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ROLE OF FIRE IN SEED GERMINATION OF WOODY TAXA IN CALIFORNIA CHAPARRAL¹

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Abstract. Germination behavior of 45 tree, shrub, subshrub, and liana taxa from fire-prone coastal sage scrub and chaparral was investigated. Seeds were sown on filter paper or potting soil, in the light or dark, with or without powdered charred wood (charate), and after heating treatments of 1 h at 70°, 5 min at 100°, 5 min at 120°C, or no heat. Germination medium had a significant effect on >70% of the species, although the pattern of response to other treatments remained the same on both media. Germination of over half of the species was inhibited in the dark, but two species were light inhibited. Charate significantly enhanced the germination of approximately a quarter of the species. A similar proportion of species exhibited heat-stimulated germination. In only a few species did both heat and charate play a role in stimulating germination. Nearly a third of the species had seeds that germinated readily upon wetting, and germination was not further stimulated by any fire-related cue. These different germination syndromes are correlated with different life history syndromes. Most coastal sage subshrubs germinate readily in the absence of fire-related stimuli and thus are capable of colonizing other forms of disturbance. For many of these species, germination was inhibited in the dark. This may result in a portion of the seed pool remaining dormant until fire since, in the case of several species, dark inhibition is overcome by charate. Chaparral shrubs and trees that germinate readily upon wetting seldom establish seedlings after fire. Their persistence in these fire-prone environments is due to resprouting after fire. Seedling establishment and population expansion for such species is dependent upon extended fire-free periods. In contrast, woody species that fail to germinate without some fire-related cue have seedling establishment and potential population expansion restricted to postfire conditions. The present mixture in species composition may be maintained by variable burning regimes.

Key words: chaparral; charred wood; coastal sage; germination; heat; life history; light.

INTRODUCTION

The semi-arid mountains of southern and central California are dominated by two major scrub vegetation types of quite different physiognomy. Coastal sage scrub, consisting of subligneous shrubs 1–1.5 m tall, many of which have drought-deciduous foliage, covers the more xeric slopes at lower elevations (Mooney 1977). Chaparral is composed of shrubs 2–4 m tall with evergreen sclerophylls; it dominates much of the landscape between coastal sage vegetation at lower elevations and woodlands at higher elevations (Hanes 1977).

Wildfires are an integral part of the ecology of these shrublands. Typically fires in chaparral and coastal sage kill all aboveground biomass, although much belowground matter (e.g., roots, lignotubers, seeds) survives. In the first growing season after fire, all of the pre-fire dominants are present in the form of resprouts or seedlings. Seedling recruitment after fire arises from a previously dormant seed bank in the soil, and fire seems to play a crucial role in stimulating germination. Resprouts arise from the root crown or from buds on specialized woody lignotubers.

Life history studies of coastal sage and chaparral

species reveal there are marked differences in mode of re-establishment (Zedler 1981). Some species of *Ceanothus* (Rhamnaceae) and *Arctostaphylos* (Ericaceae) have no capacity for vegetative regeneration after fire, and thus are totally dependent upon the seed bank for re-establishment. Other species, such as *Adenostoma fasciculatum*, resprout from lignotubers and establish numerous seedlings. Finally, there are species that seldom establish seedlings after fire, and their continued presence is insured only by an ability to resprout vigorously.

Seed germination behavior of certain shrubs in chaparral has been shown to be dependent upon heat from fire for scarification, e.g., *Ceanothus* species, *Adenostoma fasciculatum*, and *Rhus ovata* (Quick and Quick 1935, Stone and Juhren 1951, 1953). Others, such as *Arctostaphylos* species, are notorious for difficulty in obtaining germination by any but highly artificial means such as soaking in sulfuric acid (Berg 1974). Recently it has been documented for *Emmenanthe penduliflora* (Hydrophyllaceae) (Wicklow 1977, Jones and Schlesinger 1980) and for other herbaceous species in recently burned chaparral (Keeley et al. 1985) that charred wood (but not ashed wood; Sweeney 1956) plays a crucial role in cueing germination to the postfire environment. The general importance of this factor for

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the woody flora has not been previously studied. Further, only for a few chaparral species has the effect of light on germination behavior been examined (Keeley 1984). The role of any of these factors in the germination of the vast majority of shrubs in coastal sage and chaparral has not been studied.

