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Source: Madroño, 68(4) : 360-365

Published By: California Botanical Society

URL: <https://doi.org/10.3120/0024-9637-68.4.360>

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CAUSES AND CORRELATES OF INTERANNUAL VARIATION IN FLOWERING OF
Calochortus plummerae (LILIACEAE)

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ABSTRACT

Calochortus plummerae Greene (Liliaceae) is a mariposa lily that is restricted to five counties in southern California. Although rarely observed in late seral chaparral during most years, it flowers abundantly after fires. In the spring of 2004, a population of *C. plummerae* was discovered in recently burned chaparral on the campus of California State University, San Bernardino. Long-term study plots were established to monitor year-to-year variation in flowering of *C. plummerae*, and to explore potential causes of this variation. We explored the relationship between annual precipitation and flowering of *C. plummerae*. We also examined the relationship between precipitation and growth of the strap leaf. Finally, we tested effects of experimental herbivory (leaf cutting) on current-year flowering. Flowering was monitored for 10 years, and leaf characteristics (leaf size and leaf loss to herbivory) were monitored for six years. During the driest year of our study, no plants flowered, but a substantial number flowered during wet years. Plants also produced narrower leaves during the driest years of the study. Leaf loss (experimental removal of most of a strap leaf) resulted in failure to flower. Overall, flowering between fires appears to be suppressed by factors that reduce current-year carbon gain: drought and leaf loss to herbivory. Although our data on herbivory were too incomplete to assess its importance in driving the dynamics of flowering in years after fire, the remaining two factors we studied (time since fire and annual rainfall) were sufficient to predict the number of *C. plummerae* plants that flowered each year.

Key Words: *Calochortus plummerae*, chaparral, fire, flowering, geophyte, herbivory, precipitation.

Calochortus plummerae Greene (Plummer's Mariposa Lily) is a geophyte of California chaparral that flowers abundantly after fire. It is endemic to five counties in southern California and has a California Rare Plant Rank of 4.2 ("plants of limited distribution; fairly threatened in California"; California Department of Fish and Wildlife 2021). It usually produces a single, basal strap leaf from an underground corm in the spring, which withers before the plant flowers. Flowering, if it occurs, takes place between May and July (Fiedler 2012). In years between fires, *Calochortus* species often remain in a vegetative state, putting up leaves in the spring (e.g., Christensen and Muller 1975; Keeley et al. 2006). Horton and Kraebel (1955), however, suggested that the corms of *C. plummerae* also become dormant as shrub cover increases in the years after fire, and that the plants produce leaves only in exceptionally wet years.

Fire-stimulated flowering is common among geophytes in Mediterranean climates, including that of *C. plummerae*'s range, and flowering of some species is more tightly restricted to post-fire years than that of others (Stone 1951; Horton and Kraebel 1955; Christensen and Muller 1975; Keeley et al. 1981; Le Maitre and Brown 1992; Rundel 1996; Lamont and Downes 2011). Factors that may contribute to this post-fire bloom include reduced competition for resources (light, nutrients, and water), release of soil nutrients by fire, reduced herbivory, and, potentially, stimulatory effects of smoke on flowering (Christensen and Muller 1975; Keeley 1993; Light et al. 2007; Borchert and Tyler 2009). Furthermore, flowering

itself may deplete energy reserves, contributing to low growth rates and low incidence of flowering after the post-fire bloom (Tyler and Borchert 2003; Borchert and Tyler 2009). In years between fires, geophytes may grow vegetatively or their underground organs may become dormant for some period (Keeley and Davis 2007).

In the fall of 2003, multiple wildfires burned a large fraction of *C. plummerae*'s range, providing an opportunity to study plant fate and phenology in the years following fire. The largest of these were the Simi Fire, the Old Fire, the Grand Prix/Padua Fire, which together burned over 105,000 ha across Ventura, Los Angeles, and San Bernardino Counties (Clark et al. 2003). Prolific flowering of *C. plummerae* the following spring made it apparent that the species was not as rare as had previously been believed. Among the newly discovered populations of *C. plummerae* that year was one on the campus of California State University San Bernardino, a campus that partially burned in the Old Fire (Williams et al. 2006).

