

## FIRE SEVERITY AND PLANT AGE IN POSTFIRE RESPROUTING OF WOODY PLANTS IN SAGE SCRUB AND CHAPARRAL

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### ABSTRACT

Postfire resprouting by woody plants confers a marked advantage in rate of recovery over species that regenerate entirely from seed. However, the predictability of this advantage varies markedly between species, with some showing nearly 100% rootcrown survival and others often much lower. This study examined patterns of fire-caused mortality and tested the relative importance of fire severity and plant age between various shrubs and subshrubs characteristic of chaparral and sage scrub associations. Resprouting success varied from about 10% for *Eriogonum fasciculatum* to a high of 98% for *Quercus berberidifolia*. For most of the shrub species, skeletons of resprouting plants were significantly taller than those of dead individuals of the same species, indicating less biomass consumption, and thus lower severity fires were associated with higher resprouting success. This pattern was less strongly the case with sage scrub species. Shrubs and subshrubs, however, differed in the effect of aboveground plant age (as estimated by basal diameter) on resprouting success. For most chaparral shrubs, age was not related to resprouting success, whereas in four out of five subshrub species, including *Artemisia californica*, *Eriogonum fasciculatum*, *Salvia leucophylla*, and *S. mellifera*, the youngest plants exhibited the highest resprouting success. I hypothesize that the reason for this inverse relationship between age and resprouting in certain sage scrub species is that, as these subshrubs age, there is a tendency to lose the resprouting ability and the mechanism is quite possibly because adventitious buds responsible for sprouting become buried by woody tissues. Patterns of character evolution in these sage scrub lineages support the hypothesis that the herbaceous perennial mode of seasonal aestivation evolved early and lignification is a more recently derived trait and this may have negative effects on resprouting as the plant ages.

Key Words: burl, chaparral, fire, lignotuber, resprouting, sage scrub.

California shrublands are among the most fire-prone ecosystems in the world. The mediterranean-climate produces a seasonal distribution of precipitation and drought that are highly conducive to fire. Winter rains of typically 250–600 mm are coupled with cool winter temperatures that reduce evaporative loss and produce moist soil conditions that results in abundant primary production during the 4–6 mo growing season. The summer and fall dry season dries foliage sufficiently such that much of this growth is available fuel for fires. The extended dry season also favors shrubs over trees, and as a consequence much of the primary growth is maintained near the ground resulting in dense fuel packing, leading to high intensity stand-replacing crown fires that feed on canopies rather than surface litter. Growing season conditions also contribute to dense contiguous shrubland landscapes that further contribute to the spread of large wildfires. Today, most fires in California are anthropogenic in origin, however, prior to human entry into the region summer convection storms provided a source of ignitions. Although there is debate over the timing of the origin of the

mediterranean climate, there is evidence that seasonal fire-type climates have been present in various parts of the world throughout the evolution of land plants (e.g., Glasspool et al. 2004; Cressler 2001; Falcon-Lang 2000; Scott and Stea 2002) and that fire was an important ecosystem process by at least the late Tertiary (e.g., Keeley and Rundel 2005).

Many plant traits have adaptive value in fire-prone environments, although debate remains as to which of these traits are true fire-adaptations, meaning they evolved in response to fire. In a crown-fire ecosystem, resprouting after top-kill is one such trait that is widely distributed in all mediterranean-climate shrublands of the world. The nearly ubiquitous distribution of resprouting in woody dicotyledonous plants (Wells 1969) suggests a very ancient origin, although this alone would not rule out fire as a primary driver since there is evidence that fire type environments have been present somewhere on the landscape throughout land plant evolution. Today, it is evident that resprouting has adaptive value following a variety of stresses including freezing (Mooney 1977) and grazing (Moreno and Oechel

1991), and thus it is perhaps prudent to think of resprouting as an adaptation to disturbance, and that fire was one of several selective agents. In some mediterranean-climate shrublands, resprouting is associated with enlarged basal tubers referred to as basal burls or lignotubers (James 1984). Although these more specialized resprouting structures show a marked association with mediterranean-climate shrublands, they are not characteristic of all resprouting species in those associations, and there is little consensus on their adaptive role (Keeley 1981; James 1984; Canadell and Zedler 1995).

