

# Drought prolongs leaf life span in the herbaceous desert perennial *Cryptantha flava*

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## Summary

1. Drought-deciduous leaves are common in habitats with predictable, seasonal drought, and a reduction in transpirational surface area is generally considered an important drought-response strategy. Yet leaf demographic responses to unpredictable drought events that can occur at any time during the growing season have been little studied in ecological systems.

2. We created drought in a natural population of the herbaceous desert perennial *Cryptantha flava* (A. Nels.) Payson (Boraginaceae) in north-eastern Utah, USA, by installing rainout shelters just before and during the early part of the growing season, from 1 March until mid-June in 1998, and from 1 March until mid-May in 1999.

3. Droughted plants exhibited water stress through lower rates of midday photosynthesis and conductance, and by producing leaves with a smaller surface area and greater specific mass than plants exposed to ambient precipitation.

4. Under drought, leaf life span increased on flowering stalks and vegetative rosettes and new leaf production decreased, reducing leaf turnover and increasing standing leaf crop in droughted plants.

5. A larger number of leaves under drought conditions compensated in area for their smaller size, which means that transpirational surface area was not reduced.

6. The reduction in photosynthetic rate and the increase in leaf life span are consistent with a more general pattern in response to other low resource conditions, paralleling leaf-level responses to shortages of nutrients and light.

7. Plants in the drought and ambient precipitation treatments responded to late-season rainfall with increased leaf production, providing an additional example of developmental plasticity in response to temporal heterogeneity in water availability.

*Key-words:* Desert perennial, drought, leaf life span, phenotypic plasticity, photosynthesis

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## Introduction

The birth and death rates of leaves have important physiological consequences for the whole plant. These leaf-level demographic traits determine the total leaf surface area over which transpirational water loss can occur and the rate of leaf turnover, which is inextricably linked to the plant's carbon and nutrient economies. Together with photosynthetic rate, leaf longevity figures in the total carbon return from a leaf, and new leaf construction places demands on existing carbon, nutrient, and water resources.

For these reasons, leaf demographic characters are likely to change in response to water availability. At

least two considerations with opposite predictions are relevant. Firstly, when photosynthesis is reduced for any reason, including drought, it could be advantageous to increase leaf life spans and reduce rates of leaf turnover in order to minimize leaf construction costs (Chabot & Hicks 1982). Conversely, maintenance of leaves may be costly when water is limiting because transpirational water loss increases proportionally with leaf surface area, increasing demands on water uptake by roots and on the hydraulic architecture of the plant. Therefore early leaf senescence may be favoured under dry soil conditions as a means of reducing water requirements and avoiding low water potentials that may cause xylem dysfunction. Historically, the advantages of reducing leaf surface area during drought have dominated ecologists' thinking (Begg 1980; Kikuzawa 1989; Kikuzawa 1995;

Kozłowski 1973; Jones 1992; Lambers, Chapin & Pons 1998).

Consistent with this reasoning, the short leaf life span associated with drought-deciduous growth has long been recognized as advantageous in habitats with predictable, seasonally distinct dry seasons. Studies have largely focused on the distribution of drought-deciduous versus evergreen growth forms over climatic gradients of seasonal water availability (Harrison, Small & Mooney 1971; Mooney & Dunn 1970).

In contrast, ecologists have not given much attention to leaf demographic responses to unpredictable drought events that can occur at any time during the growing season. Most relevant data have come from agricultural systems, which use largely annual species. Studies with crop species show that while plant responses to drought are complicated and varied, involving changes in cell- and leaf-level physiology as well as development, changes in leaf demography are an important component (Blum 1996). In sorghum a 14–26% reduction in canopy photosynthesis during drought is fully accounted for by a reduction in leaf surface area, not by a reduction in stomatal conductance (Garrity, Sullivan & Watts 1984). In general, reduced leaf expansion appears to be a common means of reducing leaf area when drought occurs early in plant growth, while drought after flowering often speeds leaf senescence (Blum 1996).

Our study examined the drought response of physiological and demographic leaf traits in the semidesert perennial *Cryptantha flava* (A. Nels.) Payson (Boraginaceae). Drought was applied experimentally to natural populations early in the spring growing season. The leaves of this drought-deciduous species normally senesce as soils dry during the summer months. To test whether drought applied early in the growing season either prolongs or shortens leaf longevity, we compared leaf life span, new leaf production, and the standing number of leaves throughout the growing season between droughted plants and those receiving ambient amounts of precipitation. Leaf life span was followed on vegetative rosettes and flowering stalks. Measurements of leaf area, leaf specific mass, photosynthesis and stomatal conductance allowed us to determine the impact of drought on leaf physiological performance, and to assess the relationship between physiological performance and leaf life span.

