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## SEED PRODUCTION, SEED POPULATIONS IN SOIL, AND SEEDLING PRODUCTION AFTER FIRE FOR TWO CONGENERIC PAIRS OF SPROUTING AND NONSPROUTING CHAPARRAL SHRUBS<sup>1</sup>

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**Abstract.** A study of seed production, seed storage in the soil, and seedling production after fire was undertaken for a sprouting and a nonsprouting congeneric pair of species of *Ceanothus* and *Arctostaphylos*. All species exhibited large fluctuations in annual seed production. There was a significant correlation between fruit production and precipitation in the previous year. It is hypothesized that high carbon gain in years of high precipitation results in high numbers of floral primordia which, in these species, remain dormant until the following year. It was also noted that high fruit production was not dependent upon high precipitation the same year; suggesting that the fruits were utilizing carbon stored from the previous year. All 4 species were capable of producing more seeds in a single season than were stored in the soil. Apparently the soil seed pools do not represent a steady accumulation of seeds in the soil but rather are the result of dynamic fluctuations in seed inputs and outputs. Each species also had more seeds in the soil, by several orders of magnitude, than seedlings after fire in an adjacent burned stand.

The sprouting and seeding reproductive strategies are quite different in the two genera. The information from this study coupled with that from other studies indicate 4 reproductive modes: sprouting and seedling production (*C. leucodermis*), abundant seedling production (*C. greggii*), low seedling production but better "equipped" seedlings (*A. glauca*), and predominantly sprouting (*A. glandulosa*).

**Key words:** *Arctostaphylos*; California; *Ceanothus*; chaparral; reproductive strategies; seed production; soil-seed pools.

### INTRODUCTION

California chaparral is a distinctive vegetation composed of closely spaced shrubs, with small, heavily sclerified, evergreen leaves. This high density of shrubs, coupled with long summer droughts characteristic of mediterranean climates, produces a vegetation susceptible to periodic widespread fires. All chaparral shrub species have the ability to regenerate rapidly after fire; for this reason it is presumed that fire has played an important role in their evolution (e.g., Sampson 1944, Horton and Kraebel 1955, Hanes 1971).

Some shrub species regenerate after fire by seedlings and by sprouts from belowground burls, however many species are restricted to just one or the other of these modes of reproduction. This division between sprouting species and obligate-seeding species is very pronounced in the two largest genera of chaparral shrubs, *Ceanothus* (Rhamnaceae) and *Arctostaphylos* (Ericaceae) (Wells 1969). These sprouting and nonsprouting species have quite different life history patterns. In the immediate postfire years, the sprouting shrubs rapidly regain their prefire size, but few seedlings become established (Jepson 1916, Plumb 1961, Vogl and Schorr 1972). The nonsprouting shrubs, on

the other hand, are replaced after fire by an abundance of seedlings which require 10 to 20 yr to reach maturity.

It is presumed the greater seedling production by these nonsprouting shrubs is due to their greater seed production (Jepson 1939, Sampson 1961, Wells 1969). Since seedlings are produced only after a fire, it is assumed that these nonsprouting shrubs accumulate a large number of seeds in the soil. However, there are no published studies on flower or fruit production for any chaparral shrubs, nor are there any studies on seed populations in the soil beneath chaparral vegetation. Thus, we know very little about the dynamics behind these two reproductive strategies. The purpose of this study was to investigate seed production and seed storage in the soil and relate these parameters to seedling production after fire for shrub species representing the sprouting and seeding reproductive modes. The following questions were examined: (1) what is the magnitude of variation in seed production from year to year, (2) what are the reasons for annual fluctuations in seed production, (3) what is the relationship between the number of seeds produced and the size of seed populations in the soil, (4) what is the relationship between the size of seed populations in the soil and seedling production after fire, and (5) how do these sprouting and nonsprouting species differ with respect to seed production, seed populations in the soil, and seedling production after fire?

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## METHODS

*Species and site selection*

The species studied were selected for the purpose of comparing shrubs which were similar in many aspects of their general ecology except for their degree of dependence upon seedling production for postfire regeneration. A pair of *Ceanothus* species and a pair of *Arctostaphylos* species were chosen. One species of each congeneric pair was a nonsprouting shrub (i.e., entirely dependent upon seedling production for post-fire establishment) and the other was a sprouting shrub (i.e., not entirely dependent upon seedling production). The species were: *Ceanothus greggii* Gray var. *perplexans* (Trel.) Jeps. (nonsprouter), *C. leucodermis* Green (sprouter), *Arctostaphylos glauca* Lindl. (nonsprouter), and *A. glandulosa* Eastw. (sprouter).

