

RESILIENCE TO FIRE DOES NOT IMPLY ADAPTATION TO FIRE: AN EXAMPLE FROM THE CALIFORNIA CHAPARRAL

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ABSTRACT

The California chaparral vegetation is resilient to frequent fires. Some species have adapted their reproductive biology to take advantage of these disturbances. Fire-adapted shrubs such as *Adenostoma fasciculatum*, *Arctostaphylos* spp., and *Ceanothus* spp. have specialized seeds which lie dormant in the soil until germination is triggered by fire. These species have evolved to exploit the conditions after fire for population expansion. One consequence of this specialization is a dependence upon fire for successful seedling establishment. Other shrubs, e.g., *Quercus dumosa*, *Heteromeles arbutifolia*, *Prunus ilicifolia*, and *Rhamnus* spp., however, do not have postfire seedling recruitment. These species persist in the face of recurrent fires because they are vigorous resprouters, but they require long fire-free periods to establish seedlings. As a consequence of these different character syndromes, opportunities for population expansion increase after fire for some species, but for others opportunities for population expansion increase only in the absence of fire. Equilibrium in species composition is probably enhanced by variable burning regimes.

INTRODUCTION

High intensity wildfires are common in the chaparral vegetation of California (Keeley and Keeley 1988). There are two reasons for this. Extended drought from midspring to midfall each year produces tinder dry fuel that is easily ignited. Additionally, mild temperatures during the wet winters and early spring, produce conditions suitable for growth of a dense shrub cover which forms a contiguous fuel. Although humans are responsible for most of the acreage burned in chaparral, lightning ignitions are frequent enough to have been an important source of ignition in prehistoric eras.

Wildfires typically kill all aboveground biomass in chaparral. Shrubs are resilient to such disturbance in that species present before the fire quickly regenerate their populations (e.g., Horton and Kraebel 1955, Hanes and Jones 1967). Some species regenerate from basal sprouts and others from seeds which lay dormant in the soil until stimulated by fire. While all chaparral shrub species are resilient to fire, not all species benefit equally from wildfires.

How might a species benefit from disturbance? High intensity chaparral fires improve site conditions by removing competing shrub cover, mineralizing nutrients, and temporarily reducing pathogens and herbivores (Rundel 1981). Some species have evolved to take advantage of fires by timing seedling establishment to the first post-fire growing season. Thus, fires represent an opportunity for population expansion and such fire-adapted species can be described as "fire-recruiters."

FIRE-RECRUITER SPECIES

Although other species may be included under this heading, good examples include *Adenostoma fasciculatum* (chamise) and species of the very diverse genera *Arctostaphylos* (manzanita) and *Ceanothus* (California lilac, buckbrush). These species flower prolifically on an annual or biennial basis, but a large portion of the seeds which are dispersed have an imposed dormancy and they accumulate in the soil beneath the shrub canopy (Keeley 1987). Those that do germinate under the shrub canopy rarely survive more than a few days or weeks.

The majority of seeds, however, persist in the soil seed bank until germination is triggered by fire. Two cues are important; either intense heat cracks the testa of "hard-seeded" species or charred wood chemically induces germination in other species (Table 1). Seedling establishment in these species is restricted to the first growing season after fire. In most *Arctostaphylos* and *Ceanothus* species, resilience to fire is completely dependent on postfire seedling recruitment because the burned shrubs are unable to resprout. For these fire-recruiter species, the postfire year is the only opportunity for population expansion.

Table 1. Germination patterns of chaparral species with heat shock stimulated germination, charred wood stimulated germination and non-refractory seeds. Seeds were heat treated dry, prior to sowing in potting soil. Charred wood was ground to a fine powder and added to the potting soil. Seeds were incubated in the light. (Data from Keeley 1987.)

| Temperature (°C) | Control | Percentage Germination | | |
|--|---------|------------------------|-----|-----|
| | | 70 | 100 | 120 |
| Time (min) | | 120 | 5 | 5 |
| <i>Ceanothus megacarpus</i> (Fire-recruiter) | | | | |
| Control | 11 | 41 | 48 | 80 |
| Charred wood | 2 | 40 | 40 | 61 |
| <i>Romneya trichocalyx</i> (Fire-recruiter) | | | | |
| Control | 0 | 0 | 0 | 0 |
| Charred wood | 24 | 33 | 34 | 24 |
| <i>Quercus dumosa</i> (Fire-persister) | | | | |
| Control | 77 | 0 | 57 | 55 |
| Charred wood | 68 | 0 | 53 | 27 |

Other characteristics illustrate specialization to postfire seedling establishment. These taxa produce propagules which are not highly specialized for long distance dispersal and the bulk of the seed bank accumulates near the parent plant. Angevine and Chabot (1979) describe this mode as the "temporal disperser strategy;" the seeds wait in the soil until a disturbance comes to them and creates a safe site for establishment. Another specialization exhibited by these obligate seeding species is the evolutionary loss of the resprouting ability. Wells (1969) maintains that these taxa were derived from crown-sprouting ancestors. Vegetative regeneration is nearly ubiquitous in woody dicots and its absence in these chaparral taxa makes these species dependent upon seedling regeneration for surviving fires.