In light of the diversity of species in coastal sage scrub and chaparral and the diversity of modes of re-establishing after fire, I hypothesized that germination behavior would differ markedly between species. This study compares the effect of heat, powdered charred wood (charate), and light on germination of 45 shrub, subshrub, and liana taxa from coastal sage scrub and chaparral. Limited experimentation was done on nine of these species.

METHODS AND MATERIALS

Selection of species was based on availability of plants with mature seed crops (Appendix). Vouchers have been deposited at LOC (Occidental College). Nomenclature is according to Munz (1974), except for *Malosma (Rhus) laurina* Nutt. ex Abrams. Most species disperse seeds in late spring and summer (see Appendix) when soil moisture levels are low, and germination is delayed until the following winter or spring. It is possible that many of these species have an innate dormancy at the time of dispersal, but this phenomenon was not studied. In general, seeds were collected at the time of maturation in summer and fall of 1983 and maintained in paper bags prior to germination tests the following winter and spring. Collections were from San Diego, Orange, Riverside, Los Angeles, Ventura, and Mariposa counties, all below an elevation of 2000 m. Seeds were cleaned by removing fruit tissues that would normally be lost in dispersal. In many cases (see Appendix) the "seed" that was sown included fruit tissues, e.g., endocarp in drupes or the entire fruit, such as in achenes. For species in the Ericaceae, multiple seeds are embedded in a resinous endocarp and dispersed as a single diaspore; 30 such diaspores were sown and the number of seeds enclosed was estimated by subsampling other diaspores.

Previous studies have reported different germination responses on filter paper and soil (Wicklow 1977, Jones and Schlesinger 1980, Keeley and Nitzberg 1984). My experiments were designed to compare results on these two media, so all treatments described below were duplicated on both media. Seeds were sown in 60 × 15 mm Petri dishes, either fitted with two sheets of Number 42 Whatman filter paper or filled with 15 g (fresh mass) of commercial potting soil, sifted to pass a 2-mm screen (Gro-lite; see Keeley 1984 for chemical comparison of this soil with soil from a stand of chaparral).

Heat treatments of 70° for 1 h, 100° for 5 min, or 120°C for 5 min were applied to the seeds prior to sowing. A control group was not heated. These treatments were selected to cover a range of conditions potentially encountered by seeds in the soil on open

sites or during fire and within the range of temperatures shown in prior studies to be stimulatory to some species (Sweeney 1956, Christensen and Muller 1975, DeBano et al. 1979). One set ($n = 3$) of each of these heat treatments (including controls) was incubated in the presence of charate and another (control) group was not given charate.

Charate was made by charring (but not ashing) fresh stems (5–15 mm diameter) of the chaparral shrub *Adenostoma fasciculatum* and grinding in a Wiley Mill to pass a 1-mm screen. Each charate treatment received an application of 0.25 g (on filter paper) or 0.50 g (on soil) of this powdered charred wood. This level of charate has been shown to be stimulatory to *Emmenanthe penduliflora* and *Eriophyllum confertiflorum*, although levels two orders of magnitude lower are also stimulatory (Keeley and Pizzorho 1986). This entire experiment was duplicated in the light (12-h photoperiod, $350 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and in the dark.

Experiments were initiated by adding 1.5 mL of deionized water to filter paper dishes (2.0 mL with charate) or 8.0 mL to soil dishes (10.0 mL with charate). Seeds of some species require a period of low-temperature treatment (stratification) in order to overcome embryo dormancy. This phenomenon was not studied; rather, all dishes were stratified for 1 mo at 5° and then incubated in either the light or the dark for 3 wk at 23°. (Previous unpublished studies in this laboratory have shown that while cold stratification may not be required for germination, it is seldom detrimental.) This cycle of 1 mo stratification and 3 wk incubation was repeated once more before ending the experiment. Germination was scored every 2 wk in the cold and every week at 23°, and seedlings removed. Seeds in the dark were scored under indirect green light.

