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## ROLE OF ALLELOPATHY, HEAT AND CHARRED WOOD IN THE GERMINATION OF CHAPARRAL HERBS AND SUFFRUTESCENTS

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### SUMMARY

(1) Herbaceous and suffrutescent species are uncommon in mature chaparral but dominate after fire. Colonization is largely from dormant seeds in the soil. This study examined the role of allelopathic inhibitors and fire-related cues in the control of germination of species in the major life-history groups.

(2) Herbaceous perennials are often dormant under the chaparral canopy and their presence in burnt areas is due to sprouts from bulbs or rhizomes. Their seeds germinated readily without any treatment and they were not inhibited by leachate from living *Adenostoma fasciculatum* foliage, but high temperatures were lethal to seeds of many species.

(3) Suffrutescents are not present under the chaparral canopy and their presence in burnt areas is due entirely to seed. Their germination was stimulated by heat, or powdered charred wood, or both, although a portion of the seeds of some species germinated without treatment.

(4) Opportunistic annuals have polymorphic seeds; a portion germinated readily whereas others germinated only after heat or charred wood treatment. The non-refractory seeds account for colonization into gaps in the canopy and the refractory portion accounts for their abundance immediately after a fire. Whether or not the non-refractory seeds are inhibited by allelopathic leachate from the *Adenostoma fasciculatum* canopy is equivocal; leachate did inhibit the germination of two of the twenty-two annual species investigated, but the germination of one-third of the species was stimulated by leachate.

(5) Fire-annual species are largely restricted to recently burnt chaparral sites and the seeds of these species remain dormant in the soil between fires. There is little germination without cues relating to fire. Some species responded to heat but the highest germination was with the charred wood or heat plus charred wood treatments.

### INTRODUCTION

Chaparral is a dense evergreen sclerophyllous scrub vegetation, widely distributed on moderately xeric sites throughout California. Fires are common during the summer and autumn drought, and shrubs exhibit a number of traits that have been interpreted as evolutionary responses to fire; for instance, lignotubers that resprout and seedling recruitment that is restricted to the first year after a fire.

Herbaceous and suffrutescent plants are a minor part of the total cover in mature chaparral but dominate after fire (Horton & Kraebel 1955). Their greatest diversity is in the first spring after a fire, although their peak cover may not be until the third or fourth year (Keeley *et al.*, 1981). More than 200 herbaceous and suffrutescent species have been reported from burnt areas of chaparral and the majority of these are annuals, some of which disappear after the first year and have been termed 'pyrophyte endemics' (Hanes 1977).

The colonization of burned sites in the first spring is largely, if not entirely, from seed in the soil although some weed (usually non-native) species may invade in subsequent years (Sweeney 1956). The mechanisms that cue germination to the post-fire environment have been the subject of controversy. There are two theories: (i) the seeds are chemically inhibited under the mature canopy (either by allelopathic substances leached from the shrubs or by microbial toxins produced in the litter) and these chemicals are eliminated by fire; (ii), the seeds require a stimulus from fire (heat, or chemicals from charred wood).

Sweeney (1956) tested over twenty species of chaparral herbs and found that one-third of the species germinated readily without treatment, one-third required an extended cold treatment, and one-third required scarification of the seed coat. A leachate from chaparral litter had no inhibitory effect. Species with seeds requiring scarification did germinate without scarification if planted in soil and treated by burning wood shavings on the surface of the soil. Sweeney's attempts to duplicate this stimulatory effect using heat largely failed, as have many subsequent attempts to show heat-stimulated germination of chaparral herbs (McPherson & Muller 1969; Christensen & Muller 1975a). Sweeney (1956) also showed that wood ash had no stimulatory effect, although Wicklow (1977) and Jones & Schlesinger (1980) demonstrated that charred (but not ashed) wood stimulated the germination of the pyrophyte endemic *Emmenanthe penduliflora*\*. It is unknown what component of charred wood stimulates germination of this species, but it is known that its germination can be induced by an aqueous extract of charred wood but not by unburned wood or activated charcoal (Keeley & Nitzberg 1984; S. Keeley unpublished).