Due to the very long lived soil seed bank, fire-recruiter species may be resilient to very long intervals between fires. Due to the absence of vegetative regeneration in most of these species, they are not resilient to fires that occur at intervals shorter than the time required to build up a soil seed bank. Although most fire-recruiter shrubs reach reproductive maturity within 10 years after fire, many may require two decades or more to accumulate a seed bank sufficient to replace the population. Thus, these fire-recruiter species may not be resilient to short intervals between fire, despite the fact that they are entirely dependent upon fire for reproduction. This dependence upon fire is what gives chaparral the reputation for being a fire dependent type vegetation. However, many chaparral dominants merely persist in the face of recurrent fire, and these "fire persisters" are not dependent upon fire.

FIRE-PERSISTER SPECIES

Many chaparral shrubs persist in the face of recurrent fires by resprouting from underground stems or roots but rarely establish seedlings after fire. Such species are resilient to fire but show no obvious adaptation to fire; vegetative regeneration is so widespread in the plant kingdom, there is little to suggest it has been selected for by fire. These species do not take advantage of postfire conditions for seedling establishment.

In the short-term, such species appear resilient to fire, but in the long-term, these populations may be threatened by repeated burning. Despite being vigorous resprouters, none of the shrub taxa spread vegetatively and thus, after fire, the best they can do is replace their populations. However, 100% of the population does not necessarily survive; i.e., there is some attrition from the population following each fire. Consequently, managing for long term survival of these species requires knowledge of their reproductive biology.

Chaparral shrubs included here are *Quercus dumosa* (scrub oak) *Prunus ilicifolia* (chaparral cherry), *Heteromeles arbutifolia* (chaparral holly), *Rhamnus crocea* (redberry) and *R. californica* (California coffeeberry). These shrubs produce acorns or fleshy fruits which mature in fall and winter and are animal dispersed. Germination typically occurs within weeks of the first fall or winter

rains and does not require fire-related stimuli (Table 1). The seeds are short-lived and thus a persistent seed bank does not develop. Seedling establishment of these shrubs is largely nonexistent in most mature chaparral stands.

The widespread lack of seedling recruitment in such species, despite substantial reproductive energy allocated to flower and seed production, led Paul Zedler (pers. comm.) to remark, "perhaps these species are in need of genetic counseling?" I suggest, however, that the reproductive cycle of these fire-persister species is dependent upon a fire regime seldom experienced in the anthropogenically controlled landscape of contemporary California.

CHAPARRAL FIRE REGIMES

Almost universally, when fire ecologists address the question of what impact humans have had on the modern landscape, it is pointed out that the policy of fire suppression has reduced the frequency of fires in most landscapes. I suggest that such has not been the case in the chaparral region of California (Keeley et al. 1989). The main reason is that fire prevention is relatively ineffective in southern California. As can be seen in Table 2, the vast majority of all acreage that is burned is the result of human ignitions. In all fairness though, fire prevention efforts have had some impact, for example in the adjacent landscape of Baja California, where fire prevention is not practiced, the number of human caused wildfires is several times higher (Minnich 1983).

Table 2. Average number of hectares burned per year by lightning-ignited and human-ignited fires on U.S. Forest Service districts in California, arranged from south to north (based on data for 1970 decade, from Keeley 1981).

| Forest District | Hectares burned per year per million hectares of forest | |
|------------------|--|----------------|
| | Lightning-ignited | Person-ignited |
| Cleveland | 36 | 12,101 |
| Angeles | 1,256 | 20,190 |
| San Bernardino | 184 | 3,919 |
| Los Padres | 2,237 | 1,734 |
| Mendocino | 24 | 1,619 |
| Six Rivers | 4 | 36 |
| Klamath | 597 | 171 |
| Shasta-Trinity | 47 | 1,709 |
| Sequoia | 98 | 1,559 |
| Inyo | 25 | 115 |
| Sierra | 44 | 1,879 |
| Eldorado | 24 | 593 |
| Stanislaus | 130 | 558 |
| Lake Tahoe Basin | 19 | 122 |
| Tahoe | 101 | 99 |
| Plumas | 209 | 530 |
| Lassen | 200 | 52 |
| Modoc | 1,699 | 396 |

Perhaps the current fire regime, which results in most of the landscape experiencing a wildfire every 20 years, is not typical of the natural environment. I view natural fires as having had a stochastic distribution in time and space; some sites at some points in time may have burned at short intervals and at other times have remained fire-free for long periods of time.