## Materials and methods

### SPECIES AND STUDY SITE

*Cryptantha flava* grows in sandy soils throughout most of the semiarid Colorado Plateau of eastern Utah and parts of adjoining states of the USA (Higgins 1971). The plant's narrow, nearly vertical, oblanceolate leaves are organized in basal rosettes that are connected by a branched, woody caudex (mostly underground stem) to a single tap root. The plants are herbaceous perennials,

with the woody caudex maintaining dormant meristems at ground level during the cold winter periods. In north-eastern Utah, where this study was conducted, the growing season generally begins in mid-April, when the 10–15 new leaves that make up the spring cohort on each rosette expand almost simultaneously. Additional leaves are produced and old ones die throughout the growing season, but few green leaves remain past late July. New rosettes arise from the axils of lower leaves on existing rosettes. A rosette apical meristem continues this pattern of seasonal leaf production, sometimes for several years, until the meristem converts from leaf to flower production and the rosette bolts to produce an erect stem bearing evenly distributed leaves and terminated by an inflorescence, usually in mid-May. No new leaves arise on a flowering stalk after the inflorescence forms, and the entire stalk dies as seeds ripen in mid-July.

The study site (1730 m elevation) is located on land managed by the US Bureau of Land Management (40°30' N, 109°22'30" E), where the vegetation is dominated by the shrubs *Artemisia tridentata* Nutt., *Chrysothamnus nauseosus* (Pallas) Britt, and the small tree *Juniperus osteosperma* (Torr.). Monthly mean temperature ranges from –8.4 °C in January to 21.3 °C in July (Western Regional Climate Center, Reno, NV, USA; <http://www.wrcc.dri.edu>). Annual precipitation averages 215 mm, but is highly variable (Forseth, Wait & Casper 2001); most precipitation occurs in spring and fall. Although the species grows both under shrubs and away from them, the plants used in this study all occurred in fully exposed microhabitats.

### WATER TREATMENTS

Drought treatments were applied in 1998 and 1999, using different methods. In 1998, precipitation was reduced in each of six 5 × 5 m study plots by unrolling an opaque canvas cover over an inclined metal frame (1–2.5 m in height) only during rain storms from 1 March (Julian date 60) to 17 June. Mid-May is typically the period of peak flowering, approximately half-way through the main growing season. In 1999, the frames were erected on six different plots from 1 March to 23 May, but the tarpaulin was replaced with stationary polyethylene roofing material that transmits photosynthetically active radiation (400–700 nm) and infrared radiation (Reynolds *et al.* 1999). Six additional plots received ambient precipitation in both years, and served as controls. Precipitation at the site was measured from 1 March to 3 August in 1998, and 1 March to 26 September in 1999.

### LEAF PHYSIOLOGY AND MORPHOLOGY

Photosynthesis and stomatal conductance were measured in 1999 for individuals in droughted and control plots. To minimize light limitations to photosynthesis, midday (1000–1400 MST) photosynthetic rates were

measured using ambient solar radiation only under cloudless conditions. One, two or three leaves of unknown age on vegetative rosettes were enclosed in the 0.25 l chamber of a Li-Cor 6200 closed photosynthesis system (Li-Cor, Lincoln, NE, USA). Photosynthetic CO<sub>2</sub> depletion within the cuvette was measured over two consecutive 15 s periods, and the average of these two measurements was taken as the photosynthetic rate. The area of leaves enclosed in the cuvette was estimated from the product of length × width.

These physiological measurements were made approximately weekly from mid-May to the end of June. Measurements collected on consecutive days were pooled, with the resultant sample periods being 18 May (Julian date 138), 23–26 May, 1 June, 8–9 June, 16–18 June and 30 June. Approximately 10 plants per plot in three to six plots of each of the two water treatments (droughted in 1999, and controls) were measured in a given sampling period. Because we suspected that physiological response to drought varies with plant size (Casper 1996), physiological measurements were made on plants of two different size categories within each plot, small plants with <15 rosettes and large plants with ≥15 rosettes. ANOVA was used to examine photosynthesis and stomatal conductance (ln-transformed). Each was examined as a function of water treatment (fixed effect), plot nested within treatment (random effect), date (random effect) and size (fixed effect) using JMP IN (SAS Institute, Inc., Cary, NC, USA). The nature of this ANOVA model requires the calculation of synthetic error terms, and interactions between date and the other independent variables could not be evaluated. All other statistical analyses were performed using STATISTICA (Stat Soft, Inc., Tulsa, OK, USA).

