

FREMONTIA

JOURNAL OF THE CALIFORNIA NATIVE PLANT SOCIETY

SPECIAL ISSUE: CHAPARRAL

CALIFORNIA CHAPARRAL

MANZANITAS

FREEZING AND CHAPARRAL PATTERNS

CHAPARRAL AND FIRE

CHAPARRAL BULBS AND FIRE

THE COST OF LIVING WITH CHAPARRAL

POST-FIRE RECOVERY OF CHAPARRAL IN SAN DIEGO

FREMONTIA

VOL. 35, NO. 4, FALL 2007

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California Native Plant Society

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CNPS carries out its mission through science, conservation advocacy, education, and horticulture at the local, state, and federal levels. It monitors rare and endangered plants and habitats; acts to save endangered areas through publicity, persuasion, and on occasion, legal action; provides expert testimony to government bodies; supports the establishment of native plant preserves; sponsors workdays to remove invasive plants; and offers a range of educational activities including speaker programs, field trips, native plant sales, horticultural workshops, and demonstration gardens.

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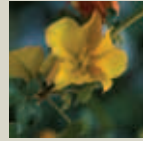
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Printed by Premier Graphics: www.premiergraphics.biz

CONTENTS

CHAPARRAL: PURE CALIFORNIA by Richard W. Halsey 2

Chaparral is the most extensive ecosystem in California, yet it is both misunderstood and underappreciated. Although fire plays a role in shaping chaparral, the system is not “fire dependent” as many believe, but rather extremely sensitive to specific fire regimes.



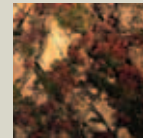
DIVERSITY AND EVOLUTION OF ARCTOSTAPHYLOS AND CEANOTHUS by V. Thomas Parker 8



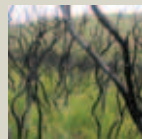
The diversity of Arctostaphylos and Ceanothus and their central role in California chaparral lies in how their life histories interact with California’s multiple topographic, edaphic, and climatic gradients. Their dormant seed banks and wildfire create conditions for rapid change. Glacial epochs, migrations, and hybridization have kept the process of speciation ongoing.

CHAPARRAL ZONATION IN THE SANTA MONICA MOUNTAINS: THE INFLUENCE OF FREEZING TEMPERATURES by Stephen D. Davis, Anjel M. Helms, Marcus S. Heffner, Anthony R. Shaver, Amory C. Deroulet, Nicole L. Stasiak, Spencer M. Vaughn, Caleb B. Leake, Han D. Lee, and Eli T. Sayegh 12

Patterning of chaparral vegetation in Southern California landscapes has largely been attributed to gradients in moisture availability, fire frequency, and soil types. The role of freezing has been neglected. This article presents evidence for the zonation of chaparral species in response to a gradient in freezing as demonstrated by the freeze on January 14, 2007.



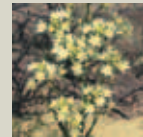
CHAPARRAL AND FIRE by Jon E. Keeley 16



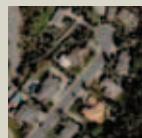
Chaparral shrublands have had a long evolutionary history in association with fire. Some species have finely tuned their life histories to take advantage of post-fire conditions and exhibit traits that are reasonably interpreted as fire-adaptations. However, this does not apply to all plant species in this community, as many are more successful in the absence of fire.

CHAPARRAL GEOPHYTES: FIRE AND FLOWERS by Claudia M. Tyler and Mark I. Borchert 22

Geophytes (bulbs) are a striking component of the post-fire flora in chaparral, flowering profusely in the first spring after a burn. Why is this reproductive display limited to immediately after fire in some species? What happens with these plants in the decades between fires? The authors describe their findings related to two geophyte species.



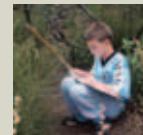
MAN AND FIRE IN SOUTHERN CALIFORNIA: DOING THE MATH by Hugh D. Safford 25



The 2003 fires in Southern California significantly increased Californians’ consciousness vis-à-vis the threat of fire, but basic misunderstandings about the nature of fire in chaparral abound, and maladaptive decisions regarding fire preparedness and land development continue to be made across the State.

FROM ASHES TO LIFE: EFFECTS OF FIRE ON A SAN DIEGO CHAPARRAL COMMUNITY by David M. Cohn III 30

When the 2003 Cedar Fire in San Diego County came close to his home in 2003, 11-year-old David Cohn had no experience with botany. Once the flames were extinguished, David embarked on a four year study to discover how the native chaparral ecosystem would recover. This is a summary of his findings.



THE COVER: Chaparral vegetation in the Trabuco Ranger District, Cleveland National Forest. Photograph by R. Halsey.



Classic Californian chamise-dominated chaparral on a granitic hillside in western Riverside County. All photographs by the author.

CHAPARRAL: PURE CALIFORNIA

by Richard W. Halsey

If there was ever a native plant community in California that deserved to be designated as the official state ecosystem, chaparral would certainly qualify. A shrub-dominated habitat covering many of the state's mountainsides with a dense carpet of green velvet, chaparral is found in every single county. Both the state bird, California quail, and the state flower, California poppy, can be found within the chaparral's extensive range. Chaparral was also the

favored habitat of the California grizzly bear, a magnificent animal that was last seen in 1924 near Sequoia National Park, the bear's last refuge from a rapidly changing world.

Unfortunately, many Californians do not recognize or appreciate the remarkable natural resource value chaparral provides, but rather view it with disdain, unaware of the system's inherent beauty. Pejoratively referred to as "brush" or "decadent vegetation," chaparral is seen

by some as only a fire threat, a risk in need of constant mitigation.

The last time *Fremontia* dedicated an entire issue to chaparral was in 1986. A significant amount of new information has been revealed since then, changing our understanding of the chaparral's relationship to fire, its response to the Mediterranean-type climate in which it thrives, and how best to manage it during a time of expanding development and global climate change.

It is time to pay another visit to California's most extensive ecosystem.

CHAPARRAL BASICS

Chaparral is a drought tolerant plant community dominated by sclerophyllous, woody shrubs and shaped by a Mediterranean-type climate (summer drought and mild, wet winters) and naturally recurring wildfires. The term sclerophyllous, meaning "hard-leaved," was first coined by the German botanist Andreas F.W. Schimper in his classic 1898 text, "Plant Geography Upon a Physiological Basis." Its most characteristic species, the fine-leaved chamise (*Adenostoma fasciculatum*), is the most widely distributed shrub in the state. Other species that help define chaparral include manzanita (*Arctostaphylos* spp.), wild lilac (*Ceanothus* spp.), scrub oak (*Quercus* spp.), mountain mahogany (*Cercocarpus* spp.) and silk-tassel bush (*Garrya* spp.).

Chaparral dominates many foothills and mountain slopes from the Rogue River Valley in southwestern Oregon, down through California, to patches in Baja California's Sierra San Pedro Martir. Interesting stands of chaparral also exist in mid-elevation areas in central and southern Arizona, such as those in the Catalina Mountains above Tucson.

The essence of becoming a botanist is to become familiar with individual plants so that both the familiar and unfamiliar will stand out. "To be able to call the plants by name makes them a hundredfold more sweet and intimate," wrote Henry Van Dyke in his 1895 collection of essays titled "Little Rivers." Distinguishing between various types of chaparral is an equally interesting task, turning what previously appeared to be amorphous green hillsides into distinctly different vegetation communities. In pursuit of this endeavor, a recent CNPS organized effort has identified over



50 different alliances (Keeler-Wolf et al. unpublished). These range from types in which one shrub species, such as chamise or ceanothus, create almost pure stands over many acres, to various forms of mixed chaparral, each with its own unique combination of plants. Highly endemic types have also been identified such as those found on serpentine deposits in the Clear Creek area of San Benito County.

When encountered and studied in the early 1900s by some land managers from the eastern United States, California shrublands violated traditionally accepted patterns of succession whereby shrubs were merely a transitional stage toward the development of a mature forest, not a climax community unto itself. Unlike forests, chaparral is auto-successional, meaning pioneer and climax communities are basically the same. After the system has been disturbed by natural processes, the most common of which is fire, chaparral immediately begins to replace itself through seeding and resprouting. In an attempt to correct this "problem," over one million conifers, a substantial share of which were non-native, were planted in the San Gabriel Mountains in Los Angeles



Top: Lichens growing on old growth chaparral burls of mission manzanita (*Xylococcus bicolor*), Bernardo Mountain, San Diego County. • Middle: Flannel bush (*Fremontodendron californicum*). • Bottom: Manzanita, the definitive chaparral shrub. Mexican manzanita (*Arctostaphylos pungens*), Descanso, San Diego County.

County during the 1920s. Most were eventually killed by fire or drought, convincing foresters to let nature be and allow chaparral to protect the region's watersheds naturally.

This does not mean, however, that succession is completely absent in chaparral. As most botanists eagerly anticipate, the first year or two after a fire, recovering chaparral stands explode with a remarkable variety of herbaceous growth and colorful wildflowers. Usually within ten years, the canopy closes and shrubs dominate the scene again. On drier, south facing hillsides, the community can be dominated by obligate-seeding, woody shrub species like *Ceanothus* (obligate seeders recolonize post-burn sites by seed germination alone). As time goes on, individual shrubs will drop out, frequently due to drought stress, with gaps in the canopy being filled in by surrounding species. On moister, north facing slopes that

have remained unburned for a century or more, groves of manzanita can grow up to 20 feet tall, with thick, shiny red trunks, creating remarkably beautiful old-growth chaparral stands. Such communities are extremely rare in the southern part of the state today because of increased fire frequency from human activity. Consequently, the best examples remain in central and northern parts of California where moisture levels are higher and fires are less frequent.

MISCONCEPTIONS

Possibly because chaparral research and fire ecology are relatively young fields, a significant number of misconceptions about California chaparral plant communities continue to persist. The most common deal with fire and include assumptions such as "chaparral needs to burn to remain healthy" and "chap-

arral is adapted to fire," both of which incorrectly imply that without frequent fire, chaparral will disappear.

While fire plays an intimate role in shaping chaparral systems, fire at the wrong time or frequency can eliminate them. This fact has been known for years by ranchers who have endeavored to "improve" and expand pastures by repeatedly burning native shrublands. Native Americans likely did the same in order to encourage the growth of herbaceous plants that produced edible seeds and increased deer populations. In the southern part of the state where fire frequency has increased dramatically over the past century, vast areas of chaparral have been converted to non-native, weedy grasslands (see Keeley article in this issue for more information on fire regimes in California chaparral).

In contrast, there has been no compelling research indicating that

A tunnel through an old-growth chaparral stand of Ramona lilac (*Ceanothus tomentosus*) in San Diego County.



long fire-return intervals are harmful to the ecological health or vitality of chaparral plant communities. In fact, extended fire-free periods are required for the seeds of many chaparral plants to germinate successfully, for specialized lichen colonies to form, and for old-growth stands to create the type of habitat that would have been favored by the grizzly bear (Keeley et al. 2005, Knudsen and Magney 2006, Storer and Tevis 1955).

Another misconception that is frequently found in various reports and articles is that chaparral shrubs produce allelopathic toxins that prevent the emergence of seedlings beneath the shrub canopy. Allelopathy is often cited to support the belief that “chaparral needs to burn” because fire is supposed to rid the soil of accumulated poisons. Not only is this untrue but many of the identified toxins actually increase in post-fire environments. With a few possible exceptions, seeds of chaparral species are innately dormant with their germination stimulated by particular fire cues, not the removal of inhibiting soil chemicals (Halsey 2004).

