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Factors Affecting Germination of Chaparral Seeds

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Abstract.—Factors affecting germination of chaparral seeds by Jon E. Keeley. *Bull. Southern California Acad. Sci.*, 83(3):113–120, 1984. Seedling establishment is uncommon under mature chaparral but abundant after fire. Germination from soils collected beneath chaparral and in an adjacent burned site were compared after various treatments. Application of an aqueous leachate from the dominant overstory shrub (*Adenostoma fasciculatum*) failed to produce any inhibition of seedling emergence from the mature chaparral soil but rather increased germination. Soil heating and powdered charred wood (charate) stimulated germination of dicots but not grasses. Tests of specific species showed *Phacelia cicutaria* and *Salvia columbariae* markedly stimulated by charate whereas *Cryptantha muricata* and *Lotus salsuginosus* were not. Grasses were abundant in the burn soil and germinated readily without treatment; their residence time in the soil, however, may be limited as they were uncommon in the mature chaparral soil. Light was a significant factor in germination of both monocots and dicots. Continuous darkness significantly reduced germination over a 12 hour photoperiod at ~230 $\mu E\ m^{-2}\ s^{-1}$ or ~20 $\mu E\ m^{-2}\ s^{-1}$ or periodic (several hours/week) light of variable intensity.

Chaparral is an evergreen scrub vegetation which dominates much of the undeveloped landscape in southern California. Widespread wildfires are relatively frequent in chaparral due to the dry fuels (resulting from the mediterranean-climate summer drought) and the dense contiguous nature of the vegetation (resulting from the winter and spring rains which are coincident with mild temperatures). Today, man supplies the ignition source for the vast majority of wildfires, though lightning-ignited fires are not uncommon (Keeley 1982). Wildfires are thought to have played a major role in the evolution of chaparral, as the shrubs exhibit a number of adaptations which have been interpreted as evolutionary responses to fire; e.g., seedling recruitment largely restricted to the first postfire year and sprouting from specialized basal burls.

Herbaceous species are generally uncommon in mature chaparral, however, they dominate the post-fire environment for one to several years (Hanes 1977; Keeley et al. 1981). The presence of many of these herb species on recently burned sites is due to seeds dormant under the chaparral and dating back to the previous fire.

Two classes of theories have been proposed to account for relatively depauperate shrub and herb seedling establishment under mature chaparral, but abundant recruitment after fire. Seeds of these species are either 1) inhibited from germinating by chemical components of the environment (e.g., allelopathic substances produced by the overstory shrubs or microbial by-products produced in the litter), or 2) the seeds are refractory and require a stimulus from fire (cues that may stimulate germination include heat, which may crack hard seed coats or melt waxy coverings, and chemical stimulants released from charred wood).

The evidence for chemical inhibition of seed germination under the shrub canopy is not compelling. Sweeney (1956) found that a leachate made from chaparral litter had no inhibitory effect on the germination of various native seeds. McPherson and Muller (1969) could only demonstrate inhibition on four native seeds and only after scarifying them and applying a highly concentrated (10×) leachate from the *Adenostoma fasciculatum* shrub canopy (names according to Munz 1974). Christensen and Muller (1975) found that a leachate from *Adenostoma* did inhibit the germination of two native and two non-native chaparral herbs but had no effect on six of the more typical "pyrophyte endemics." Kaminský (1981) suggested microbial toxins produced in chaparral soils could inhibit germination of native herbs and demonstrated such an effect on lettuce seeds. Also, he found that soils from a second year burn showed no inhibitory effect. Recently Pack (1985), using native herb seeds and 6 mature and 6 burn soils, was not able to duplicate Kaminsky's results.

Attempts to demonstrate that fire-related cues play a role in stimulating germination have likewise produced conflicting results. Sweeney (1956) found that excelsior burned on top of soil did stimulate germination of native herb seeds but attempts to attribute this to either a chemical product from burned wood or heat were unsuccessful. Likewise McPherson and Muller (1969) and Christensen and Muller (1975) were unable to demonstrate heat stimulated germination of herbs although the latter study as well as others (e.g., Stone and Juhren 1951; Hadley 1961; Quick and Quick 1961) have shown heat stimulated germination of shrub seeds. Although Sweeney (1956) could not demonstrate any effect of ashed wood products, Wicklow (1977), and later Jones and Schlesinger (1980), demonstrated that partially charred wood stimulated germination of *Emmenanthe penduliflora*.