McPherson & Muller (1969) did extensive experimental work which implicated allelopathic inhibition by the *Adenostoma fasciculatum* shrub canopy as the factor which prevented herb germination in mature chaparral. They concluded that heat from fire destroys the toxin and thus releases the seeds from inhibition. These conclusions are widely accepted despite the following drawbacks in their experiments and conflicts with other results. (i) They studied mostly non-native herbs which seldom occur on recently burnt areas. (ii) Most of their work focused on the effect of leached inhibitors on *growth*, not on *germination*. (iii) Inhibition of germination was demonstrated for four species of native herbs only after the seeds had been scarified and treated with a 10× concentrate of the leachate from *A. fasciculatum* foliage. (iv) Soil and litter from beneath the canopy was not inhibitory unless additional concentrated leachate was added. (v) Temperatures applied to the soils, which resulted in enhanced germination, were far lower than the temperatures needed to degrade the suspected toxins (McPherson, Chou & Muller 1971). (vi) The concentration of toxins necessary for inhibition (McPherson, Chou & Muller 1971) were much higher than those found in soils (Kaminsky 1981). (vii) The concentration of suspected allelopathic toxins was greatest in burned soils from recently burned sites (Christensen & Muller 1975a). (viii) Seeds in soil which was heat treated, but then returned to beneath the shrub canopy, showed high germination (Christensen & Muller 1975b). (ix) Seeds of many species fail to germinate even if they are never exposed to so-called allelopathic toxins. (x) Nearly all of the evidence for allelopathy in chaparral is based on laboratory bioassays and the literature supports Stowe's (1979) contention 'that perhaps any species can be shown to have allelopathic properties in bioassays'.

Christensen & Muller (1975a) demonstrated that *A. fasciculatum* foliage leachate inhibited the germination of two native and two non-native chaparral herb species but had no effect on six of the more typical pyrophyte endemics. After further experimentation they

\* Nomenclature according to Munz (1974).

'concluded that numerous ecological factors associated with the chaparral understory result in an extremely low probability of seedling survival. [and] ... This has resulted in selection for dormancy mechanisms in some species which minimize seed germination during periods of low survival probability' (Christensen & Muller 1975b).

Kaminsky (1981) hypothesized that seed dormancy is induced by inhibitors from microbes in the litter under chaparral and demonstrated such an effect with cultivated lettuce seeds. Pack (1985) repeated Kaminsky's experiments with five native herb species and eight chaparral soils and found no evidence of microbial by-products inhibiting germination.

Part of the confusion surrounding chaparral herb germination behaviour is the assumption that one mechanism works for all species as suggested by certain investigators working on a single non-native species. We consider that the herb and suffrutescent species in chaparral include a diversity of life histories and of seed germination behaviours. We divide the 'temporary' post-fire flora into four groups: (i) herbaceous perennials; (ii) suffrutescents; (iii) opportunistic annuals; and (iv) fire annuals. In this study we examine the role of allelopathy, heat and charred wood in the control of seed germination of species from each of these groups.

## METHODS

Twenty-eight herbaceous and two suffrutescent species, representing each of the four life-history types, were selected for study. Seeds were collected in late spring and the experiments were begun in late summer.

The treatments were: (i) heating prior to sowing; (ii) media treatments during incubation. The seeds were heated 'dry' on open Petri dishes in a forced convection oven at 80 °C for 2 h, at 120 °C for 5 min, and at 150 °C for 5 min. The media treatments were: aqueous leachate from the foliage of *Adenostoma fasciculatum* (hereafter called *Adenostoma*); powdered charred *Adenostoma* wood; and leachate and powdered charred wood combined. All treatments were carried out in combination for a total, including controls, of sixteen treatments per species. Each was replicated eight times.

Germination tests were carried out in 10 cm diameter × 1.5 cm deep plastic Petri dishes with about 50 ml of sterilized potting soil (Gro-Lite) sifted through a 3-mm screen. The seeds were sown on top of the soil after heat treatment. For most species fifty seeds were sown per dish but some species had too large a seed for this number—see tables. Charred wood treatments received about 2.5 g of powdered charred wood. For dishes receiving the leachate, 25 ml of leachate were applied; 25 ml of deionized water were applied to all other dishes. Soon after the experiments began the charred wood treatments were given an additional 2 ml of water to compensate for the absorption by the powdered charred wood.

Leachate and 4× concentrated leachate from living *Adenostoma* foliage was prepared in mid- to late-summer (when the concentration of 'allelopathic toxins' should have been close to its peak) as described by McPherson & Muller (1969). Briefly, foliage was placed in a 1-m<sup>2</sup> funnel and 3 l of deionized water were applied in a fine mist over a period of 2 h. The liquid was stored at 5 °C until it was applied, usually within a week of preparation.

Powdered charred wood was prepared by charring (not ashing) with a torch of living *Adenostoma* stems (<20 mm diameter) and grinding them in a Wiley mill to pass a 1-mm mesh screen.

The Petri dishes were wrapped in plastic bags to prevent desiccation and, as in earlier studies described in the literature cited previously, incubated in the dark, although counting

was under normal room light. Since it was unknown which species might require a cold stratification treatment, all the dishes were incubated at 5 °C for 20 days followed by incubation at 23 °C for 15 days. This regime was repeated twice for a total germination period of more than 100 days. The germination was recorded every 10 days in the cold treatment and every 5 days at room temperature and all germinated seeds were removed.