While the phrase “old-growth” is commonly invoked to inspire the vision of ancient forests, it is equally valid for use in describing many mature chaparral stands. With trunks of toyon and manzanita more than waist thick, gnarled stems of ceanothus supporting canopies filled with blue and white blossoms high above, and twisted branches of chamise covered with wildly colorful displays of lichen, the richly descriptive phrase “old-growth” is more than suitable. If one were to closely examine the diversity of all life thriving in such ancient landscapes, words like “decadent” and



This large big-berry manzanita (*Arctostaphylos glauca*) was killed outright by a fire.

“senescence” would be clearly inappropriate.

The unique natural resource value old-growth chaparral provides Californians demonstrates why misunderstandings about fire can be so damaging. If land managers and private citizens believe chaparral “needs” fire and that it is a “good thing” when it burns, then beautiful, legacy manzanitas and ancient chaparral stands are perceived as having little value. In addition, the threat of converting native shrublands to non-native grasslands due to increased fire frequency is not adequately recognized.

CHAPARRAL ACROSS CALIFORNIA

There is little mystery why chaparral is not as well known as many other native California plant communities; the name is more commonly used to identify everything from housing developments to herbal remedies. The four Southern California National Forests are actually not dominated by forested sys-

tems at all, but chaparral. In fact, more than 90% of the Cleveland National Forest is covered by native shrublands. Changing the name of some of these public lands to National Chaparral Recreational Areas may begin to help Californians properly recognize the native plant communities in which they live.

There are a number of remarkable chaparral stands across the state. One exists on the north side of Guatay Mountain in San Diego County. The local Kumeyaay Indians call it Na-wa Ti'e and believe it is protected by a spirit guardian. For fear of angering Na-wa Ti'e, in-

habitants in the village that once occupied the valley below never ventured up the mountain's slopes. Legend has it that the mountain has never burned because of the guardian's watchful eyes. Today, it remains a sacred place, both for the Kumeyaay and those who value the unique natural resources that can be found there. On its northern exposure resides the last, ancient Tecate cypress (*Cupressus forbesii*) grove in California and one of the last, intact old-growth stands of chaparral in the region.

Punching out of a dense, eight-foot thick carpet of Eastwood manzanita (*Arctostaphylos glandulosa*), cupleaf ceanothus (*Ceanothus greggii*), and scrub oak (*Quercus berberidifolia*) are islands of 20-foot tall, multi-trunked canyon live oak (*Quercus chrysolepis*).

The vigorous Tecate cypress grove is at least 145 years old (Gautier and Zedler 1980). These trees are truly remarkable with their thin, reddish bark, large trunks, and fine, scale-like leaves. They can reach up to 30 feet and form an airy canopy decorated with quarter-sized cones

that remain closed until the parent branch dies either by fire or injury. Although they have been labeled as fire-dependent, multiple fires in other groves have seriously compromised the reproductive success of the species in California. Therefore, it is better to view the Tecate cypress, as well as all other plants that have some type of fire-adaptive reproductive trait, as “fire regime sensitive.” Fire is a disruptive force that can have various impacts depending on its time of arrival.

ISOLATED TREASURES

Clinging on to a geological island near the central California town of Ione, a unique type of chaparral named after the town struggles to maintain its grip. Abandoned mining activity and road cuts expose the soils upon which the community exists—fine, white sands and strange layers of ancient marine sediments laid down 35 to 57 million years ago during the Eocene. All share high levels of acidity, lots of aluminum, and poor fertility.

Covering the ground in low mounds are the intermingled mats of Ione manzanita (*Arctostaphylos myrtifolia*), the characteristic species of this isolated patch of fragile ecology. In fall the mats are covered with bright red, nascent inflorescences, immature flower buds ready

to release urn-shaped blossoms in late winter. Randomly scattered between the olive-green shrubs is the occasional sticky whiteleaf manzanita (*Arctostaphylos viscida*) standing out with its contrasting lighter color. Combined with the varied foliage and unusual soil hues, the area takes on a quality best described by the brush of an Impressionistic painter.

First identified in 1886 by Charles Parry, Ione manzanita survives on a patchwork of sites totaling approximately 1,000 acres, portions of which are being preserved through a cooperative effort between landowners and various interested parties (including CNPS). Currently the Bureau of Land Management (BLM) manages two reserves of 86 and 20 acres, each with CalTrans managing populations along its right-of-way. Large portions of Ione chaparral are on the private Arroyo Seco Ranch whose owners have expressed an interest in protecting the endangered system.

Unfortunately, large mats of Ione manzanita have been dying throughout its small range, leaving behind only pale, woody skeletons. The die-back appears to have been occurring at least since 1988. According to George Hartwell, a talented naturalist who once lived in the area, the fungus responsible for madrone canker (*Fusicoccum aesculi*) has been

found in Ione manzanita tissue. Another fungus that causes root and crown rot (*Phytophthora cinnamomi*) was found to be infecting the plants in 2001. Drought stress may be the primary cause of the problem with fungal infections dealing the final blow. Whatever the cause for the die off, the future of the remaining stands of Ione manzanita chaparral is questionable.

CHAPARRAL BY THE SEA

The Elfin Forest Preserve in Los Osos, right across the bay from Morro Rock, is a model example of how a group of dedicated individuals can restore a seriously damaged ecosystem and protect it for future generations. Due to the efforts of local residents, the 90-acre maritime chaparral landscape was purchased between 1987 and 1994. Although many ancient pygmy coastal live oaks (*Quercus agrifolia*), endemic Morro manzanitas (*Arctostaphylos morroensis*), and wedgeleaf ceanothus (*Ceanothus cuneatus*) remained in the lower, relatively pristine portion of the preserve, a large area had been severely compromised by motorcyclists and non-native veldt grass (*Ehrharta calycina*). Through steadfast volunteer efforts, the area is recovering nicely.

A walk along the preserve's boardwalk is like traveling back in time, when large portions of coastal California were covered with the varied and colorful foliage of a maritime form of mixed chaparral shaped by ocean influences. Yellows from mock heather (*Ericameria ericoides*), subtle grays from California sagebrush (*Artemisia californica*), and creamy whites, scarlet reds, and lupine purples decorate the landscape like floral confetti.

At one juncture along the way, you'll find a bronze plaque dedicated to the Fairbanks family. The reason for its presence is clear. It is a tribute to Jeff and Ann Fairbanks, along with their three daughters,

Ione chaparral featuring the endangered Ione manzanita (*Arctostaphylos myrtifolia*).



Courtney, Galen, and Siena, who were strong supporters of protecting the Elfin Forest. "The beauty of this county is one of the major reasons for living here," Jeff wrote as the editor of the local *Telegram-Tribune* newspaper. "We are all responsible for it."

The plaque also reminds us of the fragility of life. Jeff, Ann, and their daughter Siena lost their lives in a horrible traffic accident in 1995. "Stand here for a moment," the dedication concludes, "close your eyes and see the Elfin Forest through a child's eyes. That is Siena's view."

THE FUTURE

Chaparral provides the closest and easiest way many Californians have to make contact with nature. Exploring it, studying its remarkable botanical diversity, and sharing its beauty with others are essential if we intend to preserve the continued vitality and survival of chaparral as well as that of other native plant communities.

Although at present there may appear to be a significant amount of chaparral in California, continuing drought conditions, increased fire frequencies, and ignorance about the system can easily change that over the next 100 years. If current drought conditions are a reflection of the ongoing change in global climate, California may witness a dramatic redistribution of native plant communities over the next century.

In Southern California, experienced wildland firefighters are noting large populations of scrub oak, ceanothus, and chamise dying from desiccation in numbers they have never seen before. Vegetation moisture levels dropped to record lows this past summer, which led to highly unusual wildfires. The lightning-caused July blaze in the Inyo National Forest burned more than 35,000 acres, a place that was once referred to as the "asbestos forest" because of its resistance to burning.



The Elfin Forest Preserve in Los Osos, San Luis Obispo County, features the endemic Morro manzanita (*Arctostaphylos morroensis*) in the middle ground of this photograph.

Record low moisture levels have changed that, as well as changing fire patterns throughout the West.

Although extended droughts have occurred in the past, this time things are different. California's population has increased dramatically, and human activity is now having a significant impact on the redistribution of native plant communities because humans cause most of the fires. As a consequence, anthropogenic fire in shrubland systems is unnaturally accelerating ecosystem change, seriously compromising normally resilient native habitats. Such change will likely be one of California's most challenging environmental issues for years to come.

Although there is not much we can do about long-term drought, we do have the ability to encourage the development of appropriate land management plans designed to protect the native landscapes we love. Our success depends a lot on awareness. This is why your interest in the natural world and the efforts of the California Native Plant Society are so important; learning to enjoy native plant communities and help-

ing others do the same is the key to their continued existence, especially those that are underappreciated.

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The rare and newly described Gabilan manzanita (*Arctostaphylos gabilanensis*) in its habitat at the headwaters of Pescadero Creek in the Gabilan Mountains of Monterey County. All photographs by the author.

DIVERSITY AND EVOLUTION OF ARCTOSTAPHYLOS AND CEANOOTHUS

by V. Thomas Parker

Few genera evoke an image of chaparral more than *Arctostaphylos* (manzanitas), *Ceanothus* (California lilacs) or *Adenostoma* (chamise). *Adenostoma* contains only two species, one of which is quite common and widespread. This scarcity of species contrasts to the large number of endemic and widespread species characterizing the other two genera. *Arctostaphylos* and *Ceanothus* both have a center of diversity in California, especially along the central coast. In California, *Arctostaphylos* and *Ceanothus* together are represented by more than 150 taxa!

These are large numbers for woody plants in such a small spatial area. Many of these species are quite rare and can be found on CNPS rare plant lists. Why are so many of these plants difficult to distinguish from one another, and how did California end up with so many of them? Be careful asking those kinds of questions. I've been working with Mike Vasey of San Francisco State University, on *Arctostaphylos* for nearly the past 20 years, and more recently with Jon Keeley of the U.S. Geological Survey, trying to understand the evolution of these plants. What a wonderful group.

Arctostaphylos evolved at least as far back as the Miocene, 15 million years ago, which corresponded to a time of global warming, while *Ceanothus* is thought to be an even older genus. Yet relatively few taxa are found in the fossil floras for most of their history. Only during the last 1.5 million years have large numbers of new fossil types rapidly appeared. Currently we have some 95 species and subspecies of *Arctostaphylos* within the political boundaries of California, and 104 of the world's 105 species and subspecies have some or all of their distribution within the California Floristic

Province that includes parts of Oregon and Baja California, Mexico. *Ceanothus* is not much different with about 75% of the 76 known species or varieties found in the California Floristic Province. Not only do these two genera have a lot of species, they also are peculiarly Californian.

The increase in the diversity of species in these two genera started about 1.5 million years ago, and is thought to have been a response to changes in the physical structure of California's geography, and a significant shift in climates. Tectonic changes were one important aspect, as the whole region was folded, faulted, elevated, and dissected at about the time the burst of diversity began. Such changes opened up new soil types, depths, and levels of development, produced windward slopes and rain shadows, and variously created a diversity of ecological opportunities that selected for new species. Our summer-dry Mediterranean climate developed and spread during the same general time period. Lack of summer rain forced the extinction of numerous plant groups that were unable to adapt and subsequently were eliminated from the region. However, their loss provided yet more opportunities for chaparral species like manzanitas to spread into new areas.

