



Reproduction and growth of the chaparral geophyte, *Zigadenus fremontii* (Liliaceae), in relation to fire

Claudia Tyler^{1,*} and Mark Borchert²

¹Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA; ²Los Padres National Forest, Ojai, CA 93023, USA; *Author for correspondence (e-mail: tyler@lifesci.ucsb.edu; phone: +1 805 455 5711; fax: +1 805 893 2578)

Received 2 October 2000; accepted in revised form 4 April 2001

Key words: Bulb, Fire-dependent reproduction, Fire-induced flowering, Long-lived, Postfire, Seedling establishment

Abstract

Zigadenus fremontii is often a striking component of the flora following fire in the chaparral. Like other geophytes, it produces large numbers of flowers in the first spring after a burn. Although these plants are most conspicuous in the early postfire environment, the question that remains is, how do they persist in the interval between fires? To address this we investigated differences in the growth and reproduction of *Z. fremontii* in burned and unburned chaparral. We monitored marked individuals for nine years at three sites: two that were burned in 1990 and one in the same area that was in unburned mature chaparral. We measured leaf area, and production of flowers and fruits. We also conducted seed experiments in the field to determine the rates and timing of germination. We found that reproduction occurs only in the immediate postfire period: flowering and production of fruits and seeds in the first year following fire, and seedling establishment by year 3. There was a cost of reproduction; plants that flowered (in the burn area) had negative growth rates the following year. In contrast, plants in unburned chaparral, which did not flower, had positive growth rates over the same period. Moreover, plants that produced the most flowers had the lowest growth rates. In the unburned chaparral site, plants were not dormant as predicted from previous literature; instead they produced leaves nearly every year. In most years the average leaf area per plant was greater than that in the burned sites. Our results indicate that postfire reproduction depends on growth and carbohydrate storage in the inter-fire period. We also suggest that this species is relatively long-lived for a herbaceous perennial.

Introduction

Plant species found in environments with periodic fires possess a wide-range of life history strategies that allow them to persist. One such plant group, which has not been well studied, is geophytes, perennial herbaceous plants whose overwintering buds are below the soil surface (Raunkiaer 1934). Geophytes survive fire because their bulbs, corms, or rhizomes are buried deeply enough that they are not killed by high soil surface temperatures. These perennial herbs are present in the first year following fire as resprouts (Keeley and Keeley 1988).

Although found in a variety of habitats throughout the world, geophytes occur in the greatest diversity in Mediterranean plant communities, including California chaparral (Rundel 1996). Here they form a striking component of the postfire “bloom” because nearly all species flower profusely in the first spring after a burn (Horton and Kraebel 1955; Keeley et al. 1981; Le Maitre and Brown 1992). As the shrub canopy closes over time, these plants remain in the understory, unlike most other postfire herbaceous species. They may flower sporadically, but it has been suggested that in the mature community geophytes probably decline in productivity and may go dormant (Keeley and Keeley 1988; Parker and Kelly 1989).

However, to our knowledge, field studies on the behavior of these plants in the interval between fires have not been done. Previous studies on herbaceous perennials have focused on the early postfire period ((Sweeney 1956; Keeley et al. 1981), but see Borchert (1989)).

Zigadenus fremontii Torr. (Liliaceae) is conspicuous in postfire chaparral. This synanthous geophyte (common name, Star Lily or Chaparral Zygadene) produces basal leaves and a tall flowering stalk in the first spring after fire. During the summer dry period, the aerial portions of the plant die back to underground bulbs; new basal leaves resprout in the subsequent wet season (generally annually). The pattern of postfire reproduction has been described for chaparral geophytes in general. Keeley (1994) describes geophytes as “disturbance dependent recruiters” because seeds are produced following fire; whether reproduction is obligately or facultatively fire dependent is unknown for this species or other chaparral geophytes. Thus, the current thought is that growth and reproduction occur in the immediate postfire period, with little occurring in the decades between fires. In order to test this assumption, we examined differences in growth and reproduction of *Z. fremontii* in burned and adjacent unburned chaparral, and monitored plants for nine years to determine the patterns of temporal variation in these attributes.

Methods

Research was conducted in the Santa Ynez Mountains, 10 km northwest of Santa Barbara, California (34°29' N, 119°46' W; elevation 360 m). Approximately 1700 hectares of chaparral in the Santa Ynez mountains burned in a wildfire on June 27, 1990. Our three study sites were located within the burn perimeter. Dominant shrub species at these sites were *Ceanothus megacarpus*, *Adenostoma fasciculatum*, *Cercocarpus betuloides* and *Heteromeles arbutifolia*. All sites were moderately steep with slope angles from 5° to 25°. The area burned last in a wildfire in 1964. The climate is Mediterranean, with hot, dry summers and cool, wet winters. Mean annual rainfall is 681 mm. Annual precipitation for the years 1990 – 1999 ranged from 290 mm to 1499 mm (Figure 1).