This experiment was run on 36 species. For 9 other species, only limited seed stocks were available, and thus the number of treatments had to be reduced for these species. These seeds were treated with either heat or charate, but not with heat plus charate together. The treatments, in both light and dark conditions, were: control, 70° for 1 h, 100° for 5 min, 120° for 5 min, and charate; all of these were run for two cycles of stratification and incubation.

RESULTS

For 36% of the 36 species tested in the main experiment, germination medium had no significant effect on germination (Table 1). The remaining species were roughly divided between species that germinated significantly better on soil and species that germinated better on paper. For some species this difference was quite marked; for example, germination of *Eriodictyon crassifolium* was nearly double on soil as compared with filter paper, whereas the opposite applied to *Romneya trichocalyx*. The most extreme example was *Clematis lasiantha*; germination completely failed on paper but was as high as 70% on soil. Although the absolute

TABLE 1. Percentage germination of 36 chaparral and coastal sage scrub species in light or dark and in response to heat treatments and the application of powdered charred wood (charate); $n = 3$ Petri dishes of 20 or 30 seeds (number indicated in parentheses following species name).†

	Percentage germination								Significance of F			
	Light				Dark				Medi- um	Light	Charate	Tem- per- ature
	Control	70°C 1 h	100°C 5 min	120°C 5 min	Control	70°C 1 h	100°C 5 min	120°C 5 min				
Anacardiaceae												
<i>Malosoma laurina</i> (30, paper)												
Control	10 ^a	9 ^{a#}	9 ^{a#}	6 ^a	4 ^{a#}	9 ^{b#}	6 ^{ab}	8 ^b	***	NS	**	**
Charate	3	8 ^{a#}	11 ^{a#}	11 ^a	2 ^a	8 ^{b#}	3 ^{a#}	12 ^b				
<i>Rhus integrifolia</i> (20, soil)												
Control	62 ^a	65 ^{a#}	53 ^{a#}	55 ^a	43 ^a	22 ^a	45 ^a	27 ^a	***	***	**	NS
Charate	47 ^a	57 ^{a#}	53 ^{a#}	82	88 ^a	73 ^a	72 ^a	52 ^a				
<i>Rhus trilobata</i> (20, soil)												
Control	38 ^a	45	37 ^a	72 [#]	17	5	3	13 [#]	NS	***	**	**
Charate	65 ^a	62 ^a	53 ^a	62 ^{a#}	28 ^a	25 ^a	12 ^b	12 ^{b#}				
<i>Toxicodendron diversifolia</i> (20, soil)												
Control	10 ^a	10 ^a	17 [#]	5 ^{a#}	3 ^a	5 ^{a#}	3 ^a	7 ^a	**	***	***	**
