# Reproduction of Chaparral Shrubs After Fire: A Comparison of Sprouting and Seeding Strategies

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# Reproduction of Chaparral Shrubs After Fire: A Comparison of Sprouting and Seeding Strategies

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ABSTRACT: The relative ability of sprouting and nonsprouting chaparral shrubs to recover from fire was studied by examining population of congeneric pairs of species in burned and adjacent unburned areas. The pairs of species selected, with the nonsprouting species named first, were *Arctostaphylos glauca* − *A. glandulosa* and *Ceanothus greggii* − *C. leucodermis*. Data were also obtained on certain associated species, particularly *Adenostoma fasciculatum*. The numbers, sizes and condition of the component species at each of the sites were measured.

Both sprouting and nonsprouting species showed vigorous recovery from fire. It seemed likely that the burned stands would eventually reach a state of development comparable to that shown in the preburn stand without any significant shifts in composition Mortality of shrubs resulting from the fire was complete for nonsprouters but varied in sprouting species. In some there was essentially no mortality, while in others, especially *Adenostoma*, it was rather high. Seedling establishment in the shrub species varied markedly and seemed to be correlated with the degree of fire-caused mortality.

A profound difference was observed in the life histories of the two nonsprouting shrubs. Whereas *Ceanothus greggii* produced a very high number of seedlings after fire, *Arctostaphylos glauca* produced substantially fewer. A comparison of the density-size distribution of live and dead stems indicated that *C. greggii* suffers high mortality early in succession, but *A. glauca* loses very few individuals even after 90 years without fire. In light of these results a model is proposed which we believe explains the adaptive significance of the obligate-seeding strategy in the southern California chaparral.

## INTRODUCTION

It is well known that the chaparral vegetation of California has the capacity for rapid regeneration after fire (*e.g.,* Cooper, 1922; Sampson, 1944; Horton and Kraebel, 1955). This is accomplished by the production of seedlings from seed stored in the soil and sprouts from belowground vegetative parts. Sometimes these two modes of reproduction are combined in a single species, but often a species reproduces after fire almost exclusively by one or the other of these means.

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This contrast between sprouting and nonsprouting modes of re-establishment is especially striking in the chaparral members of the genera *Arctostaphylos* and *Ceanothus*. Jepson (1916) was the first to recognize the significance of this marked difference in fire response, and discussed its ecological and taxonomic significance for *Arctostaphylos*. He noted that in *Arctostaphylos* only those species with a basal burl sprouted, and later, Wieslander (1939) discovered that this burl was a normal morphological feature of the sprouting species which appeared early in the seedling stage of development. It is now known that the correlation between the presence of a burl and the ability to sprout is characteristic of other genera in the chaparral as well.

These observations led to a generally accepted view that the ability to sprout was an adaptation which was selected for by fire (Cooper, 1922; Sweeney, 1967; Wright, 1971; Biswell, 1974). While the question of the origin of the burl remains open, Wells (1969) has made a convincing case for the view that sprouting in itself is an ancestral trait and therefore those species which sprout after fire are, with respect to that trait, less "specialized" for the chaparral than related species that rely upon seed reproduction.

Wells noted that in *Arctostaphylos* and *Ceanothus*, the majority of the species found in the chaparral environment are of the nonsprouting type which have virtually 100% mortality as a result of fire, and re-establish themselves solely from seed stored in the soil. These shrubs, referred to as "fire-type" by Jepson (1939) and "obligately-seeding" by Wells (1969), are thought by Jepson and Wells to have evolved this seeding behavior in response to fire. They argue that the abundant production of seed, which is dependent upon fire to germinate, is more "biologically specialized" to the fire cycle of the chaparral than is sprouting.

Since both modes of reproduction are important and coexist in the chaparral, it is apparent that each is adapted to the prevailing conditions. But they are also strikingly different, and populations of the two types respond quite differently to fire and to the subsequent processes of establishment and competition. One would expect that the relative rates of mortality and establishment of the two reproductive types would change with changing patterns of environmental disruption, especially changing fire frequencies. Thus, an understanding of the population dynamics of the two types of reproduction is important to understanding the selective pressures which may have existed in the past and to intelligently selecting management procedures for the future.

The different response to fire of sprouters and obligate-seeders raises some questions. First, it would seem that a long-lived species with the ability to survive fires and resprout vigorously should have an overwhelming advantage in competition. Once such a species had appropriated space, it would occupy it for a long time. After fire, the well-developed root system should make it almost immune from seri-

ous competition for some years. Moreover, an abnormally short length of time between fires would be only slightly damaging to a sprouting species, and reproduction could be safely deferred or reduced for the first years after fire and all energy dedicated to growth.

In contrast, the obligate-seeding life history seems less obviously advantageous. Since all of the adults die in the fire and no significant seed germination takes place except after fire, species with this life history are dependent upon accumulating seeds in the soil. This would suggest allocation of a large proportion of energy to annual seed production. But this must either go to an extreme, resulting in evolution toward an herbaceous form, or some balance must be struck between growth and reproduction. Too much allocation to growth, though, would be very risky should the interval between fires occasionally be relatively short.

In attempting to explain this coexistence of sprouters and seeders, three basic life history features, with respect to fire, seem of importance: (1) the relative ability to survive fires; (2) the relative ability to establish seedlings after fire, and (3) the relative longevity and competitive ability between fires. The focus of this study was to obtain information on these three aspects of life history for sprouting and obligate-seeding shrub species.

