Spring 2010

The Response of Zigadenus fremontii to Variation in Fire Regime

Shannon Elizabeth Dinis
San Jose State University

THE RESPONSE OF *ZIGADENUS FREMONTII* TO VARIATION IN FIRE REGIME

A Thesis

Presented to

The Faculty of the Department of Biological Sciences

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Shannon Elizabeth Dinis

May 2010

The Designated Thesis Committee Approves the Thesis Titled

THE RESPONSE OF *ZIGADENUS FREMONTII* TO VARIATION IN FIRE REGIME

by

Shannon Elizabeth Dinis

APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCES

SAN JOSÉ STATE UNIVERSITY

May 2010

Dr. David K. Bruck	Department of Biological Sciences
Dr. Susan Lambrecht	Department of Biological Sciences
Dr. M. Beth Dawson	Department of Biological Sciences

ABSTRACT

THE RESPONSE OF *ZIGADENUS FREMONTII* TO VARIATION IN FIRE REGIME

by Shannon Elizabeth Dinis

California's chaparral shrub communities are naturally exposed to dry-season fire. It could be reasoned that prescription burns set during the wet season by land managers would have more detrimental effects on plant regeneration than dry season fires because wet season burns are more likely to kill newly emergent seedlings and damage newly emerged leaves of mature plants. Six field sites with flowering *Zigadenus fremontii*, an herbaceous perennial geophyte common to chapparal and part of the post-fire bloom, were established at Henry W. Coe State Park in Nothern California. Three sites were part of the September 2007 Lick Wildfire and three were part of a February 2007 prescription burn. The sites were monitored for *Z. fremontii* regeneration over two years. *Z. fremontii* exposed to the prescription burn fared better than the wildfire plants, with inflorescence height being significantly higher in prescribed burn sites. Bulbs were transplanted into soil from the prescription burn, wildfire, and unburned area to determine differences in regeneration due to soil characteristics. There were no significant differences due to soil types, but only bulbs from the prescription burn sites had the ability to produce flowers in multiple years subsequent to fire. Differences in germination rates between seeds grown in soil from the wildfire, prescription burn, and unburned soil were investigated via a controlled germination experiment. There was a trend for increased germination in burned soils compared to unburned soils. The evidence from this study suggests that geophytes can benefit from fires set outside of the natural fire season of chaparral.

ACKNOWLEDGEMENTS

I would like to thank Dr. Winslow Briggs for his enthusiasm and support in the beginning stages of this project. His insight and novel ideas helped bring this project to life. I thank my advising committee, Dr. David Bruck, Dr. Susan Lambrecht, and Dr. M. Beth Dawson for ongoing support and helpful comments throughout this process. I thank Lucy Dinis, Joe Dinis, Daniel Johnson, Katie Rodriguez, and Carmel de Bertaut for their assistance in the field. Thank you to my funding sources for this project: San Jose State University Department of Biological Sciences Research Fellowship and the California Native Plant Society, Santa Clara Valley Chapter, Graduate Scholarship.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Introduction

Wildfire is the principal source of disturbance in many plant communities. It provides soil nutrients by depositing ash from burned materials, and it controls diseases by removing infected or dead plants (Keeley 2006; Zald et al. 2008). Fire also plays an essential role in regeneration of many fire-adapted species by opening cones or releasing seeds from dormancy (Keeley et al. 1985; Franklin et al. 2005). In these ways, fire affects biodiversity by providing conditions under which a variety of species thrive.

California's chaparral shrub communities are well adapted to fire, frequent occurrences in the Mediterranean climatic and soil conditions that characterize these communities. Several chaparral herbaceous species, such as the subshrub golden yarrow (*Eriophyllum confertiflorum*), the fire annuals caterpillar phacelia (*Phacelia cicutaria*) and grand gilia (*Gilia splendens*), and opportunistic annual coastal lotus (*Lotus salsuginosus*), have been found to require the heat of fire, charrate (charred wood deposited on the soil after fire), or both to release seeds from dormancy (Keeley et al. 1985). Shrub species, such as many within the genus *Ceanothus* also require fire temperatures for seed germination (Keeley 1987). Smoke has also been found to stimulate germination in herbaceous chaparral species such as whispering bells *(Emmenanthe penduliflora*) and giant flowered phacelia (*Phacelia grandiflora*) (Keeley & Fotheringham 1998). Sucrose lineolate, a compound found in seeds of whispering bells (*Emmenanthe penduliflora*) and *Phacelia* spp., has been determined to be responsible for maintaining dormancy in the inter-fire period (Egerton-Warburton & Ghisalberti 2001). Along with seed adaptations to fire, many shrubs and herbaceous perennials in chaparral shrublands are fire tolerant with the ability to sprout from an underground storage organ or above ground axillary buds after fire (Bond & Midgley 2003; Knox & Clarke 2006b). Because many species have the ability to resprout after a disturbance, this adaptation likely evolved as a response to frequent disturbances or defoliation, which then became a valuable trait in fire-prone ecosystems such as chaparral (Lloret et al. 1999). Other shrub communities, such as the sclerophyllous woodlands of Australia, show similar adaptations to fire in terms of bud resprouting and seed release from dormancy. The typical fire regime in both chaparral and sclerophyllous shrub communities amounts to high intensity crown fires that consume much of the vegetation and occur at intervals of 20 years or more (Keeley 2002, 2006).

Most fire studies in shrub communities have focused primarily on the effect of fire frequency on flora diversity. This focus has been due at least in part to concerns over the invasion of opportunistic annual grasses into vegetation gaps produced by fire. High frequency, low intensity fires especially produce gaps that lead to the conversion of chaparral to grassland (Keeley 2006). Knox and Clarke (2006a) studied the effects of increased fire frequency on resprouting ability of shrub species in an Australian sclerophyllous shrub community, comparing the size of the lignotuber in several species before and after fire. The fire intervals in their study sites ranged from 7 to 22 years. In all of the species examined, larger lignotubers sprouted more often after fire leading to higher survival rates. There was no significant change in sprouting frequency with increased fire frequency, indicating that species with the ability to resprout after fire were able to survive with higher frequency fires. Obligate seeder species significantly decreased in percent cover when fire frequencies were high in a sclerophyllous shrub community in Spain (Lloret & Vila 2003). The authors concluded that, at high fire frequencies (two fires within 2-3 years), new seedlings lack the time for growth and maturation.