Charate	20 ^a	38	10 ^{a#}	12 ^{a#}	8 ^a	7 ^a	0 ^a	3 ^a				
Asteraceae												
<i>Artemisia californica</i> (30, soil)												
Control	73 ^{a#}	56 ^{a#}	47 ^a	56 ^{a#}	0 ^a	10 ^a	3 ^a	0 ^a	***	***	***	NS
Charate	78 ^{a#}	80 ^{a#}	81 ^a	87 ^{a#}	62 ^a	49 ^a	64 ^a	50 ^a				
<i>Haplopappus squarrosus</i> (30, paper)												
Control	34 ^{a#}	34 ^{a#}	3 ^{b#}	1 ^{b#}	17 ^{a#}	14 ^{a#}	4 ^b	0 ^{b#}	*	NS	NS	***
Charate	18 ^{a#}	28 ^{a#}	7 ^{b#}	0 ^{b#}	24 ^{a#}	16 ^{a#}	17 ^a	0 [#]				
<i>Viguiera laciniata</i> (30, paper)												
Control	79 ^{a#}	61 ^{ab#}	53 ^{b#}	94 ^{a#}	52 ^{a#}	52 ^{a#}	42 ^{a#}	74 ^{a#}	NS	NS	NS	NS
Charate	78 ^{a#}	73 ^{a#}	87 ^{a#}	70 ^{a#}	74 ^{a#}	56 ^{a#}	58 ^{a#}	61 ^{a#}				
Caprifoliaceae												
<i>Lonicera subspicata</i> (20, paper)												
Control	88 ^{a#}	80 ^{a#}	82 ^{a#}	68 [#]	83 ^{a#}	70 ^{ab#}	85 ^{a#}	63 ^{b#}	***	NS	NS	***
Charate	73 ^{a#}	75 ^{a#}	78 ^{a#}	53 [#]	90 ^{a#}	77 ^{ab#}	80 ^{a#}	62 ^{b#}				
Ericaceae												
<i>Arctostaphylos glandulosa</i> (30, paper)												
Control	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^{a#}	0 ^a	*	NS	***	NS
Charate	5 ^a	3 ^a	2 ^a	3 ^a	8 ^a	13 ^a	3 [#]	7 ^a				
<i>Arctostaphylos patula</i> (30, paper)												
Control	1 ^{a#}	3 ^{a#}	4 ^{ab#}	6 ^{b#}	6 ^a	12 ^{a#}	10 ^a	7 ^{a#}	***	***	**	NS
Charate	1 ^{a#}	3 ^{a#}	1 ^{a#}	4 ^{a#}	17 ^a	19 ^{a#}	18 ^a	10 [#]				
<i>Comarostaphylis diversifolia</i> (30, paper)												
Control	69 [#]	22 [#]	12 ^a	9 ^{a#}	42 [#]	17 ^{a#}	37 [#]	18 ^{a#}	*	***	**	***
Charate	63 [#]	23 [#]	46	8 [#]	36 [#]	17 ^{a#}	43 [#]	17 ^{a#}				
Fabaceae												
<i>Lotus scoparius</i> (30, paper)												
Control	43 ^{a#}	51 ^{ab}	43 ^{a#}	60 ^b	41 ^{a#}	40 ^{a#}	43 ^{a#}	59 [#]	***	**	*	**
Charate	40 ^{a#}	22 ^a	40 ^{a#}	36 ^a	50 ^{a#}	32 ^{b#}	37 ^{b#}	47 ^{a#}				
Fagaceae												
<i>Quercus dumosa</i> (20, soil)												
Control	77 [#]	0 [#]	57 ^{a#}	55 ^a	66 ^{a#}	0 [#]	60 ^a	47 [#]	*	NS	NS	***
Charate	68 [#]	0 [#]	53 [#]	27	70 [#]	0 [#]	40 ^a	50 ^{a#}				
Garryaceae												
<i>Garrya flavescens</i> (30, soil)												
Control	4 ^a	12 ^a	10 ^a	6 ^a	24 [#]	1 ^a	4 ^a	0 ^a	NS	**	***	**
Charate	65 ^a	34 ^b	54 ^a	19 ^b	17 ^{a#}	47 ^b	57 ^b	28 ^a				