To compare postfire growth and reproduction of *Z. fremontii* to that in unburned mature chaparral, we selected two sites in the burn, and one site in an extensive unburned patch of chaparral. (This patch did

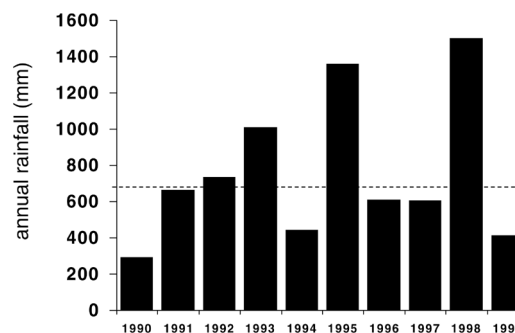


Figure 1. Annual rainfall during the study period. Dashed line represents the mean annual rainfall from 1951 to 1999. (Data from the Santa Barbara County recording station #395, elevation 365m, approximately 2 km from the study sites.)

not burn due to erratic fire behavior, not because of differences in vegetation type or age.) One of the sites that burned (BURN 1) had a predominately north/northwest aspect (320°). The other two sites (BURN 2 and UNBURNED) were on two adjacent ridges, and were approximately 1 km west of the first site; these two sites had predominately south/southwest aspects (200°).

Density of *Z. fremontii* varied among the three sites. BURN 1 (north-facing slope) had the lowest density (0.2/m²), BURN 2 (south-facing slope) the highest density (5.0/m²), and UNBURNED was intermediate (0.5/m²). At each site we marked 60 individual plants. In two of the sites (BURN 1, UNBURNED), where the plants were relatively widely spaced, we marked all the plants in the single large patch where they occurred (126 m², and 270 m², respectively). In the third site (BURN 2), where plant density was high, we selected plants randomly within the larger patch (812 m²). Individuals were marked by placing a metal stake with a numbered tag 9 – 15 cm downhill from the plant; distance and compass direction from the stake to the plant were recorded for each individual. We monitored the plants each spring from 1991 – 1999. Vegetative characteristics recorded included number of basal leaves, basal leaf lengths and maximum widths, and whether or not the leaves had been grazed. (The term “basal” is used to distinguish between the primary leaves and the few short leaves that are found on flowering stalks.) These measurements were taken in the late spring, just before leaves started to senesce and thus were as close as possible to the maximum leaf size reached each year. We estimated leaf area as leaf length times maximum width. Using leaves from unmarked plants, we deter-

mined that estimated area (leaf length \times maximum width) correlated well with actual leaf area ($y = 0.68x$; $n = 141$, $r^2 = 0.99$, $P < 0.001$).

Annual relative growth rates were calculated as: $\log(\text{basal leaf area}_{yr\ 2}) - \log(\text{basal leaf area}_{yr\ 1})$. Our assumption in calculating growth rates is that leaf area is positively correlated with bulb size, and thus leaf area is an index of total plant size. Previous workers have demonstrated a positive relationship between bulb mass and basal leaf area for *Zigadenus fremontii* (D. C. Odion, unpublished data), for *Z. nuttallii* in both burned and unburned sites (Knapp 1986), and in other geophyte species (Fiedler 1987; Boeken 1989; Snow and Whigham 1989).

We also recorded flower stalk (raceme) height; number, length and width of flower stalk leaves; number of flowers; and number and length of fruit pods. To estimate the number of seeds produced per plant, we collected ripe fruits from unmarked plants to determine the relationship between fruit length and seed number ($y = 1.52 * e^{1.28x}$; $n = 285$, $r^2 = 0.65$, $P < 0.001$).

We also conducted experiments in the field (at site BURN 1) to determine timing and rates of seed germination. Fifteen 26 cm \times 26 cm \times 3.5 cm open "boxes" were constructed of redwood lathe and partitioned into four equal-sized quadrats with interior dimensions of 11.5 cm \times 11.5 cm. Plastic window screen was attached to the bottom of each box to hold soil but to allow for drainage. Soil collected from the site was microwaved on high intensity for 20 minutes to kill any seeds and then was spread into each quadrat to a depth of 3.0 cm. In October 1991, four months after natural seed dispersal, fifty *Z. fremontii* seeds were sown at a depth of 1.0 cm in each quadrat (200 seeds per box). The boxes were placed in a transect 1 m apart on a gentle ($< 5^\circ$), north-facing slope above the site. Seedlings were counted in April 1992. Soil from one randomly chosen quadrat per box was collected in October 1992 and in July 1994 and examined for intact seeds, empty seed hulls, and bulbs. To determine germinability of the remaining intact seeds, these were sown in potting soil and placed in a laboratory germinator at 25 $^\circ\text{C}$ in continuous light until germination was complete.

Since two sites were within a single burn area and the other site in a single unburned patch, inferences about the effects of fire are unavoidably based on pseudoreplication (Hurlbert 1984). Thus, statistical analyses comparing sites were not performed.

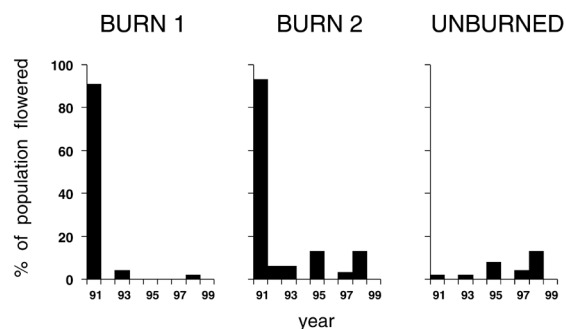


Figure 2. Variation in flowering, among sites and years. Shown is the percentage of plants in the sample population that produced a flowering stalk in a given year at each site.

