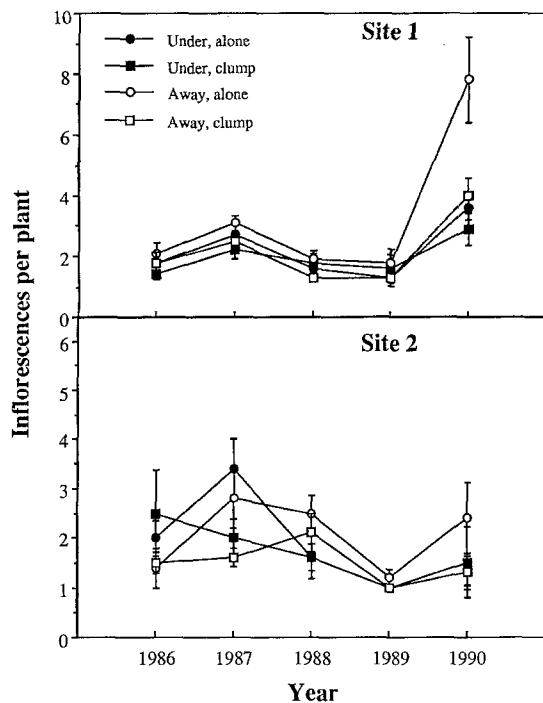

Fig. 5 Annual mean number of inflorescences (± SD) per flowering individual separated by microhabitat and density. Note the different scales for the two sites

The relationship between number of rosettes and vegetative biomass was the same in the drought year of 1989 as it was in 1990. The number of rosettes provides a robust measure of aboveground vegetative biomass. For 1989, $y = 0.070x$, where y = biomass (g) and x = number of rosettes ($r^2 = 0.86$), and for 1990, $y = 0.078x$ ($r^2 = 0.94$). The slopes of these regression equations were not statistically different ($F_{1,19} = 0.11$; Sokal and Rohlf 1981).

Size specific response to drought

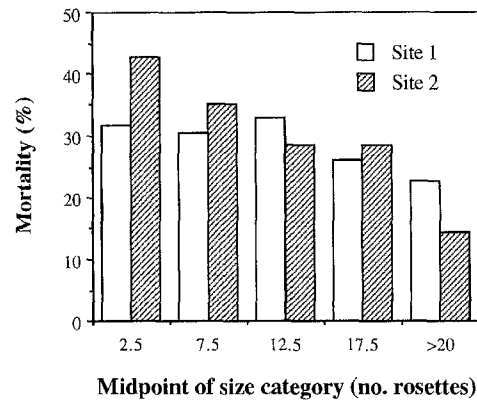There was a negative relationship between the number of leaf rosettes in 1988 and the absolute change in leaf ro-

Fig. 6 Mortality between 1988 and 1989, the drought year, as a function of plant size category. Mortality did not differ among size categories at either site

settes between 1988 and 1989. That is, nearly all large plants lost leaf rosettes between 1988 and 1989 while many smaller plants grew during the same period. ANOVAs examining the change in number of rosettes as a function of plant size the previous year and microhabitat (pooling density categories) verified that absolute growth decreased with initial plant size between 1988 and 1989 (parameter estimate = -0.6251; $P < 0.001$ for Site 1 and parameter estimate = -0.3863; $P < 0.001$ for Site 2) while in all other years the relationship between plant size and growth was positive or statistically non-significant. These analyses revealed no differences between the shrub and open microhabitats in growth during drought, independent of plant size.

Mortality during the drought year (Fig. 6) was not size-specific at either site (log-linear analysis). The apparent trend toward lower mortality with larger size, especially at Site 2, is partly attributable to smaller sample sizes in the larger size categories.

Effects of density

Mortality and flowering during the drought year were independent of density at both sites. Despite the large increase in mortality compared with other years, plants growing alone were just as likely to die as plants growing with at least one other plant (Site 1, $\chi^2 = 0.30$; Site 2, $\chi^2 = 0.01$). Neither the proportion of plants flowering (Fig. 4, Table 1) nor the number of inflorescences per flowering individual (Fig. 5, Table 2) varied with density during drought.