Resprouting confers a marked advantage in rate of postfire recovery over species that regenerate entirely from seed (Keeley and Zedler 1978; Malanson and O'Leary 1982; Keeley and Keeley 1984; Tyler and D'Antonio 1995). However, the predictability of this advantage varies markedly between species. Some evergreen chaparral shrubs, including *Quercus berberidifolia*, *Heteromeles arbutifolia*, and *Malosma laurina*, are usually just top-killed and commonly 90–100% of the rootcrowns survive and resprout (Keeley et al. 2006). Others, such as “resprouting species” of *Arctostaphylos* and *Ceanothus* (subgenus *Ceanothus*), and the widespread *Adenostoma fasciculatum* may have a substantial portion of the population completely killed; in the latter species mortality varies from 0–100%, but typically is <50% (Rundel et al. 1987; Keeley et al. 2006). Likewise, the smaller stature semi-deciduous sage scrub exhibits marked differences between species in mortality and subsequent resprouting success, varying between 1–50% of the population (Keeley and Keeley 1984; Keeley et al. 2006).

Five factors have been hypothesized to explain differences in resprouting success: i) fire intensity, ii) plant size and biomass, iii) stem age, iv) seasonal differences in physiological condition, and v) fire frequency effects on plant condition. These are not mutually exclusive hypotheses and potentially more than a single factor is important in any given instance. It is likely that the importance of each varies spatially and temporally, as well as taxonomically.

A number of studies support the contention that fire intensity, which is the energy output of the fire, is one of the more important factors in shrub resprouting. Direct measures of fire intensity have shown effects on density of *Adenostoma fasciculatum* (chamise) resprouting stems (Moreno and Oechel 1994). Mortality of *A. fasciculatum* shrubs also has been shown to increase with increased fuel loading, presumably due to increased fire intensity (Moreno and Oechel 1994). Since fire intensity measures are usually only available for prescribed fires, most studies of wildfires use surrogates for fire intensity such as biomass loss, which are considered

to be metrics of fire severity; e.g., Moreno and Oechel (1989) and Perez and Moreno (1998) have reported a significant relationship between heat output from a fire and the diameter of the smallest twig remaining on the shrub skeleton. Using this measure of fire severity there is a negative relationship with survival of resprouting shrubs and subshrubs ( $r^2 = 0.17$ ,  $P < 0.001$ ,  $n = 90$  sites; Keeley unpublished analysis of data reported on in Keeley et al. 2005, 2006).

Rundel et al. (1987) found that plant size (measured by the aboveground lignotuber area) is a critical factor in postfire survival of resprouting *A. fasciculatum*, as has been noted for other chaparral shrubs (Keeley and Zedler 1978; Moreno and Oechel 1993), but other studies have failed to find such a relationship (Anfuso 1982; Stohlgren 1985). Although not tested in the context of fire, it has been reported that plant age may be an important factor in resprouting of the coastal scrub species *Baccharis pilularis* following cutting (Hobbs and Mooney 1985).

Seasonal effects on mortality and subsequent resprouting have also been documented and it appears that springtime depletion in rootcrown carbohydrate stores may be the primary factor in causing reduced resprouting success at this time (Laude et al. 1961; Parker 1987; Rundel et al. 1987; Beyers and Wakeman 2000). High fire frequency when repeat fires occur only a few years apart also is known to reduced resprouting success (Zedler et al. 1983; Haidinger and Keeley 1993), perhaps due to reduced recovery time for replenishment of rootcrown carbohydrates.

The purpose of this study was to examine patterns of fire-caused mortality and test the relative importance of fire severity and plant age across various shrubs and subshrubs characteristic of chaparral and sage scrub associations. In order to eliminate seasonal effects, I have studied sites that all burned during mid-autumn and during the same year.