The raw data were analysed with two-way and one-way analysis of variance. Fisher's least significant difference (LSD) was calculated for significant one-way analysis of variance tests.

## RESULTS

### *Interaction of leachate, heat and charred wood*

All the herbaceous perennials had seeds which germinated readily without any treatment (Table 1). Heat was lethal to many seeds, although the lethal temperature varied between species; the seeds of the dicotyledons *Marah macrocarpus* and *Paeonia californica* were more sensitive to 2 h at 80 °C than to 5 min at 120 °C, whereas the opposite applied to the monocotyledons *Stipa coronata* and *Zigadenus fremontii*. Five minutes at 150 °C

TABLE 1. Percentage germination of herbaceous perennial species from Californian chaparral after treatment with heat in combination with aqueous leachate from living *Adenostoma fasciculatum* foliage, or powdered charred stems, or both (L+C).

Temperature (°C) Time (min)	Control	Heat treatment		P	LSD
		80 120	120 150		
<i>Marah macrocarpus</i> (8 dishes of 10 seeds)					
Control	73	19	25	9	** 25
Leachate	89	0	34	4	** 12
Charred wood	84	0	51	1	** 19
L + C	88	0	41	21	** 32
P	N.S.	**	N.S.	N.S.	
LSD		13			
<i>Paeonia californica</i> (8 dishes of 20 seeds)					
Control	68	1	6	2	** 10
Leachate	79	6	21	5	** 22
Charred wood	55	0	13	1	** 13
L + C	42	0	13	1	** 13
P	**	N.S.	N.S.	N.S.	
LSD	17				
<i>Stipa coronata</i> (8 dishes of 30 seeds)					
Control	90	83	23	0	** 13
Leachate	87	88	53	0	** 20
Charred wood	80	82	13	0	** 11
L + C	68	74	14	1	** 7
P	**	N.S.	**	N.S.	
LSD	16		26		
<i>Zigadenus fremontii</i> (8 dishes of 50 seeds)					
Control	84	71	9	0	** 15
Leachate	83	71	33	1	** 20
Charred wood	68	55	5	2	** 19
L + C	73	88	6	1	** 8
P	N.S.	**	**	N.S.	
LSD		24	10		

\*\*  $P < 0.01$ .

N.S.,  $P > 0.05$ .

killed nearly all seeds. *Adenostoma leachate* had no significant effect on germination, although charred wood tended to inhibit the germination of some species. Two-way analysis of variance showed a significant interaction between heat and media treatment for the two dicotyledons although there is no obvious interpretation for this. The results are not shown for two other herbaceous perennials. *Calystegia macrostegius* had highest germination under control conditions and it was most sensitive to 80 °C for 2 h; however, its maximum germination was only 21%. *Sisyrinchium bellum* had very low germination although it tended to be enhanced by leachate and reduced by charred wood and heat.

These patterns contrast with those observed for the two suffrutescent species (Table 2). *Eriophyllum confertiflorum* had very low germination under control conditions and showed no enhancement from heat treatments alone. Charred wood, however, increased its germination tenfold and there was an additional enhancement with 120 °C plus charred wood treatment. This synergistic effect of heat plus charred wood may account for the significant interaction effect in the two-way analysis of variance. The control seeds, which largely failed to germinate after 105 days, were truly dormant since their germination increased from 4% to 53% when powdered charred wood was added after the end of the experiment. Approximately one-quarter of the *Helianthemum scoparium* seeds germinated without treatment although their germination nearly doubled by treatment at 120 °C.

Annuals showed a range of responses. These species are arranged in Table 3 from the more opportunistic to the more fire dependent. For the two annual grasses, *Avena barbata* (non-native) and *Festuca magalura*, germination occurred readily without treatment. *Festuca magalura* showed a slightly significant enhancement of germination with either leachate or charred wood. *Avena barbata* germination was greatly inhibited by 150 °C treatment but *Festuca magalura* germination was not.

Two of the opportunistic-type annuals (the first nine in Table 3) germinated readily without treatment, although the germination of six of the other seven species doubled with either heat or charred wood treatment. A similar pattern was observed for two annual

TABLE 2. Percentage germination of suffrutescent species from Californian chaparral after treatment with heat in combination with aqueous leachate from living *Adenostoma fasciculatum* foliage or powdered charred stems, or both (L + C).  $n = 8$  dishes of 50 seeds each.