Leaf area and leaf specific mass were measured on a separate set of leaves collected from a total of 12 small and 12 large plants from each water treatment on 4 June 1999 (Julian date 155). One leaf was sampled from each plant. Leaf area (cm<sup>2</sup>) was measured on fresh leaves using a portable leaf-area imager (Model CI 420, CID Inc., Vancouver, WA, USA) and image analysis software (CIAS IMAGE ANALYSIS ver. 2., Jandel Scientific, San Rafael, CA, USA). Leaves were then dried to constant mass. Leaf specific mass was calculated as dry mass (g) divided by area. The effects of water treatment on leaf area and leaf specific mass were assessed using a two-way ANOVA.

#### LEAF DEMOGRAPHY

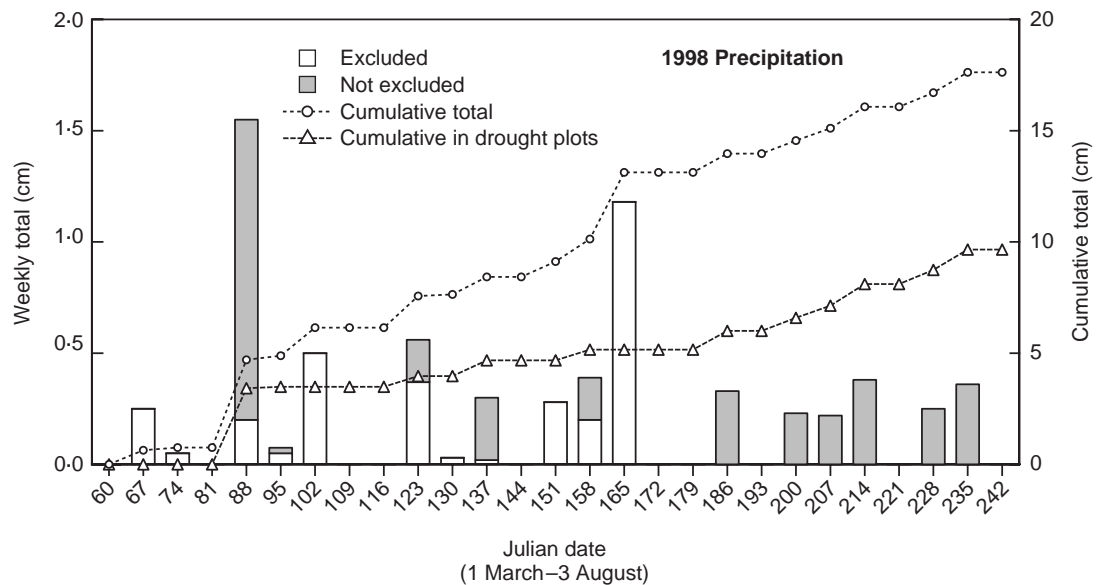
Plants used in the leaf demography studies were chosen without regard to size, but all were mature plants with at least five vegetative rosettes. Leaves on flowering stalks were followed in 1998, beginning on 20 May (Julian date 140), when a single flowering stalk was marked on each of 22 plants located within drought plots, but near enough to a plot edge that they could be reached without entering the plot. Flowering stalks

were similarly marked on 26 control plants located <10 m from a drought plot. Repeated visits are necessary for leaf demography studies, so control plants were selected outside the delineated control plots to minimize foot traffic near plants being used for physiological measurements. Coloured thread was tied around the middle of each stem to give a positional reference for following individual leaves. The total number of living leaves, both below and above the thread, was recorded at censuses conducted every 2–3 days. Leaves were considered to be alive as long as some green tissue was evident. While data from all census dates were compared graphically, a repeated-measures ANOVA was used to examine the number of surviving leaves per flowering stalk as a function of water treatment on three regularly spaced census dates: 20 May (Julian date 140), 28 May and 5 June. Experimental plot was treated as a random variable in this and subsequent ANOVA models.