Results

Reproduction

In 1991, the first year after fire, there was abundant flower, fruit, and seed production at the burn sites. At BURN 1, plants produced an average of 15.1 fruits (s.e. 3.1) and 142.6 seeds per plant (s.e. 28.9). At BURN 2, where plants were larger, the average was 27.7 fruits (s.e. 3.4) and 336.9 seeds per plant (s.e. 48.3). However, reproduction (i.e., seed production) was essentially confined to the first year after fire (Figure 2). In 1991, 90% of the plants in the burn areas produced large flowering stalks, fruits and seeds. In contrast, flowering occurred only rarely in the unburned site or in subsequent years in the burned areas. At these other times, when plants did produce a flowering stalk, these often did not develop, nor did the plants produce seeds.

Flower production increased with plant size (Figure 3; linear regression of $\log(\text{no. of flowers per plant})$ vs. $\log(\text{basal leaf area})$: BURN 1: $r^2 = 0.97$, $P < 0.001$; BURN 2: $r^2 = 0.99$, $P < 0.001$). Similar significant relationships were observed for other reproductive characters including number of fruits and number of seeds. These relationships were all non-linear; that is, a steep increase in flower, fruit and seed production occurred with plants whose leaf area was greater than 100 cm^2 .

Results indicate that there was a cost of reproduction in terms of plant growth. Plants that produced the most flowers (and fruits and seeds) in 1991 had the lowest relative growth rates between 1991 and 1992 (Figure 4; BURN 1: $y = -0.004x - 0.212$; $r^2 = 0.55$, $P < 0.001$. BURN 2: $y = -0.002x - 0.299$; $r^2 = 0.29$, $P = 0.001$). Comparing relative growth rates at each burn site of plants that produced above vs. below the

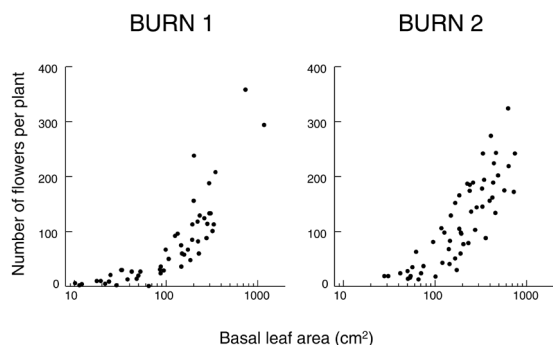


Figure 3. Relationship between leaf area (log) and number of flowers produced in the first spring following the fire in burned populations of *Zigadenus fremontii*.

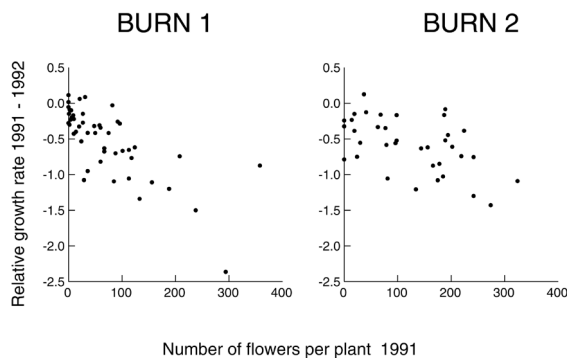


Figure 4. Relationship between flower production and relative growth rate ($\log(\text{basal leaf area}_{\text{yr } 2}) - \log(\text{basal leaf area}_{\text{yr } 1})$).

median number of flowers in 1991, we found that, on average, individuals that produced above the median number of flowers in 1991 had significantly lower relative growth rates than the plants that produced the fewest flowers (Table 1). In addition, in comparing growth rates for plants in burned vs. unburned areas, we found, contrary to our expectations, that plants in the two burn sites had negative growth rates, whereas plants in the unburned site had higher, positive growth rates (Table 1).

Vegetative growth

The number of leaves produced and leaf area per plant varied among sites and years (Figure 5). The most striking pattern was that, while the two burn sites were similar to each other, plants in the unburned chaparral had the greatest number of leaves and the greatest leaf area. In 1992, two years after fire, plants were smaller (BURN 1: number of leaves 2.6, s.e. 0.1; basal leaf area 38.9 cm², s.e. 5.4. BURN 2: number of leaves 3.2, s.e. 0.2; basal leaf area 70.1

cm², s.e. 10.8) compared to the unburned site (UN-BURNED: number of leaves 5.3, s.e. 0.4; basal leaf area 447.0 cm², s.e. 56.8). Also noteworthy was the finding that in the burn areas, leaf area and number of leaves per plant was high in the first year, but was lower in nearly all subsequent years (Figure 5). Particularly striking was the decline in leaf area and number of leaves between 1991 and 1992 in the two burn areas (Figure 5). With the exception of the first year, the pattern of variation in leaf area at all sites was similar – some years all sites had high leaf areas relative to other years. Comparing leaf area among sites for all years, we found that leaf area was highly correlated among sites (Table 2).

We examined the frequency of resprouting at each site (Figure 6). A high proportion of plants resprouted nearly every year of the study period at all sites. However, not all plants resprouted every year; in some years (e.g., 1994 in all sites) only a small proportion of the study population had resprouted. Contrary to expectation, we found that in unburned chaparral resprouting was common; nearly 80% of the marked plants resprouted in 7 of the 9 years of the study period (Figure 6).

Several factors may affect variation in leaf area or resprouting among years. Grazing by herbivores varied markedly among years (Figure 7). Beginning in the fourth year following the fire (1994), we observed an abundance of small rabbit scat (probably *Sylvilagus* sp.) at all sites, particularly in the burn areas. In 1994 at BURN 2, and in 1999 at BURN 1, when rabbit scat was especially dense, many plants were not present, and we found uneaten leaves that were completely cut off near where marked individuals should have been found. However, we did not detect relationships between growth of *Zigadenus* and either precipitation or grazing. There were no significant relationships between leaf area or proportion of population resprouting, and the rainfall of the current or previous year, nor the proportion of population grazed in the current or previous year at any site ($P > 0.10$ for all.)