It is clear that no single study is likely to completely clarify the situation. The purpose of this study is to extend these previous investigations to examine how "allelopathic leachate," charred wood and heat affect germination of seeds from natural chaparral soils. In addition, the role of light, which has previously been ignored, was investigated.

Methods

The top 2–4 cm of soil was collected (in early fall) either from beneath mature chaparral (~75 yrs as determined by ring counts) or an adjacent burn (after the end of the second year of regrowth). These sites were in the San Gabriel Mtns. at 900 m, 1 km north of the Monte Cristo Ranger Station. Soils were sieved with a 3 mm screen and the few seeds that did not pass through were added back. The soil was spread to ~3 mm depth on a tray and heated in a forced convection oven at 80°C for 2 hrs or 120°C for 5 min. Petri dishes (100 × 15 mm) were filled with 50 cc of this soil and leachate or charate (see below) treatments were applied.

Leachate from *Adenostoma* foliage was prepared as described by McPherson and Muller (1969). Branches from the upper canopy were cut and placed in a 1 m^2 funnel and 3 liters of deionized water were applied in a fine mist over a period of 2 hrs. The concentrate was prepared by warming and stirring leachate on a hot plate, maintained below 50°C as suggested by McPherson and Muller (1969).

Charate was prepared from *Adenostoma* wood by charring stem segments with a torch and grinding in a Wiley mill to pass through a #20 mesh screen. Approximately 2.5 g of powdered charate were applied per dish.

For dishes receiving the leachate treatment, 25 ml of leachate were added. Charate treatments received 27 ml of deionized H_2O, and 25 ml dH_2O were added to all other dishes. Dishes were stacked on trays and covered with black plastic bags to reduce evaporation. The material was then incubated at 5°C for 1 wk, followed by 23°C for 1 wk; and this cycle was repeated two times for a total of 6 weeks. The seeds of four herb species were then added and incubated in the same manner.

In these experiments seeds were incubated in the dark but were exposed to several hours of light each week when germinated seeds were scored. An additional experiment, using some of the treatments described above, was done with seeds in continuous darkness for 6 wks (scoring was done under a green light) or under a 12 hr light regime. The latter dishes were covered with clear plastic bags and placed 150 mm beneath fluorescent lamps where they received ~230 $\mu E\ m^{-2}\ s^{-1}$.

The two soils, as well as a commercial potting soil (for comparison) were analyzed for major inorganic nutrients by an outside commercial soil testing lab.

Results

Fertility of the soils from mature and burned chaparral are compared with a commercial potting soil in Appendix I. Relative to the potting soil, both chaparral soils were markedly depauperate in several important elements. The major soil changes after fire included an increase in pH, Na^+, PO_4^- and CO_3^{-2} but a decrease in NO_3^-.

The buffering capacity of all soils was similar with respect to *Adenostoma* leachate. For example the pH of this leachate varied from 3.5 to 3.8, dependent on concentration. When added to either soil, leachate lowered the pH of the soil solution by 0.1 pH unit. Charate had a pH of 7.4 and when added to burn soil it did not change the pH of the soil solution, but when added to the mature soil the pH increased from 5.6 to 6.0. Since the organic matter was largely broken down in the burn soil it tended to absorb much less water and thus these soils tended to be wetter. Because of this difference it is possible that seeds were exposed to different osmotic pressures in the two soils. Circumstantial evidence suggests

Table 1. Germination from soil collected beneath mature *Adenostoma* chaparral and in an adjacent second year burn (n = 84).

		Seedlings/50 cc soil							
	Soil	Control	1× *Adenostoma* leachate	4× *Adenostoma* leachate	*Adenostoma* charate	80°C (2 hrs)	120°C (5 min)	*P*	LSD
Dicots	Mature Chaparral	0.67	1.16	0.90	1.57	1.12	1.11	**	0.40
	2nd yr Burn	4.76	4.70	4.48	3.55	4.68	3.18	**	0.92
Monocots[a]	Mature Chaparral	0.23	0.15	0.05	0.17	0.04	0.11	*	0.13
	2nd yr Burn	10.82	11.25	10.75	10.77	9.08	4.46	**	2.32

* $P < 0.05$, ** $P < 0.01$.