## METHODS

Ninety study sites were selected from 16 fires that burned over 80,000 ha across an area of more than 10,000 km<sup>2</sup> in southern California USA in late October and early November 1993 (further details in Keeley et al. 2005). Roughly comparable numbers of apparently low and high severity fires, and of chaparral and sage scrub sites were selected. Sampling was in spring 1994 and precipitation during this first growing season was only 80% of the long-term average for the region. Sampling was done in 20 × 50 m (tenth ha) sites with 10 nested 100-m<sup>2</sup> square subplots. Prefire woody plant density was based on a census of skeletal remains of shrubs and subshrubs in each subplot. All skeletons were recorded by species, which were identifiable based on form,

TABLE 1. COMPARISON OF DEAD AND RESPROUTING SHRUB SKELETONS FOR CHAPARRAL AND SAGE SCRUB RESPROUTING SPECIES. \*\*\*P < 0.001, \*P < 0.05, <sup>ns</sup>P > 0.05. fs = facultative seeder, or = obligate resprouter.

	Mode	Skeleton height (cm)			Skeleton basal diameter (mm)		
		Dead (n)	Resprouts (n)	t-value P	Dead	Resprouts	t-value P
<b>Shrubs</b>							
<i>Adenostoma fasciculatum</i>	(fs)	37.6 (873)	102.4 (1467)	-28.091***	31.4	32.0	-0.828 <sup>ns</sup>
<i>Adenostoma sparsifolium</i>	(or)	102.3 (19)	235.8 (116)	-6.119***	43.6	61.4	-3.076*
<i>Arctostaphylos</i> spp.	(fs)	17.7 (44)	67.5 (24)	-4.246***	40.5	33.6	1.729 <sup>ns</sup>
<i>Ceanothus spinosus</i>	(fs)	56.1 (135)	202.9 (197)	-11.106***	48.1	53.9	-1.323 <sup>ns</sup>
<i>Malosma laurina</i>	(fs)	34.5 (23)	63.6 (585)	-1.954 <sup>ns</sup>	48.0	38.7	1.325 <sup>ns</sup>
<i>Quercus berberidifolia</i>	(or)	102.5 (16)	174.9 (296)	-2.774*	45.1	46.1	-0.291 <sup>ns</sup>
<i>Rhus integrifolia</i>	(fs)	12.8 (168)	105.1 (365)	-17.029***	49.6	69.5	-7.161***
<b>Subshrubs</b>							
<i>Artemisia californica</i>	(fs)	18.3 (958)	32.2 (410)	-6.438***	32.2	11.7	32.912***
<i>Eriogonum fasciculatum</i>	(fs)	6.4 (1489)	7.6 (247)	-1.038 <sup>ns</sup>	24.6	9.1	30.895***
<i>Salvia apiana</i>	(fs)	12.7 (201)	24.6 (333)	-6.323***	22.5	21.9	0.561 <sup>ns</sup>
<i>S. leucophylla</i>	(fs)	42.2 (116)	46.2 (276)	-0.905 <sup>ns</sup>	33.4	19.8	8.544***
<i>S. mellifera</i>	(fs)	17.9 (973)	52.0 (182)	-10.601***	33.9	20.7	14.806***

branching pattern, and bark. On some sites, skeletons were burned to ground level but characteristics of root-crown shape allowed us, in most cases, to assign a species name. In a small percentage of cases (<1%), skeletal remains were unidentifiable to species. These skeleton populations are inferred to represent the prefire shrub population density; however, I lack a measure of the amount of error associated with this method. In general, skeletons at densities and spacing similar to that observed in unburned stands were observed and so I assumed that they represented an acceptable estimate of the prefire population of living shrubs. It seems likely that this estimate comprises mostly living shrubs prior to the fire, as dead shrubs would be more likely to be completely consumed by fire and not leave a recognizable skeleton. Nomenclature is according to (Hickman 1993).