Seed germination

Out of 50 sown seeds, there was an average of 4.6 (s.e. 1.6) seedlings per quadrat in Spring of 1992. This was likely an underestimate of seedling emergence; we observed large rabbit scat (probably from *Lepus californicus*) both in and around the seed boxes, so newly emerging seedlings may have been

Table 1. Annual relative growth rates of plants that produced above vs. below the median number of flowers per site in the first year after fire, and all plants at a site. Relative growth rates calculated as $\log(\text{basal leaf area}_{\text{yr2}}) - \log(\text{basal leaf area}_{\text{yr1}})$. Data are means per site (plus 1 s.e.).

	Median # flwrs produced per plant	Relative Growth Rate (1991 – 1992)		All plants
		ABOVE median # flwrs produced	BELOW median # flwrs produced	
BURN 1	49	-0.79 (0.10)	-0.27 (0.06)	-0.53 (0.07)
BURN 2	99	-0.77 (0.09)	-0.40 (0.07)	-0.58 (0.06)
UNBURNED	-	-	-	0.17 (0.04)

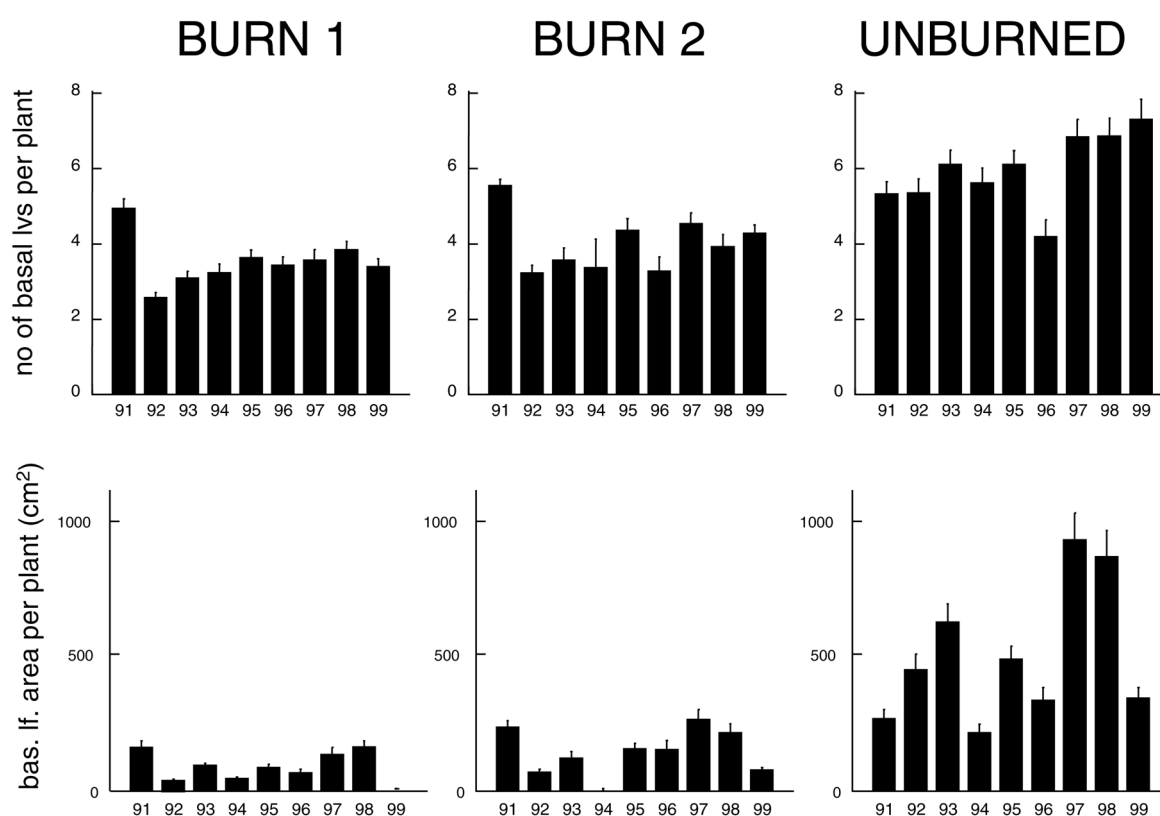


Figure 5. Variation in number of leaves and basal leaf area per plant among sites and years. Data are means (plus 1 standard error) of plants that resprouted.

Table 2. Between site correlation of average plant leaf area per year. Matrix of Pearson correlation coefficients (r) and Bonferroni probabilities (P).

	BURN 1		BURN 2	
	r	P	r	P
BURN 2	0.83	0.03	-	-
UNBURNED	0.89	0.01	0.86	0.02

removed before we sampled. In October 1992, we recovered 74% of the sown seed as intact seeds, empty seed hulls, and new bulbs (Table 3). Since there was,

on average, 21 intact seeds or bulbs remaining, some seeds had been lost to predation or other sources of mortality. Of the intact seeds that were recovered, 43% germinated in the greenhouse, indicating that, while most seeds germinate or are killed in the first winter following seed dispersal, there is some carry-over into the next winter. However, by July 1994, no intact seeds were present in soil samples.