The primary goals of this study were to quantify changes in flowering of *C. plummerae* in the years following fire, describing the degree to which flowering was restricted to the post-fire environment, and to explore correlates of interannual variation in flowering (in particular, variation in rainfall). Three years into the study, however, we expanded the focus to measure plant survival, potential dormancy, interannual variation in leaf size, and herbivory. We did not measure seedling recruitment because we could not distinguish seedlings of *C. plummerae* from

seedlings of *Calochortus splendens* Douglas ex Benth., which was also present on the site (Williams et al. 2006). Flowering was monitored for 10 years and vegetative characteristics (leaf emergence, leaf size, and leaf loss to herbivory) were monitored for six years. We explored the relationship between annual precipitation and flowering of *C. plummerae* plants, we documented year-to-year variation in the size of the strap leaf produced (specifically, leaf width), and we tested effects of reducing leaf area (experimental herbivory or leaf clipping) on current-year flowering.

METHODS

Flowering, Survival and Dormancy

In June 2004, we established three 5 m × 5 m plots on Badger Hill, an outcrop of Pelona schist surrounded by alluvium (Miller and Matti 2001), on the campus of California State University San Bernardino (34.186°, -117.315°). We sited plots so that each contained a large number of plants of *Calochortus plummerae*. Plots were located along ridges and on northeast-facing slopes, at elevations of 540–565 m. We mapped all individuals of *C. plummerae* in the plots and marked each with a small colored stake located 5 cm to the east of each plant (or in another direction when rocks precluded stake insertion). We censused plants between May and June every year for 10 years to determine if they had produced a flowering stalk that year. New individuals that flowered over the course of the study were also marked and mapped.

In 2007, to better assess plant survival and dormancy, we began censusing plants twice a year: once during the flowering season, as described above, and once earlier in the season (March or April). Leaves were still alive during the earlier census, but generally dead and/or missing during the later census. Censusing twice allowed us to detect plants that produced leaves but did not flower.

Relationship of Flowering to Rainfall and Time Since Fire

We explored the effect of annual precipitation on flowering of *C. plummerae* by using a multiple regression approach that modeled flowering as a function of annual precipitation and time since fire. The number of plants flowering (pooled data from the three plots) was regressed against total precipitation received during the preceding year (July through June) and a function of time that described how flowering decreased after the initial post-fire bloom. We used precipitation records from a weather station in Redlands, California, approximately 20 km southeast of the study site, due to the incomplete nature of precipitation records closer to the study site (NOAA 2020). One month of precipitation data was missing from the Redlands record, so it was estimated from the rainfall patterns observed at

nearby stations. To validate the model, flowering data was taken periodically after the study (in 2014, 2016, and 2019) and compared to model predictions. Regression analyses were performed with JMP statistical software (JMP Pro 15.0.0, SAS Institute Inc., Cary, NC).

Interannual Variation in Leaf Size and Herbivory

During the early-season surveys we mapped and marked all newly encountered *Calochortus* plants in the plots. Those too small to flower were identified to genus only, because *Calochortus splendens* also occurred in the area (Williams et al. 2006) and was difficult to distinguish from *C. plummerae* prior to flowering. We measured the strap leaves of all *Calochortus* plants (length and width) and noted any herbivore damage to the leaves. Herbivory that left less than 3 cm of leaf length was arbitrarily scored as “severe” herbivory for the purposes of quantifying year-to-year variation in herbivore damage. Apart from 2009, when we missed the early-season survey, these surveys were conducted from 2007 to 2013.

Effect of Simulated Herbivory on Flowering

To determine the effect of herbivory on flowering of *C. plummerae*, we simulated herbivory by clipping leaves. On 17 February 2013, 24 plants with large strap leaves (>1.0 cm in width, median length ~ 46 cm) were located along the ridges of Badger Hill. We caged half of the plants with hardware cloth (16 mm mesh) to prevent herbivory, and we clipped the strap leaves of the other half to simulate herbivory. Leaves were clipped to a length of 3 cm. Plants were assigned to treatments in a stratified-random manner based on leaf size: plants were matched by leaf width then assigned at random to either the control or clipping treatment. All plants were mapped and marked with a large nail inserted 3 cm east of the plant. Plants were censused on May 10 to determine whether they had flowered or not. The effect that clipping had on the probability of flowering was tested with a Fisher’s exact test.