METHODS

*Basic design of the study.*—This study concentrates on the genera *Arctostaphylos* and *Ceanothus,* both of which are important throughout the chaparral region and have numerous species, many of which are locally sympatric. They also exhibit a marked sprouter-nonsprouter division within each genus. To clarify the role of fire, a paired stand approach was used, in which recently burned areas adjacent to unburned areas of similar vegetational composition and age, and similar soil type and topographic position were studied. All the burned areas used were the result of wildfires.

Two pairs of species, one from *Arctostaphylos,* the other from *Ceanothus,* were selected and the stands chosen so that they contained at least one of the pairs of species in both the burned and unburned paired sites. With this approach, it was possible to observe the response of species in the same genus differing in mode of reproduction.

*Species and site selection.*—To insure the greatest generality, the species were picked with the following criteria in mind: that they (1) be widespread; (2) occur predominantly in the chaparral, and (3) frequently occur on the same sites. The species chosen were *Arctostaphylos glauca* (nonsprouter), *A. glandulosa* (sprouter), *Ceanothus greggii* var. *perplexans* (nonsprouter) and *C. leucodermis* (sprouter). Nomenclature is according to Munz (1959).

Two sites were selected: one for *Arctostaphylos* and one for *Ceanothus.* The criteria for each site were: (1) that the unburned chaparral stand be contiguous with the burned stand; (2) that both stands in each site be of the same age previous to the fire; (3) that

both congeneric species be important components of the vegetation of the area, and (4) that the burned stands of both sites burned in the same month and year.

The *Arctostaphylos* site was located at the junction of Japatul-Lyons Valley Road and Lawson Truck Trail, approximately 10 km S of Interstate Hwy. 8, in San Diego Co., California (elevation 675 m). Both the unburned and burned stands were on E-facing slopes of an iron rich vertisol soil. The shrubs in the unburned stand were ca. 90 years old, determined by ring counts taken from several *Arctostaphylos glauca, A. glandulosa* and *Ceanothus greggii*. The burned stand was part of the Laguna Fire of September 1970.

The *Ceanothus* site was off Boulder Creek Road approximately 11 km N of Interstate Hwy. 8, in San Diego County (1300 m). Both unburned and burned stands transected N- and S-facing slopes of adjacent drainages on a soil of decomposed granite. The shrubs in the unburned stand were 23 years old, determined by ring counts from several *C. greggii*. The burned stand was part of the Boulder Fire of September 1970.

For both the *Arctostaphylos* and the *Ceanothus* sites, similarity in size of the shrub remains in the burned stand with those in the adjacent unburned stand was taken as evidence that both stands were the same age prior to the fire.

*Sampling.*—All sampling was done in June 1972. For the stands burned in autumn 1970 this was ca. 1 year after recovery had begun. The shrub species in the unburned portion of the *Arctostaphylos* site were sampled using eight parallel 70-m transects, 10 m apart. Four 2 x 4 m plots were placed along each transect using a random numbers table to select the points. Due to the often "vine-like" growth pattern of these shrubs, particularly in older chaparral (Davis, 1973; Keeley, 1975), it was believed that basal area, rather than areal coverage of foliage, would better reflect the population structure. Basal diameter of all species was measured 10 cm above the ground for each stem in the plot. Stems from the same individual were recorded together, and dead stems were recorded separately. For sprouting species, length and two widths of the burl—narrowest and widest—were recorded. Due to the resistance of the burls to destruction by fire, this measure was useful in estimating the similarity of the prefire vegetation in the burned stand with the vegetation in the unburned stand.

The vegetation in the burned stand at the *Arctostaphylos* site was sampled using the same procedure as in the unburned stand. In addition, *Arctostaphylos glauca* and *A. glandulosa* were sampled in a 20 x 30 m plot for an additional estimate of seedling production by these two species. Because of the fusion of several seeds into a single fruit, *Arctostaphylos* seedlings often occur in groups. Due to the close proximity of the seedlings which emerge from the same fruit or segment and the resultant competition between them, all but one usually die within the first few years. Thus, the total number of seedlings does not adequately reflect the reproductive potential of these species, so

the number of such "seedling groups" was also recorded. Since ground-dwelling seed predators use *Arctostaphylos* fruits (Keeley and Hays, 1976), some of these seedling groups may be due to animal caches as observed from other shrub species (Sanderson, 1962; West, 1968).

The sampling at the *Ceanothus* site was similar to that at the *Arctostaphylos* site with the following exceptions. Eleven parallel 50-m transects, 10 m apart, were laid out. Due to the density of stems at this site, three plots, only 2 x 2 m each, were randomly placed along each transect. In the additional 20 x 30-m plot in the burned stand, only *Ceanothus greggii* and *C. leucodermis* were sampled.

Basal area was calculated from the stem diameter on the assumption each stem was circular. Relative dominance (from live basal area) and relative density were calculated for each species (Cox, 1967). Burl area of the younger globose burls was estimated by calculating area from measured diameter. The area of older, irregular and generally more elongated burls was estimated as a rectangle by multiplying total length at the ground surface times the average of two widths.

Although adjacent burned and unburned stands may be broadly similar, for critical comparisons we believed it best, due to local shifts in the vegetation, to check this with an estimate of the prefire vegetation in the burned stand. Short of sampling prior to a fire, this could be done best by a comparison of plant remains in the burned area with the existing vegetation in the unburned area. Sprouting species lend themselves very nicely to this comparison, since the basal burl is quite resistant to destruction by fire and usually recognizable to species even when it does not resprout. Species without burls are a more serious problem since the dead aboveground stems in the burn are the only indication of the prefire vegetation, and destruction by fire is generally greater for aboveground stems than for burls. Estimates for these species may therefore be relatively low on the burned site.