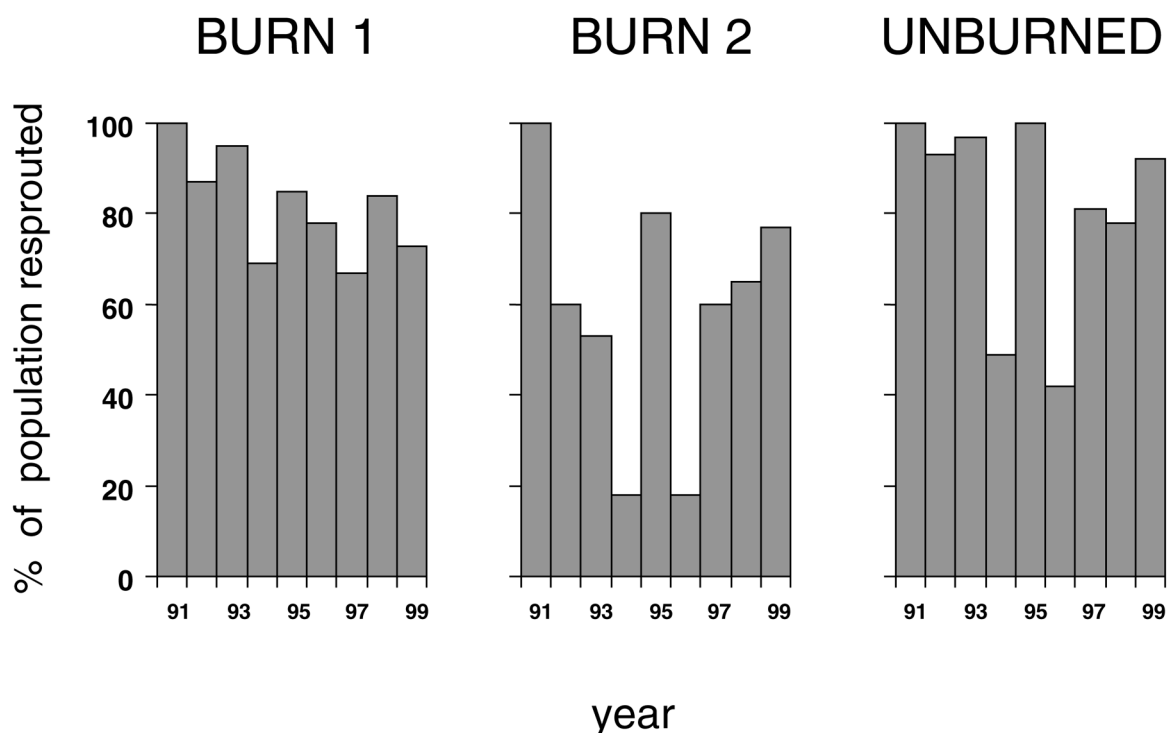


Figure 6. Annual variation in the percentage of the study population that resprouted at each site.

Discussion

Induction of flowering

We found that most flowering and all seed production of *Zigadenus fremontii* occurs only in the first winter and spring following fire. This is explained in part by fire-stimulated flowering, which has been reported for other geophytes in chaparral (Stone 1951; Muller et al. 1968; Keeley et al. 1981). Although few experimental studies have been conducted, the factors that have been found to stimulate flowering in other geophytes include both direct effects (e.g., heat, smoke, chemical addition) and indirect effects (e.g., increased soil nutrients, increased light levels due to shrub removal, removal of other inhibitors) of fire. Keeley (1993) found that the South African fynbos geophyte, *Crytanthus ventricosus*, was stimulated to flower by smoke. Observing fire-stimulated flowering in the lily, *Blandfordia nobilis*, Johnson et al. (1994) noted that the one-time pulse of flowering was closely associated with changes in soil chemistry during the postfire period, suggesting that fire-induced changes in soil attributes may play a role in the direct induc-

tion of flowering. Others have demonstrated that indirect factors are the primary cues for flowering. Le Maitre and Brown (1992) found that clearing vegetation resulted in the same flowering rates as burning in the geophyte, *Watsonia barbonica*. Brewer and Platt (1994) reported that fire-stimulated flowering in the perennial forb, *Pityopsis graminifolia*, was due to canopy and litter removal. Stone (1951) demonstrated that increased illumination resulted in higher proportions of plants flowering in the chaparral geophyte, *Brodiaea ixioides* (now *Triteleia ixioides*), and suggested that shade removal was the primary factor responsible for postfire flowering.

For *Z. fremontii*, we speculate that induction of flowering results from the interaction of several factors, including 1) high light levels, and 2) adequate carbohydrate storage in the bulb. The fact that some plants produced flowering stalks in the mature chaparral, and in the later years in the burn area, indicates that the cue that stimulated flowering was not a direct effect of fire, and that flowering was facultatively fire-dependent. We observed that the few *Z. fremontii* that flowered in the mature chaparral appeared to be in or near light gaps. However, if shade-removal were the