All 4 species are broadly similar in their flowering and fruiting phenology. Both *Ceanothus* species flower in early to mid-spring and their seeds disperse in late spring. The *Arctostaphylos* species flower in late winter and their seeds disperse in late summer. The *Ceanothus* species produce capsules (50–100 mg/capsule dry weight); each contains 3 seeds (5–10 mg/seed) which are ejected at maturity. The *Arctostaphylos* species produce a drupe with 4–10 seeds embedded in a hard resinous endocarp which is surrounded by a leathery (*A. glauca*) or pulpy (*A. glandulosa*) pericarp. The fruits of *A. glauca* (600–800 mg) have an average of 5.6 seeds/fruit whereas the fruits of *A. glandulosa* (50–100 mg) have an average of 6.4 seeds/fruit ( $n = 100$ ). For both species the fruits fall from the shrub intact, but the pericarp is soon lost. In *A. glauca* fruits the seeds remain permanently fused within the endocarp so that 1 fruit results in one multiseeded propagule. Fruits of *A. glandulosa*, on the other hand, split into propagules of 1 to several seeds, averaging 3.6 propagules/fruit ( $n = 100$ ).

Two study sites were selected: 1 for the *Ceanothus* species and 1 for the *Arctostaphylos* species. The criteria for site selection were: (1) an unburned chaparral stand contiguous with a recently burned stand, (2) both stands at each site of the same age previous to the fire, and (3) both congeneric species major components of the vegetation. The sites were selected with a view to relating seed production and seed populations in the soil in the unburned stand to seedling production in the adjacent burned stand.

The *Ceanothus* site was off Boulder Creek Road  $\approx 11$  km north of Descanso, in south San Diego County, California (elevation 1,300 m). Both unburned and burned stands transected north- and south-facing slopes of adjacent drainages on a soil of decomposed granite. The shrubs in the unburned stand were 23 yr old, determined by ring counts from several *C. greggii*. The burned stand was part of the Boulder fire of September 1970. The *Arctostaphylos* site was located at the junction of Japatul-Lyons Valley Road and Lawson Truck Trail,  $\approx 12$  km south of Descanso, in

San Diego County (675 m). Both the unburned and burned stands were on east-facing slopes of an iron-rich vertisol soil. The shrubs in the unburned stand were  $\approx 90$  yr old, determined by ring counts taken from several *A. glauca*, *A. glandulosa*, and *C. greggii*. The burned stand was part of the Laguna fire of September 1970. For both the *Ceanothus* site and the *Arctostaphylos* site, the similarity in size of the shrub remains in the burned stand with shrubs in the adjacent unburned stand was taken as evidence that both stands were the same age prior to the fire (see Keeley 1973).

*Vegetation sampling*

Vegetation sampling was undertaken to determine the coverage and density of each species under study in both the unburned stand and the adjacent burned stand. All sampling was carried out in the summer of 1972; for the burned stands this was after 1 full year of recovery from the fires of 1970. At the *Ceanothus* site, three 2-  $\times$  2-m plots were randomly placed along each of 11 parallel 50-m transects through the unburned stand. Height, basal diameter, and areal diameter were recorded for both *Ceanothus* species. In the burned stand the same sampling procedure was used, plus an additional 20-  $\times$  30-m plot was sampled. At the *Arctostaphylos* site the same procedure was used except that four 2-  $\times$  4-m plots were placed along 8 parallel 70-m transects.

*Seed sampling*

All seed sampling was undertaken in the unburned stand at both sites and was divided into 2 parts: (1) estimating seed production over a several-year period, and (2) estimating the size of the seed populations in the soil at one point in time.

Estimates of seed production for the *Ceanothus* species were made in the late spring or summer of 1973, 1974, and 1975. Two parallel lines were laid out through the unburned stand, and for both *Ceanothus* species the areal spread and number of fruits was recorded from the first 50 shrubs encountered. In 1974 all the shrubs had an exceptionally heavy fruit-set, thus for each shrub only the fruits on 1 randomly selected quarter were counted. Total seed production in the stand was obtained for each species by multiplying the no. of fruits/metre<sup>2</sup> of areal coverage by the areal coverage/hectare (obtained from the vegetation sampling) by the no. of seeds/fruit.

Estimates of seed production by the *Arctostaphylos* species were made in the summers of 1972, 1973, 1974, 1975, and 1976 using the same sampling procedure described for the *Ceanothus* species, except that in 1976 only 25 shrubs of each species were sampled. Relative fruit production (i.e., fruits/square metre of areal coverage) was converted to both seeds/hectare and propagules/hectare with the conversion factors given above.

For both *Ceanothus* and *Arctostaphylos* species,

TABLE 1. Shrub and population characteristics of the *Ceanothus* species at the *Ceanothus* site

Species	Unburned stand				Burned stand		
	Ht (m)	m <sup>2</sup> of areal coverage/shrub	Shrubs/ha	cm <sup>2</sup> of basal area/ha	m <sup>2</sup> of areal coverage/ha	Resprouts/ha	Seedlings/ha <sup>a</sup>
<i>C. greggii</i>	1.78**	1.37 <sup>NS</sup>	7,900	218,400	11,000	0	14,350
<i>C. leucodermis</i>	1.60**	1.12 <sup>NS</sup>	3,540	41,800	4,000	1,170	2,050

\*\* Difference between species is significant at  $P < .01$ .

<sup>NS</sup> Difference between species is not significant ( $P > .05$ ).

