store it (with the exception of geophytes). They must be able to quickly exploit moisture when available and survive in between. It is a remarkable evolutionary achievement.

Fire Adaptations

Fire is viewed as separate from life, a destroyer of things. When studying biology in school, the subject is conspicuously absent from the curriculum, even at the university level. The omission is regretful because in many ecosystems, fire is as important as rainfall in shaping community structure and the organisms that live there. In especially fire-prone environments like California chaparral, a lack of specialized fire adaptations prevents a species from existing there. This does not mean the chaparral "needs to burn" to remain healthy or that it is immune from fire as a destructive force. It merely illustrates the system's ability to continue existing in the face of a powerfully disruptive force under natural conditions.

In their response to fire, chaparral shrubs and herbaceous perennials can be classified into five different groups, each with its own survival strategy: obligate resprouters, obligate seeders, endemic fire followers, facultative seeders, and frequent fire followers (fig. 1-12).

STRATEGY	STUMP SPROUT	SEEDS	PLANT TYPE	EXAMPLE
Obligate resprouter	Yes	Transient seed bank. No fire response. Seed life: less than one year.	Shrub, Herbaceous perennials	*Quercus berberififolia, Heteromeles arbutifolia, Prunus ilicifolia.* Geophytes
Obligate seeder	No, plant dies	Large seed bank. Germinate after fire. Seed life: decades.	Shrub, Herbaceous perennials	Most *Artcostaphylos* species. 80% of *Ceanothus* species. *Dicentra chrysantha* Serotinous pines
Endemic fire followers	No, annual life span	Large seed bank. Germinate only after fire. Seed life: decades.	Annuals	*Emmenanthe penduliflora Phacelia grandiflora Phacelia brachyloba*
Facultative seeder	Yes	Large seed bank. Germination can be fire dependant or not. Seed life: decades.	Shrub, Herbaceous perennials	*Adenostoma fasciculatum Malosma laurina* 20% of *Ceanothus* species. Five *Arctostaphylos* species.
Frequent fire followers	No, annual life span	Polymorphic seed banks. Germination enhanced by fire cues. Seed life: dormant-type for decades.	Annuals	*Antirrhinum coulterianum Lupinus bicolor Cryptantha micromeres*

Fig. 1-12 Reproductive Response to Fire. *Chaparral plants are able to recover from fire by using one of five strategies. Obligate refers to an organism with only one lifestyle. Obligate resprouters survive a fire only by resprouting. Facultative refers to a double lifestyle. Facultative seeders survive fire by resprouting and by post-fire seed germination.*

Obligate resprouters are possibly relic species from a time when the climate of southern California was sub-tropical and fires played a smaller evolutionary role than they do today. Consequently, these plants are found in more mesic environments such as north-facing hillsides and canyon bottoms. They survive burns because of their ability to stump sprout. Their seeds, frequently surrounded by some fruity covering, are short-lived and likely do not survive into the fire season, either succumbing to decay or by being eaten. A thick layer of leaf litter is typically required for their successful germination, which is one reason seedlings of obligate resprouters are seldom observed in mature chaparral stands less than 50 years old (Keeley 1992). Toyon *(Heteromeles arbutifolia)* (#52) and holly-leafed cherry *(Prunus ilicifolia)* are obligate resprouters.

Obligate seeders die in fires, but their populations recover because their seeds survive to germinate. Most are fire-dependant, producing seeds requiring some kind of fire cue such as heat, charred wood, or smoke to stimulate their germination. Obligate seeder shrubs are typically found in concentrated, even-aged stands. These homogenous populations exist for two reasons. First, their seeds are small and do not have structures encouraging animal or wind distribution. Most go no further than the canopy directly below the mother plant (Keeley 1991a). Secondly, since the seeds respond to the same fire cue at the same time, all the adult plants have the same birthday. Cupleaf ceanothus *(Ceanothus greggii)* (#47) and bigberry manzanita *(Arctostaphylos glauca)* (#23) are classic obligate seeders. In contrast to obligate resprouters, obligate seeders are frequently found in xeric areas like ridge tops, flat mesas, and south-facing hillsides.