Temperature (°C) Time (min)	Control	Heat treatment			P	LSD
		80 120	120 5	150 5		
<i>Eriophyllum confertiflorum</i>						
Control	4	6	4	1	*	3
Leachate	8	6	6	1	N.S.	
Charred wood	52	58	66	2	**	12
L + C	58	63	65	3	**	11
P	**	**	**	N.S.		
LSD	12	9	10			
<i>Helianthemum scoparium</i>						
Control	23	15	43	3	**	10
Leachate	29	17	50	11	**	14
Charred wood	23	16	37	4	**	10
L + C	25	17	40	9	**	12
P	N.S.	N.S.	N.S.	N.S.		

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

N.S.,  $P > 0.05$ .

TABLE 3. Percentage germination of annual species from Californian chaparral after treatment with heat in combination with aqueous leachate from living *Adenostoma fasciculatum* foliage or powdered charred stems or both (L+C). Species are listed in order from the most opportunistic to the most fire dependent.  $n = 8$  dishes of 50 seeds each except where otherwise stated.

Temperature (°C) Time (min)	Control	Heat treatment		P	LSD	
		80 120	120 150 5 5			
<i>Avena barbata</i> (n = 8 dishes of 30 seeds)						
Control	91	69	78	35	**	26
Leachate	80	71	66	20	**	20
Charred wood	96	76	96	26	**	14
L + C	87	76	78	17	**	14
P	N.S.	N.S.	**	N.S.		
LSD			19			
<i>Festuca megalura</i> (n = 8 dishes of 30 seeds)						
Control	85	66	89	96	**	12
Leachate	93	78	89	91	*	11
Charred wood	97	70	96	73	**	20
L + C	95	84	100	88	N.S.	
P	*	N.S.	**	N.S.		
LSD	8		11			
<i>Brassica nigra</i>						
Control	28	69	56	54	**	13
Leachate	60	80	89	74	**	10
Charred wood	4	26	17	11	**	17
L + C	28	65	59	39	**	21
P	**	**	**	**		
LSD	19	19	18	32		
<i>Descurainia pinnata</i>						
Control	12	10	9	3	**	6
Leachate	31	32	35	31	N.S.	
Charred wood	12	7	8	9	N.S.	
L + C	9	10	13	7	N.S.	
P	**	**	**	**		
LSD	14	27	28	17		
<i>Camissonia hirtella</i>						
Control	30	49	66	69	**	10
Leachate	52	59	59	80	**	19
Charred wood	26	33	22	20	N.S.	
L + C	45	51	30	58	*	18
P	**	*	**	**		
LSD	20	18	20	18		
<i>Cryptantha muricata</i>						
Control	24	20	37	7	**	15
Leachate	52	65	35	19	**	22
Charred wood	67	85	64	10	**	18
L + C	79	73	63	7	**	18
P	**	**	**	N.S.		
LSD	21	21	17			
<i>Lotus salsuginosus</i>						
Control	24	30	40	21	**	13
Leachate	21	32	31	12	**	9
Charred wood	20	34	30	12	**	9
L + C	26	30	37	16	**	9
P	*	N.S.	N.S.	N.S.		
LSD	5					

TABLE 3.—(contd.)

Temperature (°C) Time (min)	Control	Heat treatment			P	LSD
		80 120	120 5	150 5		
<i>Chaenactis artemisiaefolia</i>						
Control	39	39	39	8	**	12
Leachate	49	30	46	1	**	10
Charred wood	53	53	49	4	**	16
L + C	57	56	48	5	**	17
P	**	**	N.S.	*		
LSD	13	15		5		
<i>Apiastrum angustifolium</i>						
Control	7	25	14	0	**	9
Leachate	12	21	23	0	**	9
Charred wood	6	17	7	0	**	6
L + C	8	26	12	0	**	10
P	*	*	*	N.S.		
LSD	4	7	9			
<i>Phacelia cicutaria</i>						
Control	5	11	6	0	**	6
Leachate	13	20	13	1	**	9
Charred wood	32	45	57	0	**	16
L + C	38	51	33	0	**	13
P	**	**	**	N.S.		
LSD	15	10	15			
<i>Phacelia grandiflora</i>						
Control	4	1	2	3	N.S.	
Leachate	7	7	12	3	**	7
Charred wood	8	6	10	1	**	7
L + C	11	21	21	7	**	7
P	*	**	**	**		
LSD	2	8	7	5		
<i>Phacelia fremontii</i>						
Control	4	4	5	4	N.S.	
Leachate	4	3	4	3	N.S.	
Charred wood	11	6	8	7	N.S.	
L + C	4	7	9	7	N.S.	
P	**	*	N.S.	N.S.		
LSD	6	3				