<sup>a</sup> Includes both live and dead seedlings.

fruit production was compared between years within a species and between congeneric species within a year with Student's *t*-test. Where the variances were nonhomogeneous, an alternative method was used (Sokal and Rohlf 1969, p. 374).

Seed populations were estimated from soil samples taken from plots used in the vegetation sampling. A square wooden frame, with an inside width of 28.5 cm, was laid down in the middle of a plot and the duff and soil was cut out to a depth of 10 to 15 cm. Everything that was retained on a no. 20-screen sieve was put in a bag and returned to the laboratory. Seeds were separated from the soil and litter by the procedure of Quick (1956) with minor modifications (Keeley 1973). At the *Ceanothus* site, a soil sample was taken from each of the 20 plots which had the greatest number of *Ceanothus* shrubs present, and only *Ceanothus* seeds were retained. At the *Arctostaphylos* site, a soil sample was taken from each of the 20 plots which had the greatest number of *Arctostaphylos* shrubs present, and only *Arctostaphylos* seeds were retained.

Since these species do not have well-developed (long-distance) seed dispersal mechanisms, it is likely that the greatest concentration of seeds occurs nearest the shrub. Therefore, sampling only plots in which *Ceanothus* or *Arctostaphylos* shrubs were present gave an upper estimate of the size of the seed populations in the soil. However random sampling would have required a much larger sample size in order to avoid the less desirable alternative of underestimating the size of the seed populations. This procedure did

TABLE 3. *Ceanothus* seed populations in the soil at the *Ceanothus* site

Species	Seeds/ha	Estimated seed viability	
		<i>N</i>	% viable
<i>C. greggii</i>	$369 \times 10^4$	170	71
<i>C. leucodermis</i>	$87 \times 10^4$	30	96

not bias the estimates in favor of the more common species since at both sites, the 20 plots included all those plots in which the less frequent species had occurred.

Estimates of seed viability were made on random samples of seeds from the soil and from the shrubs. Seeds were cut in half and the embryo was scored as "viable" if plump and white, and scored as "inviable" if shrunken or discolored. This classification was supported by preliminary tests using the tetrazolium test described by MacKay (1972). Undoubtedly some seeds scored as viable were not viable, however this was a good upper estimate of seed viability since there was little chance that seeds scored as inviable were viable.

## RESULTS

### *Ceanothus* site

In the 23-yr-old unburned stand, *Ceanothus greggii* shrubs were significantly taller than *C. leucodermis* shrubs and tended to have larger areal spreads (Table 1). The density and areal coverage of *C. greggii* was

TABLE 2. Fruiting characteristics of the *Ceanothus* species at the *Ceanothus* site

Year	Species	Fruits/m <sup>2</sup> of areal coverage <sup>a,b</sup>	Seeds/ha	Estimated seed viability	
				<i>N</i>	% viable
1973	<i>C. greggii</i>	$340 \pm 67^{\text{NS}}$	$11.1 \times 10^6$	1,300	51
	<i>C. leucodermis</i>	$230 \pm 57^{\text{NS}}$	$2.7 \times 10^6$	2,200	53
1974	<i>C. greggii</i>	$5,252 \pm 456^{**}$	$170.2 \times 10^6$	1,300	49
	<i>C. leucodermis</i>	$2,454 \pm 262^{**}$	$29.2 \times 10^6$	1,000	44
1975	<i>C. greggii</i>	$0 \pm 0.0^{**}$	0	...	...
	<i>C. leucodermis</i>	$4 \pm 0.8^{**}$	$47.6 \times 10^3$	...	...

<sup>a</sup>  $\pm$  SE of the mean ( $N = 50$ ).

<sup>b</sup> Differences between years (within a species) are significant at  $P < .01$ .

<sup>NS</sup> Difference between species is not significant ( $P > .05$ ).

\*\* Differences between species are significant at  $P < .01$ .

TABLE 4. Shrub and population characteristics of the *Arctostaphylos* species at the *Arctostaphylos* site

Species	Unburned stand				Burned stand		
	Ht	m <sup>2</sup> of areal coverage/shrub	Shrubs/ha	cm <sup>2</sup> of basal area/ha	m <sup>2</sup> of areal coverage/ha	Resprouts/ha	Seedlings/ha <sup>a</sup>
<i>A. glauca</i>	2.68**	6.35**	860	152,700	5,500	0	8,500
<i>A. glandulosa</i>	1.79**	3.03**	1,560	148,400	4,700	860	1,050

\*\* Differences between species significant at  $P < .01$ .

<sup>a</sup> Includes both live and dead seedlings.

≈2.5× greater than that of *C. leucodermis*, and *C. greggii* had nearly 5× as much basal area. In the adjacent burned stand *C. greggii* seedling density was 7× greater than that of *C. leucodermis*.

Fruit production by the *Ceanothus* shrubs in the unburned stand fluctuated greatly from year to year (Table 2). In 1973 and 1974 *C. greggii* produced more fruits than *C. leucodermis*. In 1975 *C. greggii* did not fruit and *C. leucodermis* produced only a fraction of the amount of the previous year. For these 3 years, *C. greggii* produced 5× as many seeds/hectare as *C. leucodermis*. At least half of the seeds produced by each species were not viable (Table 2), due largely to the abortion of one seed in each capsule very early in development.