Serotiny, used exclusively by conifers, represents an interesting twist to the obligate seeding strategy. Serotiny refers to conifers that produce serotinous cones, meaning they remain closed and on the tree for a year or more after maturity, opening to release their seeds only after being fire-stimulated. The seeds then scatter over the burned ground, setting the stage for the next generation. The seeds do not depend on a fire cue per se, rather the heat of the fire to set them free. Although trees are not a component of chaparral, there are localized populations where conifers punctuate the shrubbery, especially as remnants of larger stands in the past and at higher elevations. The Tecate cypress *(Cupressus forbesii)*, restricted to Orange and San Diego Counties and northern Baja California, is one example. These are truly remarkable trees with crimson bark and tiny cones about the size of a quarter. One old growth population, nestled within the canyons of the northern Santa Ana Mountains, once contained an individual with a trunk eight feet in diameter until it burned in 2002.

There are various levels of serotiny. The Coulter pine *(Pinus coulteri)* has a varied serotinous nature depending on the community in which it lives. In some stands, serotiny is uncommon, but for trees within chaparral the cones can remain attached and closed for as long as 25 years (Lanner 2002). Interestingly, the Torrey pine, found in maritime mixed chaparral is only partially serotinous. Although it will release its seeds over several seasons without a heat stimulus, it can retain cones for up to 15 years (Lanner 2002). A noteworthy population of Knobcone pine *(Pinus attenuata),* whose cones are tightly sealed with resin, exists on Pleasants Peak in the Santa Ana Mountains. Since these trees are unable to compete with the surrounding chaparral, they are often found inhabiting islands of nutrient poor serpentine soil where shrubs are stunted and sparse.

In addition to obligate seeding woody species and perennials there are a number of annuals that have overwhelming dependence on fire for proper germination. These are the **endemic fire followers**, partially responsible for the explosive post-fire wildflower bloom observed after winter rains (frequent fire followers make up the rest). Once they have grown, set seed and died, most of these species will not reappear until after the next fire. As with obligate seeding shrubs, these fire following annuals, like *Phacelia brachyloba* (#15), can blanket entire hillsides to the exclusion of almost any other species.

Facultative seeders play both sides of the fire survival game; seed germination as well as being able to resprout from a root burl. These include dominant shrubs such as chamise *(Adenostoma fasciculatum)* (#50), laurel sumac *(Malosma laurina)* (#5), and whitebark ceanothus *(Ceanothus leucodermis)* (#48).

Ceanothus and manzanita, the definitive chaparral shrubs, have a number of facultative members. Of the five manzanitas that resprout, only one, *Arctostaphylos glandulosa,* is common in southern California. About 20% of the ceanothus, mostly in the subgenus *Ceanothus*, resprout. An interesting variation exists with the common blue flowering Ramona lilac, *Ceanothus tomentosus* (#47). The northern California populations in the Sierra Nevada are resprouters, but disjunct (widely separated) populations in southern California are non-resprouters. There is speculation the loss of the resprouting trait may have something to do with the evolutionary selection pressures created by climatic change, but the answer remains elusive (Schwilk 2002).

Some facultative seeders, like *Arctostaphylos glandulosa* and chamise, are especially fire responsive. Their seeds require a fire cue to germinate despite their resprouting ability. This duplicitous response to fire has led at least one fire ecologist to humorously suggest the species are in serious need of genetic counseling (J.E. Keeley 2004, personal communication).

Frequent fire followers are annuals with polymorphic seeds, a percentage of which remain dormant in the soil and are cued to germinate after a fire. The common bicolor lupine *(Lupinus bicolor)* (#27) and the little popcorn flower *Cryptantha micromeres* (#16) are in this group.

Earth Plants

Geophytes deserve special mention regarding response to fire. These are strictly herbaceous (having only soft, fleshy plant parts) and emerge from an underground storage organ such as a bulb, corm, or enlarged root. Monocot geophytes are the plants that produce some of the most magnificent wildflowers after a fire. Species such as wild hyacinth *(Dichelostemma capitatum)* (#60), mariposa lily *(Calochortus species)* (#57), and soap plant *(Chlorogalum parviflorum)* (#55) color the scene with delightful blossoms perched on tall, thin stalks waving in the breeze. Paradoxically, these plants emerge from deep underground structures that are unaffected by the flames above. Their prolific response to fire raises an intriguing question. Why would fire have any influence on their flowering patterns? Claudia Tyler and Mark Borchert (2003) did a nine-year investigation of one geophyte, Fremont's camus *(Zigadenus fremontii)* (#58), and provided some answers.