Because these were wildfires and covered large areas, direct measures of fire intensity were unavailable. I used a measure of biomass loss as a surrogate for fire intensity that is best referred to as a measure of fire severity. This measure of fire severity is justified since fire intensity is defined by the amount of biomass consumed (e.g., Byrum 1959). Our metric was the height of the shrub or subshrub skeleton, measured for 5 skeletons of each species in the subplots. Because of the even-aged nature of these crown-fire ecosystems, most shrubs are approximately the same height in mature communities and this is even more so within the same species. Thus, it was assumed that height of the skeleton was inversely related to fire intensity. Since there are no prior studies relating shrub skeleton height to fire intensity, we used least squares regression to evaluate the correlation between average skeleton height at a site with diameter of the smallest twig

on skeletons, which is a parameter that has been shown to correlate with fire intensity (e.g., Moreno and Oechel 1989).

In order to examine the relationship between resprouting success and plant age, and obtain large samples of all dominant species, we were not able to age each individual shrub. Therefore, we assumed that age was correlated with basal diameter of the largest prefire stem, so basal diameter was measured with calipers on these same 5 skeletons.

Initial analysis showed that skeleton characteristics roughly followed a normal distribution of sizes. Thus, statistical comparisons between dead and resprouted plants were done with a two-tailed pooled t-test.

## RESULTS

Resprouting success varied from about 10% for *Eriogonum fasciculatum* (average of 36 sites) to a high of 98% for *Quercus berberidifolia* (average of 6 sites). In order to relate resprouting shrub survivorship to fire severity (a surrogate for fire intensity) we used height of the remaining shrub skeleton for each shrub. Using site averages for skeleton height and diameter of the smallest twig on skeletons we found a significant relationship between these two measures ( $r^2 = 0.24$ ,  $P < 0.001$ ,  $n = 90$ ); since the twig diameter has been shown to correlate with fire intensity (Moreno and Oechel 1989) we infer skeleton height is a measure of fire intensity. Skeleton characteristics of resprouting versus dead individuals for the 12 most abundant species are shown in Table 1. For most of the shrub species, skeletons of resprouting plants were significantly taller than those of dead individuals of the same species, indicating lower severity (intensity) fires

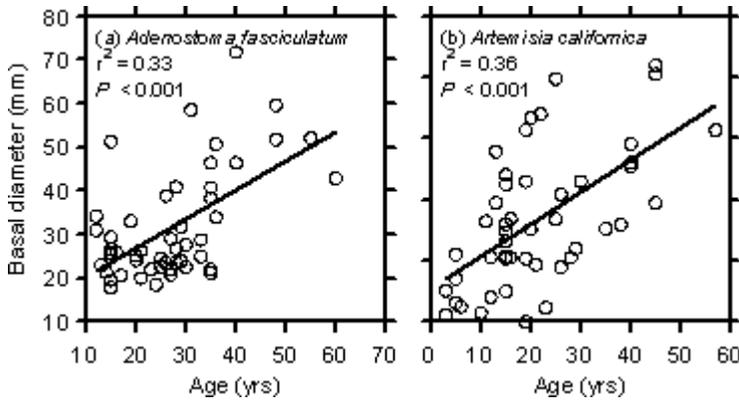


FIG. 1. Relationship between basal diameter of postfire skeletons and prefire stand age for one of the most widely distributed (a) shrubs in this study, *Adenostoma fasciculatum* (chamise), found at 50 sites and (b) subshrubs, *Artemisia californica* (California sagebrush), found at 47 sites.

were associated with resprouting success. This pattern was less strongly the case with sage scrub species; two of the five species exhibited no relationship between measures of fire severity and resprouting.

In order to relate resprouting to plant age, we depended upon the basal diameter of the largest stem on skeletons as a surrogate for plant age. This assumption is supported by the significant relationship between basal diameter and stand age for the most widely distributed shrub (Fig. 1a) and subshrub (Fig. 1b). Shrubs and subshrubs differed markedly in the effect of plant age (as estimated by basal diameter) on resprouting success (Table 1). For most shrubs, age was not related to resprouting ability, whereas in four out of five subshrub species it was. Particularly surprising is the fact that for subshrubs the youngest individuals with the smallest diameter stems (see for example, Fig. 2a) had a significantly greater likelihood of sprouting than older larger subshrubs (e.g., Fig. 2b).