A comparison of seed populations in the soil (Table 3) indicated that in 1972 *C. greggii* had 4× as many seeds in the soil as did *C. leucodermis*. The difference in viability between the seeds from the shrubs and the seeds from the soil is accounted for by the fact that many of the seeds scored as inviable from the seed crops were so badly shrivelled that they were not picked up in the soil samples.

#### *Arctostaphylos* site

In the 90-yr-old unburned stand of chaparral, the nonsprouting *A. glauca* shrubs were much larger than

the sprouting *A. glandulosa* shrubs (Table 4). There were fewer of the former species so in terms of basal and areal coverage both species were equivalent at this site. In the adjacent burned stand, the nonsprouting *A. glauca* produced over 5× more seedlings than *A. glandulosa*.

Fruit production by these 2 species fluctuated by several orders of magnitude during the years of this study (Table 5). In the even-numbered years, *A. glandulosa* produced from 2 to 10× more fruits/square meter of areal coverage than *A. glauca*. In 1974 both *Arctostaphylos* species showed a highly significant increase in fruit production from the previous 2 yr. Neither species flowered in 1975. The ratio between the 2 species for seeds/hectare was similar to the ratio for fruits/square meter of areal coverage. However, due to the characteristic splitting of *A. glandulosa* fruits, the number of propagules/hectare in the even-numbered years was almost a magnitude greater for *A. glandulosa*. During the years of this study, *A. glandulosa* produced 4× as many seeds/hectare as did *A. glauca*. However, for all the years sampled, seed viability was highest for *A. glauca*.

A comparison of seed populations in the soil (Table 6) indicated that in 1972 there were 27× more *A. glandulosa* propagules in the soil than *A. glauca* propagules. This represented ≈7× more *A. glandulosa*

TABLE 5. Fruiting characteristics of the *Arctostaphylos* species at the *Arctostaphylos* site

Year	Species	Fruits/m <sup>2</sup> of areal coverage <sup>a,b</sup>	Seeds/ha	Propagules/ha	Estimated seed viability	
					N	% viable
1972	<i>A. glauca</i>	3.8 ± 1.0**	117,000	20,900	560	90
	<i>A. glandulosa</i>	10.0 ± 2.1**	300,800	178,600	325	48
1973	<i>A. glauca</i>	1.6 ± 0.7*	49,300	8,800	560	81
	<i>A. glandulosa</i>	0.0 ± 0.0*	0	0	...	...
1974	<i>A. glauca</i>	349.5 ± 56.3**	10.8 × 10 <sup>6</sup>	1.9 × 10 <sup>6</sup>	560	79
	<i>A. glandulosa</i>	916.8 ± 161.7**	32.2 × 10 <sup>6</sup>	19.2 × 10 <sup>6</sup>	650	68
1975	<i>A. glauca</i>	0.0 ± 0.0 <sup>NS</sup>	0	0	...	...
	<i>A. glandulosa</i>	0.0 ± 0.0 <sup>NS</sup>	0	0	...	...
1976	<i>A. glauca</i>	50.7 ± 11.8**	1.56 × 10 <sup>6</sup>	27.9 × 10 <sup>4</sup>	...	...
	<i>A. glandulosa</i>	598.8 ± 92.1**	18.0 × 10 <sup>6</sup>	10.1 × 10 <sup>6</sup>	...	...

<sup>a</sup> ± SE of the mean ( $N = 50$  except in 1976 where  $N = 25$ ).

<sup>b</sup> Differences between years (within a species) are significant at  $P < .01$  for all comparisons except *A. glauca* between 1972 and 1973 ( $P < .05$ ), and *A. glandulosa* between 1973 and 1975 and between 1974 and 1976 ( $P > .05$ ).

\*\* Differences between species are significant at  $P < .01$ .

\* Difference between species is significant at  $P < .05$ .

<sup>NS</sup> Difference between species is not significant ( $P > .05$ ).

TABLE 6. *Arctostaphylos* seed populations in the soil at the *Arctostaphylos* site

Species	Propagules/ha	Seeds/ha	Estimated viability			
			Seeds		Propagules	
			N	% viable	N	% viable <sup>a</sup>
<i>A. glauca</i>	$102 \times 10^4$	$346 \times 10^4$	381	54	113	55
<i>A. glandulosa</i>	$2,716 \times 10^4$	$4,116 \times 10^4$	552	7	366	9

<sup>a</sup> Propagules with at least 1 viable seed.

fruits in the soil. There were 12× more *A. glandulosa* seeds/hectare than *A. glauca* seeds, however the vast majority of these seeds were not viable (Table 6).

#### DISCUSSION

A summary of the results obtained for all species (Table 7) will be helpful in discussing the questions which were set out in the **Introduction**.