\*  $P < 0.05$ .\*\*  $P < 0.01$ .N.S.,  $P > 0.05$ .

species not shown in Table 3; *Calyptidium monandrum* doubled its germination with 80 °C treatment and *Salvia columbariae* doubled its germination in response to charred wood plus leachate. Two other species not shown in Table 3, *Claytonia perfoliata* and *Nicotiana attenuata*, had very low germination and no treatment had a significant effect. Of the first seven species in Table 3 only the two grasses and *Lotus salsuginosus* did not show a highly significant interaction between heat and media treatments with the two-way analysis of variance. *Brassica nigra* (non-native), *Camissonia hirtella*, *Cryptantha muricata* and *Descurainia pinnata* showed a highly significant enhancement of germination with the application of leachate.

Fire annuals (the last three species in Table 3) showed a significant enhancement of germination with charred wood. Significant interactions with two-way analysis of variance were evident with two *Phacelia* species. The combination of heat plus charred wood



treatments produced a synergistic enhancement for *P. cicutaria*; it increased germination ten times over the control. The combination of leachate and charred wood enhanced germination of *P. grandiflora* although it is unclear what this unnatural combination means. Two of the *Phacelia* species shown in Table 3 as well as five other fire annuals (not shown) did not have very high germination. *Antirrhinum coulterianum*, *Phacelia brachyloba* and *P. viscida* had less than 5% germination for most treatments; leachate was the only treatment that tended to enhance their germination. *Gilia splendens* had less than 1% germination under control conditions but 28% with a combination of leachate plus charred wood. *Emmenanthe penduliflora* had less than 5% germination and showed no response to charred wood as reported in the literature cited previously. However, this same seed stock was tested 2 years later under the same conditions and 72% germinated in response to charred wood compared to 4% for controls. This apparent ageing requirement is not common to all *E. penduliflora* populations as other populations have germinated (when treated with charred wood) immediately after collection (J. Keeley unpublished). Subsequent experiments with *E. penduliflora* reported in the next section utilized seeds obtained from C. Jones (the seed stock utilized by Jones & Schlesinger (1980)).

The rate of germination varied widely among species (Fig. 1). For many species, half to three-quarters of the total germination occurred during the 3-week cold treatment, whereas other species did not germinate until moved to room temperature and, in some species, the majority of seeds did not germinate until exposed to a second or third cold treatment. It is clear from Fig. 1 that the rate of germination was unrelated to life history. In some instances the rate of germination varied with treatment. For example, *Chaenactis artemisiaefolia* had two germination peaks: one during the first cold treatment, and one after the second cold treatment; 80% of the first peak was due to the charred wood treatments and most of the second peak was due to non-charred wood treatments. Other species with multiple germination peaks did not show such a dichotomy with respect to treatment.

#### Additional experiments with charred wood

It is apparent that the degree of charring is not critical to the charred wood response (Table 4). *Adenostoma* stems charred only on the outside (and ground to a powder) were as effective as thoroughly charred stems in stimulating germination. Also, the amount of powdered charred wood required to stimulate germination does not appear to be critical. The percentage germination of *Eriophyllum confertiflorum* was not significantly changed when the amount of charred wood was reduced 100 fold (data not shown).

The charred wood response is obviously not due to an inorganic 'fertilizer' effect as Hoagland's solution did not enhance germination (Table 5).

TABLE 4. Percentage germination of species from Californian chaparral with powdered charred wood from *Adenostoma fasciculatum* stems charred only on the surface or completely charred (but not ashed).  $n = 8$  dishes of 50 seeds each.

	Control	Partially charred wood	Completely charred wood	<i>P</i>	LSD
<i>Antirrhinum coulterianum</i>	0	7	12	**	6
<i>Chaenactis artemisiaefolia</i>	27	87	84	**	9
<i>Emmenanthe penduliflora</i>	0	17	20	**	11
<i>Eriophyllum confertiflorum</i>	11	56	61	**	17

\*\*  $P < 0.01$ .