RESULTS

Flowering, Survival and Dormancy

As expected, the number of *C. plummerae* plants flowering was highest in the first year after fire (Fig. 1A). Year to year variability was high. Flowering completely failed in the driest year (the 2006–2007 season) but reached a level equivalent to 27% of the post-fire bloom eight years after fire (in 2011; Fig. 1A). Plants that bloomed in 2004, right after the fire, constituted a smaller and smaller fraction of the blooming population as the years passed, but one survivor still bloomed in 2013 (Fig. 1A).

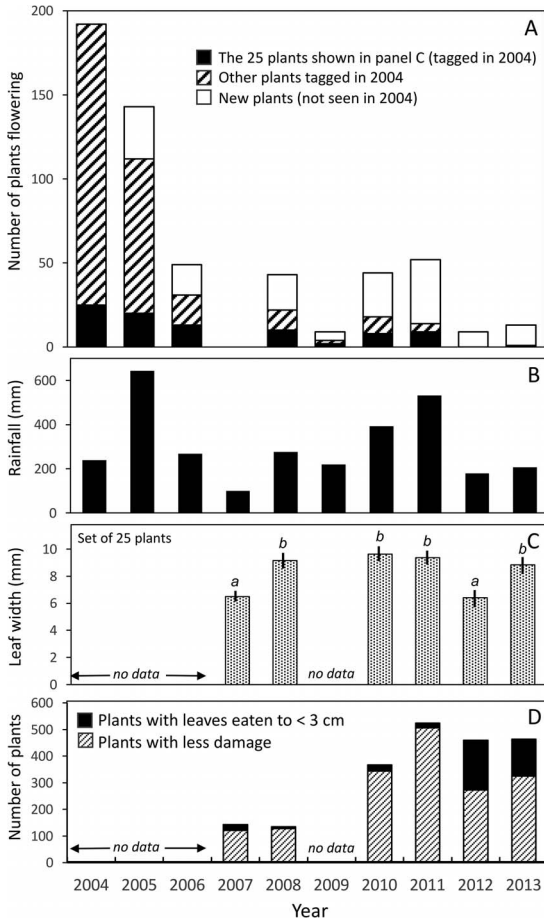


FIG. 1. Year-to-year variation in plant performance (flowering and leaf width) and potential controlling factors (rainfall and herbivory). A. Total number of *C. plummerae* plants flowering in plots. Stacked bars show flowering plants that were originally marked in 2004, separating the set of 25 plants included in the leaf-width analysis (black bars) from others (hatched bars), and flowering plants that were new, or not encountered in 2004 (white bars). B. Rainfall from July of the previous year through June at Redlands, CA. C. Leaf width (mean \pm SE) of 25 individuals for which measurements were available from every census. Bars labeled with the same letter were not significantly different from each other according to multiple pair-wise t-tests with a Bonferroni correction. D. Number of plants of *Calochortus* spp. that experienced severe herbivory (leaving < 3 cm of leaf length; solid bars) and those that experienced less severe or no herbivory each year.

Thirty percent of the originally marked plants were observed in 2013, having survived at least 10 years. The fraction of the originally marked population that produced a leaf during the six years with early-season surveys (i.e., were neither dead nor dormant) ranged from 25% to 30% (25% in 2007, 28% in 2008, 32% in 2010, 31% in 2011, and 30% in both 2012 and 2013). Approximately 60% of the

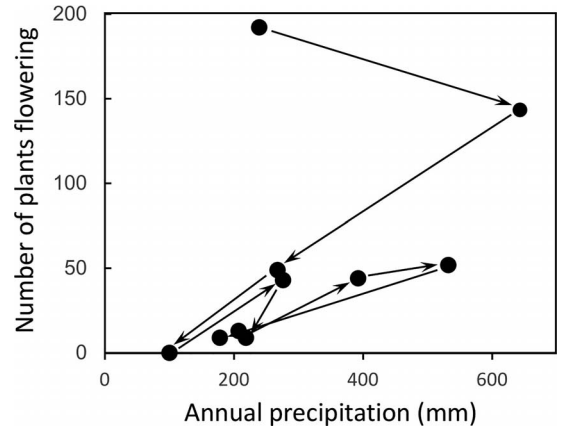


FIG. 2. Relationship between annual rainfall (July–June) and number of *C. plummerae* plants flowering in plots at the end of the season (late May to early June). Arrows indicate the trajectory over time, from the number of plants flowering in 2004 (top) to the number flowering in 2013 (bottom).