PECULIAR RELATIONSHIP TO FIRE: DIFFERENT LIFE HISTORIES

The abundance of taxa in *Arctostaphylos* and *Ceanothus* result not only from California's marked topography, edaphic (soil) diversity, and the shift to a drier climatic, but also from wildfire, a process that arises more frequently under those conditions. The species rich-

ness reflects more than the physical environmental diversity and dry climate; it also reflects a mutual inter-relationship between fire and plant life history characteristics.

Arctostaphylos and *Ceanothus*, along with *Adenostoma*, have strongly persistent seed banks that are fire stimulated. Seeds that are not consumed by animals are slowly incorporated into the soil, where they remain until a wildfire occurs. Other woody shrub genera in California either lack these types of seed banks, or only a small fraction of their seeds may remain dormant. Persistent seed banks compress the recruitment process, the germination of seeds and the establishment of new individuals, to a single year after each fire, regardless of the interval between fires. This is an important process we will come back to later.

Additionally, a characteristic that distinguishes *Arctostaphylos* and *Ceanothus* from all other shrub genera in chaparral is that they contain species with different life histories.

The characteristic rich red-brown smooth bark on the twisted branches of the common manzanita (*Arctostaphylos manzanita*) in a Sonoma County woodland edge.



One group of species has burls or root crowns with dormant buds that permit resprouting of the plants after wildfire. These individuals usually survive a large number of fires, and indeed, unless shaded out by larger plants, may persist indefinitely.

A second, larger group of species in these genera is killed by fire. Their populations are completely dependent on the germination and establishment of new individuals arising from the soil seed banks. They have been termed "obligate seeders" as a consequence. This life history style may seem risky, and it is, but the benefits appear to be rapid and successful growth in chaparral and the ability to adapt to changing conditions. Almost 40 years ago, Phil Wells, at the University of Kansas, pointed out that not only do *Ceanothus* and *Arctostaphylos* have a peculiarly large number of taxa compared to other chaparral genera, but that diversity is concentrated in those taxa killed by fire, the obligate seeders. Researchers ever since

have accepted that this life history style contributes to more rapid rates of speciation. Other plants associated with chaparral may also display an obligate seeding lifestyle, as for example the closed-cone species in *Pinus* and *Cupressus*. Other Mediterranean-climate regions show similar patterns, with a few genera developing obligate seeding life histories and becoming more species rich compared to other groups.

RECENT HISTORY

The high diversity of these two genera emphasize the importance of the origin of a summer-dry Mediterranean-climate, the incredible topographic, edaphic, and climatic diversification of

California, and the development of both sprouting and obligate seeding life histories in the context of frequent fire. Of course, there is even more to the story of this rapid radiation of species. Glacial periods have also occurred during the last two million years or more, and have significantly impacted the distribution of plants. Glacial advances and retreats force the shifting of plant distributions. The last glacial period finally retreated a little over 10,000 years ago. During the time since the last ice age, climates have not been stable, with a particularly dry and warm period occurring from about 4,000-8,000 years ago. Chaparral expanded north into the Columbia River Basin, followed by a retreat back into California when the climates moderated again.

These climatic fluctuations stimulated migration of populations adapted to narrow climatic conditions and brought into contact populations that formerly were geographically quite separate. During such times of rapid change, not only are populations rapidly advancing to follow climatic shifts, but they also leave behind relict populations—remnants of formerly widespread species that persist in relatively isolated areas. Hybridization becomes possible between formerly separated populations as their migrants and relicts overlap, and new genetic recombinants may have a better set of adaptations to shifting local conditions than their progenitors. This is especially possible for the obligate seeders of *Arctostaphylos* and *Ceanothus*. Hybridization appears to be quite easy among a number of the species in these genera; geographic separation is the current primary reproductive barrier. The advantage to obligate seeders is that fire eliminates all the adults and permits selection among those new, and genetically diverse, seedlings arising from the seed bank. If there were new recombinants with better adaptations, models indicate that it would

take only a little over 20 fire cycles for a completely new species of hybrid origin to take over a habitat. Importantly, the original adults, killed by the wildfire, are not around to genetically swamp out these new recombinants. That is presumably a principal reason obligate seeding genera are so species rich worldwide.

Consider the San Francisco Bay Area as an example. The Bay Area was a forested river valley during the last glacial period. As glaciers retreated, climates rapidly shifted to moderate conditions, followed by a rapid shift to much drier and warmer conditions that lasted until around 4,000 years ago, then changed to conditions similar to those of today. Species of *Arctostaphylos* and *Ceanothus* were especially favored during that dry and warm period as forests and woodlands retreated to wetter sites and fires swept the tree communities. Today relict stands of forest, woodland, and savanna within broad tracts of chaparral attest to the spread of chaparral.

Currently, the region from San Francisco Bay to Monterey contains 42 species or subspecies of *Arctostaphylos*, 32 of which are narrow endemics to sites that were probably forested only 10,000 to 20,000 years ago. Almost all the narrow endemics are obligate seeders. *Ceanothus* exhibits a similar pattern in the same region, although it is not as species rich. These narrow endemic species, the rare species, are important to consider. Influential botanist, geneticist, and evolutionary biologist, G. Ledyard Stebbins, and others, have estimated that the maximum age for many of these narrowly endemic species is only 10,000 to 20,000 years. Hybridization and recombination under intense ecological selection could account for this rapid radiation; in fact, these are just about the only set of processes that could account for that speed of adaptation. Having such a

recent origin, one can imagine that many of these species may have only slightly changed in morphology from their predecessors, making them difficult to identify.

Overall post-glacial distributions of a number of narrow endemics suggest that their origins are based on two different paths of evolution. One origin is relict populations that have been left behind as populations moved north after the retreat of glaciers, and subsequently have been ecologically selected to local conditions. *Arctostaphylos columbiana* may fit this model, widespread to the north with morphologically similar narrow endemics to the south, such as Marin manzanita (*A. virgata*), found only in the foggy areas of Marin County, and *A. montereyensis* found at Fort Ord and nearby areas of Monterey County.

The second potential origin is from hybridization between more rapidly migrating species moving north as they encounter lagging or relict populations of other species. Hybridization under these circumstances might result in recombination and the development of a new species. *Arctostaphylos canescens* seems to provide a number of examples as a potential parent to species of possible hybrid origin. For example, *A. luciana* near San Luis Obispo, *A. auriculata* on Mt. Diablo, *A. glutinosa* in the southern Santa Cruz Mountains, and *A. malloryi* on volcanics north of the Bay Area all seem to share an unusually large number of features with *A. canescens*. At the same time, other characters indicate the influence of other evolutionary lineages, such as the arrowhead-shaped auriculate leaves found in *A. auriculata*, *A. luciana*, and *A. glutinosa*. Similarly, the widespread big berry manzanita (*A. glauca*) also appears to be a potential parent in the origin of a number of taxa, such as *A. gabilanensis* and *A. refugioensis*.

Arctostaphylos also seems to have a process of species origin lacking in

other chaparral species. Two old lineages appear to exist in manzanitas, but reproductive isolation between these lineages is not complete. However, hybridization appears limited which suggests some fertility barriers. Unlike *Ceanothus* or other chaparral shrubs, *Arctostaphylos* has species at both a diploid level (2 sets of chromosomes) and a tetraploid level (4 sets of chromosomes). Research on a number of these tetraploids, which make up almost a third of the taxa, indicate they are of hybrid origin arising from crosses of species from the two lineages. Polyploidy is a common process in plants that permits regaining complete fertility from combinations that may be partially infertile. Most of these tetraploids contain a large number of subspecies, like *A. tomentosa*, *A. cruceata*, *A. glandulosa*, and *A. manzanita*. Adaptive hybridization may be the source of the diverse and difficult to identify tetraploids and their many subspecies.

CONCLUSIONS

At this point, the diversity of *Ceanothus* and *Arctostaphylos* and their central role in California chaparral lies in how their life histories interact with California's multiple topographic, edaphic, and climate gradients. Their dormant seed banks and wildfire create conditions for rapid change. Glacial epochs, migrations, and hybridization have kept the process of adaptation and speciation ongoing. Recent research using molecular genetic techniques indicates that for both *Arctostaphylos* and *Ceanothus* there are two old and distinct lineages. However, when it comes to the current species, the genetic levels explored so far indicate little differentiation exists. Future work will eventually tease out these patterns of history and give us a richer understanding of the extent and multitude of evolutionary pathways that these plants have wandered.



A very old specimen of Montara manzanita (*Arctostaphylos montaraensis*) growing on Montara Mountain in San Mateo County with huckleberry (*Vaccinium ovatum*) and bracken fern (*Pteridium aquilinum* var. *pubescens*).

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Zonation of chaparral, in response to freezing, along Malibu Canyon Road from the ocean near Malibu to inland Tapia Park. Shrubs with bright red leaves are laurel sumac (LS, *Malosma laurina*), which our data have shown undergo leaf death at -6°C and nearly 100% embolism of their stem xylem (Pratt et al. 2005; Davis et al. 2005; Davis et al. 2007). There are less red leaves high on the slopes in the background, which suggests temperatures were above -6°C on higher slopes. All photographs by the author.

CHAPARRAL ZONATION IN THE SANTA MONICA MOUNTAINS: THE INFLUENCE OF FREEZING TEMPERATURES

by Stephen D. Davis, Anjel M. Helms, Marcus S. Heffner, Anthony R. Shaver, Amory C. Deroulet,
Nicole L. Stasiak, Spencer M. Vaughn, Caleb B. Leake, Han D. Lee, and Eli T. Sayegh

A principal objective in plant ecology is to explain the distribution of species and vegetation patterning. In the case of the chaparral shrub community in the Transverse Mountain Ranges of Southern California, previous explanations of chaparral zonation have focused on differential water resources, exposure to solar radiation, and edaphic factors (Davis et al. 1999). Here we examine an

alternate possibility, gradients in freezing temperatures.

The Pacific Ocean near Malibu, California, ameliorates fluctuations between minimum temperatures at night and maximum temperatures during the day. Minimum temperatures rarely dip below 0°C on cold winter nights. In contrast, just 5 kilometers inland, deep canyons reduce the ocean's ameliorating influence, reduce insolation, and increase

cold air drainage, enhanced by radiative heat loss from plants to cold skies on calm, clear nights. These factors can lead to a steep 12°C gradient in minimum temperature over a short distance of 5 kilometers (Figure 1, page 13). This gradient in temperature is accompanied by a dramatic shift in chaparral species composition, with coastal greenbark ceanothus (*Ceanothus spinosus*), bigpod ceanothus (*C. megacarpus*),

and laurel sumac (*Malosma laurina*) dominating the Malibu landscape while inland wedgeleaf ceanothus (*C. cuneatus*), hoaryleaf ceanothus (*C. crassifolius*) and sugar bush (*Rhus ovata*) dominate the landscape near Tapia Park (Figure 1).