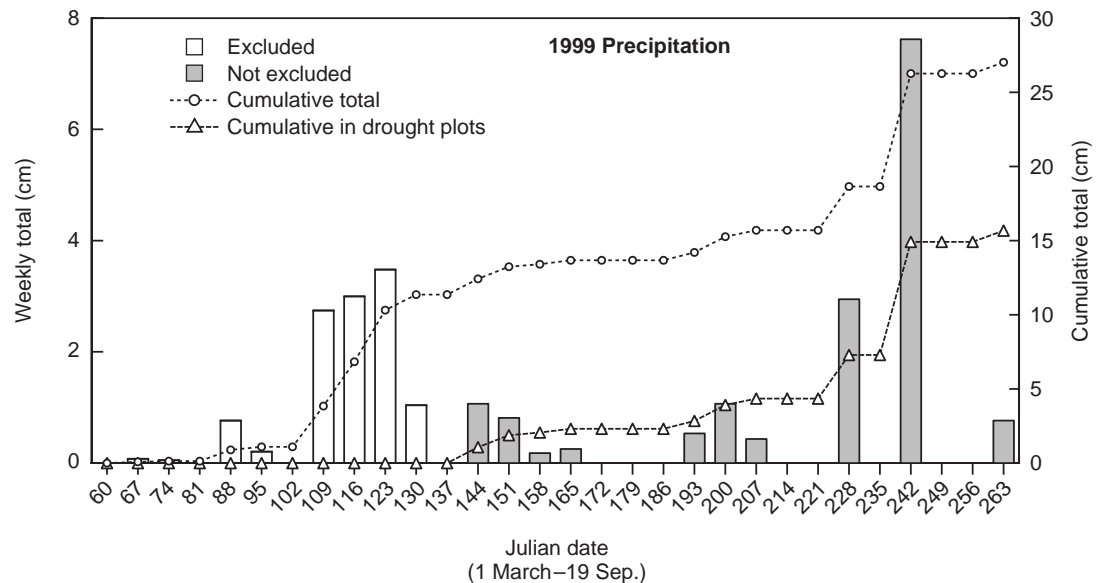
In 1999, leaf demography was followed on a single vegetative rosette on each of 23 plants located within drought plots, and on 21 control plants outside the plots; these were different individuals from the plants whose leaves were followed in 1998 but were similarly located with respect to the plots. Because vegetative rosettes continue to produce new leaves throughout the growing season and because the stem does not elongate sufficiently to place markers on it, it was necessary to mark leaves individually. Mature leaves were marked by applying a small (<2 mm diameter) dot of oil-based paint to the adaxial surface using a felt-tipped pen. The paint caused no obvious damage to mature leaves, but could not be applied to expanding leaves because it interfered with leaf expansion. Expanding, unmarked leaves were still uniquely identified by their order on the stem. At censuses conducted every 3–4 days, each leaf was checked for survival using the criteria described above. A leaf was considered 'born' when its length reached at least 1 cm.

Comparisons were made between droughted and control plants in 1999 for the number of standing leaves per rosette; the number of new leaves produced between the first census and 24 July; and leaf life span as a function of birth date. 24 July was an arbitrary date at the end of the period of most active plant growth. The numbers of standing leaves present at all census dates were compared graphically between drought and control treatments. A repeated-measures ANOVA was used to compare standing leaf number as a function of water treatment and over four relatively evenly spaced censuses – 8 May (Julian date 128), 27 May, 17 June and 10 July. The cumulative number of new leaves (ln-transformed) in each rosette between the first census and 24 July was also compared between treatments.

Leaf life span (measured in days) was examined separately for leaves already present at the first census and for leaves that appeared after the first census, and therefore whose birth date was known. The average



**Fig. 1.** Actual and cumulative precipitation for the drought and control treatments during the 1998 growing season. Precipitation excluded from the drought plots is indicated by white bars; precipitation falling on both drought and control plots is in grey.



**Fig. 2.** Actual and cumulative precipitation during the 1999 growing season. Drought and control plots are indicated as in Fig. 1.

longevity of all leaves present at the first census was calculated for each plant, and these values were compared between droughted and control plants using ANOVA. Leaves that were born between the first and fourth censuses were classified by their date of first appearance, and life span was examined using an ANOVA that included birth date as an additional factor. When a plant had produced more than one new leaf between two census dates, one leaf was selected at random for the analysis. Life span could not always be determined for leaves produced after the fourth census because some survived until October, when not all markings on leaves remained visible.