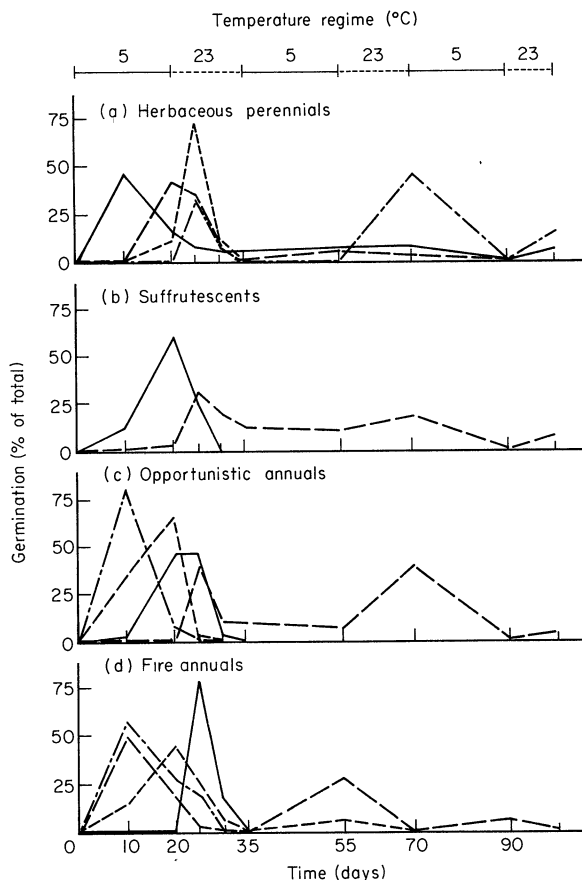


FIG. 1. Rate of germination for representative species from Californian chaparral. (a) Herbaceous perennials: (—), *Calystegia macrostegius*; (— · — ·), *Paeonia californica*; (— · — ·), *Sisyrinchium bellum*; (— · — ·), *Zigadenus fremontii*. (b) Suffrutescents: (—), *Eriophyllum confertiflorum*; (— · — ·), *Helianthemum scoparium*. (c) 'Opportunistic annuals': (—), *Apiastrum angustifolium*; (— · — ·), *Camissonia hirtella*; (— · — ·), *Festuca megalura*; (— · — ·), *Lotus salsuginosus*. (d) 'Fire annuals': (—), *Antirrhinum coulterianum*; (— · — ·), *Chaenactis artemisiaefolia*; (— · — ·), *Gilia splendens*; (— · — ·), *Phacelia cicutaria*. Data from all treatments (Tables 1–3) combined,  $n = 128$ .

TABLE 5. Percentage germination of species from Californian chaparral with half-strength or double-strength Hoagland's solution or powdered charred wood.  $n = 8$  dishes of 50 seeds each.

	Control	Hoagland's $\times 0.5$	Hoagland's $\times 2$	Charred wood	<i>P</i>	LSD
<i>Chaenactis artemisiaefolia</i>	27	29	26	84	**	10
<i>Eriophyllum confertiflorum</i>	11	9	3	61	**	13

\*\*  $P < 0.01$ .

#### Further heat treatments

Although three of the *Phacelia* species in Table 3 did show significant enhancement with charred wood, only *P. cicutaria* had very high germination. In an effort to obtain higher germination for *Phacelia* species, a greater range of temperature treatments was tried

## Germination of chaparral herbs

TABLE 6. Percentage germination of *Phacelia* species from Californian chaparral after treatment with heat and in combination with powdered charred wood. The last column is a compilation of results for four treatments.  $n = 5$  dishes of 100 seeds each.

Temperature (°C) Time (min, unless otherwise indicated)	Control	Heat treatment				P	LSD
		50 2 weeks	80 120	130, 170, 5 5	200, 220 2 2		
<i>P. brachyloba</i>							
Control	1	1	1	0	**	2	
Charred wood	0	0	1	0	**	1	
<i>P. cicutaria</i>							
Control	9 **	11 **	7	0	**	7	
Charred wood	14	51	10	0	**	16	
<i>P. fremontii</i>							
Control	1 **	4 **	2	0	**	5	
Charred wood	16	17	3	0	**	6	
<i>P. grandiflora</i>							
Control	4	3 **	4 **	0	**	4	
Charred wood	8	12	9	0	**	6	
<i>P. parryi</i>							
Control	0	0 **	0 **	0	**	4	
Charred wood	1	3	4	0	**	2	
<i>P. viscida</i>							
Control	4	5 **	2 **	0	**	2	
Charred wood	7	19	9	0	**	9	

\*\*  $P < 0.01$ .

For control *v.* charred wood treatments not marked with an asterisk,  $P > 0.05$ .

(Table 6). Although some species still had low germination, several points are clear. Approximately 130 °C for 5 min appears to be the lethal temperature for the six *Phacelia* species tested. Five of the species were significantly enhanced by charred wood and several showed significantly higher germination with a particular combination of heat and charred wood. Two weeks at 50 °C did not enhance germination; however, for three species, this heat treatment coupled with charred wood did increase germination over charred wood alone. This response to 50 °C was investigated further with a treatment more nearly simulating summer soil conditions—50 °C 8 h per day (alternating with 25 °C for 16 h) for 2 months. The same species which showed significantly higher germination with charred wood plus 50 °C for 2 weeks (over charred wood alone) responded similarly with this 2-month temperature treatment.