[a] All but one of the monocots were grasses.

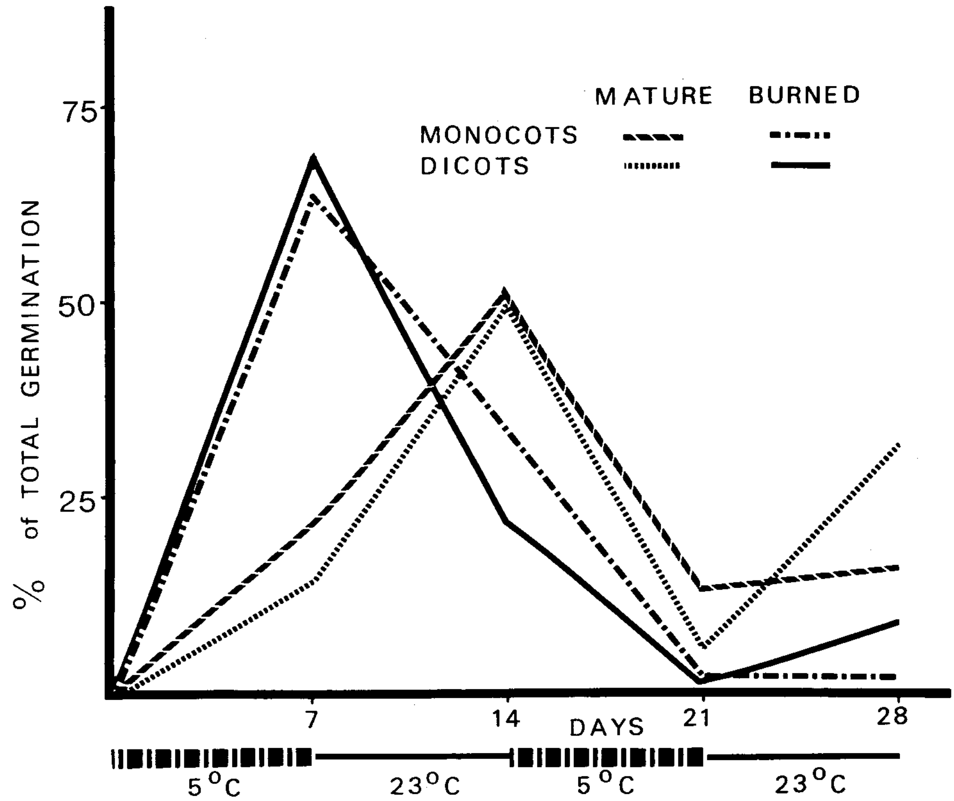

Fig. 1. Rate of germination of monocots and dicots from soils collected from mature chaparral and an adjacent two year burn.

this was not a complication. As will be seen below, germination of *Cryptantha muricata* did not differ on the two soils yet a separate test showed it was sensitive to elevated osmotic pressure; germination was reduced from 77% (S.D. = 12, N = 3) in distilled water controls to 24% (S.D. = 7) in 0.2 M mannitol.

Dicot seedling emergence from mature soils was significantly increased by all treatments, including the supposedly "allelopathic" leachate treatments (Table 1). Charate produced significantly greater germination than any other treatment; sixteen dicot species emerged from these plates: 51% were herbs, largely *Descurainia pinnata, Camissonia hirtella, Gnaphalium californicum* and the remaining 49% were nearly all *Adenostoma fasciculatum.*

From the second year burn soil, dicot germination was much greater than from the mature chaparral soil and no treatment increased germination over controls. No shrub seedlings emerged from these soils though many of the herb species were the same as those from the mature soil. Addition of charate to this soil significantly reduced germination.

Monocot seeds were rare in mature chaparral soil but abundant in burned chaparral soil. These seeds were essentially all from grasses, largely *Bromus tectorum* and *Festuca megalura.* Heat reduced germination of these grasses in both soils.