##### Variability in seed production

Annual seed production can fluctuate by several orders of magnitude for both *Ceanothus* and *Arctostaphylos* species (Table 7). These shrubs have years of high, intermediate, and low fruit production. The observation that in the same year all 4 species produced a large number of fruits, whereas in another all produced a low number, suggests that these annual fluctuations may be directly related to climatic fluctuations. A comparison of the fruit production patterns with climatic patterns during the study is shown in Fig. 1. In all years, the pattern is one of decreasing precipitation in late spring as temperatures increase. In midsummer, when temperatures are high, precipitation is low; as precipitation increases in fall and winter, temperatures decrease. Characteristic of this mediterranean climate is the small seasonal as well as annual fluctuations in temperature relative to the very large annual fluctuations in precipitation.

The importance of this interplay between moisture availability and temperature to the growth of chaparral shrubs has been repeatedly demonstrated (e.g., Cooper 1922, Bauer 1936, Miller 1947, Major 1963, Harvey and Mooney 1964, Dunn 1975). In gener-

al there is strong evidence that annual carbon fixation by chaparral shrubs is directly related to annual precipitation, and there is also evidence that it is only slightly limited by temperature (Mooney et al. 1975). Thus, there is good reason to expect a strong correlation between precipitation and fruit production. If so, we might expect high fruit production in years of high precipitation. However, in this study there was low fruit production in 1973, a year of high precipitation, whereas medium to high fruit production occurred in 1974 and 1976, years of low precipitation.

Another hypothesis is that fruit production is dependent upon the carbon gained in the previous year, in which case there should be a correlation between fruit production and the amount of precipitation in the previous year. There is support for this idea: 1972 and 1974 had low precipitation and each was followed by a year of low fruit production, whereas 1973 had high precipitation and was followed by a year of high fruit production, and 1975 had close to normal precipitation and was followed by a year of medium fruit production. The correlation between fruit production and precipitation in the previous year is striking: for *Arctostaphylos glauca*  $r_s = 0.9$  and for *A. glandulosa*  $r_s = 0.97$  (Spearman's rank correlation,  $P < .05$ ,  $N = 5$ ). Although I am unaware of any previous discussion of this phenomenon in chaparral shrubs, there is some evidence that it is widespread. For example, Van Rensselaer (1942, p. 56) noted that 1939 was "the heaviest ceanothus blooming season observed in years in southern California." Climatic data shows that 1939 was a year of subnormal rainfall in southern California, but it followed a year with "more than double the usual amount" of precipitation in midspring (Bowie 1938, 1939).

TABLE 7. Summary of seed production, seed storage in the soil, and seedlings produced after fire for all species

Species	Unburned stand					Viable seeds in the soil/ha (1972)	Burned stand Seedlings/ha <sup>b</sup>
	Viable seeds produced/ha						
	1972	1973	1974	1975	1976 <sup>a</sup>		
<i>Ceanothus greggii</i>	...	$560 \times 10^4$	$835 \times 10^5$	0	...	$262 \times 10^4$	$144 \times 10^2$
<i>C. leucodermis</i>	...	$145 \times 10^4$	$128 \times 10^5$	$230 \times 10^2$	...	$835 \times 10^3$	$205 \times 10$
<i>Arctostaphylos glauca</i>	$105 \times 10^3$	$399 \times 10^2$	$853 \times 10^4$	0	$130 \times 10^4$	$187 \times 10^4$	$850 \times 10$
<i>A. glandulosa</i>	$144 \times 10^3$	0	$220 \times 10^5$	0	$104 \times 10^5$	$288 \times 10^4$	$150 \times 10$

<sup>a</sup> Viability this year was taken as the average of the previous years.

<sup>b</sup> Includes both live and dead seedlings.