Some of the dead burls and stems in the burn may have died prior to the fire. To correct for this, the area of dead burls of burl-forming species and of dead stems of the nonsprouters was measured in the unburned area. These burl areas, expressed as a percentage of the living basal areas, gave a correction factor which could be used to estimate the proportion of prefire mortality in the burned stands.

Nonsprouting shrubs, as the name suggests, suffer 100% mortality from fire. Sprouting shrubs are theoretically capable of 100% regeneration after fire, but do suffer some mortality, and an estimate of fire-caused mortality for the dominant sprouting shrubs was needed. Since it was not possible to know whether a burl in the burn was dead before the fire, values of postfire mortality were interpreted with respect to the percent of prefire mortality. In addition, the size of "individual" sprouting shrubs can vary greatly, so an estimate of the numbers of shrubs killed by fire is not as good as one which takes size into account. Thus, we estimated mortality for a sprouting species as the percent of total burl area contributed by dead individuals. Fire-

caused mortality was then estimated as the percent of dead burl area in the burned stand minus the percent of burl area dead in the unburned stand.

## RESULTS

*Population structure before and after fire:* Arctostaphylos *site.*— Comparison of the relative dominance (from live basal area) and relative density indicates that the burned and unburned stands were similar in species composition, but there were marked differences in species importance (Table 1). This results largely from the relative decline in basal area of the nonsprouters and the great increase in density of species reproducing by seed. In the unburned stand, *Arctostaphylos glauca* and *A. glandulosa* were the dominant shrubs, followed by *Adenostoma fasciculatum* (just *Adenostoma* from here on) and *Ceanothus greggii*. In the burned stand the sprouting species *Adenostoma* and *Arctostaphylos glandulosa* were the initial dominants, and the greatest densities were for those species with large numbers of seedlings, *Adenostoma, C. greggii* and *Arctostaphylos glauca*.

The range in seedling production—basal areas (*Arctostaphylos glauca*) and burl areas (*A. glandulosa*)—for the two samples in the burned stand compared with the unburned stand (Table 2) indicates that populations of *A. glauca* and *A. glandulosa* comparable in age and density to the existing populations in the unburned stand produced approximately 10,600 and 1500 seedlings per ha, respectively. The data on seedling groups (*i.e.,* one or more seedlings arising from nearly the same point) indicate that in both *Arctostaphylos* species the number of seedlings theoretically capable of reaching maturity was about half the total number of seedlings. The other two dominant shrubs at the *Arctostaphylos* site, *Adenostoma* and *Ceanothus greggii,* both produced high numbers of seedlings. A prefire population of *Adenostoma,* perhaps half the size of the population in the unburned stand, produced over 14,000 seedlings/ha. There were nearly 19,000

TABLE 1.—Vegetation comparison of the unburned and burned stands at the *Arctostaphylos* site; nonsprouting species are indicated by NS, sprouting species by S

| Species | Repro-ductive type | Relative dominance[a] | | Relative density | |
|---|---|---|---|---|---|
| | | Unburned | Burned | Unburned | Burned |
| *Arctostaphylos glauca* | NS | 33.2 | 1.4 | 8.4 | 16.6 |
| *A. glandulosa* | S | 32.2 | 26.9 | 14.0 | 1.6 |
| *Adenostoma fasciculatum* | S | 19.3 | 49.8 | 48.0 | 29.1 |
| *Ceanothus greggii* | NS | 9.4 | 3.9 | 15.9 | 44.9 |
| *Quercus dumosa* | S | 5.0 | .... | 2.5 | .... |
| Eleven other shrubs or subshrub species | .... | 0.9 | 18.0 | 11.2 | 7.8 |
| Total density, all species (numbers/ha x $10^{-3}$) | .... | .... | .... | 12.0 | 41.4 |
| Total basal area, all species[a] (cm²/ha x $10^{-3}$) | .... | 463.9 | 26.3 | .... | .... |

[a] From basal area of live stems

TABLE 2.—Comparison of cover in the unburned stand with an estimate of prefire cover in the burned stand and seedling densities for each of the dominant species at the Arctostaphylos site. The two samples taken in the burned stand for *A. glandulosa* and *A. glauca* are presented separately to illustrate the relationship between seedling density and prefire cover

| Species | Stand | Cover[a] (m²/ha) | Seedlings[b] #/ha | % Dead | # Alive/ha | Arctostaphylos seedling groups[c] #/ha | % Dead | # Alive/ha |
|---|---|---|---|---|---|---|---|---|
| *Arctostaphylos glandulosa* | Unburned | 316.0 | 0 | ... | ........ | ...... | ... | ........ |
| | Burned (Transect) | 109.0 | 550 | 71 | 160 | ...... | ... | ........ |
| | Burned (20 x 30 m plot) | 296.0 | 1,550 | 55 | 700 | 800 | 28 | 630 |
| *A. glauca* | Unburned | 16.4 | 0 | ... | ........ | ...... | ... | ........ |
| | Burned (Transect) | 17.9 | 10,600 | 33 | 6,440 | ...... | ... | ........ |
| | Burned (20 x 30 m plot) | 2.3 | 6,400 | 44 | 3,560 | 3,000 | 30 | 2,130 |
| *Adenostoma fasciculatum* | Unburned | 251.0 | 0 | ... | ........ | ...... | ... | ........ |
| | Burned | 107.0 | 14,400 | 39 | 8,784 | ...... | ... | ........ |
| *Ceanothus greggii* | Unburned | 7.4 | 0 | ... | ........ | ...... | ... | ........ |
| | Burned | 0.0 | 18,900 | 2 | 18,500 | ...... | ... | ........ |

[a] This is burl area, live and dead, for the burl-forming species (*A. glandulosa* and *A. fasciculatum*) or basal area, live and dead, for the nonburl-forming species (*A. glauca* and *C. greggii*), excluding seedlings (*i.e.*, for the burn this represents an estimate of the prefire population size)

[b] After 1 full year of recovery

[c] Consisting of one or more seedlings arising from nearly the same point (*see* Methods)

*C. greggii* seedlings/ha, but the lack of any remains of *C. greggii* in the burned stand makes an estimate of its prefire population size impossible.