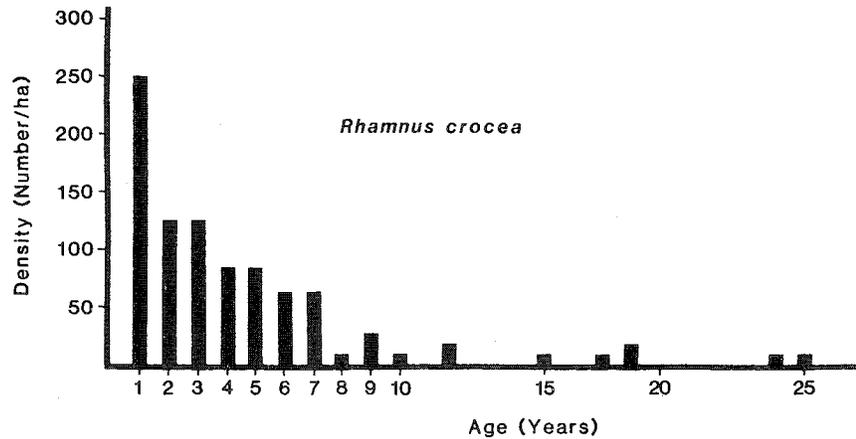
One of the more compelling pieces of evidence for this hypothesis is that fire-persister species require very long fire-free intervals for seedling establishment. Although seedling recruitment by these species is seldom observed, it has been reported from very old stands of chaparral (Patric and Hanes 1964, Zedler 1981, Keeley et al. 1986). As can be seen in Table 3, *Quercus dumosa*, *Prunus ilicifolia*, *Rhamnus crocea*, and others are capable of substantial seedling recruitment on sites free of fire for 75 years or more. It is not known why successful seedling establishment is absent in younger stands, although one possibility is that these seedlings may require soils with higher organic matter, and thus greater water holding capacity, typical of soils in old chaparral. Fire-persister species are generally much more sensitive to water stress than fire-recruiter species (Keeley and Keeley 1988) and thus seedlings of fire-persister species may also require the development of a dense, shady canopy that may reduce summer water stress. Not surprisingly, fire-persister species are more shade tolerant than fire-recruiter species. It is important to note that seedling establishment in older chaparral is only characteristic of fire-persister species; fire recruiter species, such as *Arctostaphylos* spp., *Ceanothus* spp., and *Adenostoma fasciculatum* do not recruit seedlings in old chaparral stands.

An example of the age structure for *Rhamnus crocea* from a stand unburned for 120 years is shown in Figure 1. If we assume roughly constant annual recruitment of seedlings, it is obvious that there is marked attrition from cohorts as they age. Even so, there are some which establish successfully and potentially will be recruited into the mature population.

Table 3. Density of dominant shrubs and seedlings/saplings in older stands of chaparral (Keeley unpublished data).

| Species | Density (#/ha) | | |
|---|----------------|-------------|--------------------|
| | Live Shrubs | Dead Shrubs | Seedlings/Saplings |
| San Ignacio Site (77 years since last burned) | | | |
| <i>Quercus dumosa</i> | 1,720 | 0 | 8,890 |
| <i>Adenostoma fasciculatum</i> | 580 | 280 | 0 |
| <i>Rhamnus crocea</i> | 420 | 0 | 1,330 |
| <i>Prunus ilicifolia</i> | 220 | 0 | 13,000 |
| <i>Ceanothus cuneatus</i> | 0 | 170 | 0 |
| Silverado Site (120 years since last burned) | | | |
| <i>Quercus dumosa</i> | 2,110 | 310 | 1,300 |
| <i>Heteromeles arbutifolia</i> | 310 | 0 | 50 |
| <i>Ceanothus crassifolius</i> | 470 | 1,110 | 0 |
| <i>Adenostoma fasciculatum</i> | 420 | 250 | 0 |
| <i>Rhamnus crocea</i> | 140 | 0 | 920 |

Figure 1. Age structure of seedlings and saplings of *Rhamnus crocea* from a stand of chaparral unburned for 120 years (Keeley unpublished data).



Whether or not the age structure of these seedling/sapling populations are sufficient to maintain, or even increase the adult population, requires careful consideration. Observations indicate that most saplings that persist in these older chaparral sites grow very slowly. Few, even after 10 years, reach the canopy and then only in gaps which are few and far between. It is unknown whether or not these saplings are able to survive and resprout after fires in these very old stands. If so, they may represent a form of “advance reproduction,” ultimately dependent upon return of fire to the site.

CONCLUSIONS

These observations are of more than academic interest. Sound land management must recognize that in order to preserve the biodiversity of fire-prone chaparral, there are taxa that may persist in the face of frequent fires, but long-term survival requires intervals of fire-free conditions for their successful reproduction. The proper fire regime for management of California chaparral may be one that includes a diversity of fire frequencies.

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