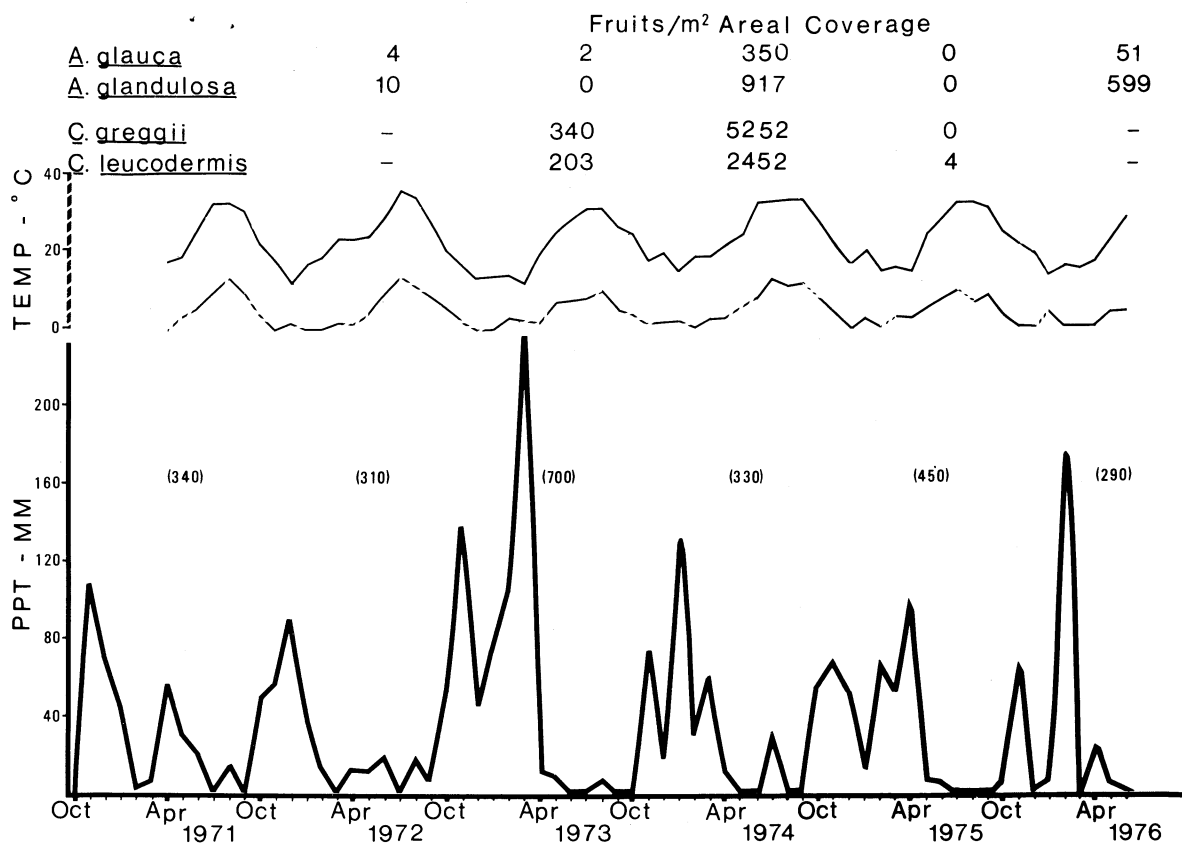


FIG. 1. A comparison of annual fruit production with monthly mean maximum and minimum temperatures and monthly mean precipitation for the nearest station, Descanso, San Diego County (1,000 m). Annual totals, July-June, are given in parentheses (21 yr mean is 551 mm, mode is  $\approx$ 500 mm). Precipitation data prior to April 1971 is from the U.S.D.A. Forest Service Station, and climatic data past this date are from Dr. P. C. Miller, San Diego State University (*personal communication*).

If this relationship between fruit production and precipitation is reflective of a dependence upon carbon gain in the year prior to fruit production, then an important question is why? One obvious explanation is that fruit maturation is dependent upon stored carbon rather than currently-produced carbon. This has been shown for *Aesculus californica* (Spach) Nutt. and *Aesculus parryi* Gray, 2 mediterranean-climate plants of California (Mooney and Hays 1973, Mooney and Bartholomew 1974). Fruits mature during summer and fall, the period in which these drought deciduous plants are leafless, thus, fruit production is directly dependent upon the current year's stored carbon. On the other hand, in the evergreen chaparral plants *Quercus agrifolia* Neé and *Heteromeles arbutifolia* M. Roem., the fruits act as a sink for currently produced carbon and rely very little on stored photosynthates (Mooney and Hays 1973, Mooney and Chu 1974). Since *Ceanothus* and *Arctostaphylos* species studied are also evergreen shrubs, one might expect them to do likewise. However, one piece of evidence suggests that dependence upon stored carbon cannot be ruled out; in *Ceanothus* and *Arctostaphylos* species, fruit maturation occurs during the spring (con-

comitant with vegetative growth), whereas in *Q. agrifolia* and in *H. arbutifolia* fruit maturation occurs during the summer and fall (after vegetative growth is completed). This distinction may be very important since Mooney and Hays (1973) noted that vegetative growth and the beginning of fruit maturation overlap slightly in *Q. agrifolia*, and it is at this time that there is some dependence upon stored carbon.

Another way fruit production could be linked to the amount of carbon gained in the previous year is through flower bud production. *Arctostaphylos* and *Ceanothus* species both produce floral primordia in the late spring of the year prior to flowering and fruiting (J. E. Keeley, *personal observation*). In many plants the production of floral primordia is directly dependent upon carbohydrate levels in the plant at the time of bud initiation (Singh 1948a, b, Davis 1957). Because high fruit production is in part dependent upon high flower production, this may be the link between a year of high precipitation preceding a year of high fruit production in these species. This is reflected in the number of floral buds produced by *A. glauca* at the *Arctostaphylos* site (1973, 120/m<sup>2</sup> of areal coverage; 1974, 0; 1975, 17; 1976, 19; *N* = 50 except

1976 where  $N = 25$ ). In the odd-numbered years fruit production was very low, so a greater production of floral buds in 1973 is very likely the result of more carbon gained as a result of the greater precipitation that year. A strong dependence of fruit production upon bud production is also suggested by the nearly identical ratios of floral buds to fruits the following year for 1973–74 and 1975–76 in *A. glauca*.