The primary zonation (1° Zonation) is from the ocean inland (0°C to -12°C) but superimposed on this pattern is a secondary zonation (2° Zonation) from hilltop to valley floor. The latter results from cold air drainage and thermal inversion (Langan et al. 1997; Ewers et al. 2003). Perhaps readers have felt the chill of entering a valley floor on early morning hikes in the Santa Monica Mountains. This thermal inversion of temperature (colder at low elevations) is five- to ten-fold steeper, and in the reverse direction, to the standard lapse rate calculated for decreasing temperature with elevation in high mountains (drop in 5°C for every 1,000 meter increase in elevation).

This temperature inversion may be counter-intuitive, but over microclimate scales (hill-valley effects) and in the Santa Monica Mountains where a contiguous elevation gradient is lacking, thermal inversions dominate and impact species distribution somewhat paradoxically. For example, it has been established that greenbark ceanothus typically grows in moist, shaded ravines but bigpod ceanothus is restricted to drier, more exposed microsites. Thus why does greenbark ceanothus not extend its distribution into moist valley bottoms near Tapia Park (photograph, page 14)? Apparently low temperature (winter freezes) prevents their establishment and survival at these relatively moist sites. Why does hoaryleaf ceanothus which typically thrives at the high elevation, snow-belt region of the San Gabriel Mountains, occupy the low valleys in the Santa Monica Mountains (Fig. 2A)? This is probably because of cold air drainage in the Santa Monica Mountains.

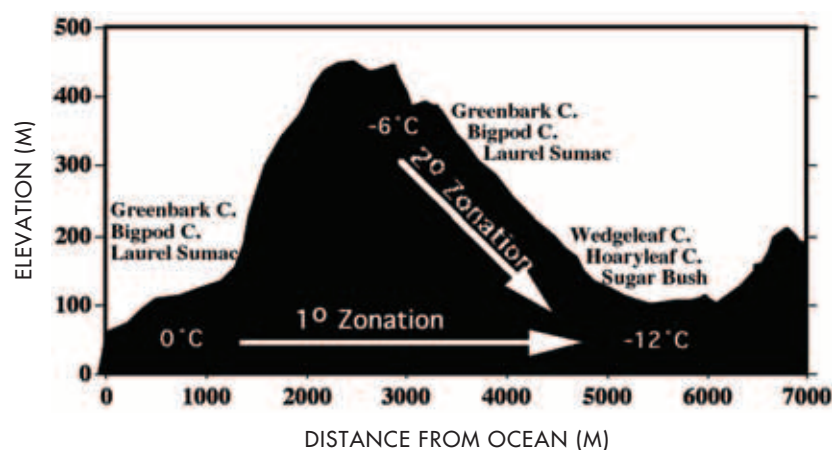


Figure 1. Profile of the change in dominant shrub species of chaparral along a South to North (left to right) transect from the coastal bluffs near Malibu to inland regions near Tapia Park in the Santa Monica Mountains. The transect roughly follows Malibu Canyon Road and the hillsides along this road allow visualization of a vegetation response to this 12°C temperature gradient between the ocean and Tapia Park, approximately 5 km inland (see photograph on page 12).

Consistent with this interpretation, our measurement of freeze-tolerance among species has shown that leaves of coastal species are much more susceptible to freeze damage than inland species. Whether one used a vital stain, variable fluorescence, electrolyte leakage into a bathing solution, or simply the color change of leaf pigment with freezing injury, the lethal temperature for 50% cell death was -6°C for laurel sumac and -10°C for greenbark and bigpod ceanothus. In contrast, the leaves of inland species were more tolerant of freezing with 50% cell death of -16°C for sugar bush and -18°C for hoaryleaf ceanothus (Boorse et al. 1998). We have not measured 50% cell death for wedgeleaf ceanothus but field observations suggest it is below -10°C (bottom photograph, page 15).

This year (2006-2007) has been the driest in recorded history for the Santa Monica Mountains (seasonal total of 87 mm, normal is 380 mm), but also one of the coldest winters on record (minimum temperatures of -12°C at Tapia Park on January 14, 2007). Furthermore, the summer drought of 2006 extended into the winter months causing a "perfect storm" in terms of plant survival in response to environmental

stress. That is, plants were severely dehydrated when they also experienced a hard freeze, a combination that is catastrophic to the water transport system of some species and a serious threat to chaparral shrubs that must maintain year-round water supplies for persistence of evergreen leaves (Langan et al. 1997; Ewers et al. 2003; Pratt et al. 2005; Davis et al. 2007).

Typically plants under field conditions rehydrate overnight as stomata close, atmospheric humidity increases, and temperature declines. This allows sufficient time for the root system and plant tissues to return to approximate equilibrium

Close-up of leaf dieback on sugar bush (SB, *Rhus ovata*). The pattern of browning suggests that portions of the leaf closest to the water supply in midveins remain green longer than margins, presumably due to freeze-caused embolism.



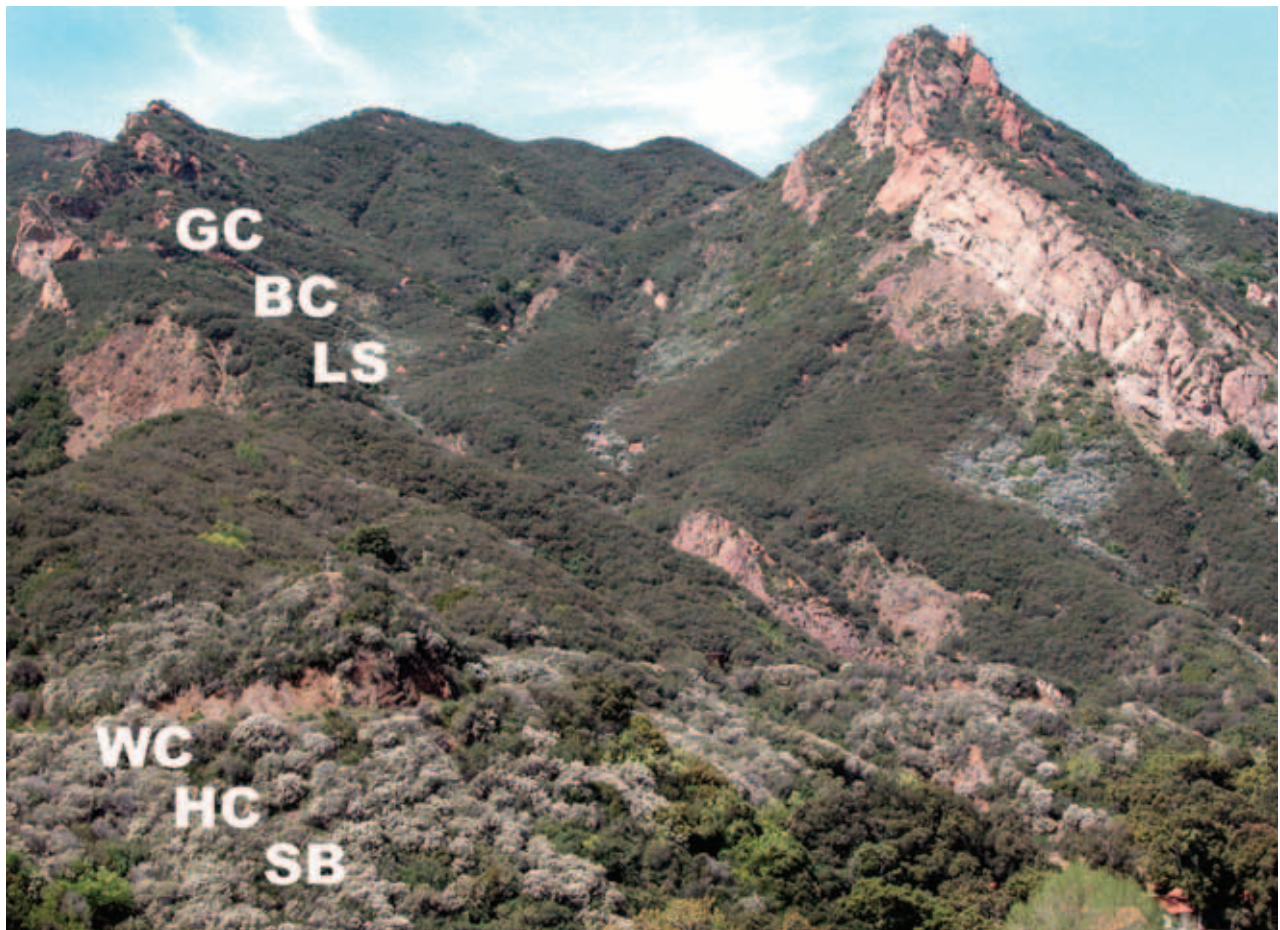
with stored soil moisture in the bulk-rooting zone. Thus plant water status measured just before sunrise represents the most hydrated state of chaparral shrubs during their 24-hour cycle, and also coincides with the lowest 24-hour temperature (Langan et al. 1997). The pre-dawn water status of plants generates modest negative pressures in the water pipes of stems (xylem vessels), ranging between -2 to -4 atmospheres (atm) of pressure (-30 to -60 pounds per square inch of pressure or psi) during the cool, rainy winters of our Mediterranean-type climate. To place these values in perspective, automobile tires are fully inflated at +2 atm of pressure and crop plants such as corn and beans lose turgor (cell pressure) and

visibly wilt around -15 atm. Surprisingly, at the time of severe winter freeze on January 14, 2007, pre-dawn water status for our chaparral shrubs at Tapia Park ranged between -36 atm for greenbark ceanothus (*Ceanothus spinosus*) to -56 atm for hoaryleaf ceanothus (*Ceanothus crassifolius*). These values are two to four times drier than the wilting point of crop plants. This was particularly worrisome to us because previous data in our laboratory have demonstrated that low water status at the time of a freezing event could cause catastrophic xylem dysfunction leading to leaf drop and shoot death (Ewers et al. 2003). This is precisely what happened at the cold edge (ecotone) of our 1° and 2° Zonations shown in Figure 1 on

page 13 (see photographs on pages 13 and 15 for examples of injuries due to freezing).

The mechanism by which water stress interacts with freezing to increase embolism formation in chaparral species is well understood (Langan et al. 1997; Davis et al. 1999b; Davis et al. 2007). When water turns to ice, any gases dissolved in the water come out of solution because of decreasing gas solubility in ice. Thus bubbles appear with ice formation. Perhaps readers have noticed how clear water often appears opaque after it is frozen into ice cubes in a freezer. The same occurs in the frozen water pipes of plant stems (xylem vessels). At the time of thaw, just after sunrise on cold winter nights, these ice bubbles in xylem

Inland 2° zonation of chaparral vegetation in the Santa Monica Mountains near Tapia Park as diagrammed in Figure 1 (page 13). Upper warmer slopes are occupied by coastal chaparral species greenbark ceanothus (GC, *Ceanothus spinosus*), bigpod ceanothus (BC, *Ceanothus megacarpus*), and laurel sumac (LS, *Malosma laurina*), whereas the lower and colder valley bottom is occupied by wedgeleaf ceanothus (WC, *Ceanothus cuneatus*), hoaryleaf ceanothus (HC, *Ceanothus crassifolius*), and sugar bush (SB, *Rhus ovata*).



conduits must redissolve into liquid water; otherwise small bubbles will coalesce to form large bubbles that occlude water transport (xylem embolism). Under hydrated conditions, -2 atm to -4 atm, gas bubbles readily dissolve at the time of thaw, but under unusually dry conditions, -36 atm to -56 atm, bubbles are pulled by the negative pressure of water stress to rapidly expand to form xylem embolism. Higher plants can only survive severe embolism in xylem conduits for one or two weeks. They must either reverse xylem embolism (highly unlikely if dry conditions persist, as in 2007) or grow new xylem tissue to replace non-functional conduits (also unlikely if dry conditions prevent positive turgor formation and cell expansion, as in 2007).