originally marked plants were not observed at all during the last seven years of the study and were, therefore, presumed dead. The remaining 10% were not observed during the last year of the study, but we could not determine whether they were dead or merely dormant.

Of those plants that were found in the last year of the study, only 58% were observed above ground every year during the six years with early-season surveys. The rest were not observed during some years, reappearing after a one year “absence” (28%) or an “absence” of two or more years (14%). These “absent” survivors were either dormant, or their leaves were eaten so early and so thoroughly that they could not be detected.

Flowering and Rainfall

The statistical effect of rainfall on flowering only became significant when a second factor was included in the model to account for the stimulatory effect of fire. Annual rainfall varied widely over the course of the study, ranging from 100 mm in the 2006–2007 season to 643 mm in 2004–2005 (Fig. 1B). The number of plants that flowered in a year was not well predicted by annual rainfall alone ($R^2 = 0.22$, $P = 0.17$). However, examination of the trajectory of flowering over the years suggested that flowering did increase with rainfall, but that the effect decreased over time (Fig. 2). A multiple-regression model that incorporated both rainfall and an asymptotically decreasing effect of time since fire yielded a good estimation of the number of *C. plummerae* plants flowering in our plots over the 10 years of this study ($R^2 = 0.98$, adjusted $R^2 = 0.97$, $P < 0.001$). It also predicted increased flowering in a subsequent wet year (28 plants in 2019) fairly closely (Fig. 3). The equation obtained was

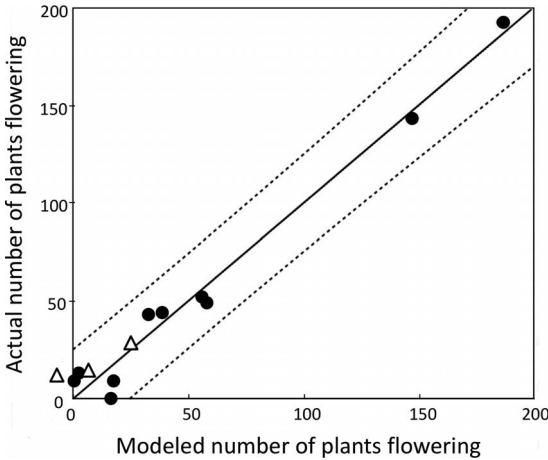


FIG. 3. Number of plants flowering vs. model estimate based on precipitation and time since fire. Closed circles represent data used to form the model, and the dotted lines represent the 95% prediction interval for those data. Triangles represent data taken later, in 2014, 2016, and 2019. Unrealistic predictions of negative numbers of plants flowering in dry years was the result of the model being a simple regression model with a negative intercept, rather than a biological or mechanistic model.

$$F = 0.148R + \frac{199}{T} - 48$$

where F was the number of *C. plummerae* plants flowering in plots, R was the annual rainfall the preceding year (mm), and T was time since fire in years, with year one being the spring following fire. Both rainfall (t-test, $t = 6.97$, $P < 0.001$) and the inverse of time since fire (t-test, $t = 15.37$, $P < 0.001$) contributed significantly to the predictive capacity of the model.

Interannual Variation in Leaf Size and Herbivory

The size of the leaf produced by a plant varied from year to year (Fig. 1C). Since leaf length was often affected by herbivory, we took leaf width as a better measure of the size of leaf that was produced by a plant. Furthermore, to focus on year-to-year variation in the leaf widths of the same individuals, we only used data from *C. plummerae* plants for which we had adequate leaf-width measurements from every early-season census (i.e., not grazed below the widest part of the leaf). Only 25 plants met this criterion. The leaf widths of these plants varied significantly among years (repeated measures ANOVA, $F_{(5,120)} = 15.95$, $P < 0.001$). Average leaf width of these individuals was not well predicted by a simple regression model based on annual rainfall ($R^2 = 0.59$, $P = 0.07$). However, plants produced significantly narrower leaves during the two driest years (post-hoc pairwise t-tests on square-root-transformed data to improve normality with a Bonferroni-adjusted alpha level of 0.0033 (0.05/15); Fig 1C).