Only a few studies have concerned the effects of fire severity (intensity/temperature) in chaparral shrub communities. Keeley et al. (2008) compared the effects of various fire severities generated by the 2003 fires in Southern California. The wildfires burned in a mosaic pattern, with differences in completeness of burning attributed to both topography and species density. Fire intensities increased with slope steepness because fire moves more rapidly and pre-heats vegetation more quickly up steep slopes, leading directly to higher fire temperatures. Fire severity was found to increase with stand age due to accumulation of debris and dry fuel. Crown fire intensity also varies with shrub density. Higher severity fires are harmful to many exotic species that commonly invade chaparral communities, so maintaining high intensity crown fires may be beneficial to the preservation of this plant community (Keeley 2006).

As urban expansion has encroached on wilderness areas, many homes have been constructed in wildfire danger zones. It is difficult for firefighters to facilitate the beneficial effects of wildfires on the environment while preventing property damage. Prescription burning, a land management tool that is used often and chiefly during the wet season in fire-prone ecosystems, permits the beneficial effects of wildfires in a more controlled fashion. Prescription burns are usually difficult to conduct in the natural late summer fire season due to concerns over air quality and increased difficulty for fire fighters to control these fires.

Most prescription burns used for fuel-load reduction are set during the wet season when plants are likely to have higher moisture content that slows the progression of a fire and makes it easier to manage. Knapp and Keeley (2006) compared prescribed burns occurring in early and late season in a mixed conifer forest for their ability to generate a patchy mosaic of low and high intensity burn areas. Early season plots were found to have less burned area than late season burn plots. In both early and late season burn plots, adjacent unburned areas served to provide seed that spread into areas burned more severely. As with chaparral communities noted above (Keeley et al. 2008), it was also found that variation in topography at both early and late season burn plots allowed for a variety of fire severities across the landscape. Unburned sites adjacent to burned sites can then provide a source of seed for repopulation of burned sites. These beneficial processes have been corroborated in other studies and likely mimic natural fire effects (Lloret & Vila 2003).

Very few studies have investigated the impact of variation in fire season on chaparral regeneration (Beyers & Wakeman 1997). Prescription burns during the wet season may have more detrimental effects on seedling regeneration than dry season fires because wet season burns are more likely to kill newly emergent seedlings or seeds that have recently imbibed or germinated. They may also have harmful effects on resprouting species by damaging newly emerged leaves, causing the plants to spend more energy making new leaves and less energy on flowering and seed production. Although prescription burns have been shown to have beneficial effects on forest vegetation (Knapp & Keeley 2006; Peterson & Reich 2008; Zald et al. 2008), they may not be beneficial to chaparral shrublands. Prescription burns in chaparral have failed to reduce fire hazard (the primary reason for conducting them) and are suspected to cause resource damage by decreasing biodiversity and reducing the watershed protection value of shrub species in this plant community (Keeley 2002). Knox and Clarke (2006a) observed seedling emergence after both wet season and dry season fires in sclerophyllous shrublands. Eight of the thirteen species studied had increased seedling emergence following dry season than wet season fires compared to non-sprouting species. The authors concluded that increased germination following dry season fires was due to increased soil temperatures following fire as compared to cooler soil temperatures following wet season fires, and cooler soil temperatures were found to inhibit germination (Knox & Clarke 2006a).

Although Knox and Clarke (2006a, b) examined the effects of fire season on the shrub species in this plant community, as is common in most chaparral studies, herbaceous perennials were not examined. This exclusion may be due to the difficulty in finding and reaching these small plants among the taller and more expansive sclerophyllous shrubs. Fire effects on herbaceous species have been studied routinely as part of grassland fire studies and forest understory fire studies (Knapp 1986; Emms 1996; Hiers et al. 2000; Dodson et al. 2008).

Chaparral star lily [*Zigadenus fremontii*, Torrey (Liliaceae)] is an herbaceous perennial geophyte that is often part of the post-fire bloom in California chaparral. All members of the genus are considered to be toxic, producing alkaloids that made members of the Lewis and Clark expedition ill, resulting in the common name of death camas (Hickman 1996). It emerges after fire from an underground bulb, although the reason for its prevalence in the post-fire bloom is largely unknown. Very few investigations have been conducted on this particular species or on other species within this genus. Determining how this species responds to variation in fire season will add valuable information to the study of fire ecology and the natural history of this species. The objective of this study was to investigate the regenerative growth and development of *Z. fremontii* in relation to variation in fire season using a prescribed burn in February 2007 and the Lick Wildfire in September 2007.

Materials and Methods

Study Area

Field sites were established at Henry W. Coe State Park west of Morgan Hill, California, USA. Henry W. Coe State Park covers over 86,000 acres of rugged wilderness and comprises one of the largest state parks in Northern California. Vegetation types include ponderosa pine forest, oak woodland, chaparral, and riparian. The climate is Mediterranean with average precipitation of 66.5 cm per year, and of which 90% falls in the winter between November and May. Average temperatures range from 5°C to 17°C in the winter and 13°C to 29°C in the summer. Aside from two smaller, inextensive fires in the early 2000's, the area encompassing the Lick Wildfire and the prescription burn had not been burned since the early 1960's, amounting to a fire interval of over 40 years.

Species Description

Z. fremontii is a geophyte that produces long linear basal leaves (an average of 20-30 cm long and 0.8-1.3 cm wide). The bulb can be found about 10 cm below the surface and is about 2 cm in diameter. The inflorescence is a panicle that can be as tall as 96 cm. Flowers are white and open with yellow nectaries near the base of the perianth, indicating insect pollination. The fruit is a capsule with many seeds. Epetiolate linear leaves begin to emerge from the bulb in early December to January. A maximum of eight leaves per plant was observed. Flowering begins in late January and continues until May. With the onset of summer, above ground structures senesce and the plant remains dormant until the first winter rains.

Z. fremontii is found in chamise chaparral, often beneath the shrub canopy or along the edges of the canopy. Herbivory was observed during this study, so some herbivores are able to tolerate the toxic nature of all members of this genus.

Field Study

Field sites were established in chamise chaparral along Willow Ridge Road (Table 1, Fig. 1), a site of burning in 2007. On the west side of Willow Ridge Road, land managers conducted a prescription burn in February 2007 (wet season burn), in a section whose boundary bordered the road. In September 2007, the Lick Wildfire (dry season burn) burned the landscape on the eastern side of the road. These two different fire regimes on each side of Willow Ridge Road formed an ideal experimental setup. Three plots of 5 m x 5 m were established in each burn section in April 2008. Plots were composed of blooming *Zigadenus fremontii* of densities ranging from 19 to 42 individuals. Data were collected at these sites in the spring of 2008 and the spring of 2009.

