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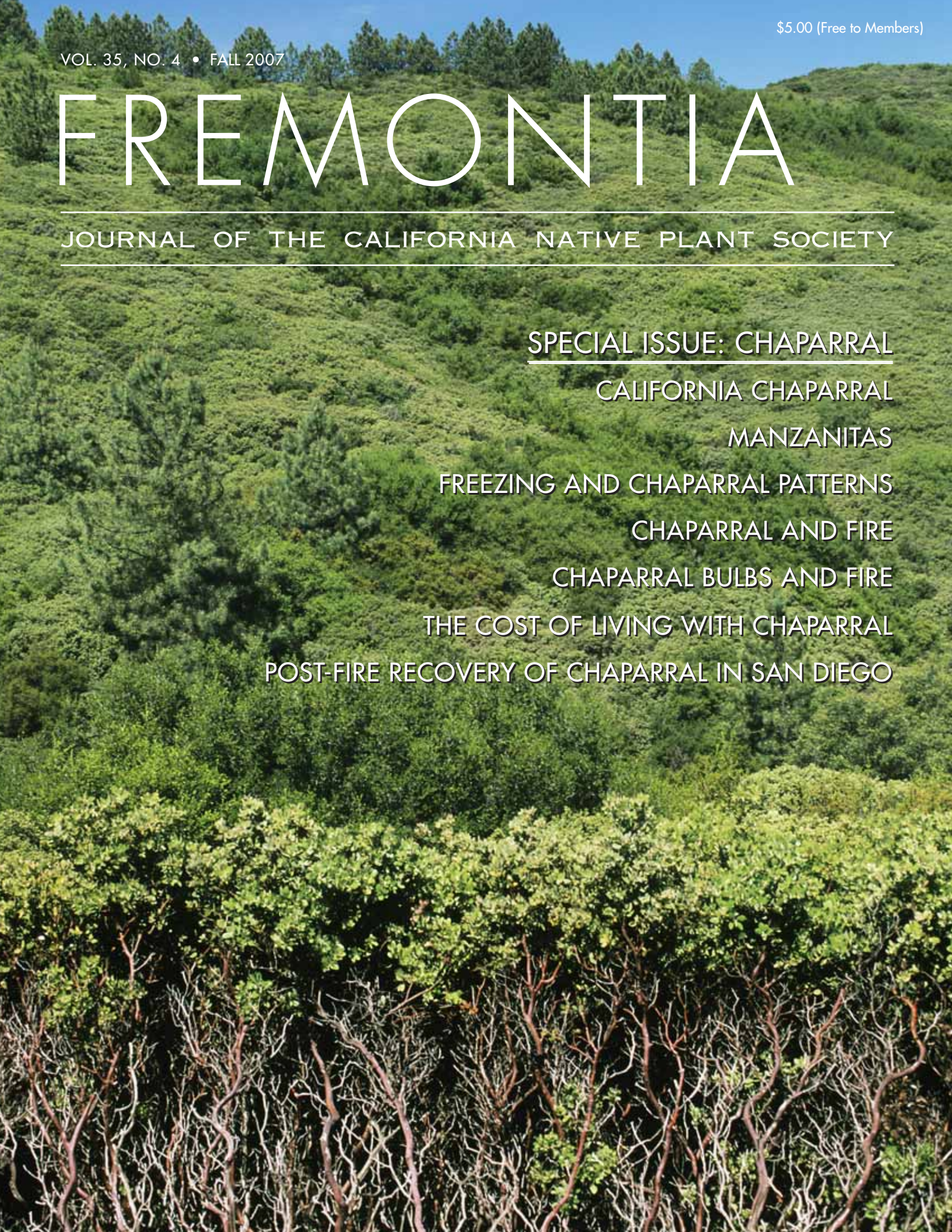