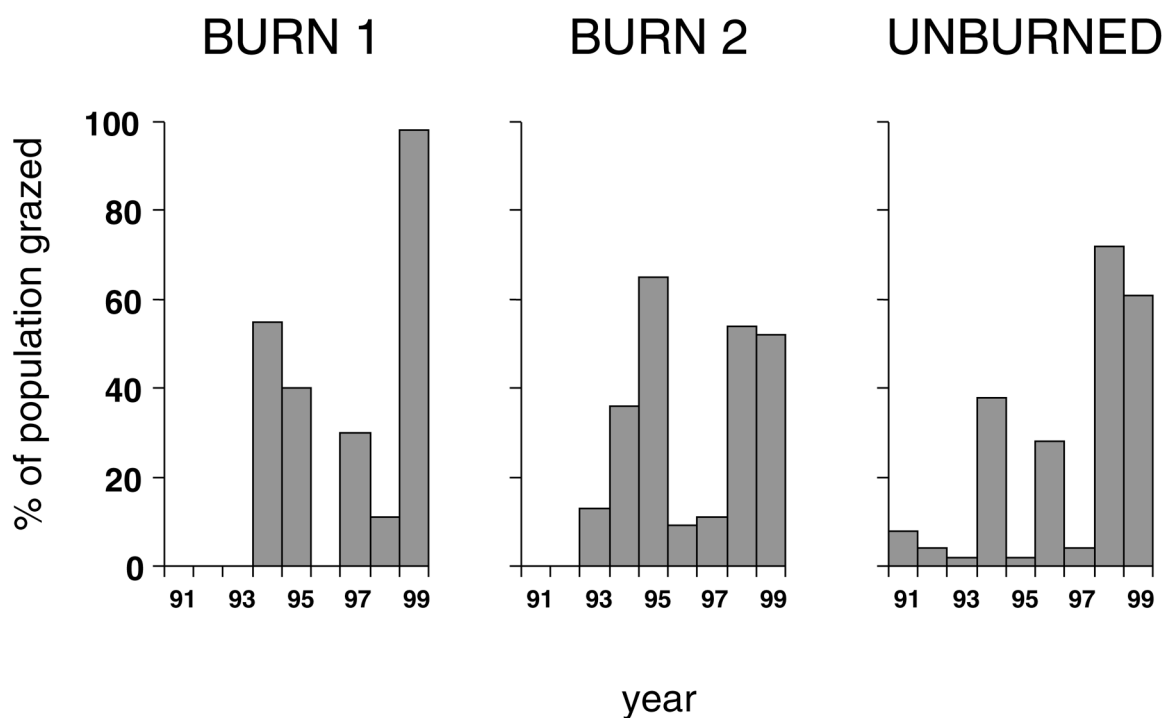


Figure 7. Annual variation in the percentage of the resprout population that was grazed at each site.

Table 3. Results of seed germination study. Numbers of intact seeds, empty seed hulls, and bulbs formed by new seedlings, collected from soil sown with 50 *Z. fremontii* seeds per 133 cm². Values are means and one standard error for quadrats collected in 1992 and 1994.

date	n	intact seeds	seed hulls	bulbs	germination of intact seeds in greenhouse
Oct 1991	15	50	–	–	–
Oct 1992	14	19.4 (2.2)	16.1 (2.1)	1.6 (0.7)	43.0% (0.1)
July 1994	15	0	20.7 (1.4)	1.1 (0.3)	–

only mechanism required for flowering, we should have also observed high rates of flowering in the burn areas in the second and even third year after fire when there was still little vegetative cover. Thus, although it appears that the cue for flowering may be a high light level, the presence of this cue is not in itself sufficient. Therefore in addition to the question of what specific cue stimulates flowering, a second question is “what prevents the production of reproductive structures?” For other geophyte species a minimum “critical” bulb size must be reached before flowering will occur (Fiedler 1987; Boeken 1989; Primack and Hall 1990; Ruiters et al. 1993). Models proposed by Dafni et al. (1981) predict that flowering in perennial geophytes with synanthous leaves will occur only after accumulation of surplus reserves, adequate to support both flowering and several successive years of

potential storage “shortages”. In the present study, we found that number of leaves and basal leaf area of plants in the burn areas were much lower in year 2 after flowering. These plants may have had too few carbohydrate reserves in the second year to produce another flowering stalk, regardless of high light levels. Our results suggest that accumulation of reserves is slow, and that at least several years are required for the plants to compensate for the cost of reproduction; in the burn areas basal leaf area was as high as it was in year 1 only after six years (Figure 5). While our observational field study presents evidence supporting the role of light and stored reserves in flowering, a controlled experiment, manipulating light, bulb size, and other factors, will be useful in identifying the mechanisms controlling the initiation of reproduction for this and other chaparral geophytes.

Success and costs of reproduction

Although the induction of flowering in *Z. fremontii* probably results from the factors discussed above, we suggest that the level of current photosynthate from leaves plays an important role in determining final seed output. In *Z. paniculatus*, defoliation did not affect the initial production of a flowering stalk, suggesting that induction of reproduction was a function of stored, not current resources (Tepedino 1982); however, *Z. paniculatus* that were defoliated produced few flowers, and most of these withered and died (Tepedino 1982). Emms (1996) also found that leaf clipping reduced seed production in *Z. paniculatus*, while addition of nutrients had no effect. Thus photosynthetic resources limited fruit and seed development in this congener. We observed that in *Z. fremontii*, flowering stalks that were produced subsequent to the first year after fire did not produce seeds. Two factors that may have limited current photosynthate production of leaves were defoliation caused by herbivores and low light levels.

By documenting decreases in growth after flowering, several other studies have shown that there is a cost of reproduction in geophyte species (Snow and Whigham 1989; Primack and Hall 1990; Emms 1996). Bulb plants are ideal for this task because both above- and below-ground portions of the plants can be measured. For example, in *Z. paniculatus*, bulbs were significantly smaller after flowering, suggesting that plants used stored reserves for production of reproductive structures (Emms 1996). In discussing the possible adaptive features of fire-stimulated flowering, Brewer (1995) postulated that the cost of flowering might be relatively low when the timing of flowering coincides with postfire increases in the availability of light and soil nutrients.