Table 1. Field site coordinates. GPS coordinates of field sites along Willow Ridge Road in Henry W. Coe State Park. Coordinates in UTM (Universal Transverse Mercator) format.

Site	*Fire Type (Month)*	*Coordinates (UTM)*
1	Wildfire (Sept 2007)	10S 0638226m E, 4112795m N
2	Wildfire (Sept 2007)	10S 0637876m E, 4112830m N
3	Prescription (Feb 2007)	10S 0636781m E, 4113518m N
4	Wildfire (Sept 2007)	10S 0636829m E, 4115051m N
5	Prescription (Feb 2007)	10S 0637129m E, 4113226m N
6	Prescription (Feb 2007)	10S 0637089m E, 4113403m N

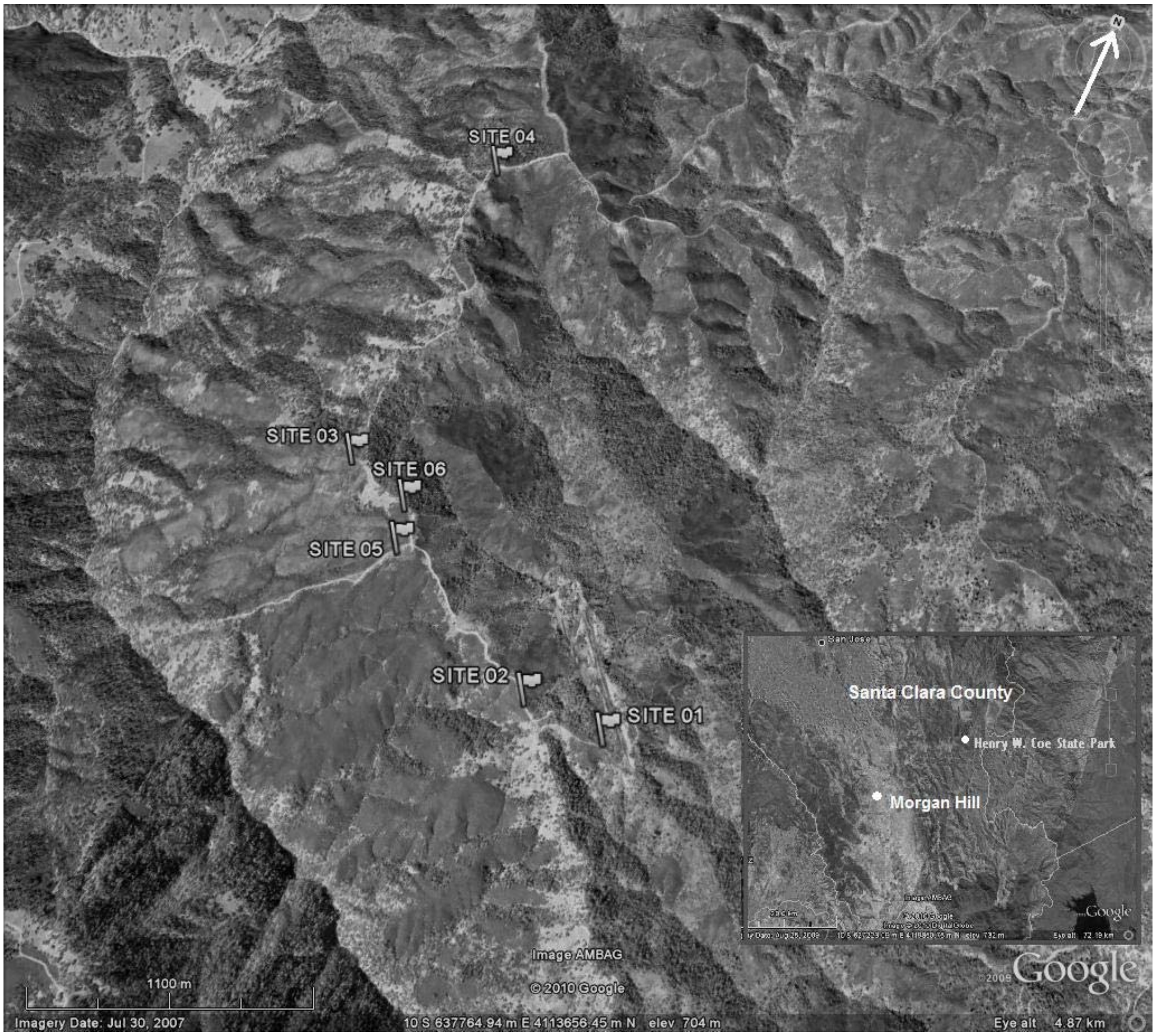

Figure 1. Field sites along Willow Ridge Road. Google Earth image of field sites established along Willow Ridge Road in Henry W. Coe State Park. Note the charred hillsides on the east side of Willow Ridge Road from the September 2007 Lick Wildfire.

To determine differences in reproductive output and productivity of plants exposed to the two fire regimes, *Z. fremontii* inflorescences were measured from the tip of the panicle to the base of the stem, and flowers (including unopened buds) were counted in two consecutive years. In spring 2009, along with the above data, total leaf area of the basal leaves was measured as an index of productivity. Leaf area was estimated from measurements of leaf length and width at the widest point. Only basal leaves (not bracts) were included in these measurements. Once capsules had fully matured and plants had gone dormant in the fall, seeds were collected for a germination study. In the late fall of 2008, 10 bulbs from the population of flowering *Z. fremontii* surrounding each plot were collected for a total of 60 plants to be used in the transplant experiment.

Transplant Experiment

In order to determine if the effects of the wildfire and prescription fire were persistent in the soil due to nutrient and charrate deposition or if the effects were short term due to some trigger directly associated with fire, such as heat or smoke, a transplantation experiment was conducted. Soil was collected from the prescription burn area, wildfire area, and unburned mature chamise chaparral. Of the 30 bulbs collected from the wildfire region, 10 were planted in soil from the wildfire, 10 were planted in soil from the prescription burn, and 10 were planted in unburned soil. Likewise, of the 30 bulbs collected from the prescription burn area, 10 were planted in each of the three different soils. All bulbs were planted in gallon-sized plastic pots. The pots were placed in a protected open courtyard. They were exposed to ambient temperature and weather, although supplementary water was periodically added to prevent desiccation in the spring. Inflorescence height, flower number, and total leaf area were measured for each plant in spring of 2009 as described above.