In their study area within the Santa Ynez Mountains, northwest of Santa Barbara, they found camus produced an abundant number of flowers and seeds the spring following a burn. In an unburned section nearby, not only were camus flowers scarce, but the few blossoms produced rarely made any seeds. However, the bulbs grew the largest and greatest number of leaves when compared to those in the burned area. As the research progressed it was discovered in nearly all subsequent years after the fire, the same plants that flowered so profusely showed dramatically reduced leaf production. The plants rarely flowered again.

Tyler and Borchert have suggested that in mature chaparral, camus gradually collects energy obtained through photosynthesis and stores the surplus in its underground bulb. Once fire eliminates the canopy, high light levels stimulate the plant to tap into those energy reserves to produce flowers. The results can be dramatic. Acres of land that have not seen camus flowers in years are suddenly covered by them. The following year, the plant's energy stores exhausted, only puny leaves are produced. Another impressive round of flower production is virtually impossible.

What of the seeds? Tyler and Borchert discovered that within four years all viable seeds germinated. Fremont's camus does not form a persistent seed bank. This means the survival of the species depends on long-lived adults that can span the time between fires. Further research is needed on other species, but from the camus investigation it appears that increased sunshine is the primary cue for the explosive, post-fire flowering response of the geophytes. However, it is important to remember that just because one study reveals data supporting a particular hypothesis, it does not necessarily eliminate all others.

In an experiment on a South African fire-lily *(Cyrtanthus ventricosus),* it was demonstrated that it would flower only after being treated with smoke (Keeley 1993). Plants exposed to sunlight alone did not germinate. It turns out that the flower buds are preformed within the bulb. No matter what time of year the fire occurs, the fire-lily will blossom five days later. Although this is unlike any species found in North America, it does demonstrate the wide variety of responses plants can have to periodic flames.

Developing Fire Survival Strategies

Evolution has shaped the chaparral and continues to do so. However, it is important to understand what exactly is evolving. To say individual chaparral plants have "adapted" to fire over time in order to survive is incorrect. Species evolve and adapt, individual living things do not. Plants cannot slowly change in order to survive an explosive inferno. They either have what it takes before hand or die. This is one of the basic principles of evolution.

The sprouting behavior of laurel sumac (#5) is an example. Upon casual observation it appears this plant has adapted to survive fire because the entire above ground portion can be incinerated yet the root stock remains alive. Within weeks, little green shoots emerge from the blackened base and after a few years the plant returns to its original size. Has laurel sumac adapted to fire in the chaparral? Not exactly. Long before the chaparral fire regime began developing approximately ten million years ago, laurel sumac was a resprouting, forest understory plant. The resprouting behavior is nothing new, but a perfect example of pre-adaptation; a characteristic that provides an organism some future advantage in a changing environment (Wells 1969). Laurel sumac did not obtain re-sprouting because of fire, it already had it. As the environment changed by becoming drier and more susceptible to fires, laurel sumac was able to survive because of a fortuitous characteristic it possessed beforehand. Other species not as fortunate were extirpated.

As time went on, a finer evolutionary process took over. Every individual is slightly different. There is always variation within a population. Some laurel sumac plants were better at resisting fire than others. Those "better resisters" produced more offspring than individuals more seriously damaged, creating a population of even better fire survivors. This is where the "adapt over time" idea comes from. Once a trait is selected by nature, in this case re-sprouting, evolution selects those individuals with better versions of the trait than others and the species as a whole becomes better adapted to fire in the chaparral. After the trait was selected, the species as a whole evolved through time improving the fire resisting characteristic. The same process goes on with all living things. The better individual survives and passes on those better characteristics to the next generation.

Obligate seeding shrubs, such as the majority of ceanothus and manzanita species, could be considered the true "chaparralians" because their life cycle requires a fire regime specific to the chaparral ecosystem. They are the new kids on the block. Their specialized fire adaptations have been fined tuned as California became dominated by a Mediterranean climate over the past 14 million years.

Fire Cues

If the complete yearly seed crop from chaparral plants were to germinate after the first winter rains, every species would be betting its entire inheritance on a single event. This is not the best survival strategy, especially in a semi-arid environment. So the question arises, when is the optimal time for germination and how is this time signaled to the seed?