#### Additional 'allelopathy' experiments

In Tables 1–3 no species was significantly inhibited by leachate from living *Adenostoma* foliage. Indeed, for some species, germination was enhanced.

In a subsequent experiment twenty species were retested for the effect of leachate as well as concentrated leachate (methods and sample sizes as in Tables 1–3). Since it was unknown what concentration may occur in the soil, a 4× concentration, as utilized by McPherson & Muller (1969), was chosen. Only three species were significantly ( $P < 0.01$ )

inhibited by concentrated leachate: in *Apiastrum angustifolium* germination was reduced from 16% to 3%; in *Cryptantha muricata* from 27% to 5%; and in *Helianthemum scoparium* from 16% to 10%. The latter two species were also inhibited with unconcentrated leachate which contrasts with the earlier experiment (Table 3) where these species were stimulated by unconcentrated leachate. The only obvious difference between these experiments was the season the leachate was prepared (and thus possibly the strength); leachate used in Tables 1–3 was prepared in mid-summer and that used in this experiment was prepared in mid-autumn prior to any rainfall.

Significantly higher germination with leachate was observed for eight of the twenty species: *Avena barbata*, *Brassica nigra*, *Calyptridium monandrum*, *Camissonia hirtella*, *Descuriania pinnata*, *Eriophyllum confertiflorum*, *Lotus salsuginosus* and *Salvia columbariae*. To test whether this enhancement was due to an inorganic ‘fertilizer’ effect, *Descuriania pinnata* was germinated with 0.5× and 2× Hoagland’s solution in place of deionized water (using the techniques as before). Both of these treatments produced 2.5 times more germination than the control.

## DISCUSSION

The results of this study support the hypothesis that the herb and suffrutescent species in chaparral include a diversity of life histories that represent a diversity of seed germination behaviours. We have divided this flora into four groups representing broadly different demographic patterns (Fig. 2) based on information gleaned from the literature and personal observations.

### *Herbaceous perennials*

Herbaceous perennials include many bulb-forming monocotyledons as well as dicotyledons. They are present under the mature canopy although, in certain years, they may remain dormant. Except for vines, which reach the canopy, flowering is uncommon

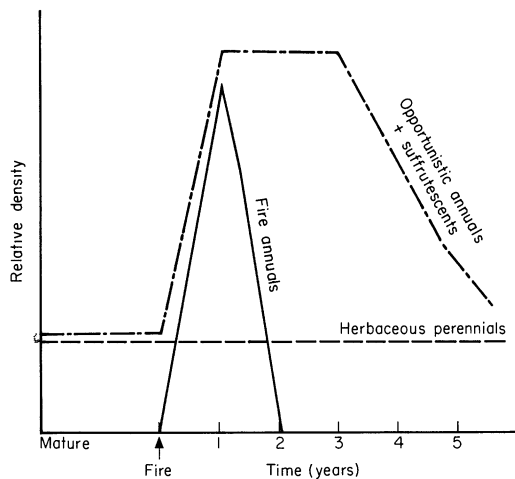


FIG. 2. Schematic outline of population changes before and after fire for Californian chaparral herbs and suffrutescents of different life histories.

and, in *Brodiaea ixoides* Wats., has been shown to be due to low irradiance under the canopy of mature chaparral (Stone 1951). In the first year after a fire all of these herbaceous perennials are present as resprouts from underground parts that survived the fire and seedlings are rare. These species flower vigorously in the first year but the timing of their seedling recruitment is unknown.

Other than a cold stratification requirement these species do not require further treatment for germination. Stratification cues germination to winter or spring conditions and this requirement may vary (both between and within species) with latitude and altitude. For example, in northern California herbaceous perennials required 2 months at 5 °C (Sweeney 1956) unlike the southern California species in the present study.

The absence of seedling establishment in the first post-fire year is related to two factors. First, since their seeds germinate readily, a dormant seed pool is not likely to accumulate between fires. Secondly, their seeds are more sensitive to higher temperatures than those of other herbs and thus are less likely to survive the fire. Seedling recruitment must occur as the shrub canopy becomes established or under the canopy itself and, therefore, it is not surprising that their germination is not sensitive to leachate from living *Adenostoma* foliage. Seedling establishment under the shrub canopy (and thus under lower irradiance) may have been the selective force for seeds which are many times larger than seeds of annual species (e.g. Salisbury 1942).