Germination Study

Differences in germination rates between seeds grown in soil from the wildfire, prescription burn, and unburned soil were investigated via a controlled germination experiment. In late fall 2009 seeds were collected from the prescription burn area and the wildfire burn area. They were sown in either prescription burn soil, wildfire soil, or unburned soil saturated with deionized water. One hundred seeds per treatment were sown from each burn type into each soil type for a total of 600 seeds. Five seeds were planted in each pot to avoid competition. The pots were covered and incubated in a controlled growth chamber (Conviron E7, Winnepeg, Manitoba, Canada) at 5°C in the dark for 28 days (Keeley et al. 1985). After this cold period, the temperature was increased to 23°C for 21 days. The cycle of cold and warmth was repeated three times for a total of 147 days. Deionized water was added to each pot to keep the soil moist, and seeds were checked for soil moisture approximately every other day. Germination was assessed weekly under green light. Green light was used because the wavelength is not absorbed by chlorophyll, therefore maintaining dark incubation.

Soil Analysis

Nutrient levels in the soil were quantified in the two burn regimes and unburned soil to explore variation in germination and regrowth of *Z. fremontii.* Eight soil samples were collected from each of the six plots as well as eight samples of unburned soil in spring 2009 for a total of 56 soil samples. Samples were sent to A & L Western Agricultural Laboratories (Modesto, California) for soil nutrient analysis.

Statistical Analysis

A MANOVA was used to analyze the data collected from the field using a General Linear Model in SPSS version 16.0. Because the data collected in the first year consisted of flower number and inflorescence height while the second year data consisted of flower number, inflorescence height, and leaf area, the MANOVA was run separately for each year. In order to compensate for multiple comparisons, a Bonferroni Correction was conducted by dividing α by the number of comparisons. In this case, $\alpha = 0.05$ and the number of comparisons is 2, so a p-value of 0.025 must be reached for each test to be considered significant.

Data collected from the transplant experiment were initially analyzed for emergence using a χ^2 test. For the remaining data with all three dependent variables (flower number, inflorescence height, and leaf area), a MANOVA was used to determine if there was a difference in growth pattern based on soil type and fire type from which the bulb originated. Data collected from the germination study were analyzed using a χ^2 test to determine if there was a difference in seedling emergence that depended on substrate collected from the wildfire, prescription burn, or unburned soil.

RESULTS

Field Study

Only inflorescence height was significantly different between the wildfire (dry season) and prescribed (wet season) burn plants, with those in the prescribed burn area being taller than those in the wildfire sites in the first year after fire ($F = 6.213$, $p = 0.014$) (Fig. 2). Mean flower number was not significantly different between the two fire seasons in the first year after fire ($F = 0.680$, $p = 0.411$). In the second year, the difference in inflorescence height was also statistically significant between fire types, with prescription burn plants having taller inflorescences than wildfire plants ($F = 8.131$, $p = 0.005$) (Fig. 2). The differences between the mean total leaf area and mean flower number in the wildfire versus prescribed burn areas in the second year after fire were not statistically significant (leaf area: F = 0.480, p = 0.489, flower number: F = 1.204, p = 0.274) (Fig. 3, 4).

Although the difference in mean flower number between wildfire and prescribed burn areas was not statistically significant in either the first or second year after fire, there was a strong difference in mean flower number between the first and second year for both wildfire and prescription burn sites (Fig 3.). Mean flower numbers in wildfire and prescription burn sites in the first year were 48 and 42, respectively. In the second year, mean flower numbers in wildfire and prescription burn sites were 9 and 12, respectively.

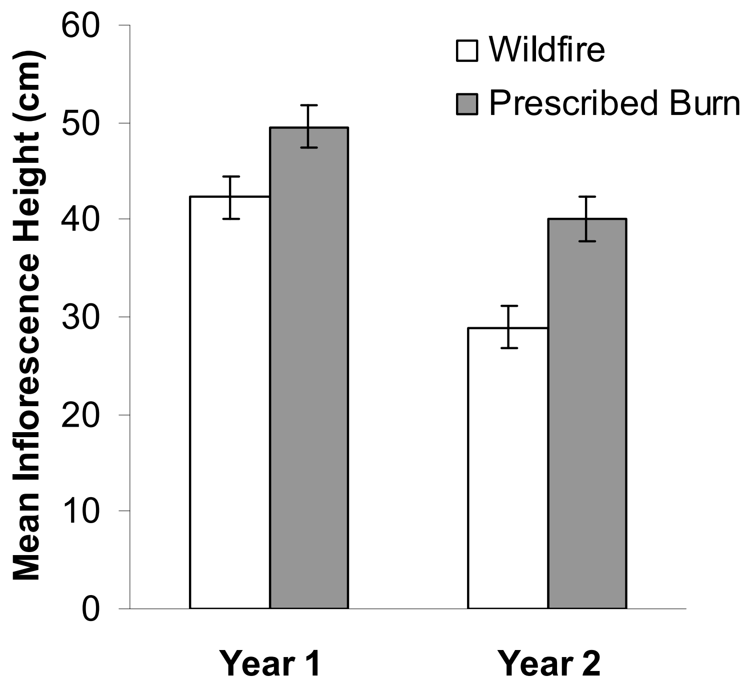

Figure 2. Mean inflorescence height with standard error (SE) by fire type (wildfire/ dry season fire and prescribed burn/wet season fire). Measurements were taken in the first spring after the fires (n = 155) and in the second spring after the fires (n = 146). Year 1: F = 6.213, p = 0.014. Year 2: F = 8.131, p = 0.005.

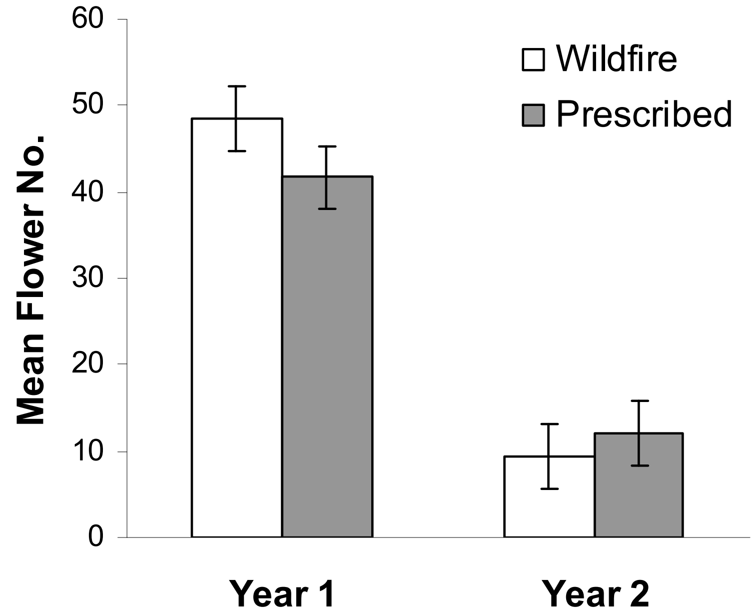

Figure 3. Mean flower number by fire type with SE. Measurements were taken in the first and second spring after fire. Year 1: F = 0.680, p = 0.411, n = 155; Year 2: F = 1.204, p = 0.274, n = 146.