Plants compete with each other for space, light, water, and nutrients. Post burn sites are like pirate's plunder. Huge amounts of acreage are cleared, the competition has been scorched, sunlight is everywhere and nutrients once locked away in the stems and leaves are lying about like gold coins. Seedlings also get a reprieve from plant nibblers since fire dramatically reduces herbivore populations. Those remaining must contend with bare ground without cover, not the best place for rodents and rabbits to scurry about unprotected from predators. This is the kind of situation designed for an evolutionary drama. Plants with seeds resistant to germinating until conditions are right, like after a fire, have an advantage over those without such innate dormancy mechanisms. Over the past ten million years, a significant number of species have evolved under such conditions, becoming dependent on specific fire regimes for their continued reproductive success. The three primary fire cues utilized for signaling the proper germination time are **heat, charred wood,** and **smoke.** Fire cues work by either physically altering the seed coat or chemically influencing the tissues beneath.

Without water, seeds cannot germinate. Since an impermeable seed coat encloses embryos within many chaparral seeds, germination will not occur until those barriers are broken by **heat**. Some species produce polymorphic seeds, meaning some require heat while others do not. For example, yellow rock rose *(Helianthemum scoparium)* (#19) splits its seed production by producing some that germinate easily with just moisture while others require temperatures approximately 250 degrees Fahrenheit for a minimum of 5 minutes. There are limits of course. Temperatures nearing 300 degrees Fahrenheit prove fatal to the little embryos (Keeley 1991b).

The other two fire cues capable of inducing seed germination are chemicals from **charred wood** or **smoke**. Chemicals leached from these substances alter internal membranes within the seed, stimulating growth. The shrub chamise *(Adenostoma fasciculatum)* (#50), and caterpillar phacelia *(Phalecia cicutaria)* (#15), a common fire-following annual, are examples of species responding to such chemicals. Interestingly, nearly all the species responding to charred wood show even higher germination rates when exposed to smoke, so apparently similar processes and chemicals are involved but are delivered more effectively with smoke. In fact, dormant seeds that show only 40% to 60% germination success from charred wood achieve 100% germination rates when exposed to smoke. Matilija poppy *(Romneya coulteri)* (#42) and whispering bells *(Emmenanthe penduliflora)* (#13) fall into this smoke-loving group. All show 0% germination with moisture alone and none of them are known to respond to heat (Keeley and Fotheringham 1998). Before drawing too many conclusions from this data, however, it's important to understand that it is more difficult to control the amount of chemical leaching off charred wood than it is when applying smoke. The lower percentage germination with charred wood data may be more reflective of experimental procedures than an accurate measurement of what happens in nature (Keeley, personal communication).

In experimental tests, smoke treated soil or smoke treated water elicit the same basic response as charred wood and direct smoke. The exact identity of the chemicals involved or the mechanism explaining how germination is induced has yet to be identified. G.R. Flematti et al. (2004) claimed to have isolated the active ingredient in smoke, but they failed to provide evidence demonstrating fire cues were required for stimulating or enhancing the germination of the seeds they tested. The search goes on.

One intriguing story relating to seed dormancy has to do with the exquisite golden eardrops *(Dicentra chrysantha)* (#40). This member of the poppy family can grow six feet tall and has bright yellow flowers with four delicate petals that look like curled earrings. This perennial exists only during the first few years after a burn, so it is clear some fire cue is required for germination. However, in multiple laboratory studies conducted by J.E. Keeley and colleagues on more than 50,000 seeds over a period of 15 years, the plant's seeds failed to germinate in response to any known fire cue. After a few insightful discussions around the lab table, they decided to bury the seeds for a while to see if some in-soil ripening was required. It was. Seeds of golden eardrops require at least a year of soil contact before they will germinate, and only then after exposure to smoke. Bush poppy *(Dendromecon rigida)* (#39) and woolly bluecurls *(Trichostema lanatum)* exhibit similar hard-to-germinate characteristics (Keeley and Fotheringham 1998).

When studying how plants respond to fire, it is important to differentiate between the actual response to fire and how the plant survives in the absence of fire. For example, deerweed *(Lotus scoparius)* (#26), an obligate seeder, responds after fire by seed germination. The adult plant dies. However, when examining the species entire reproductive cycle, its seeds will sometimes germinate in the absence of fire. Being an obligate seeder does not necessarily mean it is completely fire dependent, it just means the species responds to fire only by germination (fig. 1-13).