In conclusion, this episodic event of extreme drought at the time of a hard freeze has provided a unique opportunity for undergraduate students in my lab (co-authors on this paper) to test hypotheses concerning the interactions of drought- and freeze-caused dieback and to examine correspondence between species distribution patterns and susceptibility to freezing injury. This event is particularly significant in light of increasing evidence of impending climate change. There is wide agreement within the scientific community that such episodic events may regulate plant establishment and persistence in the landscape. Consequently, one of the main predictions of climate change models for Southern California is increasing episodic events such as droughts and wildfires. In 2007, the Malibu area (photograph, page 12) not only experienced a record freeze, but the driest year in recorded history, and three separate fire events: one on January 5, 2007, another on October 21, 2007, and a third on November 24, 2007. We hope that when post-fire, seasonal rains arrive this winter they will be gradual and gentle, and not add to the episodic list.

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Top: At the cold ecotone between plant communities, greenbark ceanothus (GC) experienced catastrophic xylem failure (98.3% embolism of stem xylem causes blockage in water transport from roots to leaves) after the freezing event of January 14, 2007, and thus virtually all leaves turned brown and dropped. Because roots are below the soil surface they avoided embolism (24.0% embolism), allowing sustained water uptake for sprouting from basal burls. Stem photosynthesis (an advantage of having green bark) evidently kept the vascular cambium alive to support new leaf emergence. By June 2007 about 10% mortality had occurred, thus most individuals will survive, although stunted in growth and lacking fruit production during the 2007 growing season. Bottom: Also at the cold ecotone, freeze-sensitive bigpod ceanothus (BC, defoliated shrubs) can be found growing next to freeze-resistant wedgeleaf ceanothus (WC, live, green leaves). Bigpod ceanothus experienced 99.5% embolism of stem xylem whereas wedgeleaf ceanothus experienced only 82.4% embolism, evidently enough to produce flowers, fruits, and seeds and avoid foliar abscission (leaf drop). About 20% of the bigpod ceanothus died by June 2007 whereas none of the adjacent wedgeleaf ceanothus died.

ating freeze-thaw stress of two evergreen chaparral species: *Rhus ovata* and *Malosma laurina* (Anacardiaceae). *American Journal of Botany* 92:1102–1113.

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Chaparral regrowth and ephemeral post-fire flora in the first spring after the 2002 Bouquet Fire, Los Angeles County (this area is in the fifth year of recovery as shown on page 20). All photographs by the author.

CHAPARRAL AND FIRE

by Jon E. Keeley

Large wildfires are an inevitable feature of chaparral. The moderate temperatures during winter promote growth of extensive stands of shrublands with contiguous fuels covering massive portions of the landscape. The summer-fall drought makes these fuels highly flammable over a relatively lengthy portion of the year. Because of widespread human influence, most fires today are anthropogenic; however, in wilderness areas lightning still accounts for some chaparral fires.

Wildfires in California shrublands pose a significant danger to

humans but are usually not a threat to sustainability of this ecosystem. Most of the flora and fauna exhibit extraordinary resilience to fire. However, although one often hears that species in this community are “fire adapted,” (indeed, I am sure I have written that many times), this is, strictly speaking, incorrect. None of the species in this fire-prone landscape are adapted to fire *per se*, but rather to a particular fire regime. Some fire regimes are destructive to chaparral species and will readily lead to their demise. The primary culprit is high fire frequency, and its

impacts will be discussed later in this article.

The California chaparral crown-fire regime is characterized by high intensity fires that burn all above-ground shrub biomass. This is in contrast to the higher elevation ponderosa pine forest surface-fire regime, where fires typically burn as low intensity fires confined to surface litter and understory plants, resulting in survival of many of the dominant trees. This profound difference in fire regime leads to very different management needs, particularly with respect to fire. Man-

agement paradigms appropriate for forested ecosystems are often inappropriate for chaparral and other crown-fire ecosystems.

RISE OF THE FLORAL PHOENIX

Most chaparral fires occur in summer and fall and typically remain as blackened landscapes until the winter rains. Fires that occur following high rainfall seasons may still have sufficient soil moisture at the time of the fire to begin regeneration sooner; for example, shrub species sometimes initiate resprouts from underground roots or stems within weeks of summer fires. However, most regeneration is initiated following the first winter rains, both from resprouts and germination of the previously dormant seed bank. Chaparral is one of a handful of ecosystems in the world that responds to fire by initiation of a post-fire ephemeral flora, composed of species that are otherwise seldom seen. This post-fire flora comprises many life forms but is dominated by annual forbs. Commonly on a single slope face there may be a couple dozen different species and the composition often changes from one slope aspect to another. These post-fire species exhibit a range of specificities to fire, some being restricted to the first and second post-fire years, others lasting somewhat longer. The most specialized are known as “post-fire endemics” (Table 1).

These species spend most of their life cycle as dormant seed banks under the closed canopy of the chaparral. Sometimes this dormant period lasts a century or more, but that interval is getting increasingly shorter. Fire triggers germination of these species following winter rains and these species are often described as having “fire-dependent regeneration.” When I was a student it was generally understood that heat from fire was the cue that

triggered germination. It is now clear that for the vast majority of this ephemeral post-fire flora heat plays no role in their germination; rather it is chemicals produced by the combustion of organic matter that stimulates germination (Table 1). In 1997 a graduate student C.J. Fotheringham and I did research that showed that smoke could trigger germination in deeply dormant seeds, and this could happen either directly or indirectly by being transferred through the gas or aqueous phase long after the fire had passed. Further we demonstrated that one of the inorganic gases in smoke, nitrogen dioxide, could trigger complete germination in some species. Organic chemists have recently reported that an organic decomposition product found in smoke also can trigger germination. One of the fascinating stories in this ephemeral flora is that of members of the Papaveraceae, e.g., bush poppy (*Dendromecon rigida*) and species of *Dicentra*. Experiments show that these species are unresponsive to any fire cue if seeds are collected directly off the plant. Rather, they must first be

allowed to “age” in the soil for perhaps as long as a year, after which they are still deeply dormant but now respond to smoke.

The ephemeral post-fire flora comprises other life forms such as geophytes and short-lived and slightly woody suffrutescent species. It is of interest that these two groups have radically different regeneration modes. Geophytes, including species of onion (*Allium*), *Brodiea*, mariposa lily (*Calochortus*), soap plant (*Chlorogalum*), blue dicks (*Dichelostemma*), and death camas (*Zigadenus*) are present at the time of fire as dormant bulbs and corms in the soil. They flower profusely after fire from resprouts and set weakly-dormant seed, which germinates after the subsequent winter rains. The suffrutescents such as deerweed (*Lotus scoparius*) and rock rose (*Helianthemum scoparium*) are present prior to fire, usually as dormant seed banks, which are heat stimulated and germinate in profusion after the first rains following fire.

Shrubs present prior to the fire are all represented in the first post-fire year, except when the interval

Burned shrub skeletons and post-fire annuals and short-lived perennials in the first spring after a fire.





Post-fire ephemeral flora. Top: California bells (*Phacelia minor*) after the Gujito Fire in 1997. • Bottom: Yellow-throated phacelia (*Phacelia brachyloba*).

between fires is unusually short. Many such as scrub oak (*Quercus berberidifolia*), coffeeberry (*Rhamnus californica*), redberry (*R. crocea*), chaparral cherry (*Prunus ilicifolia*), and mountain mahogany (*Cercocarpus betuloides*) return as vegetative re-sprouts. Their seedlings are non-existent after fire. On the other hand, many species of ceanothus (*Ceanothus cuneatus* and *C. greggii*) and manzanita (*Arctostaphylos glauca* and *A. viscida*) are present after fire from germination of dormant seed banks that are either stimulated by heat (*Ceanothus*) or by combustion

products (*Arctostaphylos*). Several species of these latter genera (e.g., *C. leucodermis* and *A. glandulosa*) both regenerate from resprouts and reproduce from seeds, as is the case for the ubiquitous chamise (*Adenostoma fasciculatum*).

The post-fire endemic story is interesting in that it is tied to chaparral and most of the taxa wear different hats in other communities, or in other words exhibit ecotypic variation. For example, whispering bells (*Emmenanthe penduliflora*) also is found in the Sonoran Desert where germination is tied to years of sufficient rainfall and fire plays no role in its life cycle. Lupine (*Lupinus succulentus*) and clover (*Trifolium wildenovii*) likewise are strictly tied to periodic post-fire environments in chaparral, but in adjacent grasslands, both may be annual components of the ecosystem showing little relationship to fire.

ALTERED FIRE REGIMES AND THE RISE OF ALIEN PLANTS

Ecologist Paul Zedler, formerly at San Diego State University, ad-

ressed the issue of threats to chaparral ecosystems due to altered fire regimes by proposing two potential risks. One was the "senescence risk," i.e., too little fire, which conceivably could lead to the local extirpation of species with fire-dependent regeneration. The other was "immaturity risk," arising due to repeat fires that occurred before fire-dependent species reached reproductive maturity, in which case soil seed banks would not be replenished at the time of fire, leading to localized extirpation.

Senescence risk does not represent a significant threat to chaparral persistence, as few areas escape fire for very long. On those occasions where chaparral stands escape fire for a century or more, studies show that they recover after fire as well as younger stands. However, immaturity risk is a very real threat because chaparral is not resilient to alterations in the fire regime that involve excessive fire frequency. This applies to both the resprouting and seeding shrubs as well as to the ephemeral post-fire flora.

Non-native grasses and forbs readily invade frequently burned shrublands and directly outcompete native herbs, perhaps favored by their early germination keyed to autumn rains. In addition, these annual alien species modify the environment to further favor their persistence. They commonly form a dense herb layer that produces highly ignitable fuels and extends the length of the fire season. Additionally, the fire regime switches to a combination of surface- and crown-fire with the alien grasses and forbs spreading fire to shrubs before the shrub canopies have closed in. Because surface fuels generate lower fire intensities, such fires favor survival of the alien seed bank, which would otherwise be destroyed in a crown-fire. Type conversion of native shrublands to alien grasslands has occurred over large portions of California. In the Coast Ranges

roughly a quarter of the wildland landscape is grassland, and nearly all is dominated by alien annuals that have displaced shrublands.

ROOTS OF FIRE ADAPTATIONS

The fossil record is replete with evidence of wildfires beginning with the earliest evolution of land plants. This record shows that similar fire regime diversity of crown fires and surface fires has been present for hundreds of millions of years. It is likely that many of the fire response traits evident in chaparral have very ancient origins. This new emerging view of fire origins is in contrast to what many of us were taught early in our careers. For example, the now deceased paleontologist, Daniel Axelrod, formerly of the University of California, Davis, wrote that fire was a relatively recent phenomenon on our landscape and that it has played little role in the evolution of chaparral species. This is perhaps understandable because until the last couple decades ecologists and geographers were generally under the belief that climate and soils determined plant distributions. Fire was often not even mentioned in textbooks as an important ecological factor.