Also in Table 2 are the values for percent mortality of seedlings in the burned stand after 1 full year of recovery from fire, obtained by expressing the number of dead seedlings counted as a proportion of all seedlings. Since it was not known whether all the seedlings which died the first summer were still present at the time of this sampling, these figures were most meaningful for relative comparisons among species. *Arctostaphylos glandulosa*, although producing the lowest number of seedlings, had the highest seedling mortality. In contrast, the largest producer of seedlings, *Ceanothus greggii*, had by far the lowest seedling mortality. Much of the mortality in *Arctostaphylos* was, however, the result of death of individual seedlings rather than seedling groups. The mortality of seedling groups was about 30% for both species, whereas the mortality of individual seedlings was 43%.

Since in most instances it was not possible to know whether a stump in the burned stand was dead before the fire, values of postfire mortality were compared with values of prefire mortality (Table 3). For example, even though 45% of the burl area of *Adenostoma* was dead after fire, over half of this may have been dead before the fire. Very little *Arctostaphylos glandulosa* was dead either before or after fire. Thus mortality due to fire was likely between 20-40% for *Adenostoma* and 1% for *Arctostaphylos glandulosa*. A comparison of the average burl area of live and dead individuals in the burned stand indicates the following: *Arctostaphylos glandulosa* shrubs with smaller burls were killed by the fire, whereas the *Adenostoma* shrubs with the larger burls were killed by the fire. In the unburned stand, dead shrubs of both species were the individuals with smaller burls.—

*Population structure before and after fire:* Ceanothus site.— Though the same species were present in both stands, there was a shift in community structure. Before the fire the nonsprouting *Ceanothus greggii* was dominant (live basal area), but after fire it was surpassed by the sprouting species *Adenostoma, Quercus dumosa* and *Ceanothus leucodermis* (Table 4). The large number of *C. greggii* seedlings suggests that this postfire dominance will be short-lived.

TABLE 3.—Percent of burl area dead and percent of individuals dead for each of the dominant sprouting species at the *Arctostaphylos* site

| Species | Stand | N | % of burl area dead | % of individuals dead | Mean burl area*** (cm²) Live | Dead |
|---------|-------|---|---------------------|------------------------|------------------------------|------|
| *Arctostaphylos glandulosa* | Unburned | 44 | 1 | 10 | 2,020 | 277 |
| | Burned | 91 | 2 | 7 | 2,414 | 430 |
| *Adenostoma fasciculatum* | Unburned | 266 | 24 | 50 | 353 | 115 |
| | Burned | 133 | 45 | 38 | 173 | 227 |

*** The size of live and dead burls differs significantly at P<0.001 by the Wilcoxon two-sample test

Table 5 compares basal areas, burl areas and seedling densities of the dominant species at the *Ceanothus* site. It appears from Tables 4 and 5 that the method of estimating prefire vegetation in the burned stand may indeed be better suited to burl-forming species. For example, *Quercus dumosa*, even though it sprouts, does not usually form a distinct burl, so a comparison was made with the basal area of stems of prefire remains in the burned stand with the basal area of stems in the unburned area. Although *Q. dumosa* is the second dominant shrub in both the burned and unburned stands, the cover values in Table 5 show that few prefire remains were found in the burn. Similar results were obtained with *C. greggii* at both the *Arctostaphylos* site and the *Ceanothus* site. This method of estimating prefire populations seems to be best suited to burl-forming species and shrubs with large trunks such as old *A. glauca*.

Since the sprouting shrub populations in the adjacent burned and unburned stands were similar in size, it is reasonable to assume that associated nonsprouting shrub populations were broadly similar before the fire. Thus, we can infer that a population of *Ceanothus greggii*, as old and as dense as that in the unburned area, produced from 10,000 to 18,000 seedlings per ha in the burned stand. In comparison, the sprouting *C. leucodermis* produced few seedlings. However, there were nearly as many seedlings per m² of prefire burl area for *C. leucodermis* as for the prolific seedling producer *Adenostoma*. No seedlings of *Quercus dumosa* were found after fire, indicating a heavy reliance by this species on resprouts in response to fire. The data for seedling mortality show that overall mortality was not as high as at the *Arctostaphylos* site. However, once again *C. greggii* had the highest number of seedlings and lowest percent seedling mortality.

Ten percent of the *Ceanothus leucodermis* burl area was dead in the 23-year-old unburned stand (Table 6). Thus, less than one-fifth of the *C. leucodermis* burl area in the burned stand may have been

TABLE 4.—Vegetation comparison of the unburned and burned stands at the *Ceanothus* site; nonsprouting species are indicated by NS, sprouting species by S

| Species | Repro-ductive type | Relative dominance[a] | | Relative density | |
|---|---|---|---|---|---|
| | | Unburned | Burned | Unburned | Burned |
| *Ceanothus greggii* | NS | 51.2 | 3.9 | 40.8 | 25.6 |
| *Quercus dumosa* | S | 20.2 | 27.5 | 8.9 | 2.9 |
| *Adenostoma fasciculatum* | S | 11.3 | 39.3 | 28.7 | 40.6 |
| *Ceanothus leucodermis* | S | 9.8 | 15.5 | 9.2 | 8.8 |
| *Arctostaphylos glandulosa* | S | 3.5 | .... | 2.4 | .... |
| Eight other shrubs or subshrub species | .... | 4.0 | 4.8 | 10.0 | 12.1 |
| Total density, all species (numbers/ha x 10⁻³) | .... | .... | .... | 28.2 | 40.6 |
| Total basal area, all species[a] (cm²/ha x 10⁻³) | .... | 412.9 | 28.9 | .... | .... |