In non-drought years, density often affected several components of plant performance at Site 1 but seldom did at Site 2. At Site 1, mortality between 1984 and 1985 and between 1986 and 1987 differed between density categories (Fig. 7). In those years, survival was higher for plants growing with at least one individual than for plants growing alone (for 1985, $\chi^2 = 7.42$, $P < 0.01$; for 1987, $\chi^2 = 4.55$, $P < 0.05$), suggesting some synergistic effect of neighbors. Density never affected survival at Site 2. Plant size varied with density in all years at Site 1

Table 1 Chi-square values for contingency table analyses of the percentage of individuals flowering at Site 1 as a function of microhabitat and density category

Source of variation	Year				
	1986	1987	1988	1989	1990
Microhabitat	3.84*	7.37*	1.81	1.01	7.16**
Density	5.55*	13.06***	6.56**	0.24	2.03
Density X microhabitat	4.00*	0.64	1.95	0.65	1.88

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$

Table 2 Parameter estimates for the ANOVA models evaluating the number of inflorescences per flowering individual as a function of microhabitat and density categories. Years when neither factor is significant are omitted. P-values were determined by randomization. The nature of the model results in the same standard errors for both variables

| Year	Site	Parameter estimates		Standard error of the estimate
		Density	Microhabitat	
1987	1	−0.581*	0.379	0.298
	2	−1.303**	−0.526	0.433
1990	1	−2.180*	2.704**	0.933
	2	−0.506	0.423	0.777

$*P < 0.05$, $**P < 0.01$

(Fig. 2, Table 3) but never did at Site 2. On average, plants growing alone were larger than those growing with at least one other individual. Density often affected inflorescence production at Site 1, where plants growing alone were, in some years, more likely to flower (Fig. 4, Table 1) and/or produced more inflorescences when they did flower (Fig. 5, Table 2). At Site 2, density never affected the proportion of plants flowering and caused a decrease in inflorescence numbers in only one year, 1987.

Effects of shrubs

The location of plants with respect to shrubs also did not affect plant performance during drought. Shrub cover did not affect percentage survival (Fig. 7), the percentage of plants flowering (Fig. 4), or the number of inflorescences per flowering individual (Fig. 5).

In non-drought years, shrubs strongly affected plant perfomance at Site 1 but only marginally did so at Site 2. In some years, percentage survival was higher for plants growing under shrubs than for those in the open (Fig. 7). Survival differed between microhabitats at Site 1 between 1986 and 1987 ($\chi^2 = 10.59$; $P < 0.01$) and at both sites between 1989 and 1990 (Site 1, $\chi^2 = 8.76$; $P < 0.01$; Site 2, $\chi^2 = 4.75$; $P < 0.05$). In contrast, shrubs negatively affected plant size and inflorescence production at Site 1. Plants under shrubs were consistently smaller than those in the open (Fig. 2, Table 1), and in most years were either less likely to flower and/or produced fewer
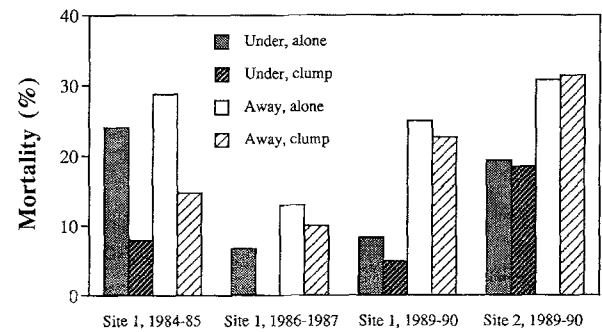
Fig. 7 Percentage mortality as a function of density and microhabitat. Data are only presented if either density or microhabitat significantly affected mortality for that particular site and year

Table 3 Parameter estimates for the ANOVA models evaluating number of rosettes per plant at Site 1 as a function of microhabitat and density categories. P-values were determined by randomization. Both variables were significant at $P < 0.001$ except as indicated. The microhabitat X density interaction was never significant. As in Table 2, the errors are the same for both variables

Year	Parameter estimates		Standard error of the estimate
	Microhabitat	Density	
1985	0.441	−0.383**	0.126
1986	1.362	−1.667	0.322
1987	2.316**	−3.706	0.685
1988	3.165	−4.967	0.880
1989	3.300	−3.768	0.831
1990	8.080	−4.645**	1.611

$**P < 0.01$

inflorescences than did plants in the open (Figs. 4, 5; Tables 1, 2). Plant size, the probability of flowering, and the number of inflorescences produced never differed between shrub and open microhabitats at Site 2.