DISCUSSION

Differential resprouting is likely a function of both innate characteristics of species as well as environmental variation during and after fire. Physiological status of storage carbohydrates has been implicated in seasonal differences in resprouting behavior (Radosevich and Conard 1980; Rundel et al. 1987), but that is not a factor in the differential survivorship of resprouters in this study since all sites burned in the same 10-day period (Keeley et al. 2005).

Fire intensity has often been invoked to explain mortality of resprouting shrubs (Moreno and Oechel 1991, 1994). In the present study, based on the premise that skeleton height is a reflection of fire intensity, there is evidence that for most shrubs, fire intensity is an important determinant of mortality (Table 1).

Alternatively, some have found that plant size, in particular rootcrown or lignotuber area is important in resprouting ability with older plants more likely to survive and resprout (Stohlgren 1985; Moreno and Oechel 1991; Vesik et al. 2004). In the present study, I have not considered this variable since sage scrub species generally lack a distinct lignotuber and don't form massive rootcrowns as is the case with some chaparral species.

A variable distinct from that of rootcrown size is the age of the aboveground plant, or in other words time since last fire. In chaparral shrubs, age does not play an obvious role in determining mortality vs resprouting. However, of particular interest is that in sage scrub subshrubs, resprouting is inversely related to plant age, and thus is more likely in younger plants (Table 1). For two common sage scrub subshrubs, *Artemisia californica* and *Eriogonum fasciculatum*, plants that resprouted typically had skeleton basal diameters of 1 cm or less (e.g., Fig. 2a). These were the largest stems on the plant and likely are indicative of plants a decade old or less. Plants with much larger diameter stems (e.g., Fig. 2b) typically did not resprout after fire. *Salvia mellifera* and *S. leucophylla* were other subshrubs on our sites that exhibited a similar pattern (Table 1). This pattern also has been reported before for the north coastal scrub subshrub *Baccharis pilularis* (Hobbs and Mooney 1985).

I hypothesize that the reason for this inverse relationship between age and resprouting in certain sage scrub species is that as these subshrubs age, there is a tendency to loose the resprouting ability. In the case of *Baccharis pilularis*, Hobbs and Mooney (1985) found that the mechanism behind this loss was that as the plant aged, adventitious buds responsible for sprouting, became buried by woody tissues, and this prevented older shrubs from resprouting.