However, today there is a large body of evidence demonstrating that fire is a major ecosystem process on many landscapes throughout the world. In chaparral there is good reason to interpret smoke-stimulated germination, coalesced fruits in *Arc-tostaphylos* (see article by V.T. Parker in this issue), and lignotubers as evolutionary responses to the crown fire regime. Even more intriguing is the work of evolutionary ecologist Dylan Schwillk (formerly with U.S. Geological Survey, now at Texas Tech University) that supports the idea some chaparral species with fire-dependent reproduction have traits that are consistent with selection to enhance flammability.

TABLE 1. POST-FIRE SPECIALISTS IN CALIFORNIA CHAPARRAL FIRE-RELATED GERMINATION CUES

	Life Form	Germination
Asteraceae		
<i>Chaenactis artemisiifolia</i>	annual	smoke*
<i>Malacothrix clevelandii</i>	annual	smoke
Boraginaceae		
<i>Cryptantha micromeres</i> , <i>C. microstachys</i>	annual	smoke
Brassicaceae		
<i>Caulanthus heterophyllus</i>	annual	smoke
<i>Guillenia lasiophylla</i>	annual	smoke
Caryophyllaceae		
<i>Silene multinervia</i>	annual	smoke
Cistaceae		
<i>Helianthemum scoparium</i>	annual	heat-shock**
Fabaceae		
<i>Lotus salsuginosus</i> , <i>L. strigosus</i>	annual	heat-shock
<i>Lotus scoparius</i>	suffrutescent	heat-shock
<i>Lupinus hirsutissima</i> , <i>L. succulentus</i>	annual	heat-shock
<i>Trifolium wildenovii</i>	annual	heat-shock
Hydrophyllaceae		
<i>Emmenanthe penduliflora</i>	annual	smoke
<i>Eucrypta chrysanthemifolia</i>	annual	smoke
<i>Phacelia brachyloba</i> , <i>P. grandiflora</i> , <i>P. parryi</i> , <i>P. suaveolens</i> , <i>P. viscida</i>	annual	smoke
Loasaceae		
<i>Menzelia micrantha</i>	annual	smoke
Onagraceae		
<i>Camissonia micrantha</i> , <i>C. californica</i>	annual	smoke
Papaveraceae		
<i>Dendromecon rigida</i>	shrub	smoke
<i>Dicentra chrysantha</i> , <i>D. ochroleuca</i>	suffrutescent	smoke
<i>Papaver californicum</i>	annual	smoke
Polemoniaceae		
<i>Allophyllum gilioides</i> , <i>A. glutinosum</i>	annual	smoke
<i>Gilia angelensis</i>	annual	smoke
Scrophulariaceae		
<i>Antirrhinum coulterianum</i>	annual	smoke
<i>Mimulus brevipes</i>	annual	smoke
Solanaceae		
<i>Nicotiana attenuata</i>	annual	smoke

* smoke, charred wood, or other combustion products from fire

** heat-shock = brief exposure to high temperatures from fire

CALIFORNIA IS A BIG STATE

Many of the generalizations about chaparral are based on ex-

tensive studies in Southern California. However, chaparral is the dominant vegetation type in the state, and historically, fire activity has been very different in other regions.

For example, in Southern California, very little if any of the chaparral landscape has escaped burning since annual record keeping began in 1911, and throughout the latter half of the 20th century most counties have had a fire rotation interval between 30-40 years, which is at the lower threshold of tolerance for chaparral. In contrast, large portions of the chaparral in the southern Sierra Nevada have escaped burning for very long periods; over 40% has never had a recorded fire.

In the mountains and valleys surrounding the East Bay of San Francisco a similar story unfolds where the fire rotation interval is estimated at about 100 years. Multiple factors account for these patterns. Differences in population density likely play a role since humans account for most fire ignitions in this vegetation. In addition, Santa Ana-type winds are rare in the southern Sierra Nevada foothills and the fire season is relatively short in the San Francisco Bay Area.

THE ODD COUPLE: CHAPARRAL FIRES AND PEOPLE

Large chaparral wildfires have been a feature of this landscape for eons. Long before humans had a dominant influence, massive wildfires occurred here; records of them are embedded in ocean sediments and Native American legends. The earliest well documented large fire in Southern California was in 1878. The fire perimeter map (stored in the U.S. National Archives) shows this fire burned from west of Pasadena north through Tujunga, but not quite to Mt. Gleason peak, then west to beyond Pacifico Mountain and was estimated at 78,000 acres. In Orange County a huge fire pushed by Santa Ana winds was reported by the *Los Angeles Times* in September 1889. The *Riverside Enterprise* (September 25, 1889) reported, "Never before have the people here witnessed such a natural pyrotechnic display. Looking eastward the entire heavens is one bright-red glare. Citizens in the entire [Santa Ana] valley are thoroughly aroused." The immensity of this fire is illustrated by the report that not only citizens on the western side of the range were impressed by the nighttime pyrotechnics but the fire was also clearly visible on the eastern side of the range: "Forest fires in the mountains east of Santa Ana raged all day and last night the light reflected upon the sky from the fire in that direction was plainly seen in this [Riverside] city." This was independently corroborated by Mr. L.A. Barrett in his 1935 book *"A Record of Forest and Field Fires in California from the Days of the Early Explorers to the Creation of the Forest Reserves."* He was 15 years old and living in Orange County at the time of the fire, and his first-hand account written many years later notes that it was the largest fire he had ever seen in his 40 year USFS career (a career



Chaparral five years after fire with resprouting evergreen chamise (*Adenostoma fasciculatum*) shrubs and seedlings embedded within a matrix of dried, but still alive, deerweed (*Lotus scoparius*) in Los Angeles County.

FIRE-PRONE YOUNG CHAPARRAL

Deer weed and other native perennials such as rock rose (*Helianthemum scoparium*) and morning glory (*Calystegia macrostegia*) are widespread in early seral stages. Their suffrutescent growth form has substantial dieback each year that provides more than enough fuel to make young chaparral highly susceptible to reburning. (Studies of similar stands show fine fuel loads are five to ten metric tons per hectare; Keeley and Halsey unpublished data.) Although these young fuels contribute to reduced flame lengths and produce fires more conducive to direct attack by fire fighters, they generally do not act as barriers to fire spread. This is one of the main reasons fire management aimed at producing "fuel mosaics" through rotational burning of chaparral has never worked in this vegetation type.

When young stands reburn they are much more susceptible to invasion by alien grasses, which in turn increases the risk of repeat fires. When fires occur multiple times within a 15- to 20-year period they can convert chaparral to alien-dominated grasslands.

that spanned some noteworthy chaparral fires such as the Matilija Fire of 1932 that burned 220,000 acres). However, until the last half of the 20th century these large fires had minimal impact due to the low density of people in the region; for example, the Matilija Fire did not destroy any homes. With the increase in population there has been a concomitant increase in human infrastructure losses, and for the last 50 years, each decade has been followed by a decade of wildfires with increasing loss of property and lives. This is despite an increase each decade in state and federal expenditures for fire suppression.

A geographer at the University of California, Riverside, Richard Minnich, has argued for more than 20 years that the fire problem in Southern California chaparral is the same as for many conifer forest surface-fire regimes in the West. Namely, that highly effective fire suppression by fire fighters has excluded fires for over a century and caused anomalously high and contiguous stands of chaparral fuels. His solution to the problem is to allow "natural" wildfires to burn during moderate weather conditions and maintain the landscape in a mosaic of young and old fuels, which he contends will fire-proof the landscape (see Box 1). This is a testable hypothesis that has captured the attention of several investigators, including Susan Conard and David Weise at the U.S. Forest Service Fire Lab in Riverside, Max Moritz at the University of California, Berkeley, and myself and a Ph.D. student C.J. Fotheringham at University of California, Los Angeles. Multiple tests of this and related hypotheses have shown that in Southern California, fire suppression has not even come close to excluding fires, and that fuel age and landscape mosaics of different aged fuels, have little effect on fire behavior during our catastrophic autumn fire season.

Unfortunately the media have exploited these studies by personalizing them as grand debates and reducing them to opposing sides or "camps." This does an injustice to the scientific method and confuses the public. As a result there is a tendency to choose sides and pick the "expert opinion" of preference. These are serious fire management issues that deserve better. In the future, scientists and the media need to do a better job of explaining the alternative models and addressing issues of data in support of one model or another. We need to move away from presenting this as a squabble between alternative and equally supportable models.

A recent Government Accounting Office report pointed out that the USFS spends over 50% of its budget on fire suppression activities and more goes to California than all of the other western US states. Most of this money goes to protect private property, and this potentially diminishes their capacity for completing other resource stewardship objectives. The report further suggested that the federal government may need to consider mechanisms for recouping some fire suppression costs from local communities. While this will certainly meet strong resistance, it may lead to greater local attention on how new and innovative approaches to land planning can diminish community vulnerability to wildfires.

Californians need to embrace a different model of how to view fires on these landscapes. Our response needs to be tempered by the realization that these are natural events that cannot be eliminated from Southern California. In this respect we can learn much from the science of earthquake or other natural disaster management. No one pretends they can stop them, rather they engineer infrastructure to minimize impacts, and in this respect there is much that can be done at the local level.

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[For related papers see also: <http://www.werc.usgs.gov/seki/keeley.asp>]

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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 pe-

riod. 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



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

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.

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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MAN AND FIRE IN SOUTHERN CALIFORNIA: DOING THE MATH

by Hugh D. Safford

The historic Southern California fire season of 2003, in which more than three-quarters of a million acres burned, thousands of homes were destroyed, and dozens of people lost their lives, brought the issue of man versus nature back to the newspaper headlines in California. Given the drought California is currently experiencing, 2007 may turn out to be another historic fire year. Although the 2003 fires significantly increased Californians' consciousness *vis-à-vis* the threat of fire, basic misunderstandings about the nature of fire in chaparral abound, and maladaptive decisions regarding fire preparedness and land development continue to be made across the state.

SOUTHERN CALIFORNIA AND FIRE: THE ECOLOGICAL REALITY

Before the arrival of Euro-Americans in Southern California, fires in montane conifer forests burned at frequent intervals, perhaps averaging 10 to 30 years between fires for most of the Southern California mountains (Keeley 2006). Fires in lower elevation chaparral-dominated systems are thought to have burned much less often, perhaps every 60 to 100 years (Keeley and Fotheringham 2001).

In both systems, the fires were caused by humans or by lightning, with the latter dominating montane forests and the former dominating lowland systems (Keeley 2006). Today, population growth in the Southern California lowlands, together with aggressive fire suppression by land management agencies, has led to a change in fire frequencies in

these two ecosystems: more than 50% of montane forestland in Southern California has not experienced a fire since the beginning of the 20th century, while about 50% of the Southern California foothills have burned two times or more and 20% three times or more (Stephenson and Calcarone 1999). Some areas have burned more than five times since 1905, and in many of these places—where fire is currently burning much more often than under presettlement conditions—chaparral stands are being converted to weedy grassland.

Today, almost all contemporary wildfires in Southern California occur in the lowlands and foothills, i.e., in chaparral or grassland. The characteristics of fire in chaparral and similar shrublands are very different from those of most conifer forests in California (Keeley et al. 2004). By definition, chaparral supports a “high severity” fire regime in which fires burn at high intensity and much of the aboveground biomass is lost. With some exceptions, before Euro-American settlement, montane conifer forests in Southern and central California tended to burn at much lower intensity and severity, with much less biomass loss. This was because frequent ground fires in these forests maintained low fuel loads which shielded much of the tree canopy from direct fire effects. In contrast to many western conifer forests—where fuel ingrowth (increasing biomass in the understory) greatly increases fire hazard in proportion to the time since the last fire—fire hazard does not increase appreciably with age in most Southern California chaparral systems. Under the right conditions, chaparral can burn at almost any age (Keeley et al. 2004).