Leaf damage by herbivores also varied substantially over the 6 yr it was measured. Among all *Calochortus* plants in our plots, including those identified only to genus, severe herbivory (scored as herbivory that left 3 cm or less of leaf length) ranged from 3% in 2011 to 41% the following year (Fig. 1D). Although insect herbivory (small bites, often along the edges of a leaf) was apparent throughout the study, damage scored as severe herbivory was usually the result of straight cuts and likely the work of small mammals. Both rabbit scat and rodent activity (soil disturbance) were observed in the plots.

Effect of Simulated Herbivory on Flowering

Simulated herbivory (leaf clipping) in February 2013 had a dramatic effect on flowering later the same spring. Four experimental plants could not be found in May, including three plants that had had their leaves clipped and one that had been caged. Of the 11 caged plants that were found, ten produced flowering stalks. Of the nine clipped plants that were found, none produced flowering stalks. This difference was highly significant (Fisher's exact test, $P < 0.0001$).

DISCUSSION

Flowering of *Calochortus plummerae* was not completely restricted to the first year or two immediately after fire, but flowering declined substantially after the initial post-fire bloom. After the second year post-fire, the density of flowering plants did not exceed 27% of that observed immediately after fire. The mechanisms responsible for both the post-fire bloom and the decrease in flowering over subsequent years were not addressed in this study but most likely include changes in plant competition. Competition was very low the first year after fire, with plots supporting only sparse growth of annual plants and very small resprouts of chaparral shrubs (primarily *Adenostoma fasciculatum* Hook. & Arn.). Although chaparral recovery was not formally measured, it followed a typical trajectory. *Acemison glaber* (Vogel) Brouillet, a rapidly growing subshrub, dominated some areas with cover peaking the third year after fire (2006). The crowns of *Adenostoma fasciculatum* continued to increase in size throughout the study, and their heights surpassed those of the faster-growing *Salvia* species (*Salvia mellifera* Greene and *Salvia apiana* Jeps.) by the fifth or sixth year of the study. Although changing competition from shrubs and subshrubs may have played a major role in the asymptotically decreasing trajectory of flowering in *C. plummerae* over the years, we cannot rule out other factors. "Time since fire" subsumed all changing factors related to post-fire recovery, allowing us to test effects of factors unrelated to fire cycles, such as variation in rainfall.

Flowering of *C. plummerae* was well predicted by annual rainfall once the overall effect of "time since fire" was factored out. This was true both at a

population level and when individual plants were followed (Fig. 1A). The set of 25 plants that consistently had measurable leaves during early-season surveys produced narrower leaves and were less likely to flower during dry years than during wetter years. Increased plant dormancy may have contributed to low flowering during dry years, but data supporting increased dormancy during dry years was weak. The fraction of the originally marked population that was active (produced a leaf) in years with early-season censuses only ranged from 25% to 32%. Even during the driest year of the study (2007), a quarter of the originally marked plants produced leaves. Plant dormancy, therefore, could not account for the complete lack of flowering that year.

Over the 10 yr of the study, there was substantial turnover in the population that flowered. A large fraction of the originally marked population (60%) was not observed at all during the last 7 yr of the study. These plants were either very deeply dormant or dead. We assumed, however, that they were dead. Studies of bulb dormancy in other *Calochortus* species have found either little evidence of dormancy (e.g., Fiedler 1987; Fredricks 1992) or a pattern similar to the pattern we found for *C. plummerae*, with the largest fraction of apparently dormant plants producing leaves after a dormant period of only one year, a smaller fraction producing leaves after a dormant period of 2 yr, and an extremely small fraction producing leaves after a dormant period of three or more years (Miller et al. 2004). The fact that more than a quarter of our originally marked plants put up leaves every year or skipped periods of only one year make it unlikely (although possible) that other individuals experienced such deep dormancy that they failed to produce leaves for 7 yr in a row. As years went by, new individuals began to flower. After 7 yr, the originally marked plants accounted for less than half of the flowering population.