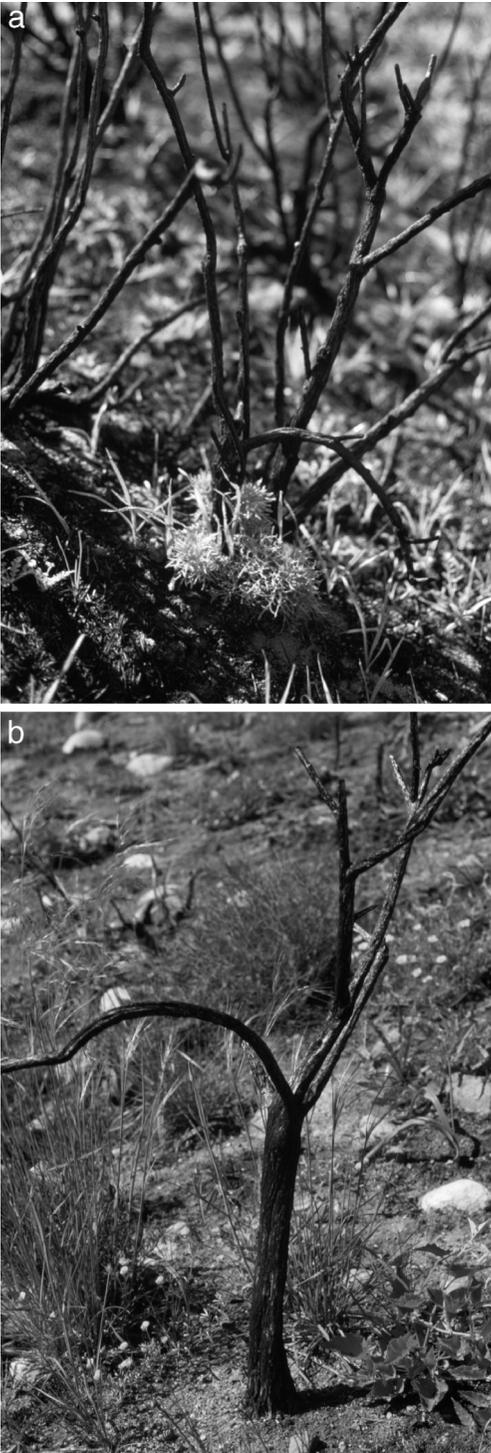


FIG. 2. First postfire year *Artemisia californica* skeletons; (a) a subshrub with prefire stem diameters <1 cm and estimated age of <5 yr that has resprouted and (b) with a basal stem diameter ca. 5 cm and an estimated age of >15 yr that was fire-killed and failed to resprout.

It is unknown if this is the mechanism responsible for the inverse age-resprouting pattern in *Artemisia californica* and *Eriogonum fasciculatum*.

I believe the age resprouting relationship differences between chaparral shrubs and sage scrub subshrubs is due to marked phylogenetic differences of the dominants. In the evergreen chaparral shrub genera of *Adenostoma*, *Malosma*, *Quercus*, *Rhamnus* and *Rhus*, all taxa are woody resprouters, as are all closely related sister genera, suggesting these are pleiomorphic traits, and the combination of woodiness and resprouting are rather ancient in these lineages.

In contrast, the sage scrub subshrubs in *Artemisia* (Asteraceae), *Baccharis* (Asteraceae), *Eriogonum* (Polygonaceae) and *Salvia* (Lamiaceae) are from largely herbaceous perennial genera and families. I hypothesize that in these lineages the herbaceous perennial mode of seasonal aestivation evolved early and lignification is a more recently derived trait. Seasonal aestivation results in aboveground die-back each dry season and resprouting from underground corms, bulbs and rhizomes the following growing season. In light of the fact that fires occur during the dormant season, it is not surprising that the vast majority of the herbaceous perennials in our shrublands are obligate resprouters (Keeley 2000). I hypothesize that resprouting is the basal condition in these lineages and secondary lignification has resulted in reduced allocation of resources to underground storage organs and increased concentration of adventitious buds in aboveground structures. As documented for *Baccharis pilularis* (Hobbs and Mooney 1985), it is hypothesized that the increased lignification in sage scrub subshrubs has diminished resprouting ability due to the inhibitory effect of burying adventitious buds.

Based on patterns of character evolution in these lineages, the herbaceous perennial mode of seasonal aestivation does indeed appear to have evolved early and lignification is a more recently derived trait. For example, Frye and Kron (2003) mapped characters onto a molecular based phylogeny for the Polygonaceae. They found evidence that the herbaceous perennial mode of seasonal aestivation evolved early in the history of the family and the woody habit was derived multiple times within the group; in eight genera including *Eriogonum*. Likewise, Carlquist (2003) studied wood anatomy of this family and also concluded that woodiness arose secondarily in the genus *Eriogonum*. Based on a variety of evidence there is also support for both *Artemisia californica* and *Salvia* spp. subshrubs being in genera where the basal condition was herbaceous perennials and woodiness is a derived state (Torrell et al. 1999; Wang 2004; Walker et al. 2004).

Thus, secondary lignification in certain sage scrub subshrubs apparently has carried with it a cost of burying adventitious buds and diminishing the resprouting capacity. As a consequence, these subshrubs are most likely to resprout when in a developmental stage most closely resembling their herbaceous perennial ancestry.

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