Table 2. Percentage germination of species planted into soils after the end of the experiment in Table 1. C.m. and P.c. were sown together and L.s. and S.c. were sown together thus n = 42 dishes for each species. Due to the large sample size, seeds were added with a small measuring spoon; mean number of seeds per spoon, ±S.E. of the mean for n = 14, was: 128 ± 6 (C.m.), 92 ± 6 (P.c.), 108 ± 5 (L.s.) and 140 ± 9 (S.c.). Note, for the heat treatment, the soils were heat treated but not the seeds of the four species added.

	Soil	Control	4× Leachate	Charate	120°C (5 min)	*P*	LSD
Cryptantha muricata	Mature Chaparral	62	72	78	74	NS	
	2nd yr Burn	64	58	72	63	NS	
Phacelia cicutaria	Mature Chaparral	17	17	26	19	**	6
	2nd yr Burn	20	20	14	18	*	5
Lotus salsuginosus	Mature Chaparral	21	19	21	19	NS	
		**	**	**	**		
	2nd yr Burn	12	12	14	12	NS	
Salvia columbariae	Mature Chaparral	9	10	52	9	**	7
		**	**	**	**		
	2nd yr Burn	25	22	27	23	NS	

NS $P > 0.05$, * $P < 0.05$, ** $P < 0.01$; $P > 0.05$ for mature vs burn comparisons not starred.

The rate of germination from these soils varied markedly (Fig. 1). For both monocots and dicots germination was much more rapid from the burn soil than from the mature chaparral soil.

After the indigenous seed pool had germinated, these same soil samples were sown with four native herb species (Table 2). There were marked differences in species responses. *Cryptantha muricata* germinated well under control conditions and was not affected by any of the soil treatments. *Phacelia cicutaria* germination was significantly increased with charate on mature soil and decreased with charate on burn soil. Germination of *Lotus salsuginosus* was significantly lower on burn soil regardless of treatment whereas *Salvia columbariae* germination was higher on burn soil unless charate was added to control soil, where germination was high.

The observation that charate enhanced germination in mature chaparral soil but inhibited germination (of some species) in burn soil (Tables 1 and 2) was surprising. In the case of *P. cicutaria* and *S. columbariae* (Table 2) the soils had

Table 3. Seedling emergence from soils incubated in the light (12 hr photoperiod at ~230 $\mu E\ m^{-2}\ s^{-1}$) and total darkness, with and without charate (n = 30).

		Seedlings/50 cc soil					
		Control			Charate		
	Soil	Light		Dark	Light		Dark
Dicots	Mature Chaparral	1.40	**	0.37	3.80	**	1.70
	2nd yr Burn	6.99	**	3.33	4.87	**	2.80
Monocots	Mature Chaparral	0.13		0.17	0.03		0.03
	2nd yr Burn	10.30	**	7.30	10.67	*	8.53

* $P < 0.05$, ** $P < 0.01$; $P > 0.05$ for light vs dark comparisons not starred.

Table 4. Percentage germination of species sown into soils after the end of the experiment in Table 3 (n = 15).

	Soil	Control Light		Control Dark	Charate Light		Charate Dark
Cryptantha muricata	Mature Chaparral	73	**	2	82	**	12
	2nd yr Burn	62	**	10	56	**	9
Phacelia cicutaria	Mature Chaparral	10	**	7	38	**	8
	2nd yr Burn	6		9	3		11
Lotus salsuginosus	Mature Chaparral	18		17	24		21
	2nd yr Burn	14		14	13		15
Salvia columbariae	Mature Chaparral	44	**	1	74	**	33
	2nd yr Burn	84	**	48	59	**	49

* $P < 0.05$, ** $P < 0.01$; $P > 0.05$ for light vs dark comparisons not starred.

been wetted and incubated for a month (to germinate the indigenous seed pool) before sowing. I hypothesized that this long pre-incubation of the soil (and in particular with the addition of charate) allowed growing microbial populations to inhibit germination. I predicted that germination would be much greater if seeds were sown into the burn soil without prior wet incubation of the soil. This was tested with *P. cicutaria* and it was found that burn soils treated as before (with prior incubation) produced 8% (S.D. = 8, N = 15) germination whereas if *P. cicutaria* were sown into burn soil without prior incubation of that soil, germination was 39% (S.D. = 5, N = 15).