The fact that leaf area removal (simulated herbivory) eliminated flowering later the same year suggests that flowering in this species is largely dependent on current-year carbon gain. There is good evidence that carbon gain in prior years and the size of the underground storage organ influence flowering of various other geophytes (e.g., Dafni et al. 1981; Tyler and Borchert 2003; Schlising and Chamberlain 2006; Borchert and Tyler 2009). Moreover, the flowering of some geophytes appears to exhaust their reserves to the extent that they grow more slowly, remain dormant, or fail to flower the following year (Eggert 1992, Tyler and Borchert 2003; Lesica and Crone 2007). Tyler and Borchert (2003) suggested that a decline in flowering of some geophytes in the years following the first post-fire year may be due, in part, to the depletion of storage reserves caused by the post-fire flowering, itself. We did not see patterns in our flowering data to suggest that the act of flowering exhausted reserves of *C. plummerae* plants to such an extent that they failed to flower the next year. In fact, a few individuals

flowered 3 yr in a row between the fifth and tenth years after fire. The dynamics of carbon gain and depletion in prior years may play a role in the flowering of *C. plummerae*, but our data suggest that current-year carbon gain is a critical determinant of flowering in this species. The pattern of increased flowering in wet years and in the period after fire (with consequently higher levels of soil nutrients and lower competition for light and water) is consistent with effects of increased resources on carbon gain and with the observation that flowering is dependent on current-year carbon gain.

Although resources released by fire may largely account for prolific flowering after fire, large fires can also reduce herbivory (Christensen and Muller 1975; Barro and Conard 1991). Patterns of herbivore damage on *C. plummerae* at our site suggested that mammalian herbivores were responsible for most instances of severe herbivory. This observation is consistent with those of Fiedler (1987) who noted that the most damaging herbivory on four *Calochortus* species that she studied along the central California coast was caused by small mammals (several rabbit species and pocket gophers) and by mule deer. While burrowing animals may survive fires, large fires have been reported to cause heavy mortality among herbivores such as brush rabbits (replaced by desert cottontails at our site) and California ground squirrels (Chew et al. 1959; Quinn 1990; van Mantgem et al. 2015). Mule deer may die in fires (Chew et al. 1959) but often flee fire and recolonize the area in the years after fire (Quinn 1990; van Mantgem et al. 2015). Therefore, herbivore damage to *C. plummerae* plants at our site may have lowest in the years immediately following fire, before we began monitoring it.

One apparent paradox in our findings was that herbivory had a strong effect on flowering, and severe herbivory varied among years, but we did not need to include herbivory in the model to obtain a good prediction of flowering. Since herbivore populations have been shown to respond to both fire and rainfall, usually in complex and species-specific ways (e.g., Christensen and Muller 1975; Barro and Conard 1991; Holmgren et al. 2001; van Mantgem et al. 2015) it is possible that impacts of herbivory on flowering were subsumed under either the "time since fire" effect or the "rainfall" effect.

Regardless of the causal mechanisms, we found interannual patterns of flowering in *Calochortus plummerae* that were consistent both with fire-promotion of flowering and with flowering that was controlled increasingly by direct or indirect effects of precipitation during the fire-free interval. Flowering was eliminated during severe drought, and this flowering failure occurred despite the continued presence of non-dormant plants on the site. Although high rainfall during the fire-free interval appeared to stimulate flowering of *C. plummerae*, the density of flowering plants in this recovering

shrubland vegetation was rarely more than a quarter of that found during the initial post-fire bloom.

ACKNOWLEDGMENTS

We would like to thank the many people who were involved in this study over the years. Among them are Larry Westrick, Kenneth Jacobs, Janelle Williams, Yolanda Osorio, George Walker, Sarah Westrick, Sam Westrick, Kimberly Spahn, and several others without whom this work would not have been possible. We are indebted to an anonymous reviewer whose comments greatly improved this paper.

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