The importance of microhabitat relative to density as a factor affecting plant size differed among years. The magnitude of the parameter estimates for density were about equal to or greater than those for microhabitat through 1989, the drought year, but in 1990, the magnitude of the microhabitat effect exceeded that of density by more than twofold (Table 3). The effects of density and microhabitat on the mean number of rosettes per plant in 1988, 1989, and 1990 were further examined using a repeated measures ANOVA. Only those plants still alive in 1990 that had not changed density categories during these 3 years were included in the analysis. The magnitude of the microhabitat effect on the number of rosettes differed among years, resulting in a significant year × microhabitat interaction (Table 4) and indicating that the importance of microhabitat as a factor affecting plant size differed among those 3 years. In contrast, the lack of a significant density × year interaction term indicates that the effect of density on plant size did not change among years.

Table 4 Repeated measures ANOVA for number of rosettes per plant in 1988, 1989 and 1990 at Site 1. Randomization procedures did not change the P-values

Source of variation	df	MS	F	P
Density	1	2852.04	18.39	0.001
Microhabitat	1	3889.03	25.08	0.001
Error	186	155.06		
Year	2	3088.10	74.50	0.001
Year X microhabitat	2	283.92	6.85	0.01
Year X density	2	37.02	0.89	NS
Error (year)	372	41.45		

Effect of shrub identity

For plants located under shrubs, their performance during the drought year depended on whether they were under *A. tridentata* or some other shrub species. Percentage mortality differed with canopy shrub identity at Site 1 while plant growth depended on shrub identity at Site 2. Of the 183 plants still alive under shrubs at Site 1 in 1988, 44% were under *A. tridentata*. Between the 1988 and 1989 censuses, 18.8% of the plants under *A. tridentata* had died compared with 37.0% under any other species ($\chi^2 = 7.20$; $P < 0.01$). At Site 2, mortality was unaffected by the identity of the shrub species. At that site 50% of the 160 plants still alive under shrubs in 1988 were under *A. tridentata*. Percentage mortality did not differ significantly for plants under *A. tridentata* (35.5%) compared with those under any other shrub species (44.2 %).

At Site 2, plants growing under *A. tridentata* did not lose as many leaf rosettes during the drought year as did plants growing under other shrub species. When plant size before drought was controlled for statistically by including leaf rosette number in 1988 as a covariate, growth differed with canopy shrub identity ($F_{1,92} = 5.718$; $P < 0.02$) but not with density. Plants under *A. tridentata* lost a mean of 0.62 (SD = 0.43) leaf rosettes while those under any other shrub species lost a mean of 1.85 (SD = 0.60) rosettes (density categories combined.) The shrub identity × density interaction term was also not significant. At Site 1, plant growth during drought was independent of both shrub identity and density.

The size of plants in 1988 suggests that growth in non-drought years was independent of shrub identity at both sites. The application of an ANOVA model that included both density and shrub identity as independent variables found no effect of either on pre-drought plant size at Site 2, and only an effect of density at Site 1 ($F_{1,179} = 9.90$; $P < 0.01$). This result is consistent with results of the ANOVAs reported in Table 3 that also detected a significant effect of density on plant size at Site 1 in all years.

Discussion

Drought did not strengthen either positive or negative plant interactions. The drought year was the only year in which neither intraspecific density nor shrub cover affected either survival or flowering in *C. flava*. The study produced no evidence, therefore, of intraspecific competition, interference by shrubs or facilitation by shrubs during drought. Evidence for at least one of these biotic interactions was found in all other years of the study. The apparent reduction in intraspecific competition is consistent with other experimental studies indicating diminished competition in drought years (Sharitz and McCormick 1973; Fowler 1986a; Bauder 1989) but is inconsistent with the prediction of Fowler (1988) that plant populations undergo density-dependent regulation during a temporal decline in resource availability. Results, likewise, do not support the expectation that facilitation is more pronounced in years of greater abiotic stress (Bertness and Callaway 1994).

Plant performance during drought did differ with canopy shrub species. Plants under *A. tridentata* had higher survival at Site 1 while at Site 2, they did not shrink as much when pre-drought size (size in 1988) was accounted for. This is consistent with *A. tridentata* supplying water to *C. flava* through hydraulic lift, but there is no direct evidence, and there are other possible explanations. Growth apparently did not differ with shrub identity in non-drought years. Survival in non-drought years could not be similarly assessed because not all shrub identities were recorded early in the experiment.