#### *Suffrutescents*

Perennials such as *Eriophyllum confertiflorum*, *Helianthemum scoparium* and *Lotus scoparius* occasionally occur in gaps in mature chaparral but never under the canopy. In the first year after a fire they are abundant as seedlings (not resprouts) and flowering usually does not begin until the second year. Their germination is markedly stimulated by heat, charred wood, or both.

As the shrub canopy returns, these species are largely eliminated. However, they can establish in gaps in the canopy and this can be accounted for by the portion of seeds which germinate without treatment. We hypothesize that this portion of the seed pool should be sensitive to 'allelopathic' leachate from the canopy which would cue germination to gaps. However, the data are equivocal. Unconcentrated leachate is not inhibitory to *Eriophyllum confertiflorum* (Table 2), *Helianthemum scoparium* (McPherson & Muller 1969), or *Lotus scoparius* (Christensen & Muller 1975a). *Helianthemum scoparium* is inhibited to some degree by concentrated *Adenostoma* leachate (McPherson & Muller 1969; this study) but it is questionable whether or not it ever experiences such conditions in the field.

#### *Annuals*

Annual species are the largest component of the post-fire flora and represent a diversity of life histories. They are considered here as two extremes. Opportunistic-annual species reach their maximum population density after a fire and, as the canopy returns, their establishment is gradually reduced to the gaps in the canopy. Examples include *Apiastrum angustifolium*, *Brassica* spp., *Camissonia* spp., *Cryptantha* spp., *Festuca* spp. and *Salvia columbariae*. Fire annuals, on the other hand, are closely associated with fire and often occur only on recently burned sites. Many of these have been reported to dominate the first year after a fire but disappear in the second year. Examples include *Antirrhinum* spp., *Emmenanthe penduliflora*, *Gilia* spp. and *Phacelia* spp. (particularly *P. brachyloba*).

Many opportunistic annuals (like certain suffrutescent species) have polymorphic seeds.

A portion are non-refractory and germinate readily without treatment and this fraction, as well as those stimulated by high soil temperature, colonize gaps in the chaparral canopy. Another portion requires some cue such as heat or charred wood. This polymorphism may be genetically or somatically controlled (Harper 1977) and need not require 'group-selection' to maintain it (Westoby 1981). We would expect the non-refractory portion of this polymorphic seed pool to be inhibited by allelopathic compounds as a means of evading unfavourable conditions under the shrub canopy. As with the suffrutescent species the data are equivocal. McPherson & Muller (1969) could not show inhibition of germination of annuals unless the *Adenostoma* leachate was concentrated tenfold. Christensen & Muller (1975a) did find a highly significant inhibition of germination of three annual species with unconcentrated *Adenostoma* leachate or with throughfall collected under *Adenostoma*. In the present study only two of the twenty-two annual species were inhibited by leachate. A major difference between these studies was the germination medium; Christensen & Muller (1975a) used glass wool saturated with leachate whereas we used potting soil—and Kaminsky (1981) has shown that soil particles absorb allelopathic substances more than seeds. However, under the conditions we used, *Apiastrum angustifolium* and *Cryptantha muricata* were strongly inhibited by 4 $\times$ -concentrated leachate. The significance of this remains to be determined since Kaminsky (1981) found that the suspected inhibitors in *Adenostoma* leachate do not occur in chaparral soils at concentrations equivalent to 4 $\times$  leachate. Even more difficult to reconcile with the theory of allelopathy is the observation that nine species in this study showed enhanced germination in response to *Adenostoma* leachate. A likely candidate for the stimulatory substance is NO<sub>3</sub><sup>-</sup> (Koller 1972) which, as a result of dry fallout (Schlesinger & Hassey 1980), is abundant in leachate (McPherson, Chou & Muller 1971; Christensen 1973).

Since opportunistic annuals colonize openings within the chaparral mosaic, it is to be expected that many of these species would possess diaspores with characteristics enhancing dispersal; e.g. *Cryptantha* spp. and *Festuca megalura* have bur-like diaspores dispersed by animals.

Fire annuals, on the other hand, have poor dispersal. The seeds of these species lie dormant in the soil until fire comes to them. They show very low germination in the absence of cues related to fire. Some respond to heat but most respond to charred wood, either alone or in combination with heat; in this study *Phacelia cicutaria* (Table 3) shows this response most clearly. These species appear to be as sensitive to high temperatures as are less fire-dependent species. Some of the other *Phacelia* species in this study (Tables 3 and 6) illustrate a pattern typically reported for fire annuals—low germination under any treatment. Possible explanations for this include: (i) a requirement for some, as yet unknown, condition; (ii) low seed viability; or (iii), a requirement for a very extended 'ageing' period. This ageing idea needs further investigation since one can imagine a strong selective basis for it in species that appear only in the first post-fire year and then disappear for many years.

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