Thus, fruit production in *C. greggii*, *C. leucodermis*, *A. glauca*, and *A. glandulosa* is apparently dependent upon the number of flower buds initiated in the previous year, which very likely is dependent upon the amount of carbon gained. Carbon gain in turn is dependent upon precipitation. In addition to total carbon gained, bud production is bound to be affected by alternative carbon demands. For example, the lack of bud production by *A. glauca* in 1974 undoubtedly reflects not only the low precipitation that year but also a high carbon demand by the extensive fruit crop. In general there is a negative correlation between number of fruits (from buds of the previous year) and number of buds (for fruits of following year) (e.g.,  $r_s = -0.55$  for *A. glauca* in 1976 with Spearman's rank correlation,  $P < .01$ ,  $N = 25$ ). It is not known whether the number of flower buds produced is simply a reflection of the amount of carbon "left over" after fruit production and vegetative growth (Davis 1957) or whether flower bud production is keyed (perhaps through a hormonal system, Kozlowski 1971, p. 403–408) to the amount of carbon which has been stored for the fruit crop of the following year. The observation that fruit production in these species is dependent upon adequate precipitation the previous year, and is much less dependent upon the amount of precipitation in the year of fruit production (Fig. 1) suggests there is a strong dependence upon stored carbon and therefore would argue for the latter mechanism.

Even though precipitation can account for much of the variability in fruit production, other factors should not be ignored. Temperature, for example, accounts for much of the variance in seed production in a number of tree species (e.g., Andersson 1965, Sharp and Sprague 1967, Lester 1967). In general these studies deal with regions having a much greater temperature range than is typical of southern California. However, occasional temperature extremes, such as late frosts, can affect fruit production even in mediterranean-climate shrubs (Hoffmann and Hoffmann 1976).

The patterns observed in this study were generally consistent for these species in the southern part of San Diego County, but not for all chaparral shrub species. For example, *Adenostoma fasciculatum* H. & A., *Heteromeles arbutifolia*, and *Malosma* (*Rhus laurina* (Nutt.) Nutt. ex Adams all had high fruit production in 1973. Perhaps this is related to their phenology of flower bud production. These shrubs differ from *Ceanothus* and *Arctostaphylos* species in that they

produce their floral primordia directly before flowering (J. E. Keeley, *personal observation*). In these species we should expect high fruit production in years of high precipitation.

#### *Seed production and seed populations in the soil*

Though annual seed production fluctuates by several orders of magnitude, each species is capable of producing many more seeds in a single good year than are stored in the soil (Table 7). This is even more striking when one recalls that these were upper estimates of the size of seed populations in the soil (see **Methods** section). This indicates that a great many of the seeds produced each year are "lost" from these stands of chaparral, either by being transported elsewhere or by being destroyed in situ.

Animal dispersal of seeds may account for some removal of seeds from these stands. For example, it is well known that coyotes relish *Arctostaphylos* fruits. I have also observed ants transporting *Ceanothus* seeds. Loss of seeds as a result of erosion is likely since erosion rates from mature chaparral of southern California can be as high as  $8,500 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  (Sinclair 1954). Deterioration of seeds could account for some of the seed loss from the soil, though there is little information on rates of seed decay in arid land soils. Seed predation may account for a great deal of the seed loss. For example, infestation of *Ceanothus greggii* seeds by the phytophagous chalcid wasp *Eurytoma ceanothi* Bugbee has been noted to reach levels  $>80\%$  (Bugbee 1971). Personal observations on *Arctostaphylos glauca* and *A. glandulosa* fruits still on the shrub have revealed that in some years, large numbers are infested by insect larvae. Additionally, several rodents are known to include large amounts of *Arctostaphylos* fruits in their diets (Smith 1942, Horton and Wright 1945, Jameson 1952). At the *Arctostaphylos* site, there is some evidence that ground-dwelling seed predators destroy substantial numbers of *Arctostaphylos* fruits and even select the larger *A. glauca* fruits over the smaller *A. glandulosa* fruits (Keeley and Hays 1976). It is not possible to evaluate the importance of each of these factors for the sites in this study.

The relationship between the quantity of seeds produced in a single season and the size of the seed populations in the soil does not indicate a steady accumulation of seeds in the soil. Illustrative of this are the relatively small seed populations in the soil at the *Arctostaphylos* site. These shrubs presumably have been producing seeds for over 75 yr, and yet in a single year they produce more seeds than have accumulated in the soil over that period of time. Perhaps a more realistic perspective of chaparral soil seed populations would be one of annual fluctuations of seed inputs and losses.

In this event, the season in which a fire occurs, as



well as the frequency of fires in the chaparral, may have important consequences for the reproduction of chaparral shrubs, particularly nonsprouting species. For example the failure to reestablish after a very early spring fire has been noted for *Ceanothus crassifolius* Torr. Extensive seed harvesting by ants had been observed and was suggested as a causal factor (Horton and Kraebel 1955). Thus these nonsprouting shrubs may be dependent upon frequent inputs of seeds into the soil for successful reproduction after fire. Additionally, due to the temporal unpredictability of fire in the chaparral environment, shrubs may not only have to cope with frequent fires but also with infrequent fires. Mechanisms which increase the longevity of nonsprouting *Arctostaphylos* shrubs (Davis 1973) and nonsprouting *Ceanothus* shrubs (Keeley 1975) may have been selected for because of a dependence upon sustained seed production.