The demographic consequences of biotic interactions in non-drought years are complicated. Shrubs neither exclusively facilitate nor interfere with *C. flava*. Shrubs negatively affected plant size and flowering performance at Site 1, where in some years individuals under shrubs were less likely to flower and/or produced fewer inflorescences. In contrast, the annual survival rate was sometimes higher under shrubs at both sites. These effects were especially pronounced the year after drought when plant growth and flowering increased greatly. Likewise, intraspecific density affected flowering and mortality in opposite ways. Plants growing alone were often more likely to flower or produced more flowering stalks when they did flower than plants growing with at least one other individual. Mortality varied with intraspecific density in only 2 years, between 1986 and 1987 and between 1989 and 1990, and only at Site 1, but in both years mortality was higher among individuals growing alone than among those growing with another individual. These opposing results suggest that flowering and survival are limited by different environmental factors. One possibility is that shading by shrubs or neighbors improves survival rates by decreasing transpirational water loss but reduces growth and flowering by causing photosynthesis to be light limited.

Drought had important effects at the population level independent of plant density or shrub cover. Drought strongly reduced survival and rearranged size hierarchies at both sites. At Site 1, seed production must have also declined drastically as a consequence of far fewer plants flowering and there being fewer inflorescences per flowering individual.

The rearrangement of population size hierarchies during drought was striking. The drought year was the only year in which large numbers of plants shrank in aboveground biomass. Because growth during drought was inversely related to size before drought, reversals occurred in the size rankings of individuals, many of which persisted for at least two years afterwards (B.B. Casper, unpublished work). These size-specific growth responses among even-aged individuals suggests a tradeoff between growth under more favorable soil water conditions and growth during drought, a phenomenon also reported for the desert shrub *Encelia farinosa*(Ehleringer 1993). Alternatively, larger plants may simply be less drought tolerant, which could occur if, for example, they require disproportionately more water per unit biomass or root/shoot ratios decrease with aboveground plant size.

A reduction in aboveground plant tissue through drought deciduous leaves, branch abscission, or reduced leaf expansion is widely interpreted as an adaptation to water stress (Hsaio 1973; Wills and Bell 1988). The death of entire vegetative rosettes in *C. flava* represents both a loss of biomass and the loss of potential reproductive meristems, which may partially account for the reduced inflorescence production during drought. Although negative growth during drought has been reported for plants in natural populations (Fowler 1986a; Wills and Bell 1988), such studies have apparently not considered whether drought causes rank reversals in size as it did here. A few other studies report an inverse relationship between aboveground plant size and some other aspect of performance during drought (Watkinson 1982; Hendrix and Trapp 1992; Rice 1990).

The large increase in growth and flowering the year after the drought may represent a compensatory response. Compensatory growth following shorter periods of water stress is well-documented and can occur either because plants draw on carbohydrates that accumulate during stress and/or because improved water availability allows for the full expansion of cells that could not occur under lower cell water potentials (Chu et al. 1979; Horst and Nelson 1979). For *C. flava*, the large number of new leaf rosettes added in 1990 could be products of carbohydrate reserves built up during the drought year. Alternatively, plants may have responded to above average precipitation in April 1990, the month when most vegetative growth occurs.

The two experimental populations of *C. flava* differed greatly in mean plant size and flowering and in whether density or microhabitat affected plant performance. Growth and reproduction were always greater at Site 1 where effects of density and microhabitat were also more likely to occur. Because nutlets used in establishing these experimental populations were all collected at Site 1, adaptation to local soil conditions could contribute to differences in performance between experimental populations. However, parallel differences between natural populations in plant size and infloresence production (B.B. Casper, unpublished work) suggest that the two sites inherently differ in productivity.

In conclusion, the pronounced demographic consequences of drought were largely independent of intraspecific density and shrub cover, although the performance of plants under shrubs was influenced by shrub species. The severe drought appeared to decrease or overshadow the importance (sensu Weldon and Slauson 1986) of biotic interactions.