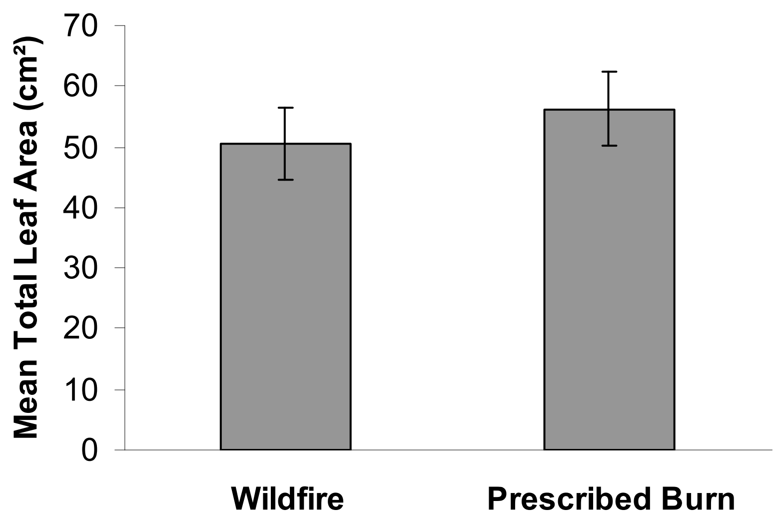

Figure 4. Mean total leaf area by fire type with SE. Measurements were taken in the second spring after fire. F = 0.480, p = 0.489.

Transplant Experiment

Plants transplanted from the wildfire area (dry season) to pots had a lower occurrence of flowering (3 bulbs out of 30 transplanted) compared to plants transplanted from the prescribed burn area (wet season) (23 out of 30) regardless of the soil in which they were planted ($\chi^2 = 43.249$, $p < 0.0001$). Most of the bulbs (22 out of 30 bulbs) from the wildfire area produced only leaves, but not flowers. In contrast, all of the prescribed burn plants that emerged produced flowers (Fig. 5). Because so few bulbs from the Lick Wildfire (dry season) produced flowers, analysis of the soil nutrient interaction with the bulbs was focused on bulbs originating from the prescribed burn area, bulbs from the wildfire area were excluded. A MANOVA revealed no significant difference between inflorescence height, flower number, or leaf area by soil type ($F = 1.769$, $p = 0.128$).

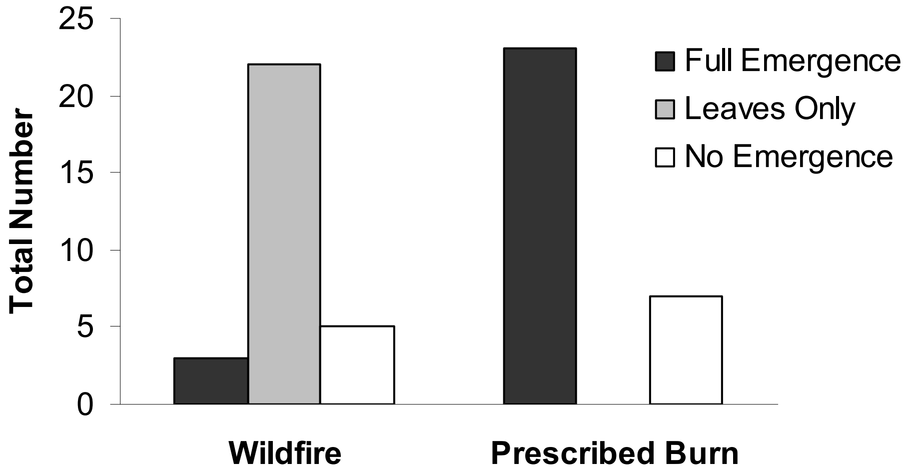

Figure 5. Total emergence by fire type in the second year after fire. Total number of bulbs that gave rise to leaves and flowers (Full Emergence), to leaves only without flowers (Leaves Only), or did not emerge at all (No Emergence). X-axis indicates whether bulb originated from wildfire or prescription burn sites ($\chi^2 = 43.249$, $p < 0.0001$, $n = 61$).

Germination Study

Of the 600 seeds planted for the germination experiment, 225 germinated. After two cycles of cold stratification (28 days each) alternating with warm periods (21 days each), 35% (78) of the seeds germinated. Following a third cold and warm temperature cycle, the remainder of the 225 germinated (147). A higher percentage of the seeds from the prescription burn area germinated than from the wildfire area (124 seeds vs. 101 seeds), although the trend was not significant ($\chi^2 = 9.365$, $p = 0.095$). Fewer seeds originating from the prescribed fire and wildfire that were sown in unburned soil germinated (62 seeds) than seeds sown in either wildfire (80 seeds) or prescribed burn soil (83 seeds) (Fig. 6).