Seedling establishment of Z. fremontii

Although the germination requirements of chaparral geophytes have been well documented in the laboratory, the timing of seedling recruitment is largely unknown. Previous studies have demonstrated that, like other geophytes, *Z. fremontii* has non-refractory seeds. Keeley et al. (1985) found that 85% of seeds germinated readily in experimental controls; heating seeds resulted in reduced germination. In the present study, we found that in the field some seeds that had not germinated in the second year were still germinable, suggesting some carry-over of viable seeds

to another year. However, by the fourth year, all seeds had either germinated or been removed. Since seed production occurs only in the first year after fire; seedling establishment is limited to the second and to a lesser extent the third year following fire, with no persistent seedbank. The tight association between fire and flowering (i.e., fire dependent reproduction) in this species indicates that seed input and thus seedling establishment occurs only once per inter-fire period, which may be several to many decades. This pulse of seedling recruitment has significant implications for the age structure of *Z. fremontii* populations, in that plants will be in even-aged cohorts spaced many decades apart.

Plant dynamics in the interval between fires

As demonstrated in the present study, and in others conducted on geophytes (Lubbers and Lechowicz 1989; Garcia and Antor 1995; Emms 1996), reproductive success (flower, fruit, and/or seed production) is positively correlated with plant size (leaf area and/or bulb size.) Since reproduction results in a decrease in plant resources, future reproductive success will be determined by carbohydrate storage in the interval between flowering events. Thus, for *Z. fremontii*, and other geophytes that are stimulated to flower by fire, growth in the interfire period is critical.

When does this critical growth occur? Based on previous reports which proposed that geophytes may be dormant or produce few leaves in long unburned chaparral (Parker and Kelly 1989; Keeley 1991, 1994), one would conclude that significant storage must occur in the immediate postfire period. Yet contrary to our expectations, we found that *Z. fremontii* in mature chaparral were not dormant; rather, leaf area, number of leaves, and relative growth rates were highest in the unburned chaparral. This result was surprising given that nutrient and light levels were presumably higher in the burn area (Christensen 1973). Even with increased input from external resources (increased nutrient supply in postburn soils) plants in the burn areas had negative growth rates during the first year after the fire, indicating that they must have used both the stored and present resources, primarily for flowering and seed production. Thus, we conclude that growth and storage of carbohydrates occurs in the long interval between fires, rather than in the immediate postfire period. We propose that this is probably also the case for other geophytes displaying fire-stimulated flowering. The importance of this

growth period in mature chaparral implies that the length of the inter-fire period can be critical to geophytes; short fire intervals would likely have negative effects both on adult plants, (since they may deplete stored resources in attempting to produce reproductive structures), and on seedling establishment (since small bulb sizes of adult plants would result in low seed production).

One possible explanation for the discrepancy between our findings and observations in the literature that chaparral geophytes are dormant in mature chaparral is that surviving plants may not have above-ground leaves in all years. Clearly, *Z. fremontii* is more visible in the first spring following fire when they are flowering. In addition, although our study plants resprouted in most years, and we have not yet noted any mortality, there were years when most plants did not resprout. Also, herbivory was intense in some years. Late in the spring, we observed that many plants that had leaves a month earlier had been defoliated. Thus, if observations of these populations were made in years when resprouting rates were low and/or herbivory was occurring, it would be reasonable to conclude that plants were either dormant or deceased. It is also possible that *Z. fremontii* contradicts the proposed model of geophyte dormancy in mature stands because it is the only common chaparral geophyte that is toxic. (The common name for this genus is “death camas.”) We have observed that other palatable geophytes (e.g., *Dichelostemma capitatum*) that resprout under the canopy in mature chaparral are often grazed. We suggest that additional surveys and long-term monitoring of geophytes in mature chaparral will be valuable to determining whether dormancy does in fact occur in older stands.

Given that inter-fire intervals may last decades (Mensing et al. 1999), we hypothesize that *Z. fremontii* is quite long-lived, relative to other herbaceous perennials. It is difficult to determine age in perennial herbs, but geophytes have been reported with lifespans of over 300 years (Garcia and Antor 1995). Our results indicate that the persistence of this species in chaparral depends on the longevity of adults, not as in most other chaparral species, on an accumulated seed bank or new seedling recruits. In *Z. fremontii*, seedling recruitment occurs perhaps only every 30 – 70 years, but seedling densities are low, and growth is slow (after 9 years most seedlings we observed in the field were small, single leaves). Mature plants must be at least the age of the inter-fire period, but because we have noted no mortality, and slow

seedling growth, it is likely that plants live more than one inter-fire period. Thus, these herbs may be among the eldest component of the fire-adapted chaparral plant community.

Acknowledgements

We thank Joseph Connell, Richard Cowling, Bruce Mahall, Dennis Odion, and two anonymous reviewers for helpful critique of this manuscript.