References

Antonovics J, Levin DA (1980) The ecological and genetic consequences of density-dependent regulation in plants. Annu Rev Ecol Syst 11:411–452

Barden LS (1988) Drought and survival in a self-perpetuating *Pinus pungens* population: equilibrium or nonequilibrium? Am Midl Nat 119:253–257

Bauder ET (1989) Drought stress and competition effects on the local distribution of *Pogogyne abramsii*. Ecology 70: 1083–1089

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Casper BB (1984) On the evolution of embryo abortion in the herbaceous perennial *Cryptantha flava*. Evolution 38:1337–1349

Casper BB (1994) Post-dispersal sibling competition and the evolution of single-seededness in *Cryptantha flava*. Evolution 48:1377–1382

Charley JL, West NE (1975) Plant induced soil chemical patterns in some shrub-dominated semi-desert ecosytems of Utah. J Ecol 63:945–964

Chu ACP, McPherson HG, Halligan G (1979) Recovery growth following water deficits of different duration in prairie grass. Aust J Plant Physiol 6:255–263

Diamond J, Case TJ (1986) Community ecology. Harper and Row, New York

Ehleringer JR (1993) Variation in leaf carbon isotope discrimination in *Encelia farinosa*: implications for growth, competition, and drought survival. Oecologia 95:340–346

Fowler N (1986a) Density-dependent regulation in a Texas grassland community. Ecology 67:545–554

Fowler N (1986b) The role of competition in plant communities in arid and semiarid regions. Annu Rev Ecol Syst 17:89–110

Fowler N (1988) The effects of environmental heterogeneity in space and time on the regulation of populations and communities. Symp Brit Ecol Soc 28:249–269

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 plants. J Ecol 63:627–632

Grime JP (1977) Evidence for the existence of three primary strategies in plants and relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Halvorson WL, Patten DT (1975) Productivity and flowering of winter ephemerals in relation to Sonoron desert shrubs. Am Midl Nat 93: 311–319

Hendrix SD, Trapp EJ (1992) Population demography of *Pastinaca sativa* (Apiaceae): effects of seed mass on emergence, survival, and recruitment. Am J Bot 79:365–375

Horst GL, Nelson CJ (1979) Compensatory growth of tall fescue following drought. Agron J 71:559–563

Hsaio TC (1973) Plant responses to water stress. Annu Rev Plant Physiol 24:519–570

Jordan PW, Nobel PS (1979) Infrequent establishment of seedlings of *Agave deserti* (Agavaceae) in the Northeastern Sonoran desert. Am J Bot 66:1079–1084

Keddy PA (1989) Competition. Chapman and Hall, London

Klemow KM, Raynal DJ (1985) Demography of two facultative biennial plant species in an unproductive habitat. J Ecol 73:147–167

Manly BFJ (1991) Randomization and Monte Carlo methods in biology. Chapman and Hall, London

McAuliffe JR (1988) Markovian dynamics of simple and complex desert communities. Am Nat 131:459–490

Muller CH (1953) The association of desert annuals with shrubs. Am J Bot 40:53–60

Newman EI (1967) Response of *Aira praecox* to weather conditions. J Ecol 55:539–566

Newman EI (1973) Competition and diversity in herbaceous vegetation. Nature 244:310

Nobel PS (1989) Temperature, water availability, and nutrient levels at various soil depths – consequences for shallow-rooted desert succulents, including nurse plant effects. Am J Bot 76:1486–1492

Rice KJ (1990) Reproductive hierarchies in *Erodium*: effects of variation in plant density and rainfall distribution. Ecology 71:1316–1323

Richards JH, Caldwell MM (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73:486–489

SAS (1985) SAS user's guide: statistics. SAS Institute, Cary

Sharitz RR, McCormick JF (1973) Population dynamics of two competing annual plant species. Ecology 54: 723–740

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, San Francisco

Steenbergh WF, Lowe CH (1969) Critical factors during the first years of life of the Saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. Ecology 50:825–834

Taylor DR, Aarssen LW, Loehle C (1990) On the relationship between *r/K* selection and environmental carrying capacity: a new habitat templet for life history strategies. Oikos 58:239–250

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. Nature 367:363–365

Turner NC, Kramer PJ (1980) Adaptation of plants to water and high temperature stress. Wiley, New York

Turner RM, Alcorn SM, Olin G, Booth JA (1966) The influence of shade, soil, and water on saguaro seedling establishment. Bot Gaz 127:95–102

Watkinson AR (1982) Factors affecting the density response of *Vulpia fasciculata*. J Ecol 70:149–161

Weldon CW, Slauson WL (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. Q Rev Biol 61:23–44

Went FW (1942) The dependence of certain annual plants on shrubs in Southern California deserts. Bull Torrey Bot Club 69:100–114

Wills RT, Bell DT (1988) Shedding of new season's shoots by *Eucalyptus erythrocorys* F. Muell: a response to water stress? In: Floret CH, Rambal S, Roy J (eds) Time scales and water stress. IUBS, Paris, pp 261–265