Another potentially confusing point relates to facultative seeders when comparing plants like chamise and laurel sumac. Both resprout and both germinate after fires, yet they have radically different reproductive cycles. Chamise is fire dependent (seeds require heat for germination), and laurel sumac is not, although some of its seeds survive after the burn to germinate. Keeping fire response and the whole reproductive perspective separate is important to avoid becoming confused.

Seeds Responding to Heat

COMMON NAME	SPECIES	FIRE RESPONSE	REPRODUCTIVE CYCLE
Cupleaf ceanothus	*Ceanothus greggii*	Obligate seeder	Fire responsive
Whitebark ceanothus	*Ceanothus leucodermis*	Facultative seeder	Fire responsive
California fremontia	*Fremontodendron californicum*	Facultative seeder	Fire responsive
Deerweed	*Lotus scoparius*	Obligate seeder	Mostly fire responsive, but has polymorphic seeds
Yellow rock rose	*Helianthemum scoparium*	Obligate seeder	Mostly fire responsive, but has polymorphic seeds
Laurel sumac	*Malosma laurina*	Facultative seeder	Fire independent, enhanced germination
White sage	*Salvia apiana*	Facultative seeder	Fire independent

Seeds Responding to Charred Wood and Smoke

COMMON NAME	SPECIES	FIRE RESPONSE	REPRODUCTIVE CYCLE
Whispering bells	*Emmenanthe penduliflora*	Endemic fire follower	Fire responsive
Golden eardrops	*Dicentra chrysantha*	Obligate seeder	Fire responsive
Matilija poppy	*Romneya coulteri*	Facultative seeder	Fire responsive
Eastwood manzanita	*Arctostaphylos glandulosa*	Facultative seeder	Fire responsive
Chamise	*Adenstoma fasciculatum*	Facultative seeder	Fire responsive
White snapdragon	*Antirrhinum coulterianum*	Frequent fire follower	Fire independent, enhanced germination
Caterpillar phacelia	*Phalecia cicutaria*	Frequent fire follower	Fire independent, enhanced germination
White sage	*Salvia apiana*	Facultative seeder	Fire independent

Fig. 1-13 Fire Cues, Fire Response, and Reproductive Cycles of Selected Southern California Chaparral Plants. *Data based on results from most recent laboratory research. Adapted from Keeley (1991b) and Keeley and Fotheringham (1998).*

The search to discover the dynamics of post-fire germination is an amazing story involving both scientific discipline and imagination. The first species to be shown to respond to charred wood was whispering bells *(Emmenanthe penduliflora)* in 1977 by D.T. Wicklow. There are other plants that retain their secrets. For example, mission manzanita *(Xylococcus bicolor)* (#24) may or may not require some fire cue for germination.

The species commonly resprouts, but seedlings of the species appear to be non-existent or extremely rare in both mature chaparral stands and post-fire environments. We do not know whether something in the environment has changed enough to prevent germination or there are other mechanisms involved.

Type Conversion

Ever since humans have been in California in significant numbers, the chaparral has been vulnerable to both purposeful and accidental elimination. It probably all started approximately 5,000 years ago when there was a dramatic shift in the diet of Native Americans. The huge Clovis spear points used to take down mastodons and other large mammals disappeared from the North American archeological record about 5,000 years ago and were replaced by mortars and other stone grinding tools. One source of energy, large mammals, was replaced by another: plants, seeds, and roots. However, deer remained important and Native Americans practiced land management to increase their numbers.

As chaparral re-dominates an area several years after a burn, deer populations slowly decrease as the amount of herbaceous browse declines. One of the ways to bring the deer back is to burn again (Biswell, et al. 1952). There are large numbers of documented accounts from early explorers that described Native Americans burning the landscape. For example, in 1792 Jose Martinez wrote, "In all of New California from Fronteras northward the gentiles (Indians) have the custom of burning the brush," (Simpson 1938). The mosaic pattern of various types of plant communities seen today in California may very well be an artifact of Native American land management practices, especially where more open habitats intrude into pure stands of chaparral (Keeley 2002). No doubt Native Americans knew that complex mosaics of habitat supported larger deer populations better than chaparral alone (Tabor 1956). Unfortunately, this artificial disturbance also set the stage for the successful invasion of Eurasian weedy annuals with the arrival of Spanish missionaries in the early 1800s.