SPECIAL ISSUE: CHAPARRAL

CHAPARRAL GEOPHYTES: FIRE AND FLOWERS

by Claudia M. Tyler and Mark I. Borchert

Flowering geophytes are among the most striking plants in post-fire chaparral. Having survived the fire because of deeply-buried bulbs or corms, these perennial herbs resprout and then flower profusely in the first spring following a fire. From unimpressive basal leaves, star lily or Fremont's zigadene (*Zigadenus fremontii*), common soap plant (*Chlorogalum pomeridianum*), mariposas (*Calochortus* species), wild hyacinth (*Dichelostemma pulchella*), and golden stars (*Bloomeria crocea*) often send up tall flowering stalks with delightful white, blue, or yellow blossoms. Although not fire-dependent *per se*, nor restricted to chaparral, these species are all well-adapted to chaparral's fireprone environment and their post-burn flowering displays are especially impressive there.

What explains the showy en masse flowering of geophytes after fire, and how do they survive long intervals between fires? To address these questions, we have been conducting long-term studies over the past nine years or more in which we have followed the fate of marked individuals in burned and unburned chaparral in the Santa Ynez and Topa Topa Mountains. We have focused on two species, *Zigadenus fremontii* and *Chlorogalum pomeridianum*, annually measuring leaf area, and production of flowers and fruits both before and after fire. We have also conducted seed experiments in the field to determine the rates and timing of germination.

FLOWERING: WHEN, WHY, AND AT WHAT COST?

We were surprised to discover that for *Zigadenus fremontii*, nearly all flowering and seed production occurred in the first winter and spring following the devastating 1990 Paint Fire near Santa Barbara. Over 90% of the plants in two burn areas produced large flowering stalks, fruits, and many seeds. In contrast, flowering was rare in the adjacent unburned site or in the nine subsequent years in the burned areas. In later years, when plants did produce a small flowering stalk, they generally did not develop fully and

Fremont's zigadene (*Zigadenus fremontii*) is one of the most characteristic chaparral geophytes. All photographs by C. Tyler.

rarely produced seeds. For *Chlorogalum pomeridianum*, flowering and seed production increased dramatically immediately after the burn, though, unlike *Zigadenus*, flowering and seed production was more apparent in later years.

What causes this conspicuous post-fire induction of flowering? This pattern has been reported for other geophytes in chaparral, and both the direct (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, reduced herbivory) of fire have been implicated. The fact that some of our plants flowered in the mature chaparral, and in the later years in the burn areas, indicates that the stimulating cue for *Zigadenus* is likely not the direct effect of fire, and that flowering is only circumstantially fire-dependent. For these two species, we suspect that the cue stimulating the initiation of flowering is high light levels that result from the elimination of the dense shrub canopy. The few *Zigadenus* that flowered in the mature chaparral in our study appeared to be in or near light gaps. We also observed these chaparral geophytes occasionally flowering in grasslands or gaps in open, low-growing maritime chaparral, indicating that flowering is not dependent on fire directly, especially where light levels are generally high.

There is a price, however, for the celebratory show of flowers and seed production after a chaparral fire. For both *Zigadenus* and *C. pomeridianum,* there was a cost of reproduction. Plants that flowered after the fire had negative growth rates the following year, indicating they were significantly smaller after using stored bulb reserves to reproduce. Moreover, plants that produced the most flowers also had the lowest (most negative) growth rates. In contrast, plants in unburned chaparral that did not flower had positive growth rates over the same period. Similar results have been reported for other geophytes, suggesting that plants use stored reserves to produce reproductive structures.

This cost of reproduction may be the key to understanding why flowering of *Zigadenus* in the chaparral is restricted to the first year after fire. If high light levels were the only mechanism required for flowering, we also should have seen geophytes in the burn areas continue to flower in the second and even third year after fire when there was still little shrub cover. We propose that induction of flowering results from the interaction of two factors: 1) high light levels, and 2) adequate carbohydrate storage in the bulb. For other geophytes, a minimum "critical" bulb size and accumulation of surplus reserves must be reached before flowering will occur. Our results with *Zigadenus fremontii* suggest this accumulation of reserves can be quite slow: five to seven years may be required for the plants in burn areas to regain basal leaf areas similar to those at the time of flowering. Thus, although the high light "cue" may be present, plants that have flowered after the fire may have too few reserves to produce another flowering stalk in subsequent post-fire years. Furthermore, by the time bulb sizes once again reach "critical" mass, shade from the returning shrub canopy may inhibit flowering in these and other chaparral geophytes. In addition, with the reestablishment of shrubs comes an increase in herbivory by small mammals, rabbits and deer.