#### *Seed populations in the soil and seedling production*

If we assume that prior to the fire the burned stand was comparable to the adjacent unburned stand at each site (this is discussed in detail in Keeley and Zedler [*In press*]), then the vast majority (over 99%) of the seeds stored in the soil do not result in seedlings (Table 7). One explanation for this apparent loss of seeds from the soil after fire may be that the number of seeds which were viable was vastly overestimated (Tables 3 and 6). This would be supported by the typically low germination of *Arctostaphylos* seeds (Rogers 1949, Berg 1974, J. E. Keeley, *personal observation*) but not by the typically high germination of *Ceanothus* seeds (Quick and Quick 1961, Hadley 1961, Gratkowski 1962).

Destruction of seeds by fire is a likely factor in accounting for such low production of seedlings. Although seed germination is greatly stimulated by fire (see Christensen and Muller 1975 for review), temperatures  $>120^{\circ}\text{C}$  destroy chaparral shrub seeds (Wright 1931, Sampson 1944, Stone and Juhren 1952, Quick and Quick 1961). Temperatures can exceed  $600^{\circ}\text{C}$  in the duff beneath chaparral during fire (Sampson 1944, Sweeney 1956), thus ensuring the destruction of many seeds. It has been observed that there are more shrub seedlings after a "light" fire than after a "very hot" fire (Hedrick 1951).

The small surface area/volume ratio and the greater endocarp/seed ratio in *A. glauca* propagules (Keeley and Hays 1976) suggests that the seeds of this species would be more resistant to destruction by fire than those of *A. glandulosa*. This may explain why there were many more *A. glauca* seedlings than *A. glandulosa* seedlings in the burned stand, even though the latter species apparently had many more seeds in the soil prior to the fire.

In general, only a very small percentage of the soil seed population will produce seedlings after fire. This

suggests that only seeds at the right level in the soil will escape destruction and still be stimulated to germinate after fire.

#### *Sprouters and nonsprouters compared*

The nonsprouting *Ceanothus* species was more abundant, had greater seed production, had more seeds in the soil, and produced more seedlings after fire than its sprouting congener (Tables 1 and 7). Based on relative seed production (seeds/square meter of areal coverage) and assuming equal abundance, the nonsprouting species would have about double the seed production of the sprouter.

This pattern is in marked contrast to that found for the *Arctostaphylos* species. In the unburned stand, the 2 species had an equivalent amount of basal and areal coverage (Table 4). The nonsprouting *A. glauca* produced fewer seeds in 3 yr and more seeds in 1 yr than the sprouting *A. glandulosa*. For the 5 yr of study, the sprouting species produced 4 $\times$  more seeds than the nonsprouting species (Table 5). The seed pool in the soil was 10 $\times$  larger for *A. glandulosa* than for *A. glauca*. This difference may be due to greater predation on *A. glauca* seeds (Keeley and Hays 1976). However, after fire the nonsprouting *A. glauca* produced many more seedlings than did *A. glandulosa* (Table 4).

An important point to consider is that although the sprouting species produced 4 $\times$  more seeds than the nonsprouting species, relatively less biomass was allocated to reproduction (Keeley and Keeley *In press*), since the fruits of *A. glauca* are about 6 $\times$  larger than those of *A. glandulosa*. In addition, *A. glauca* seeds (endosperm and embryo) are much larger and better protected (larger endocarp/seed ratio) than *A. glandulosa* seeds (Keeley and Hays 1976). Thus not only do *A. glauca* seeds stand a better chance of surviving fire, but they also have a better chance of producing established seedlings (see Keeley and Zedler *In press*). Therefore, the fact that *A. glauca* produces more seedlings after fire than *A. glandulosa* may be a result of a better "packaged" seed rather than a greater number of seeds.

These two congeneric sprouting and nonsprouting species pairs represent 4 different "evolutionary options" in reproductive strategies. The results from this study, coupled with information on the population dynamics of these species (Keeley and Zedler *In press*), suggest the following generalizations. The sprouting *Ceanothus leucodermis*, which may lose up to 50% of its population in a fire, produces many seedlings after fire. The nonsprouting *Ceanothus greggii* must reestablish after fire entirely by seedlings and does so by very high seed production and successful seedling establishment. This high seedling production is followed by high shrub mortality in the first few decades after fire as the shrub canopy closes. The sprouting *Arctostaphylos glandulosa* has low mortality

due to fire and establishes few seedlings after fire, even though it expends a great deal of energy on seed production. The nonsprouting *A. glauca* depends less on the numbers of seeds produced and more on seeds that produce successful seedlings. Due perhaps to an initially low seedling density, *A. glauca* shrub mortality is relatively low for the first several decades after fire.

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