  [a] From basal area of live stems

TABLE 5.—Comparison of cover in the unburned stand with an estimate of prefire cover in the burned stand and seedling densities for each of the dominant species at the *Ceanothus* site. The two samples taken in the burned stand for *C. leucodermis* and *C. greggii* are presented separately to illustrate the relationship between seedling density and prefire cover

| Species | Stand | Cover[a] (m²/ha) | Seedlings[b] | | |
|---|---|---|---|---|---|
| | | | #/ha | % Dead | # Alive/ha |
| *Ceanothus leucodermis* | Unburned | 42.7 | 0 | ⋯ | ⋯ |
| | Burned (Transect) | 27.4 | 2,500 | 6 | 2,350 |
| | Burned (20 x 30 m plot) | 20.0 | 1,500 | 0 | 1,500 |
| *C. greggii* | Unburned | 27.6 | 0 | ⋯ | ⋯ |
| | Burned (Transect) | 3.9 | 10,600 | 5 | 10,000 |
| | Burned (20 x 30 m plot) | 4.6 | 17,800 | 2 | 17,400 |
| *Adenostoma fasciculatum* | Unburned | 131.0 | 0 | ⋯ | ⋯ |
| | Burned | 109.0 | 13,300 | 13 | 11,600 |
| *Quercus dumosa* | Unburned | 9.0 | 0 | ⋯ | ⋯ |
| | Burned | 0.2 | 0 | ⋯ | ⋯ |

[a] This is burl area, live and dead, for the burl-forming species (*C. leucodermis* and *A. fasciculatum*) or basal area, live and dead, for the nonburl-forming species (*C. greggii* and *Q. dumosa*), excluding seedlings and resprouts in the burn (*i.e.*, for the burn this represents an estimate of the prefire population size)

[b] After 1 full year of recovery

killed by fire. *Adenostoma* had less than 1% dead burl area in the unburned stand so that 24% dead burl area in the burned stand is likely representative of mortality due to fire. Comparing average burl area of live and dead individuals in the burned and unburned stands indicates that the dead *C. leucodermis* and *Adenostoma* are smaller than the live individuals. This was particularly striking for the latter species in the unburned stand where 44% of the individuals were dead, but they represented only 0.2% of the burl area.

## DISCUSSION

The basic features of the life histories of the species studied are summarized in a qualitative way in Table 7. Three of the features, namely, relative seedling establishment after fire, early seedling mortality and adult mortality attributable to fire, were investigated directly and are based on the quantitative data from this and other chaparral studies. The fourth category, later seedling mortality, is estimated from a consideration of stand structure and general knowledge of the species behavior in San Diego County. This last trait is therefore indirectly derived and based to some extent on subjective evaluation.

It is apparent that even for these few traits expressed with a limited scale there are marked differences among the species, even within the sprouting and nonsprouting groups. One does not, of course, expect that different species will be wholly the same in life history features, but even so the diversity is striking. These comparisons show that sprouters and nonsprouters are ends of a continuum. This is brought out clearly by the correlation observed between relative seedling establishment and adult mortality from fire. A species that suffers complete mortality from fire must also establish a substantial number of seedlings. Intermediate incidence of fire-caused mortality is associated with intermediate levels of seedling establishment.

Within the sprouting species, adult mortality between fires and as the result of fires differs markedly. *Quercus dumosa* shows very little adult mortality and no seedling establishment. The acorn is poorly adapted to survive fire and to germinate in the conditions existing after fire, and it is probably very rare for oaks to establish new in-

TABLE 6.—Percent of burl area dead and percent of individuals dead for each of the dominant sprouting species at the *Ceanothus* site

| Species | Stand | N | % of burl area dead | % of individuals dead | Mean burl area*** (cm²) Live | Mean burl area*** (cm²) Dead |
|---|---|---|---|---|---|---|
| *Ceanothus leucodermis* | Unburned | 60 | 10 | 42 | 151 | 20 |
| | Burned | 49 | 20 | 39 | 160 | 64 |
| *Adenostoma fasciculatum* | Unburned | 115 | <1 | 44 | 172 | 8 |
| | Burned | 97 | 24 | 45 | 197[NS] | 79[NS] |

*** The size of live and dead burls differs by the Wilcoxon two-sample test with P < 0.001, except those marked NS in which 0.05 < P < 0.10

TABLE 7.—Qualitative conclusions about life history features of the species studied, based on the values obtained in this study and from literature on Southern California[a] chaparral succession; nonsprouting species are indicated by (NS), sprouting species by (S)[b]

| Species | Adult mortality from fire | Relative seedling establishment after fire | Early seedling mortality | Mortality of shrubs later in succession |
|---|---|---|---|---|
| *Arctostaphylos glauca* (NS) | complete[1,8] | high[1] | moderate[1] | low[1] |
| *A. glandulosa* (S) | very low[2] | low[1,6,9] | high[1,9] | low[8] |
| *Ceanothus greggii* (NS) | complete[8,9] | very high[9] | low to moderate[9] | moderate to high[8,10] |
| *C. leucodermis* (S) | moderate[8] | moderate[1,9] | low[1,9] | moderate to high[1,7,8] |
| *Adenostoma fasciculatum* (S) | moderate to high[1,2,5,8,11] | high[1,6,9] | moderate[1] | moderate[4,8] |
| *Quercus dumosa* (S) | very low[3,5] | none[1] | unknown probably high | low[4] |