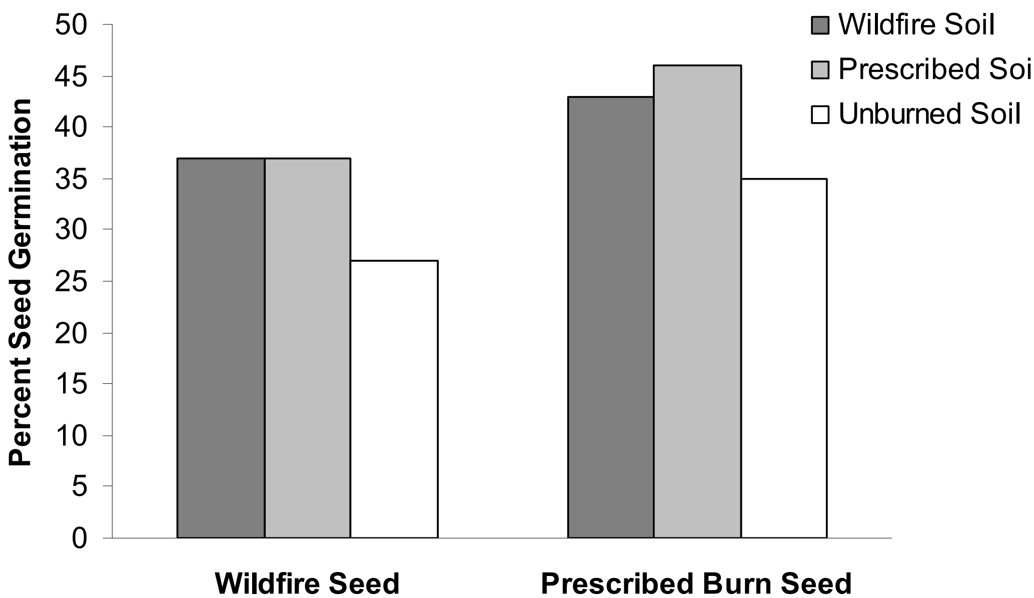

Figure 6. Percent seeds germinated over 21 weeks ($\chi^2 = 9.365$, $p = 0.095$, $n = 225$).

Soil Analysis

Due to potential interactions between the soil minerals and the large number of minerals monitored, the ideal statistical test to perform would be a principal components analysis. This test requires a very large sample size which was unattainable. Therefore, statistical analyses were not completed on soil minerals. With that in mind, trends between soil minerals in the three soil types will be considered. Of the macronutrients, nitrogen, potassium, phosphorous, magnesium, calcium, and sulfur, all but sulfur varied greatly with fire type (Table 2). N was higher in both burned soils than in unburned soil.

The wildfire soils had the highest levels of P, K, Ca, B, and Mn compared to prescription burn or unburned soil. The prescription burn soil had the highest levels of Mg, Na, Zn, Fe, and Cu. Unburned soil had the highest level of organic matter and was intermediate for all other minerals.

Table 2. Mean Soil Mineral Levels. Mean levels of macronutrients and micronutrients in soil from wildfire, prescribed burn, and unburned sites.

Soil Nutrients	*Wildfire Soil*	*Prescribed Burn Soil*	*Unburned Soil*
% Organic Matter	7.5	6.0	7.6
N (ppm)	9.6	9.9	6.1
K (ppm)	234.0	131.9	176.0
P (inorganic) (ppm)	43.3	9.0	17.4
P (organic) (ppm)	35.9	15.3	18.8
S (ppm)	7.8	7.5	7.0
Ca (ppm)	2009.7	1690.3	1694.5
Mg (ppm)	253.6	671.8	358.6
Na (ppm)	18.4	27.0	22.9
Zn (ppm)	1.8	2.3	2.1
Mn (ppm)	41.2	36.5	39.3
Fe (ppm)	27.9	29.0	36.5
Cu (ppm)	0.8	1.1	0.9
B (ppm)	0.5	0.4	0.4

DISCUSSION

Field Study

Plants in the prescribed burn area fully regenerated (flowered) more often than those in the wildfire area. Inflorescences were significantly taller in the prescription burn area than in the wildfire area in both years. The differences in mean flower number and mean total leaf area between the two fire regimes were not statistically significant. N levels were discovered to be higher in burned soils compared to unburned soils due to the high levels of N in ash in the form of ammonium rather than nitrate (Christensen 1973). Increased levels of nitrogen have been found to stimulate vegetative growth and increase flower stalk length (Marschner 1986). In horticultural species of *Lilium,* addition of nitrogen increased average stem length by 25% above that of unfertilized plants (Sajid et al. 2009). Prescription burns and wildfires apparently provided "fertilizer" to the field sites in this study, improving the mineral levels of the soil with respect to P and K in the wildfire soil and N in both fire types. So while nitrogen may contribute to increased vegetative growth, it did not account for the difference in inflorescence length as indicated by the fact that the levels of nitrogen were similar between the prescribed burn (wet season) soil and the wildfire (dry season) soil.

The increased inflorescence height in prescribed burn sites may be explained by reduction of light from incomplete burning in prescribed burn sites compared to wildfire sites. The lower intensity prescribed burn removed less vegetation and created more shade than the high intensity wildfire. The plants in the wildfire sites did not need to extend their flowers as high above the vegetation to be more accessible to pollinators as the plants in the prescribed burn sites. Studies manually removing the canopy could be conducted to verify this hypothesis.

Although the difference in flowering between the prescription burn and wildfire area in either the first or second spring after fire were not statistically significant, there was a difference in mean flower number between the first and second years for both fire types. One hypothesis to explain this pattern is that the combination of fire signals and increased light availability may trigger production of a high volume of flowers in the first year. The energy required to produce such a high number of flowers in the first year depletes reserves in the bulb resulting in lower flower production in the following year.

Tyler and Borchert (2003) found that flowering in *Z. fremontii* was infrequent beyond the first year after a wildfire. They determined that decreased flowering was a result of decreased bulb reserves from high energy flower output in the first year, suggesting that the bulb must have a minimum amount of reserves before flowering would occur (Tyler & Borchert 2003). The minimum bulb volume may also relate to decreased flower output in the second year after fire, as observed in this study.

Transplant Experiment

All bulbs collected had flowered in the spring of 2008; they were transplanted in the late fall of 2008 to pots containing one of three soil types. The following spring, all but seven of the bulbs from the prescribed burn area flowered. On the other hand, only three of the wildfire bulbs flowered while 22 produced leaves without flowers. These results concerning the plants from the wildfire sites were consistent with those of Tyler and Borchert (2003), where the incidence of flowering of *Z. fremontii* in the first year after a wildfire was about 90% compared to almost no flowering the following year, and most of the plants did produce leaves. In a study of succession of herbaceous flora in California chaparral, Keeley et al. (1981) found that herbaceous growth was stunted in the second year after fire, such that plants were shorter and species cover less in the second year compared to the first year after fire. This result was attributed to a decrease in precipitation the second year after fire. Precipitation remained fairly constant over the period of our current study (54.81 cm in the 2007-2008 season and 52.24 cm in the 2008-2009 season), making it questionable that changes in precipitation explain the flowering decline we found. The reasons for the different prescription burn response may very well involve other factors resulting from the fire, cues generated by a high intensity fire that are lacking in a low intensity controlled burn. The most likely change resulting from the high intensity fire that would carry forth to the growing season a year away to prevent flowering would be in soil characteristics such as changes in available minerals and changes in soil texture resulting in differences in water-holding capacity and light penetration.