Then, beginning in 1862, California experienced a devastating dry spell; 40% of the entire state's livestock perished. In ranch lands surrounding the little pueblo of Los Angeles, 70% of the animals died searching for food and water. Sheep outlasted the cattle and nibbled down whatever was left, roots and all (Cleland 1951). Drought was nothing new to California and its native flora of course, but the combined pressure of overgrazing and competition from exotic weeds created an ecological disaster. Native forage was devastated and much of the ground lay bare. A huge niche opened up and weeds from another Mediterranean climate across the Atlantic Ocean took advantage of the situation with a vengeance.

Because they grow faster and have more aggressive seed dispersal mechanisms, exotic weedy annuals quickly fill in areas scraped clean of vegetation, burned too frequently, or disturbed by other types of activity. Instead of ceanothus and manzanita, disturbed chaparral is typically type converted to non-native, weedy grassland with exotic grasses like wild oats *(Avena fatua)* (#63), foxtail chess *(Bromus madritensis)*, and ripgut *(Bromus diandrus)* (#64) along with non-grass immigrants such as filaree (*Erodium* species) (#62), mustard *(Brassica species)* (#61), and various thistles.

Under natural fire regimes, chaparral replaces chaparral (photos 14–17). But as fire frequencies increase, exotic grasses and weeds can easily establish themselves and begin the process of type conversion (photo 11). One possible reason for this is because the amount of fuel available to burn in recovering shrublands is less than in mature stands, thus creating a cooler fire. Cooler fires allow weed seeds to survive, whereas hotter chaparral fires do not. As the amount and type of fuels continues to change in favor of lighter ones, the invasive species alter the fire regime and then flourish under the new environment they create (Brooks, et al. 2004). These plants dry out earlier in the spring and thus increase the length of the fire season in the chaparral (Keeley 2000). In addition, they create fine, high surface to volume ratio fuels making them highly combustible (Rundel 1981), increasing the probability of ignition.

The change in fire return intervals and number of fires has been dramatic in some southern California counties over the past century (Keeley et al. 1999).

- In Los Angeles County from 1910 to 1950 there were 357 brush fires. From 1951 to 1997 they increased to 1,392.
- In Riverside County the fire return interval before 1951 was 225 years. After 1950, it decreased to 38 years.

Interestingly, while the number of fires increased during the period studied, the mean fire size decreased. For example, before 1951 the mean fire size in San Diego County was 2,319 acres. After 1950, it was 1,344 acres. This is important in terms of invasive weeds because smaller burns with large perimeter-to-area ratios are more readily invaded than larger ones (Turner et al. 1997). The presence of fuel breaks and roads adjacent to and within chaparral stands make for ready sources of non-native weed seeds (Keeley 2004b).

The first chaparral plants to vanish when fires increase are the obligate seeders, as demonstrated after two fires on Otay Mountain in southern San Diego County. The first fire occurred in 1979. In 1980, a second fire reburned a portion of the 1979 scar due to the presence of dry annual ryegrass *(Lolium multiflorum)*, which had been seeded on the mountain as an erosion control measure. The impacts were dramatic. Except for a few individuals, the obligate seeder *Ceanothus oliganthus* was completely eliminated from the site. Chamise *(Adenostoma fasciculatum)*, the most common species before the fires, was reduced in density in various study plots by up to 97%. This is interesting because chamise is a facultative seeder, able to resprout as well as germinate after a fire. Apparently the second blaze caught the exposed young sprouts when they were the most vulnerable and the supporting burl did not have enough stored energy to develop new ones (Zedler et al. 1983). All the seedlings that had germinated after the 1979 fire were killed in the 1980 fire. The 2007 fires also killed seedlings from the 2003 fires.

This type of ecological damage has occurred time and time again throughout southern California as increased fires, aided by inappropriate and largely useless post-fire erosion control measures, have transformed large tracks of native chaparral into non-native, weedy grassland. In fact, until recently, type conversion of shrublands in favor of grass was an official government land management policy (CDF 1978). Based on the average of many investigations, the threshold below which chaparral will be type converted is anywhere between ten to twenty years depending on summer drought and individual site conditions (Haidinger and Keeley 1993, Keeley 1995, Zedler 1995, Jacobson et al. 2004). Anything less threatens the chaparral's continued existence.