## Results

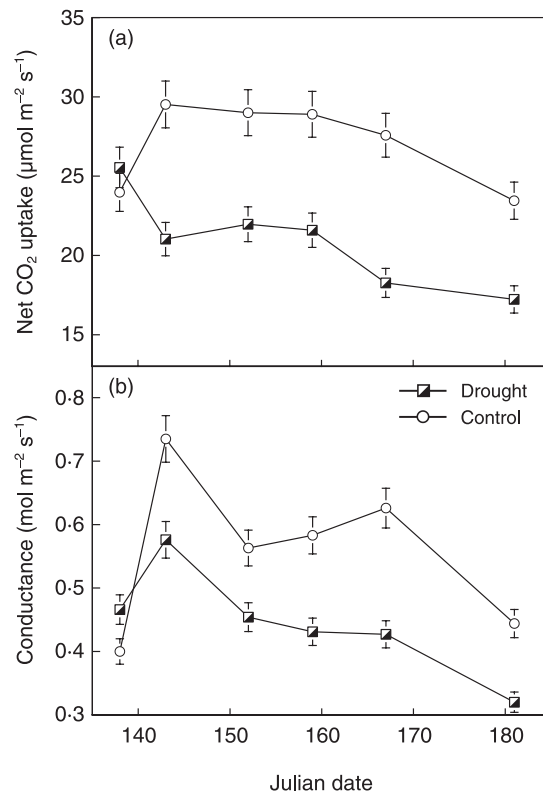
### PRECIPITATION

In 1998, precipitation was reduced by roughly half in the drought plots between 1 March and 17 June (Julian dates 60–169), at which time the shelters were removed. All precipitation was excluded from drought plots from 1 March to 23 May, 1999 (Figs 1 and 2). An unusually large amount of precipitation fell in late August and early September in 1999, and both 1998 and 1999 had above the long-term mean precipitation in this area (Western Regional Climate Center).

**Table 1.** ANOVA results for midday photosynthesis and stomatal conductance (ln-transformed) shown in Fig. 3 (the model requires synthetic error terms)

Variable	df	Photosynthesis		Conductance	
		MS <sub>effect</sub>	F ratio	MS <sub>effect</sub>	F ratio
Drought treatment	1	4493.43	64.71***	5.69	41.23***
Plot (water treatment)	14	71.76	1.38	0.14	1.01
Size	1	2.27	0.04	0.64	4.64*
Drought treatment × size	1	65.46	1.28	0.13	0.91
Size × plot (drought treatment)	14	54.11	2.28**	0.15	2.24**
Date	5	252.73	10.65***	2.28	34.99***

Degrees of freedom indicated for numerator. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .



**Fig. 3.** Midday photosynthesis (a) and stomatal conductance (b) for plants in drought treatments and control plots that received ambient precipitation. Error bars  $\pm$  SE.

#### LEAF PHYSIOLOGY AND MORPHOLOGY

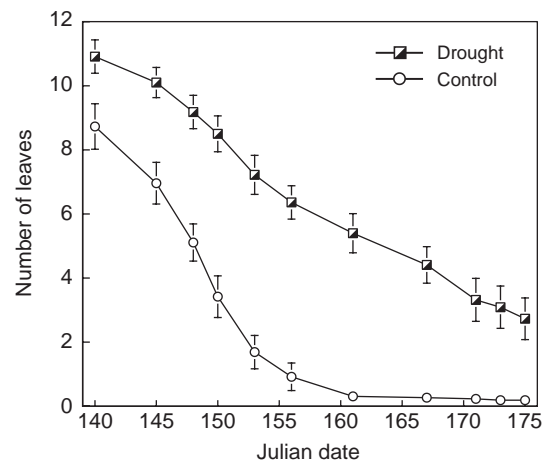
In 1999 the drought treatment reduced midday photosynthesis by 24% and stomatal conductance by 21%. ANOVA results for midday photosynthetic rates (Table 1; Fig. 3) showed highly significant effects of drought treatment and date. Plant size was not significant, but a significant plot  $\times$  plant size interaction indicates that photosynthesis varied with plant size in some plots. Conductance showed a similar pattern to photosynthesis (Table 1; Fig. 3), with significant differences between drought and ambient precipitation and among dates. Conductance also differed between plant size categories, with smaller plants having an overall 6% greater conductance. The plant size–plot

interaction term was also significant, indicating that plant size affected conductance more in some plots than in others.