Leaf emergence in *Z. fremontii* begins by early January, and flowering begins by late February. Energy from the bulb is required for leaf growth, but soon after emergence, the leaves begin generating enough photosynthate to restore carbohydrates to the storage organ (Muller 1978). Because prescribed burns are carried out during the wet season (February in this study), the fire would have destroyed newly emergent leaves, if present. Clipping the leaves of *Z. paniculatus*, a species common to sagebrush plant communities, during the growing season led to a decrease in mass of the bulb by the end of the growing season (Emms 1996). In a similar study of the effect of fire and defoliation on *Z. nuttallii*, a tallgrass prairie species, bulb mass was reduced by 70% by leaf clipping compared to control plants (Knapp 1986). Surprisingly, plants defoliated by fire during the growing season increased their bulb mass by season's end to levels similar to plants in unburned sites (Knapp 1986), indicating greater uptake from the soil or greater photosynthate accumulation. Our own findings of inflorescence height enhancement as a result of fire agree with the findings in Knapp's (1986) study, such that a fire during the wet season did not hinder growth and productivity of *Z. fremontii* and apparently led to plants in the next growing season with the capacity for both reproductive and vegetative growth. The dry season fire in our study, however, led to plants lacking in the ability to reproduce the following season.

Knapp (1986) also found that the production of a flower stalk did not affect bulb mass at the end of the season for any of the treatments suggesting that production of photosynthate by leaves is sufficient to supply resources to maintain bulb volume even during flowering. However, bulb size could be maintained despite a decrease in starch content, a parameter not measured directly in Knapp's (1986) study. So it is possible that flowering depletes reserves sufficiently to preclude subsequent flowering. Leaf production and photosynthate accumulation would have to intervene to replenish lost reserves. The prescription burn likely destroyed any *Z. fremontii* leaves in February 2007, preventing flowering in that growing season, but not necessarily leaf production after the fire. Leaves would then produce photosynthate that would replenish bulb volume before the spring 2008 growing season. Bulbs from the prescription burn area might have had a head start in terms of storage reserves that the wildfire plants were lacking. Therefore, prescription burn plants would have the ability to reproduce in subsequent years, unlike the wildfire plants. However, if the starch content of the bulbs in Knapp's (1986) study on a tallgrass prairie species of *Zigadenus* was in fact unaffected by flowering, then the seasonal fluctuation in reserve content would not account for the flowering distinctions observed between the prescribed burn and wildfire plants in this study.

Of the plants that resprouted with leaves and flowers, there was no significant difference in their response to the different soil types in inflorescence height, leaf area, or flower number and therefore to differences in available soil nutrients. Likewise, all plants in the transplant experiment were exposed to similar light levels, so increased light availability did not explain the different developmental pattern between bulbs from the wildfire and prescribed burn sites. Thus the odd response of the prescribed burn plants (flowering season after season) are difficult to explain. With a wildfire, flowering occurred after the fire then was suppressed a year later; it seems unlikely that this pattern could be explained by heat, smoke, changes in O_2 partial pressure, or other direct fire effects with the exception of the soil characteristics explored above. Several studies investigated the effect of smoke and heat on the germination of numerous species (Keeley et al. 1985), but none have investigated the effect of these factors on the process of resprouting from underground storage organs in herbaceous species.

One hypothesis for the response observed in this transplantation experiment is that the bulbs in the wildfire sites may have been injured from high intensity fires. That is, that flowering in the first year combined with injury from a high intensity fire is too much stress to result in flowering the following year. Several studies have determined that there must be a minimum bulb size in order for flowering to occur in species with underground storage organs (Tyler & Borchert 2003; Borchert & Tyler 2009). The minimum bulb size may also relate to the need to repair or regenerate injured tissues before subsequent flowering. Lower intensity prescribed fires occurring in the wet season may be hot enough to stimulate flowering without damaging the bulb, allowing for flowering in subsequent years. Further studies could investigate not only the specific fire cue related to flowering or its suppression, but also whether bulbs exposed to high intensity fires become damaged from high heat.

Germination Study

Seeds planted in burned soil, regardless of burn season, germinated more readily than those planted in unburned soil. While not statistically significant, this result was the general trend. Germination percentage was not affected by the burn area from which seeds originated. Because the seeds used in this study were from plants of *Z. fremontii* that flowered post-fire, these seeds were not exposed to direct fire cues such as heat or smoke. Instead, fire increased the concentration of available nutrients in the soil, apparently allowing for higher germination rates than seeds sown in unburned soil. Other soil characteristics, such as soil density (itself a factor or affecting light or water availability), leachate from other plants, or charrate presence, could be responsible for this difference in germination. Keeley et al. (1985) found that germination in *Z. fremontii* increased with addition of charrate and leachate residue from chamise (*Adenostoma fasciculatum*), while almost no germination resulted from heat treatments. This indicates that seeds from *Z. fremontii* are responding positively to increased nutrient availability. Germination increases after fire were observed in many herbaceous species by Ooi et al. (2004) and Williams et al. (2005), but the seeds in these studies were those deposited in the field in previous seasons as a seed bank and thus were exposed to direct fire; direct fire factors, such as heat and smoke, were cited as possible signals but indicate that soil characteristics are more likely controls.

Two cycles of 4-week cold/3-week warmth were required to generate a high proportion of germination, suggesting an extensive cold requirement for germination. This study indicates that fire-derived germination signals alone are insufficient to stimulate germination. Among stratified seeds not exposed to fire, germination occurred to some extent (31%) in unburned soils, albeit less than burned soils (41%). Therefore, cold alone is also insufficient to cause a maximum germination response. Seeds of *Z. fremontii* produced from post-fire flowering events delay germination until conditions are favorable (Bond 1984; Williams et al. 2005; Knox & Clarke 2006a). Delayed germination in Mediterranean climates is likely advantageous because it ensures that not only are seeds germinating during the wet season, but there is also reduced competition from both adult shrubs and understory herbaceous species which are removed by fire allowing more light to reach seeds and seedlings (Ool et al. 2004).

Conclusions

Prescription burns occurring in the wet season stimulated germination, vegetative regeneration, and reproduction of *Z. fremontii*. It is especially surprising to us to find that plants presumably well adapted to the natural wildfire occurrence in the chaparral community were actually better served in terms of their subsequent reproductive success by a low intensity fire in the wet season. Bulbs exposed to a wet season burn not only grew taller inflorescences, but also flowered more often in the second year than those exposed to a dry season wildfire. Prescription burns have been shown to produce a mosaic pattern of varying fire intensities, although at lower maximum temperatures, that mimics wildfire patterns as well as creating gaps near unburned locations that allow for influx of seeds into newly burned sites (Knapp & Keeley 2006). The soil from the prescription burn site was comparable to that from the wildfire site in its ability to stimulate germination exceeding that in unburned soils. This evidence suggests that geophytes can benefit from fires set outside of the natural fire season of chaparral ecosystems. For land managers, this study supports the beneficial effects of prescription burns set outside of the natural fire season and for geophytes in particular, wet season fires seem to promote increased reproductive output compared to wildfires during the dry season.