[a] Studies from other regions of California were not included mainly because of very different seedling densities reported from various sectors of the state; *e.g.*, 14,400 *Adenostoma fasciculatum* seedlings/ha reported in this study is the highest of any southern California study but much lower than the *A. fasciculatum* seedling densities of 105,500/ha (Stocking, 1966) reported from the Sierra Nevada or 117,600/ha (Sampson, 1944) and 1,400,000/ha (Sweeney, 1956) reported from northern California

[b] Numbers refer to sources which support the conclusion; numbers in italics refer to sources which report different conclusions; 1 = Horton and Kraebel, 1955; 2 = Plumb, 1961; 3 = Plumb, 1963; 4 = Patric and Hanes, 1964; 5 = Kinucan, 1965; 6 = Hanes and Jones, 1967; 7 = Specht, 1969; 8 = Hanes, 1971; 9 = Vogl and Schorr, 1972; 10 = Bradbury, 1974; 11 = Dodge, 1975

dividuals in recent burn areas. In contrast, *Adenostoma* suffers substantial adult mortality and succeeds in establishing many thousands of seedlings. These differences in fire-caused mortality are probably due to a complex of physiological, morphological and environmental factors. Rooting depth, the location of adventitious buds, the quantity of storage carbohydrates, the average amount of fuel accumulated around the base of the plant, the moisture status of the stems and roots at the time of the fire, and the size of the individual are among the factors which probably are important.

The seedling production in *Arctostaphylos glandulosa* is only a fraction of that of *Adenostoma*, and the seedlings suffer high mortality. Even though the seedling numbers are relatively low, it seems that they are greatly in excess of the numbers needed to replace individuals that have died in the interval from the previous fire (*see also* Vogl and Schorr, 1972). There are a number of alternative explanations for this seeming excess of seedlings: (1) excess seedling production may have selective value because of the greater variety of progeny for selection to act upon (Grant, 1975, p. 436); (2) excess seedling production may have been selected for colonization of new areas; (3) excess seedling production may be a conceptual mistake, *i.e.*, *A. glandulosa* seedlings suffer very high mortality so substantial seedling production may be necessary in order to produce a single mature shrub; (4) the underlying assumption of a selective basis for the presently observed relationship between seedling production and shrub replacement may be incorrect, *i.e.*, Axelrod (1973, 1975) argues that chaparral shrubs evolved under a different climate than at present; perhaps substantial seedling production was of greater adaptive value under a Pliocene summer-rain climate than it is presently.

Nonsprouting species also show differences in life history characteristics. *Ceanothus greggii*, as observed in this study, produces a large number of seedlings. In contrast, *Arctostaphylos glauca* produces fewer seedlings, even though it is a much more dominant member of the community. However, the *Arctostaphylos* seedlings are usually larger than the *Ceanothus* seedlings after only 1 year, and this differential tends to remain. It seems as if *C. greggii* is producing many seedlings each with a lesser probability of success, whereas *A. glauca* is producing fewer but more competitive seedlings. This is a difference in life history nearly as profound as that between sprouters and nonsprouters.

Indirect evidence of this difference and its consequences may be obtained by examining a frequency distribution of stem diameters at 10 cm at the *Arctostaphylos* site. Assuming that age and size are positively correlated, these data show (Fig. 1) that there were many times more dead than live *Ceanothus greggii* and that stems of nearly all size classes were dying—that is, that mortality seems to have been significant in the past and is still significant in the present. In contrast, *Arctostaphylos glauca* had a minority of stems dead, and had essentially no dead stems in the largest sizes. This suggests little

mortality in well-established individuals, and probably reduced mortality at present. It appears as though the difference noted in the seedling stage is borne out in later development. One might say that *A. glauca* is competing with size, while *C. greggii* is competing with numbers.

These observations call into question the idea, sometimes stated as a generalization, that nonsprouting species represent only a successional stage in chaparral development and are gradually eliminated from the canopy, essentially disappearing by the 3rd or 4th decade after fire. As has been shown, the 90-year-old *Arctostaphylos* stand was dominated by a nonsprouting *Arctostaphylos* and had a substantial number of nonsprouting *Ceanothus* as well. The fact that at this site less than 7% of the basal area of *A. glauca* was dead (Table 8) suggests a great longevity for this species. Over 40% of the basal area of *C. greggii* was dead after 90 years, though the data from the *Ceanothus* site (Table 8) as well as Figure 2 suggest that much of this died in the 1st 20 years after fire. We have also observed vigorous nonsprouting shrubs in other old chaparral stands in San Diego County. It is true that certain nonsprouting species are typically short-lived, but it is by no means a valid generalization (Keeley, 1975). The large number of dead nonsprouting shrubs, commonly observed in older stands, is often the result of a natural thinning of the population as a stand ages. It is not, in itself, evidence of senescence (*e.g.*, Comfort, 1956, p. 22-24).