Drought treatment affected both leaf area and leaf specific mass. Leaves on droughted plants were, on average, smaller ( $0.91 \text{ cm}^2$ ,  $\text{SE} = 0.075$ ) than leaves on control plants ( $1.28 \text{ cm}^2$ ,  $\text{SE} = 0.104$ ;  $F_{1,44} = 15.53$ ;  $P < 0.001$ ). Leaves were also smaller on small plants ( $0.80 \text{ cm}^2$ ;  $\text{SE} = 0.056$ ) than on large plants ( $1.39 \text{ cm}^2$ ,  $\text{SE} = 0.093$ ;  $F_{1,44} = 39.78$ ;  $P < 0.001$ ), but the plant size  $\times$  drought treatment interaction was not significant. Droughted plants had greater leaf specific mass ( $0.166 \text{ g cm}^{-2}$ ,  $\text{SE} = 0.004$ ) than controls ( $0.147 \text{ g cm}^{-2}$ ,  $\text{SE} = 0.005$ ;  $F_{1,44} = 9.75$ ;  $P < 0.01$ ). Leaf specific mass was also greater for small plants ( $0.165 \text{ g cm}^{-2}$ ,  $\text{SE} = 0.004$ ) than for large ones ( $0.147 \text{ g cm}^{-2}$ ,  $\text{SE} = 0.005$ ;  $F_{1,44} = 10.68$ ;  $P < 0.01$ ), but again the size  $\times$  drought treatment interaction was not significant.

#### LEAF DEMOGRAPHY

In 1998 flowering stalks produced under drought conditions began the census period with approximately two more leaves than controls (Table 2; Fig. 4). The results of ANOVA indicate time as a significant factor;

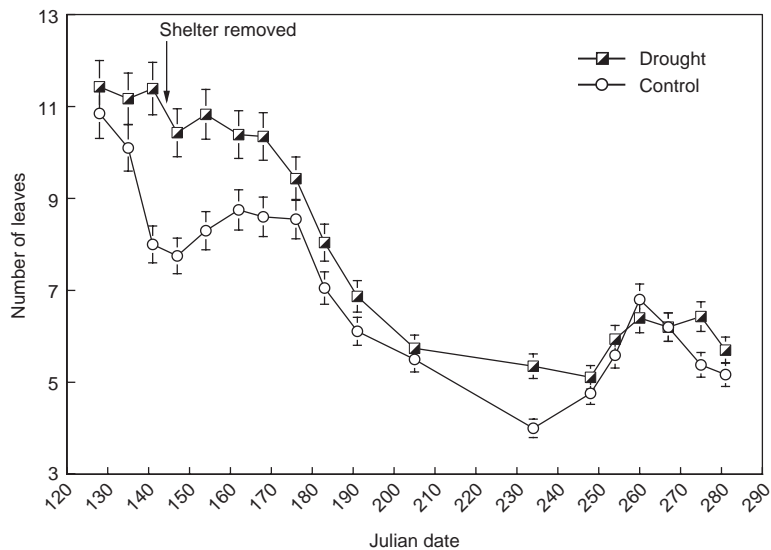


**Fig. 4.** Mean number of leaves ( $\pm$  SE) on flowering stalks for plants in the drought treatment and for controls throughout the 1998 growing season.

**Table 2.** ANOVA results for the standing leaf crop on flowering stalks in 1998 and on vegetative rosettes in 1999 (Figs 4 and 5)

Variable	Flowering stalks 1998			Rosettes 1999		
	df	MS <sub>effect</sub>	MS <sub>error</sub>	df	MS <sub>effect</sub>	MS <sub>error</sub>
Water treatment	1,4	403.48**	8.39	1,5	67.94*	7.08
Plot	4,38	25.53	22.36	5,31	16.58	11.55
Time	2,8	160.78***	0.93	3,15	160.58***	1.61
Drought treatment × plot	4,38	8.39	22.36	5,31	7.08	11.55
Drought treatment × time	2,8	16.63	4.68	3,15	8.09	2.52
Plot × time	8,76	0.93	2.10	15,93	1.61	1.83
Drought treatment × plot × time	8,76	4.68*	2.10	15,93	2.52	1.83