In terms of the life history of *Z. fremontii*, the positive response to wet season fires may suggest that its response to wet season fire may have evolved with species such as *Zigadenus nuttallii* which are exposed to wet season fires in the tall-grass prairies (Knapp 1986). Seeds of *Z. fremontii* benefit from the nutrient rich environment post-fire as shown with increased germination in burned *vs*. unburned soil, but are likely not exposed to direct fire cues due to their negative response to high heat treatments in the study by Keeley et al. (1985). Further studies exploring the effect of direct fire signals on flowering and its suppression as well as potential bulb injury from high intensity fires will add to the understanding of the life history of this species.

Literature Cited

Beyers, J. L., and C. D. Wakeman. 1997. Season of burn effects in southern California chaparral. Interface Between Ecology and Land Development in California conference, Los Angeles, CA.

Bond, W. J. 1984. Fire survival of cape Proteaceae: Influence of fire season and seed predators. Vegetatio **56:** 65-74.

Bond, W. J., and J. J. Midgley. 2003. The evolutionary ecology of sprouting in woody plants. International Journal of Plant Sciences **164**(3, Supplement: Evolution of Functional Traits in Plants): S103-S114.

Borchert, M., and C. M. Tyler. 2009. Patterns of post-fire flowering and fruiting in *Chlorogalum pomeridianum var. pomeridianum* (DC.) Kunth in southern California chaparral. International Journal of Wildland Fire **18:** 623-630.

Christensen, N. L. 1973. Fire and the nitrogen cycle in California chaparral. Science **181:** 66-68.

Dodson, E. K., D. W. Peterson, and R. J. Harrod. 2008. Understory vegetation response to thinning and burning restoration treatments in dry conifer forests of the eastern cascades, USA. Forest Ecology and Management **255:** 3130-3140.

Egerton-Warburton, L. M., and E. L. Ghisalberti. 2001. Isolation and structural identification of a germination inhibitor in fire-recruiters from the California chaparral. Journal of Chemical Ecology **27:** 371-382.

Emms, S. K. 1996. Temporal patterns of seed set and decelerating fitness returns on female allocation in *Zigadenus paniculatus* (Liliaceae), an andromonoecious lily. American Journal of Botany **83:** 304-315.

Franklin, J., A. D. Syphard, H. S. He, and D. J. Mladenoff. 2005. Altered fire regimes affect landscape patterns of plant succession in the foothills and mountains of southern California. Ecosystems **8:** 885-898.

Hickman, J. C., editor. 1996. *The Jepson Manual: Higher plants of California*. 3rd edition. University of California Press, Berkeley, California.

Hiers, J. K., R. Wyatt, and R. J. Mitchell. 2000. The effects of fire regime on legume reproduction in longleaf pine savannas: Is a season selective? Oecologia **125:** 521-530.

Keeley, J. E., B. A. Morton, A. Pedrosa, and P. Trotter. 1985. Role of allelopathy, heat and charred wood in the germination of chaparral herbs and suffrutescents. Journal of Ecology **73:** 445.

Keeley, J. E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology **68:** 434-443.

Keeley, J. E., and C. J. Fotheringham. 1998. Smoke-induced seed germination in California chaparral. Ecology **79:** 2320-2336.

Keeley, J. E. 2002. Fire management of california shrubland landscapes. Environmental Management **29:** 395-408.

Keeley, J. E. 2006. Fire management impacts on invasive plants in the western United States. Conservation Biology **20:** 375-384.

Keeley, J. E., T. Brennan, and A. H. Pfaff. 2008. Fire severity and ecosytem responses following crown fires in California shrublands. Ecological Applications **18:**1530-1546.

Keeley, S. C., J. E. Keeley, S. M. Hutchinson, and A. W. Johnson. 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.

Knapp, E. E., and J. E. Keeley. 2006. Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest. International Journal of Wildland Fire **15:** 37-45.

Knox, K. J. E., and P. J. Clarke. 2006a. Fire season and intensity affect shrub recruitment in temperate sclerophyllous woodlands. Oecologia **149:** 730-739.

Knox, K. J. E., and P. J. Clarke. 2006b. Response of resprouting shrubs to repeated fires in the dry sclerophyll forest of Gibraltar range national park. Proceedings of the Linnean Society of New South Wales **127:** 49-56.

Lloret, F., M. Verdu, N. Flores-Hernandez, and A. Valiente-Banuet. 1999. Fire and resprouting in Mediterranean ecosystems: Insights from an external biogeographical region, the mexical shrubland. American Journal of Botany **86:** 1655-1661.

Lloret, F., and M. Vila. 2003. Diversity patterns of plant functional types in relation to fire regime and previous land use in Mediterranean woodlands. Journal of Vegetation Science **14:** 387-398.

Marschner, H. 1986. *Mineral nutrition of plants*. Academic Press, London, England.

Muller, R. N. 1978. The phenology, growth and ecosystem dynamics of *Erythronium americanum* in the northern hardwood forest. Ecological Monographs **48:** 1-20.

Ooi, M. K. J., T. D. Auld, and R. J. Whelan. 2004. Delayed post-fire seedling emergence linked to season: A case study with *Leucopogon* species (Epacridaceae). Plant Ecology **174:** 183-196.

Peterson, D. W., and P. B. Reich. 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. Plant Ecology **194:** 5-16.

Sajid, G. M., M. Kaukab, and Z. Ahmad. 2009. Foliar application of plant growth regulators (PGRs) and nutrients for improvement of lily flowers. Pakistan Journal of Botany **41:** 233-237.

Tyler, C., and M. Borchert. 2003. Reproduction and growth of the chaparral geophyte, *Zigadenus fremontii* (Liliaceae), in relation to fire. Plant Ecology **165:** 11-20.

Williams, P. R., R. A. Congdon, A. C. Grice, and P. J. Clarke. 2005. Effect of season of burning and removal of herbaceous cover on seedling emergence in a eucalypt savanna of north-eastern Australia. Austral Ecology **30:** 491-496.

Zald, H. S. J., A. N. Gray, M. North, and R. A. Kern. 2008. Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. Forest Ecology and Management **256:** 168-179.