In general, we find high mortality later in succession in those species which produce large numbers of seedlings after fire, regardless
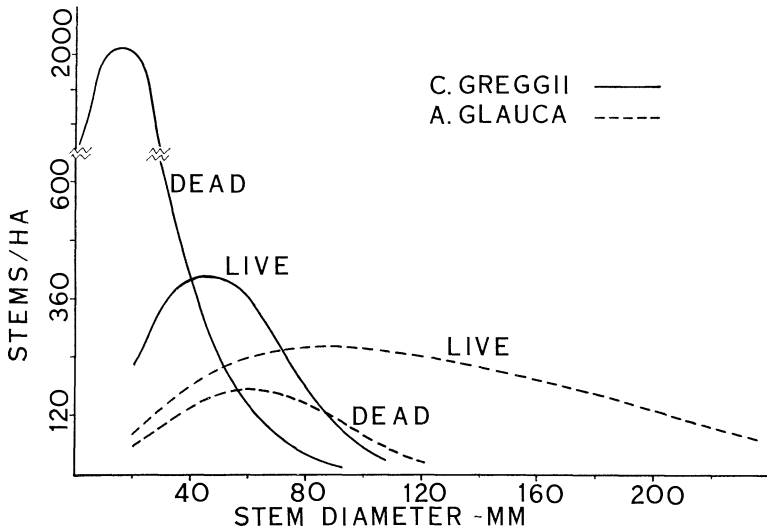


Fig. 1.—Smoothed density-size distributions for the live and dead stems of *Arctostaphylos glauca* and *Ceanothus greggii* at the 90-year-old *Arctostaphylos* site

of whether they are sprouters or nonsprouters. For example, at the 90-year-old *Arctostaphylos* site the two species with the greatest percent dead in the unburned stand, *Ceanothus greggii* and *Adenostoma* (Table 8), produced the largest number of seedlings in the burned stand (Table 2). For the species with the lowest percent dead (*Quercus dumosa*) no seedlings were found after fire. A similar relationship between initial seedling density and subsequent shrub mortality was observed by Horton and Kraebel (1955) for the nonsprouting *Ceanothus crassifolius*. Ten years after fire they found mortalities of 33, 40, 55 and 81% for initial seedling densities of 3707, 8155, 19,769 and 91,431 per ha, respectively.

This study has shown that both the sprouting and the nonsprouting species studied are well-buffered against local extinction from fire. This is true, not only in young stands of chaparral, but also in stands nearly a century old. A greater probability of fire-caused mortality seems to be balanced by a higher probability of seedling establishment. The sprouting and seeding modes are cleary ends of a continuum. Nevertheless, it still seems that a species that loses completely the ability to sprout would be in a far more precarious position than one which could sprout to at least some extent. The fact that nonsprouting species do exist strongly suggests that there must be an advantage to reestablishing totally by seedlings.

*A model for the seeding strategy.*—What is the adaptive significance of obligate seeding shrubs? Wells (1969) maintains that obligate seeding species of *Ceanothus* and *Arctostaphylos* were derived from sprouting ancestors, *i.e.*, evolutionarily they have lost the ability to resprout (*see also* Stebbins, 1974, p. 192). He argues that under conditions of recurring fire this loss means a greater number of sexual generations resulting in a greater frequency of natural selection and a quickening of the tempo of evolution in these groups. Raven (1973) has interpreted this to mean that the adaptive advantage to being an

TABLE 8.—Percent of basal area dead for the dominant species in the unburned stands at the 90-year-old *Arctostaphylos* site (A) and the 23-year-old *Ceanothus* site (C)

| Species | Site | % of basal area dead |
|---|---|---|
| *Arctostaphylos glauca* | A | 7 |
| *A. glandulosa* | A | 15 |
| | C | 21 |
| *Ceanothus greggii* | A | 41 |
| | C | 24 |
| *C. leucodermis* | C | 29 |
| *Adenostoma fasciculatum* | A | 40 |
| | C | 12 |
| *Quercus dumosa* | A | 6 |
| | C | 7 |

obligate seeder is that it affords a closer and more rapid adjustment to the environment than crown-sprouting species. That is, by establishing each new generation with sexually produced progeny, nonsprouting species gain some sort of evolutionary advantage over crownsprouting species which reestablish and even expand (Jepson, 1916) their populations by already established individuals.

We contend that arguments based solely on the advantages of increased numbers of sexual generations are insufficient to explain the evolution of the obligate seeding strategy. It has been argued (Williams, 1966, 1975; Ghiselin, 1974) that long-term advantages to sexual reproduction can only be explained (within the framework of neo-Darwinian evolutionary theory) by group selection or biased extinction. The first mechanism is undesirable for a number of reasons (Williams, 1971) but mainly because of the very intense selection pressure required to maintain it. The second mechanism, Williams argues, is unacceptable because there is no evidence that asexual taxa have gone extinct any more frequently than sexual taxa. Biased extinction is a particularly undesirable explanation in this chaparral situation, because sprouting is a very successful mode of reestablishment and reproduction. That is, sprouters and seeders coexist, so we cannot explain one group at the expense of the other. Williams has proposed that in order for sexual reproduction to be selected for, it must have an immediate effect on an individual's fitness.

We believe there are two basic questions to be answered here. One, are there conditions under which it would be advantageous to reestablish entirely by seedlings (regardless of whether or not they are sexually produced)? The other, given that *Ceanothus* and *Arctostaphylos* species are self-incompatible (Raven, 1973), what advantage is there for a seeder to reproduce sexually (presumably this would be most pertinent to obligate seeders)? We offer the following model as an attempt to answer both of these questions.