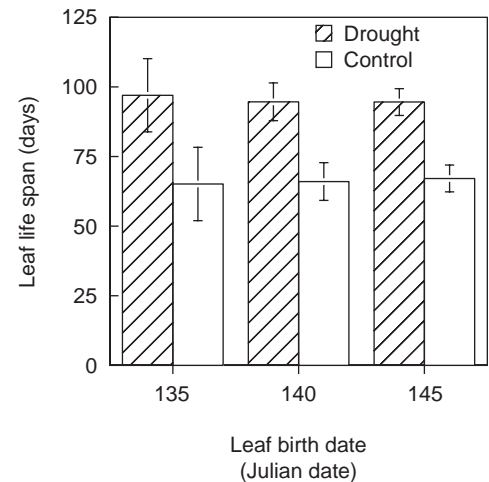
\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .



**Fig. 5.** Mean number of leaves ( $\pm$  SE) on vegetative rosettes for plants in the drought treatment and for controls throughout the 1999 growing season. Date of shelter removal is indicated.

leaf number declined as the season progressed. The drought treatment  $\times$  time interaction was nearly significant ( $P < 0.08$ ), reflecting a tendency for leaf number to decline more rapidly on control plants. By 10 June (Julian date 162), fewer than 10% of the leaves on the flowering stalks of controls still survived, while more than 50% of the leaves on flowering stalks of droughted plants were still living. Plot was not significant as a main effect, but a significant drought treatment  $\times$  time-plot interaction term suggests that the temporal decline in leaf number differed between plants receiving drought and ambient precipitation for some experimental plots.

Examination of leaf number through time for vegetative rosettes in 1999 indicates that more leaves were present on droughted plants than on controls throughout the period of most active plant growth (Table 2; Fig. 5). Leaf number per rosette differed between census dates, and the drought treatment  $\times$  time interaction was nearly significant ( $P < 0.06$ ), reflecting greater differences between treatments as the season developed. Leaf numbers increased modestly following rains on 25 May and 4 June (Julian dates 145



**Fig. 6.** Mean life span of leaves in the two water treatments ( $\pm$  SE). Julian dates 135, 140 and 145 correspond to the second, third and fourth censuses.

and 156; Figs 2 and 5) but more so for control plants than for droughted plants (Fig. 5). Early drought retarded the plants' ability to respond to rain in May and June. Standing leaf numbers increased following late-season rainfall, after Julian date 242, for plants in both treatments. Experimental plot was not significant as a main effect or as an interaction with any other factor.

During the growing season, control plants produced almost twice as many new leaves (after the initial cohort) as droughted plants. By 24 July (Julian date 205), rosettes on control plants had produced on average  $7.25 \pm 0.4$  (SE) new leaves since the first census, compared to  $4.17 \pm 0.36$  for droughted plants ( $F_{1,5} = 22.54$ ;  $P < 0.05$ ). Leaf production also differed among experimental plots ( $F_{5,31} = 2.77$ ;  $P < 0.05$ ).

Leaves present at the first census lived twice as long under the drought treatments (droughted plants =  $49.16 \pm 1.93$  days; controls =  $22.62 \pm 1.78$  days,  $F_{1,5} = 212.33$ ;  $P < 0.001$ ). For leaves that were first noted on one of the next three census dates, those on droughted plants lived roughly 1.5 times longer than those on controls (Fig. 6,  $F_{1,5} = 8.62$ ;  $P < 0.05$ ). Neither plot nor the plot  $\times$  treatment interaction was significant for either the first spring cohort or those produced subsequently.

## Discussion

Leaf demography and leaf size change in *C. flava* when unpredictable drought occurs early in the growing season, but not in ways that reduce transpirational surface area. The drought treatment induced physiological stress, as evidenced by depressed photosynthetic rate and stomatal conductance, but it neither hastened the senescence of individual leaves nor shortened the time that the leaf canopy was maintained on the plant. In fact, flowering stalks maintained leaves for longer under drought conditions. Droughted plants do produce smaller leaves, as found in other species (Larcher 1995), but the higher number of leaves per rosette compensates in total area for their smaller size. Perhaps of greater consequence to the plant, drought also reduces leaf turnover, which decreases the resources needed for new leaf construction. Lower rates of leaf construction are consistent with reduced photosynthetic rates and water uptake in droughted plants.