SEEDLING ESTABLISHMENT

Although the germination requirements of chaparral geophytes have been well documented in the laboratory, the timing of seedling recruitment has been largely undescribed. Previous studies have demonstrated that many geophytes, including *Z. fremontii* and *C. pomeridianum,* produce seeds that lack dormancy, thus, unlike many other fire followers, they germinate readily without heat or other fire-related stimulus. As described above, seed production occurs only in the first year after fire. In our field study, we found that all seeds germinated or were removed by seed predators within the first two years; thus, seedling establishment is limited to the second and to a lesser extent the third year after fire, with none remaining to form a persistent seedbank. The tight association between fire and flowering (i.e., fire-dependent reproduction) in *Zigadenus* indicates that seed input, and thus seedling establishment, occurs only once in each period between fires, which may last several to many decades. Thus, this pulse of seedling recruitment has significant implications for the age structure of *Zigadenus* populations, as plants will be in even-aged cohorts spaced many decades apart.

Wild hyacinth (*Dichelostemma pulchella*), one of the most widely distributed geophytes in California, flowers well after fires.

IN MATURE CHAPARRAL: UNDERSTATED IN THE UNDERSTORY

Unlike most other post-fire herbaceous species, geophytes remain

Fremont's zigadene (*Zigadenus fremontii*) as typically seen in its vegetative state in mature chaparral.

in the understory as the shrub canopy closes over time. It has been suggested that in mature chaparral, geophytes decline in productivity or go dormant. However, our studies of *Z. fremontii* in unburned chaparral indicate just the opposite. Contrary to our expectations, we found that leaf area, number of leaves, and relative growth rates of *Zigadenus* in mature chaparral were higher than those in the recently burned areas in most years. This was especially surprising given that nutrient and light levels were presumably higher in the burn areas.

Although there is variation in leaf area and resprouting among years—probably a function of both rainfall and herbivory—resprouting of the geophytes in the unburned chaparral was comparable to that in the burned areas. Nearly 80% of marked *Zigadenus* in mature chaparral resprouted in seven out of nine years. Since reproduction results in a decrease in stored plant resources, future reproductive success depends on and will be determined by growth and carbohydrate accumulation in the interval between fires. So, while mass reproduction of most other herbaceous species occurs in the immediate post-fire period followed by death, geophytes such as *Zigadenus* remain active, though understated, in the mature chaparral understory.

The importance of this vegetative growth while in the understory implies that the length of the period between fires can be critical to geophytes. In the typical scenario, with at least a few decades between fires, the growth and storage of carbohydrates over many years prepares these bulb plants for truly impressive floral displays. This was apparent in both species since flower, fruit, and seed production increased significantly with plant (bulb) size. On the other hand, short fire intervals may have negative effects both on adult plants, which may deplete their moderate resources in attempting to produce reproductive structures, and on seedling establishment since smaller bulbs of adult plants would result in low seed production.

Given that intervals between fires may last decades, we hypothesize that many chaparral geophytes are likely quite long-lived relative to other herbaceous perennials. Although it is difficult to determine age in perennial herbs, lifespans of over 300 years have been reported for some species of bulb plants. The persistence of geophytes in chaparral depends on the longevity of adults and not on the creation of an accumulated seed bank or new seedling recruits. In *Z. fremontii,* seedling recruitment occurs perhaps only every 30 to 70 years. In addition, seedling densities are low, and growth is slow (after nine years most seedlings we observed in the field were still small, single leaves). This strongly suggests that mature plants must be at least the age of the interval between fires. Furthermore, since mortality is low and seedling growth slow, it is likely that plants live longer than one interval between fires. Surprisingly, these herbs, which flower splendidly after fire but then remain inconspicuous in mature stands, may be among the eldest species of the fire-adapted chaparral plant community.

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