First, seedlings do not compete well against sprouters. Thus, seedlings are adapted to openings in the chaparral. Openings occur after fires. The size of the openings depends upon a number of factors. If the prefire composition is largely sprouters, then the size of the openings will depend upon the frequency and intensity of fires in the environment. That is, during succession there is a constant thinning of shrubs [note the decrease in shrub density from 23 years to 90 years in Tables 1 and 4 (*see also* Patric and Hanes, 1964; Hanes, 1971)]. As the length of the fire-free period increases, shrub size increases so that individual shrubs appropriate a greater amount of space at the expense of neighboring shrubs. This results in a reduction in the density of potential resprouts plus an increasing probability of fewer of these potential resprouts surviving the more intense fires which result from the greater accumulation of dead fuel (Dodge, 1972). Thus, the longer the fire-free period the larger the openings after fire (Fig. 2). Also, increased mortality of sprouters would tend to select for reallocation of energy from burl production to seed production (*see*

Charnov and Schaffer, 1973). We suggest that occasional long fire-free periods (*e.g.*, 100 years or more) have been a very important evolutionary stimulus for the obligate seeding strategy.

Under this model the significance of the different obligate seeding strategies becomes more apparent. *Arctostaphylos glauca* shrubs are very long-lived and reach arborescent proportions (at the *Arctostaphylos* site, 2.7 m tall, 6.4 m² areal coverage; n = 50). In effect, they appropriate a large amount of space and hold it until a fire. Fruit production is very high in these old stands (Keeley and Keeley, 1977), and after fire their very large propagules (ca. 800 mg), which are poorly dispersed, produce a new crop of seedlings in the opening directly beneath the dead shrub. *Ceanothus greggii* appropriates very little space in older stands of chaparral. However, it produces an abundance of small (ca. 7 mg) long-lived seeds which are better dispersed and result in an abundance of seedlings in any available openings after fire.

The maintenance of sexual reproduction by seeders can be explained within the framework of Williams' arguments as follows. After fire, all shrub species re-establish during the 1st postfire year, very likely a time of intense selection of seeding species (Stebbins, 1971). Depending upon environmental conditions that year, particularly precipitation which can fluctuate greatly from year to year, the 1st postfire year conditions may be quite different from one fire
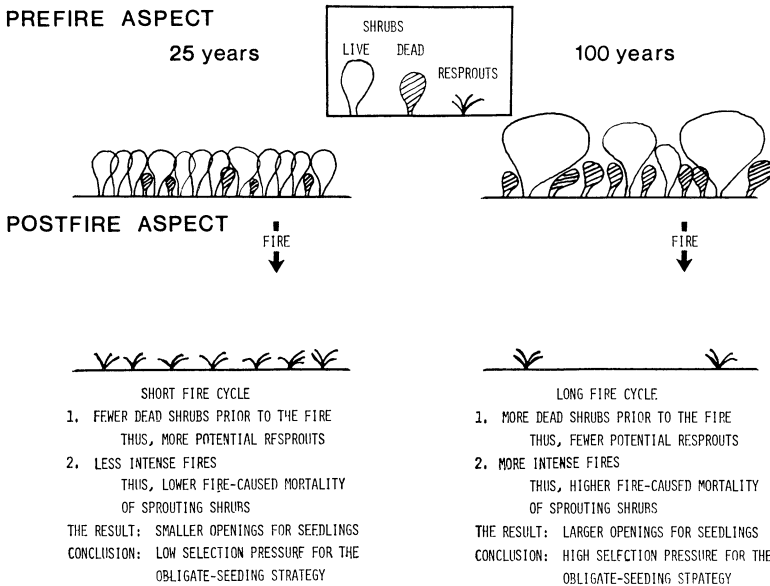


Fig. 2.—A schematic model illustrating the relationship between successional changes in the density of live shrubs and the relative abundance of postfire resprouting shrubs resulting from fires early in succession vs. late in succession

cycle to the next. In essence, the selectively relevant features of the environment are unpredictable from one generation to the next. Since all members of a population reestablish at the same time, the result will tend to be a homogeneous sampling of potential genotypes. Between fires, shrubs which fail to maximize the variety of phenotypes in which their genes occur may have their genes left out of the next fire-spawned sampling of genotypes.

One of the important conclusions from this model is that the real selective pressure for the obligate seeding strategy has been the infrequency of fire in the southern California chaparral. We envision an environment in which fire is inevitable but one in which there is a high probability of fire-free periods for as long as a century (*cf.* Wells, 1962, p. 97-99, who comes to a similar conclusion but for different reasons). Some chaparral ecologists may grimace at the thought of southern California chaparral having evolved under long fire-free periods; however, it is not an untenable hypothesis. As seen in this study, chaparral can recover after fire in 90-year-old stands (*see also* Hanes and Jones, 1967). The commonly accepted paradigm that natural fires have always burned southern California chaparral at very short and regular intervals is not beyond question. Lightning-fire frequency in California decreases radically from N to S, from high to low elevations, from the mountains to the coast and, most importantly, as the Santa Ana (low humidity, high velocity, foehn wind) season approaches (Snow and Kotok, 1923; Court, 1960; Komarek, 1967; U.S. Forest Service, unpublished fire reports from the Los Padres, Angeles, San Bernardino and Cleveland National Forests). The region of California with the lowest lightning-fire frequency is the coastal ranges; this is also the area which supports the greatest abundance and diversity of nonsprouting species. In contrast, the midelevation range (1000-3000 m) of the Sierra Nevada is a region with a very high lightning-fire frequency, and the chaparral of this area is particularly depauperate in nonsprouting species of *Arctostaphylos* and *Ceanothus* (*e.g.,* Munz, 1959; Epling and Lewis, 1942; Critchfield, 1971).

Our studies suggest that chaparral is adapted to both short and long fire-free periods. This is undoubtedly a reflection of the unpredictability of fire in the environment. With a very short fire cycle nonsprouting shrubs are eliminated. With the present man-made fire cycle of every 20-30 years, both sprouting and seeding species regenerate, but over long periods of time sprouting species may gain an advantage. With a much longer fire cycle sprouters and seeders should coexist.

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