Effect of Light

In previous experiments light was not considered; seeds were incubated in the dark although they were exposed to the light when scored. In this experiment germination under a twelve hour photoperiod was compared with germination in total darkness (Table 3). For both mature and burn soils, dicot and monocot seed germination was significantly inhibited by total darkness. The four species sown into these soils illustrate different responses to total darkness (Table 4); *L. salsuginosus* was insensitive to darkness; *C. muricata* and *S. columbariae* were markedly inhibited by total darkness with or without charate; *P. cicutaria* was inhibited by darkness only in the presence of charate.

Apparently the previous experimental conditions of dark incubation followed by scoring in the light approximated the "light stimulating" conditions of the 12

Table 5. Effect of light intensity on germination of seeds from mature chaparral soil and *Cryptantha muricata* planted in the same soil (n = 12). For C.m. seed number is as in Table 2.

	$\mu E\ m^{-2}\ s^{-1}$ ~230	~20	~0	*P*	LSD
Dicots (NO/50 cc)	1.92	1.92	0.7	**	1.39
Monocots (NO/50 cc)	0.00	0.17	0.17	NS	
Cryptantha muricata (%)	75	57	10	**	16

NS $P > 0.05$, ** $P < 0.01$.

hr photoperiod incubation. This is suggested by a comparison of the charate response in the previous experiments (Tables 1 and 2) with the charate effect under the light treatment (Tables 3 and 4). Although the absolute level of germination was higher under 12 hr photoperiod (Tables 3 and 4) than under periodic light exposure every week (Tables 1 and 2), the relative effect of charate was the same under both conditions. Table 5 shows that the light intensity may be quite low ($\sim$20 μE m^{-2} s^{-1}) and still produce a stimulatory effect on germination.

Discussion and Conclusions

This study does not support the theory that native seeds are inhibited from germinating under the mature chaparral canopy by chemical inhibitors. Indeed so-called "allelopathic" leachate from *Adenostoma* foliage stimulated germination of seeds from the mature chaparral soil. This stimulatory effect has in fact been observed for a variety of species (Keeley et al. 1985) where it has been attributed to the known stimulatory effect of NO_3^- which is abundant in the leachate. Circumstantial evidence of microbial inhibition was observed in the present study but only on burn soil.

Both heat and charred wood produce a highly stimulatory effect on germination of seeds from mature chaparral soil. However, charate stimulated the germination of *Phacelia cicutaria* and *Salvia columbariae* but not *Cryptantha muricata* or *Lotus salsuginosus.*

In comparing the mature chaparral soil and the second year burn soil it is clear that 1) the seed pools are quite different, and 2) the soils affect germination of the same species quite differently. Annual grass seeds were uncommon in the mature chaparral soil whereas they were abundant in the second year burn soil. This suggests that these species invade recently burned areas but their residence time in the soil is low in the absence of fire. Although ignored in previous studies it appears that light plays a major role in the germination of certain chaparral seeds. Certainly the evidence presented here should be sufficient warning that future studies need to examine the effect of light on chaparral seed germination.

Highest germination from mature chaparral soil was with charate under a 12 hr photoperiod. Estimates based on the range of depths soil was sampled suggest this treatment produced ca. 1500 seedlings/m^2 $\pm$ 500. Such numbers are clearly large enough to produce seedling densities typical of burned chaparral stands.

In conclusion it appears from these data that the bulk of the dormant seed pool in mature chaparral requires the stimulating effect of heat, charred wood, and light for germination. Seeds in soil from a 2nd year burned site (still largely devoid of shrub cover) germinated readily without heat or charred wood although a large portion of this seed pool required light for germination.

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Appendix I. Soil characteristics for media used in this study compared to commercial (Gro-Lite) potting soil. The mature soil pH in parenthesis is for the soil alone, i.e., without the fine litter (mostly *Adenostoma* leaves).

	Potting soil	Mature chaparral soil	2nd yr burn soil
pH	6.7	5.6 (6.6)	7.3
Na (ppm)	230	75	130
Mg (ppm)	250	21	20
Ca (ppm)	300	200	210
Fe (ppm)	0.6	1.4	1.6
Zn (ppm)	0.2	0.4	0.4
PO_4 (mg/l)	7.5	0.04	0.60
SO_4 (mg/l)	96.0	0.00	0.00
NO_3 (mg/l)	7.9	1.5	0.7
CO_3 (mg/l)	0.1	0.1	0.6