References

- Boeken B. 1989. Life histories of desert geophytes – the demographic consequences of reproductive biomass partitioning patterns. *Oecologia* 80: 278–283.
- Borchert M. 1989. Postfire demography of *Thermopsis macrophylla* var. *agnina* J. T. Howell (Fabaceae), a rare perennial herb in chaparral. *American Midland Naturalist* 122: 120–132.
- Brewer J.S. 1995. The relationship between soil fertility and fire-stimulated floral induction in two populations of grass-leaved golden aster, *Pityopsis graminifolia*. *Oikos* 74: 45–54.
- Brewer J.S. and Platt W.J. 1994. Effects of fire season and soil fertility on clonal growth in a pyrophilic forb, *Pityopsis graminifolia* (Asteraceae). *American Journal of Botany* 81: 805–814.
- Christensen N.L. 1973. Fire and the nitrogen cycle in California chaparral. *Science* 181: 66–68.
- Dafni A., Cohen D. and Noy-Meir I. 1981. Life-cycle variation in geophytes. *Annals of the Missouri Botanical Garden* 68: 652–660.
- Emms S.K. 1996. Temporal patterns of seed set and decelerating fitness returns on female allocation in *Zigadenus paniculatus* (Liliaceae), an andromonecious lily. *American Journal of Botany* 83: 304–315.
- Fiedler P.L. 1987. Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). *Journal of Ecology* 75: 977–995.
- Garcia M.B. and Antor R.J. 1995. Age and size structure in populations of a long-lived dioecious geophyte: *Bordera pyrenaica* (Dioscoreaceae). *International Journal of Plant Sciences* 156: 236–243.
- Horton J.S. and Kraebel C.J. 1955. Development of vegetation after fire in the chamise chaparral of southern California. *Ecology* 36: 244–262.
- Hurlbert S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Johnson K.A., Morrison D.A. and Goldsack G. 1994. Postfire flowering patterns in *Blandfordia nobilis* (Liliaceae). *Australian Journal of Botany* 42: 49–60.
- Keeley J.E. 1991. Seed germination and life history syndromes in the California chaparral. *Botanical Review* 57: 81–116.
- Keeley J.E. 1993. Smoke-induced flowering in the fire-lily *Cyrtanthus ventricosus*. *South African Journal of Botany* 59: 638.

- Keeley J.E. 1994. Seed-germination patterns in fire-prone Mediterranean-climate regions. In: Arroyo M.T.K., Zedler P.H. and Fox M.D. (eds), *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia*. Springer-Verlag, New York.
- Keeley J.E. and Keeley S.C. 1988. Chaparral. In: Barbour M.G. and Billings W.D. (eds), *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge, pp. 165–207.
- Keeley J.E., Morton B.A., Pedrosa A. and Trotter P. 1985. Role of allelopathy, heat, and charred wood in the germination of chaparral herbs and suffrutescents. *Journal of Ecology* 73: 445–458.
- Keeley S.C., Keeley J.E., Hutchinson S.E. and Johnson A.W. 1981. Postfire succession of the herbaceous flora in southern California chaparral. *Ecology* 62: 1608–1621.
- Knapp A.K. 1986. Ecophysiology of *Zigadenus nuttallii*, a toxic spring ephemeral in a warm season grassland: effect of defoliation and fire. *Oecologia* 71: 69–74.
- Le Maitre D.C. and Brown P.J. 1992. Life cycles and fire-stimulated flowering in geophytes. In: van Wilgen B.W., Richardson D.M., Kruger F.J. and van Hensbergen J.H. (eds), *Fire in South African Mountain Fynbos*. Springer-Verlag, New York, pp. 145–160.
- Lubbers A.E. and Lechowicz M.J. 1989. Effects of leaf removal on reproduction vs. belowground storage in *Trillium grandiflorum*. *Ecology* 70: 85–96.
- Mensing S.A., Michaelsen J. and Byrne R. 1999. A 560-year record of Santa Ana Fires reconstructed from charcoal deposited in the Santa Barbara Basin, California. *Quaternary Research* 51: 295–305.
- Muller C.H., Hanawalt R.B. and McPherson J.K. 1968. Allelopathic control of herb growth in the fire cycle of California chaparral. *Bulletin of the Torrey Botanical Club* 95: 225–231.
- Parker V.T. and Kelly V.R. 1989. Seed banks in California chaparral and other Mediterranean climate shrublands. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), *Ecology of Soil Seed Banks*. Academic Press, San Diego.
- Primack R.B. and Hall P. 1990. Costs of reproduction in the pink lady's slipper orchid: a four-year experimental study. *The American Naturalist* 136: 638–656.
- Raunkiaer C. 1934. *The Life Forms of Plants and Statistical Plant Geography*. Clarendon Press, Oxford.
- Ruiters C., McKenzie B. and Raitt L.M. 1993. Life history studies of the perennial bulbous geophyte species *Haemanthus pubescens* subspecies *pubescens* (Amaryllidaceae) in lowland coastal fynbos, South Africa. *International Journal of Plant Sciences* 154: 441–449.
- Rundel P.W. 1996. Monocotyledonous geophytes in the California Flora. *Madroño* 43: 355–368.
- Snow A.A. and Whigham D.F. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). *Ecology* 70: 1286–1293.
- Stone E.C. 1951. The stimulative effect of fire on the flowering of the golden brodiaea (*Brodiaea ixiodes* Wats. var. *lugens* Jeps.). *Ecology* 32: 534–537.
- Sweeney J.R. 1956. Responses of vegetation to fire. A study of the herbaceous vegetation following chaparral fires. University of California Publications in Botany 28: 143–216.
- Tepedino V.J. 1982. Effects of defoliation on reproduction of a toxic range plant, *Zigadenus paniculatus*. *Great Basin Naturalist* 42: 524–528.