Figure 1 (page 26) compares the 20th century fire record for the chaparral-dominated Angeles, San Bernardino, and Cleveland National Forests (“Southern California”) against the record for the Eldorado, Tahoe, Plumas, and Lassen National Forests (“Northern Sierra”), which are comprised almost entirely of coniferous forest. First, fire suppression has greatly decreased the number of fires in coniferous forest, but has had little or no effect on fire frequencies in Southern California (i.e., in the chaparral/grassland belt). Indeed, fires have been increasing in number in Southern California since the 1930s (Figure 1, top, page 26).

Secondly, mean fire size before and after fire suppression (defined here as 1940) has increased in the Northern Sierra, but has not changed in Southern California (Figure 1, middle, page 26). Finally, the proportional area burned by large fires

Old-growth chamise (*Adenostoma fasciculatum*) on Santa Catalina Island. Photograph by R. Halsey.



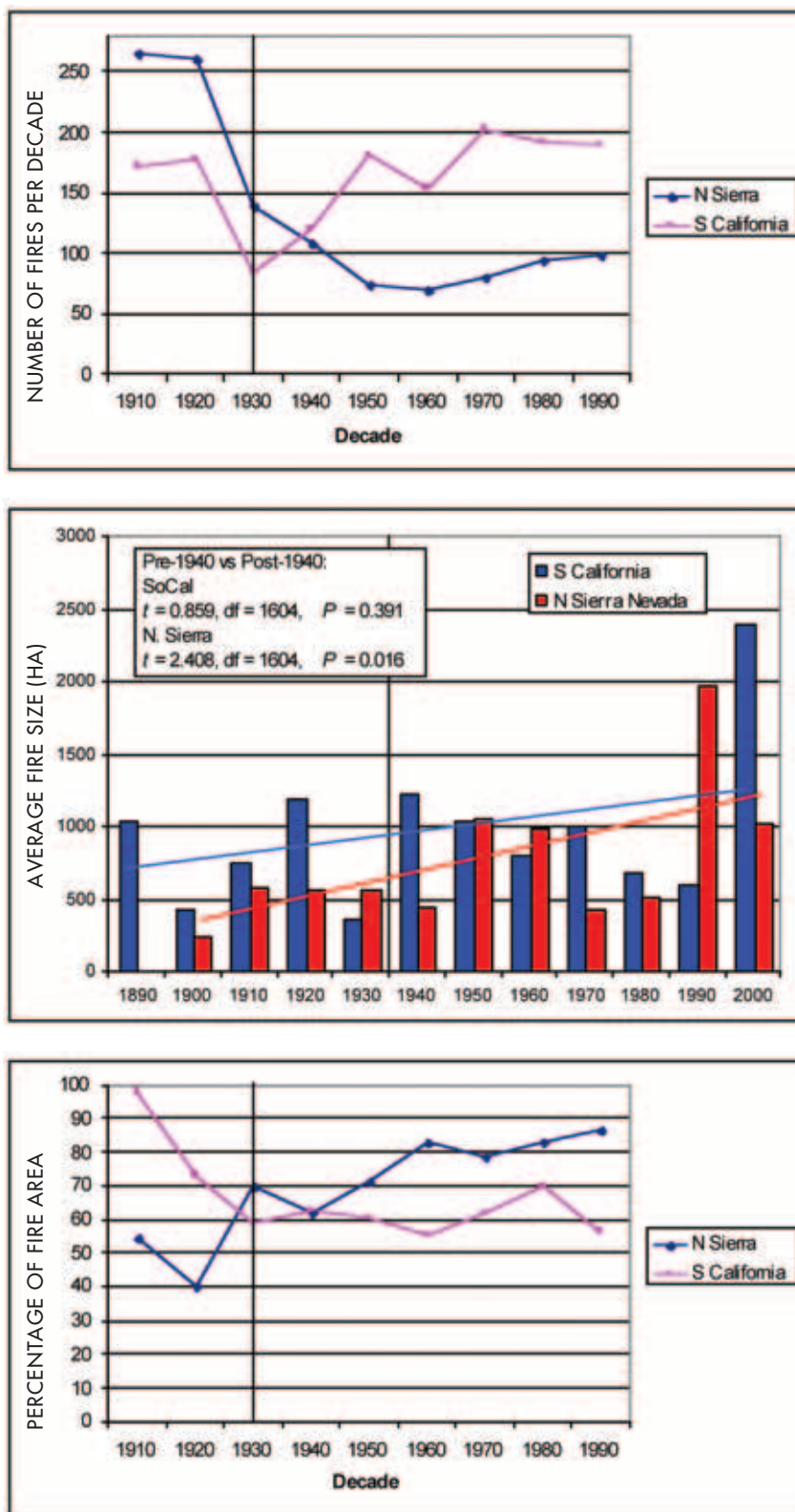


Figure 1. Fire statistics compared between the northern Sierra Nevada (conifer forest) and Southern California (primarily chaparral and non-conifer forest). TOP: Number of fires per decade; MIDDLE: Average fire size per decade; BOTTOM: Percent of the total area burned within a decade contributed by the area of the ten largest fires in that decade. The black vertical line represents the approximate beginning of federal suppression of fires. Source: <http://www.frap.cdf.ca.gov/data/frapgisdata/select.asp>

has increased over time in the Northern Sierra but has remained constant in Southern California (the high value in 1910 is an artifact of an incomplete record for that decade). In essence, big fires have always been a feature of the Southern California landscape.

SOUTHERN CALIFORNIA AND FIRE: THE SOCIOECONOMIC REALITY

Southern California cities and counties are among the fastest growing in the nation. The Los Angeles Basin and greater San Diego add over 300,000 people per year, and Southern California counties rank first through fourth in numbers of new residents added per annum in California (U.S. Census Bureau 2005). Urban areas are expanding rapidly to accommodate growing populations. Between 1970 and 1990, the size of the Los Angeles metropolitan area increased by over 1,000 square kilometers, metro San Diego expanded by almost 800 square kilometers, and the urbanized parts of San Bernardino and Riverside counties grew by over 380 square kilometers (U.S. Census Bureau 2005).

Growth rates in Los Angeles and San Diego proper have slowed slightly in recent years only because the availability of land has decreased—current growth is occurring primarily on the urban periphery, in areas bordering national forests and other public lands (SCSC 2001, USFS 2005). In these areas, the greatest increases in housing development are occurring in dispersed neighborhoods that often adjoin highly flammable wildland landscapes (Syphard et al. 2007).

Suburban expansion into former wildlands is driven as much by profits in real estate development, construction, and home sales as by population growth itself. The median price of a home in San Diego County grew from \$150,000 in 1993,

to nearly \$450,000 in 2003. Although the housing market is currently down, profits to home builders over the last two decades have been astronomical: annual net earnings for some of the development corporations operating in Southern California amounted to over one billion dollars in 2004 and 2005 (<http://finance.google.com>). Under these conditions—exploding populations, high development profits, and the relative affordability of land outside the current urban boundary—the pressure to rapidly build housing in the wildland-urban interface (WUI) is enormous.

SOUTHERN CALIFORNIA AND FIRE: WHEN REALITIES MEET

California abounds with examples of people living in harm's way: earthquakes, landslides, floods, and fires threaten the lives and property of a high proportion of the state's residents. The intersection of millions of people and rapid, poorly planned suburban growth with what has been called "the world's most flammable ecosystem" leads predictably to the sorts of calamities Southern California experienced in 2003. Eight of the ten costliest fires in U.S. history have occurred in the California WUI (Halsey 2005), and the costs of fighting wildland fires which threaten human populations are increasing rapidly. More than half of the most damaging fires in the U.S. over the last 170 years were in California, and California leads the nation in wildfire-related economic losses, as well as in fire fighter fatalities (Halsey 2005). Federal Emergency Management Agency (FEMA) expenditures in California are typically higher than in any other state, and many of these outlays relate to fire-induced losses. In the period between 1991 and 1999, California received nearly four times more FEMA money than the sec-



The vibrant red of Indian pink (*Silene laciniata*) appears amongst fire-blackened stems. Photograph by R. Halsey.

ond biggest recipient (Florida) and nine times more than the third (North Carolina).

The realities of increasing populations and fires are forcing major changes in the way that government agencies do business in Southern California. For example, although the Forest Service is usually thought of as a wildlands management agency, a large and growing portion of its budget is allocated every year to protecting private property and infrastructure in the WUI (SCSC 2001, Canton-Thompson et al. 2006). Between 1970 and 1985, the Forest Service spent about \$215 million annually in wildland fire suppression costs; since 2000 the average annual expenditure has ballooned to one billion dollars (<http://www.forestsandrangelands.gov/>). In 1999, non-fire allocations were twice the allocations for wildland fire management, but since 2001 the latter have exceeded the former by an annual average of almost 20%.

In Southern California, the budgetary imbalances are even more prominent. For example, until the mid-1990s, the Cleveland National Forest's budget allocations for fire and non-fire needs were approximately equal, but by 2002 fire allo-

cations had risen to 70% of its entire budget; today the disparity is even greater. Other agencies have had to make similar changes. Today, across all government agencies, California fields the largest fire department in the United States (and probably the world), with an annual budget for wildfire preparedness exceeding three billion dollars.

Even with these huge governmental allocations for fire control, losses of property and life continue to mount in Southern California. There are two major reasons for this trend: the nature of fire and climate in Southern California, and patterns in population growth and land development. In the first place, fire-fighting agencies simply cannot stop chaparral fires that occur under extreme weather conditions, such as Santa Ana windstorms, until those conditions abate. Although there is a persistent belief among some segments of the population that expensive aerial fire fighting technology can be employed at any time to save poorly planned and located communities from wildfire loss, such tools cannot extinguish fires. Only ground crews can accomplish this, and in any case aerial support is impossible when aircraft are grounded by smoke

and high winds. Secondly, population growth and the proportion of land occupied by dispersed housing in wildland settings are the two variables most closely linked to fire occurrence and property loss in the California WUI (Syphard et al. 2007). As populations and fires continue to grow, and as dispersed and poorly planned developments continue to spread across the region, more and more Southern Californians are coming to understand in first-hand fashion that the equation as currently constituted is unsolvable.

HOW DO WE SOLVE THIS EQUATION?

Although the first human response to catastrophes like the 2003 Southern California fires is often to blame others for our misfortune (Halsey 2005), some people have been able to get beyond the immediate shock to think constructively about how to mitigate the impacts of chaparral fires on communities, as well as the impacts of communities on fires. What is clear is that significant changes must be made in the way we build and live in California's WUI.

Over the last few decades, federal, state, and local agencies have constructed an elaborate and expensive system of wildland fuel breaks throughout Southern California. Fuel breaks are meant primarily to moderate fire behavior sufficiently to allow fire control personnel to safely engage in suppression activities. However, when destructive fires occur in Southern California they almost always occur under extreme weather conditions, i.e., low humidities, high temperatures, and strong winds. Nearly every year, fires across California provide evidence of the inability of wildland fuel breaks to stop fire spread under these types of conditions (Keeley et al. 2004).