Longer leaf life spans appear to be associated with lower photosynthetic rates under a variety of environmental conditions that limit physiological performance and plant growth. Our results parallel the increased leaf life spans and decreased photosynthetic rates documented with shortages of nutrients and light (Ackerly & Bazzaz 1995; Kikuzawa 1988; Nilsen 1986; Shaver 1981). They are consistent with the prediction of Chabot & Hicks (1982) that long-lived leaves and a conservative photosynthetic strategy should prove beneficial in dry soils. An inverse correlation between photosynthetic rate and leaf life span also holds in interspecific comparisons, even across biomes (Reich *et al.* 1999). In terms of total carbon gain, a longer life span can compensate for a reduced photosynthetic rate, which should prove particularly beneficial if leaves support developing seeds, as they presumably do on the flowering stalks of *C. flava*.

Although few comparable data sets on drought-induced changes in leaf demography and photosynthetic performance exist for natural species, at least one drought-deciduous desert shrub also shows a trade-off between instantaneous photosynthetic rate and leaf longevity similar to the results presented here. In wetter soils, *Encelia farinosa* produces leaves that are larger, more glabrous, and have a larger photosynthetic capacity than those produced under drier, warmer conditions (Cunningham & Strain 1969; Smith & Nobel 1978). Sandquist & Ehleringer (1998) found that *E. farinosa* displayed less leaf pubescence and shed its leaf canopy sooner at the wettest of three geographically separate sites. Similarly, individuals growing on dry ridge tops show greater leaf retention and lower transpiration rates than do plants from adjacent washes (Monson *et al.* 1992).

Nevertheless, it is clear that leaf abscission is associated with dry soils, as it is in *C. flava* when leaves senesce in late summer. Other species with drought-

induced leaf abscission include some herbaceous crops and desert shrubs (Kozłowski 1973; Morgan *et al.* 1977; Orshan 1954). A study of the dioecious evergreen shrub *Pistacia lentiscus* across sites differing in annual precipitation found that leaf abscission increased with a reduction in soil moisture for males, but not for females (Jonasson, Medrano & Flexas 1997). Together with the formation of fewer new leaves, this resulted in a smaller standing leaf crop in drier sites and a negative correlation between standing leaf crop and water-use efficiency. Similarly, the desert shrub *Artemisia tridentata* combines an evergreen canopy with seasonally deciduous leaves (Miller & Shultz 1987). Large leaves with a high photosynthetic capacity are produced in early spring, but these leaves abscise as summer drought develops, leaving clusters of smaller, longer-lived leaves with lower photosynthetic rates.

Our study shows that unpredictable, early season drought produces different leaf demographic responses in *C. flava* than those observed as the soil dries predictably at the end of the growing season. Response to drought varies with plant ontogeny in some annual crops (Blum 1996), but for perennials the timing of drought relative to the normal initiation and cessation of plant growth may be more critical. That the timing of water stress can be a factor in leaf abscission was demonstrated in a study of the chaparral shrub *Lotus scoparius* (Nilsen & Muller 1981). In this species, drought increases leaf abscission and reduces total leaf number, but the effect is more pronounced under long-day conditions, typical of those near the end of the growing season. Nilsen & Muller (1981) argue that in the Mediterranean climate of southern California the dual control of drought and photoperiod avoids early season leaf senescence that would limit plants' ability to respond to later rain events. On the other hand, because summer drought is so predictable in these climates, leaf abscission under a long-day photoperiod reduces water loss without sacrificing much potential carbon gain.

Specific responses to drought, such as changes in leaf demography, need to be viewed within the context of the large suite of possible responses, potentially involving multifaceted changes in physiology, development and phenology (Blum 1996). Although we found no changes in leaf demography that would reduce water loss in *C. flava*, alternative water-conservation mechanisms are available to these plants. Droughted plants exhibit lower stomatal conductance and, following dry winters, larger plants reduce leaf surface area by producing fewer rosettes at the onset of growth in the spring (Casper 1996).

The developmental repertoire of *C. flava* includes plastic responses to improved soil water status as well as drought. This is evidenced by the number of new leaves produced following substantial rains in late August and early September, even though heavy precipitation so late in the growing season is unusual

(Forseth *et al.* 2001). Variability in precipitation and soil moisture is a ubiquitous form of temporal environmental heterogeneity, which is an important factor in the evolution of phenotypic plasticity (Schlichting & Pigliucci 1995). Temporal heterogeneity is particularly pronounced in arid environments because precipitation is so unpredictable (Fogel 1981). It is in just such environments that strong plastic responses to changes in soil moisture variation should be expressed.

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