The ultimate purpose of fuel breaks is to protect human lives

and property, but it has been known for many years that home fire safety in areas of high fire hazard depends largely on local factors, such as the condition of fuels surrounding one's property, local topography, the home's design and construction, and ease of access and exit for fire fighters (Radtke 1983). For most of California, it follows that the most strategic location for fuel breaks is near human habitation, rather than far from it, and that well-considered planning and building decisions made by local communities and homeowners are ultimately more important to human safety than split-second decisions made by fire fighters in the act of fighting fires.

Although we are a stubborn species, it appears that some of the lessons of the 2003 Southern California fires have begun to sink in. For example, the Forest Service altered its general fuels management strategy for Southern California so as to focus its fuel-clearing efforts more in the immediate proximity of human communities rather than in the intervening wildlands (USFS 2005). The State of California formalized its high fire hazard area definitions (http://www.fire.ca.gov/wildland_zones.php), and for those areas, Public Resource Code 4291 was revised to require 30 meters (100 feet) of defensible space, up from nine meters (30 feet) in the

original code (since 1998 Los Angeles County has required 60 meters (200 feet)). Note that "defensible space" does not mean "moonscape" (Halsey 2005).

California Building Codes 701A to 704A go into effect January 1, 2008, and in high-fire-hazard areas they require (among other things): external ignition-resistant building materials, fire-resistant windows and doors, and fire-retardant-treated decking. Many Southern California cities have upgraded their fire fighting capabilities, and now Southern California boasts the highest density of "well-protected" communities in the nation (<http://www.iso.com>). Homeowner fire hazard assessments are also now available online, for example U.C. Berkeley's Fire Information Engine Toolkit (<http://firecenter.berkeley.edu/toolkit/>), which also offers information related to home fire protection and post-fire damage recovery.

Although these government-based efforts are laudable, in the end it will take education, assumption of personal responsibility, and real political will to change the way that fires impact communities and communities impact fires in Southern California. Before the 2003 fires, defensible space laws were already on the books, but they were often loosely enforced or not at all. Many property owners who live in WUI areas move there precisely to escape

Homes built at the top of a saddle are especially vulnerable during a wildfire. White Xs mark homes burned during the 2007 Witch Fire, San Diego County.



urban regulation, and they may resist fire safety codes that limit their freedom to build and landscape as they choose. Many property owners also perceive fire and its outcomes essentially as random and uncontrollable events and fail to see the economic payoff of investing in fire fighting infrastructure or in safeguarding their own private assets (Winter and Fried 2000). It is a distressingly common pattern for California communities to vote down increased allocations for fire protective services, while concurrently approving further haphazard development into fire-threatened landscapes (Halsey 2005; Figure 2).

Arguably the most positive development to come out of the 2003 fires has been a refocus on education. In concert with the San Diego Wildfires Education Project, a number of Southern California school districts now teach short courses in fire safety and fire ecology, and the availability of educational resources through the Internet and published information has exploded. Perhaps the most basic lesson Californians must learn is that suppression and prevention are important, but they are not the only variables in the equation. Properly doing the math will require that we understand as a society that wildfire is an inevitable component of the chaparral landscape, just as tornadoes are an unwelcome but unavoidable companion across the Midwest, and hurricanes an inescapable part of living in the coastal Southeast. Once we bring ourselves to recognize this reality, we can set about planning more intelligently for growth and development, engineering infrastructure to minimize fire impacts, and summoning the com-

mon sense, political will, and personal responsibility *to be prepared*.

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Figure 2. Many California housing tracts violate basic principles of fire safety in high-fire-hazard areas. Topography is a major factor influencing home safety. Homes built atop topographic high points require setbacks from steep slopes, as wind-driven flames and convective heat can impact these homes directly. Homes in natural chimneys are highly prone to fire-loss, as narrow canyons and saddles act as wind tunnels.

FROM ASHES TO LIFE: EFFECTS OF FIRE ON A SAN DIEGO CHAPARRAL COMMUNITY

by David M. Cohn III

On October 26, 2003, the Cedar Fire swept near the neighborhood of 11-year-old David Cohn III. "The Cedar Fire nearly destroyed my home," David told Rick Halsey. "I watched the flames come closer and closer to my house from my bedroom. After the fire, ash blanketed the hillsides of Poway as far as the eye could see. I wondered if the thriving chaparral ecosystem would recover or would the fire cause invasive species to flourish? I wanted to turn this frightening experience into something positive so I began studying the chaparral's post-fire response." This is a summary of David's work:

In November of 2003, I began documenting plant regeneration and soil chemistry changes in a biological preserve located in the

High Valley region of Poway, California.

Multiple test plots were established and site visits were conducted every three weeks. Each plant inside the test plots was identified and counted. Notable examples included laurel sumac (*Malosma laurina*), chamise (*Adenostoma fasciculatum*), chaparral candle (*Hesperoyucca whipplei*), and white sage (*Salvia apiana*).

The general area was also surveyed in an attempt to correlate the results found inside the plots to the regeneration noted in the entire plant community. During each visit, soil temperature, soil moisture level, humidity, ambient air temperature and rainfall totals were also recorded.

Every three months, soil samples

from the fire test site and from a nearby unburned soil location were taken to the laboratory at John Deere Landscaping and analyzed at home using the Rapidtest Soil Kit. Analysis of soil within the Cedar Fire burn revealed that the nitrogen levels fluctuated from 170 to 340 pounds per acre, which is normal for a chaparral ecosystem. Phosphorus levels ranged from 0 to 54 pounds per acre, below normal to normal. Potassium levels remained between 140 and 230 pounds per acre, above normal for chaparral. The nutrient levels remained relatively stable for the entire 40 months of this study. The lack of nitrogen depletion found in the burned soil may be due to the low residence time of the flames or the fire's temperature. The high potassium levels may be the results of high ash content in the burned soil and chemical weathering from potassium feldspar boulders.

Samples of unburned soil were placed in a gas kiln to simulate the effects of wildfires at various temperatures. The chaparral soil was burned at three different temperatures: 1,000°F; 1,500°F; and 2,000°F. Nitrogen became depleted as soon as heat was applied. Potassium steadily increased as the kiln temperature increased. At 2,000°F, surplus levels of potassium were noted. Phosphorus increased to surplus levels at 1,000°F and 1,500°F. Phosphorus declined to a normal level at 2,000°F.

Over the 40-month period (November 2003 to March 2007), 2,369 native plants germinated, while only 37 non-native plants appeared. The 2,369 native plants represented 35 different species. Native-plant fire

Three weeks after the Cedar Fire ravaged the High Valley area of Poway, 11-year-old David Cohn establishes one of many observation test plots. All photographs provided by the author.



followers, such as popcorn flower (*Cryptantha micromeres*) and Parry phacelia (*Phacelia parryi*), were predominant in the first 14 months. Endemic and frequent fire followers and opportunistic annuals reached their maximum populations within the first two years. The obligate-seeding deerweed (*Lotus scoparius*), seedling chamise (*Adenostoma fasciculatum*), and obligate-resprouter sawtooth goldenbush (*Hazardia squarrosa*), all showed increased density and cover by the third post-fire year.

From 2004 to 2005, the total number of species in the burn area increased from 14 to 24, a 71% increase. However, by 2006, a 21%

One year post-Cedar Fire, David measures the density of the crown-sprouting, fire-dependent chamise (*Adenostoma fasciculatum*) in his observation test plot #5.



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decline was noted and the species count dropped to 19. By the first two months of 2007, the total number of species declined further to 13. Remarkably, in only about three years time, the native fire followers disappeared, the numbers of post-fire specialists and opportunistic annuals have significantly declined, and the shrub cover and density began to increase. It was wonderfully surprising to discover that the native plants were so resilient and overwhelmingly outnumbered the invasive species.

David's now four-year science fair project has earned him a number of top awards including the Sweepstakes Award in Life Sciences at the 2006 Greater San Diego County Science and Engineering Fair, and Project of the Year at the 2006 California State Science Fair. David has also presented his project at the Smithsonian Institution National Museum of Natural History in Washington, D.C.

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Anjel M. Helms, Marcus S. Heffner, Anthony R. Shaver, Amory C. Deroulet, Nicole L. Stasiak, Spencer M. Vaughn, Caleb B. Leake, Han D. Lee, and Eli T. Sayegh are undergraduate students at Pepperdine University and worked with Stephen D. Davis documenting the effects of the freezing temperatures on the zonation of chaparral species in the Santa Monica Mountains.

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FROM THE EDITOR

Welcome to *Fremontia*'s special Chaparral Issue. Our guest editor, Richard Halsey, has assembled seven compelling articles covering an array of topics on California chaparral—that most characteristic mediterranean-climate vegetation. Other regional floras have their versions of oak woodlands, grasslands, and forests of conifers or broadleaved evergreens, but it is only in those rare summer-dry and winter-moist areas of the world that these strikingly beautiful shrublands abound.

Halsey's article sets the stage for this issue by providing an overview of the ecology and diversity of chaparral in California, and is illustrated with his superb photographs.

Parker's studies on manzanitas have been ongoing for over 20 years. This article explains the reasons why there are so many different kinds of manzanitas in California.

Davis and his students took full advantage of the unique set of circumstances following the unusually hard 2007 freeze in the Santa Monica Mountains. Such unusual conditions are responsible for some of the patterns in the chaparral that we see today.

Keeley's contribution provides an up to date explanation and review of the complex relationship between chaparral, fire, and people.

Tyler and Borchert provide new insights into the interaction between fire and chaparral geophytes (bulbs).

Safford explores the vortex of economic and political realities in our dealings with chaparral. Many hard choices remain to be made by Californians.

Student David Cohn shows what one person can accomplish while exploring and documenting the consequences of a major chaparral wildfire in his own backyard.

There are many sources of additional information on our chaparral ecosystem. If you are not familiar with Rick Halsey's California Chaparral Institute, I highly recommend that you visit its web site: <http://www.californiachaparral.com/> and then take a long hike to experience your under-appreciated local chaparral.

Bart O'Brien

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Mark I. Borchert is the province ecologist for U.S. Forest Service and is responsible for Los Padres National Forest, Angeles National Forest, San Bernardino National Forest and Cleveland National Forest.

David M. Cohn III is a fifteen-year-old student at the Rhoades School in Encinitas, California. He attributes his passion for science and the environment to his Rhoades School science teacher, Mrs. Roxanne Hunker.

Stephen D. Davis is a distinguished professor of biology at Pepperdine University who specializes in the physiological ecology of chaparral shrub communities of Southern California. The co-authors are undergraduate students who collected the data for this article as partial fulfillment of their introductory botany class, biology of plants, at Pepperdine University.

Richard W. Halsey is the director of the California Chaparral Institute, a research and educational organization focusing on the ecology of California's shrubland ecosystems, the dynamics of wildland fire, and the importance of nature education.

Jon E. Keeley is currently a research ecologist with the U.S. Geological Survey, stationed at Sequoia National Park, is an adjunct professor in the department of ecology and evolutionary biology at the University of California, Los Angeles, and is a research associate of the Rancho Santa Ana Botanic Garden in Claremont.

V. Thomas Parker is a professor of biology specializing in plant ecology at San Francisco State University and has worked on understanding *Arctostaphylos* evolution for the last 20 years or so, leading to the next treatment of the genus in the upcoming second edition of *The Jepson Manual*.



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