TABLE 1. Continued.

	Percentage germination								Significance of <i>F</i>			
	Light				Dark				Medi- um	Light	Charate	Tem- per- ature
	Control	70°C 1 h	100°C 5 min	120°C 5 min	Control	70°C 1 h	100°C 5 min	120°C 5 min				
Hydrophyllaceae												
<i>Eriodictyon crassifolium</i> (30, soil)												
Control	33 ^a	32 ^a	30 ^a	63 [#]	2 ^a #	1 ^a #	4 ^a	36 [#]	***	***	***	***
Charate	60 ^a	56 ^a	82 ^b	75 ^b #	6 ^a #	2 ^a #	28 ^b	48 ^b #				
Lamiaceae												
<i>Salvia apiana</i> (30, paper)												
Control	8 ^a #	42	9 ^a #	0 [#]	10 ^a #	3 ^a #	4 ^a #	0 ^a #	NS	NS	***	***
Charate	6 ^{ab} #	20	12 ^a #	0 ^b #	8 ^a #	7 ^a #	8 ^a #	0 [#]				
<i>Salvia mellifera</i> (30, paper)												
Control	48 ^a	37 ^{ab}	34 ^b	29 ^b	18 ^a	8 ^a	7 ^a	10 ^a #	***	***	***	***
Charate	69 ^a	68 ^a	60 ^a	47	69 ^a	60 ^a	56 ^a	28 [#]				
Malvaceae												
<i>Malochothamnus fasciculatus</i> (30, soil)												
Control	2 ^a #	7 ^a #	4 ^a #	24	3 ^a #	6 ^a #	4 ^a #	6 ^a #	*	NS	NS	***
Charate	4 ^a #	3 ^a #	3 ^a #	9 ^a	1 ^a #	0 ^a #	4 ^{ab} #	8 ^b #				
Papaveraceae												
<i>Romneya trichocalyx</i> (30, paper)												
Control	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	1 ^a	***	***	***	NS
Charate	24 ^a	33 ^a	34 ^a	24 ^a	17 ^a	11 ^a	13 ^a	10 ^a				
Polygonaceae												
<i>Eriogonum fasciculatum</i> (20, soil)												
Control	83 [#]	72 [#]	67 [#]	27	45 [#]	52 [#]	65 ^a	30	NS	***	NS	***
Charate	67 [#]	85 [#]	75 [#]	60 ^a	57 [#]	48 ^{ab} #	35 ^b	12				
Ranunculaceae												
<i>Clematis lasiantha</i> (30, soil)												
Control	32 ^a	70 [#]	47 ^a	34 ^a #	0 ^a	7 ^a #	9 ^a #	7 ^a #	***	***	***	***
Charate	79 ^a	75 ^a #	70 ^a	13 [#]	16 ^a	16 ^a #	10 ^a #	7 ^a #				
Rhamnaceae												
<i>Ceanothus cuneatus</i> (30, paper)												
Control	10 [#]	26 ^b #	52 ^a #	40 ^{ab} #	10 ^a #	3 ^a	38 ^b	28 ^b #	***	NS	**	***
Charate	10 ^a #	12 ^a #	57 [#]	34 [#]	10 [#]	32	58	46 [#]				
<i>Ceanothus integerrimus</i> (20, soil)												
Control	5 ^a #	7 ^a #	5 ^a #	5 ^a #	15 [#]	25 ^a #	45 [#]	25 ^a #	NS	***	NS	NS
Charate	3 ^a #	3 ^a #	12 ^a #	5 ^a #	7 [#]	32 ^a #	27 ^{ab} #	17 ^b #				
<i>Ceanothus leucodermis</i> (30, paper)												
Control	3 [#]	29 [#]	48 [#]	64 [#]	7 [#]	47 ^b	50 ^{ab} #	68 ^a #	***	NS	**	***
Charate	7 [#]	27 [#]	62 ^a #	47 ^a #	2 [#]	20	58 ^a #	58 ^a #				
<i>Ceanothus megacarpus</i> (30, paper)												
Control	11 [#]	41 ^a #	48 ^a #	80	6 [#]	54 ^a #	53 ^a #	88	NS	NS	*	***
Charate	2 [#]	40 ^a #	40 ^a #	61	3 [#]	40 ^a #	56 ^{ab} #	67 ^b				
<i>Ceanothus oliganthus</i> (30, soil)												
Control	0 [#]	21 [#]	42 ^a	33 ^a #	0 [#]	21 ^a #	32 ^a #	30 ^a #	NS	**	*	***
Charate	0 [#]	12 [#]	18 ^{ab}	34 ^b #	0 [#]	30 ^a #	32 ^a #	39 ^a #				
<i>Rhamnus californica</i> (20, soil)												
Control	65	5 [#]	25 ^a #	33 ^a #	75 ^a	10 [#]	60 ^a	33 [#]	NS	**	NS	***
Charate	15 ^a	15 ^a #	35 ^a #	25 ^a #	90 ^a	9 [#]	90 ^a	35 [#]				
<i>Rhamnus crocea</i> (20, soil)												
Control	48 [#]	20 ^{ab} #	22 ^{ab}	15 ^b #	3 ^a	5 ^a #	2 ^a	2 ^a #	***	***	**	***
Charate	43 ^a #	38 ^a #	65 ^a	13 [#]	32 ^a	7 ^b #	22 ^a	8 ^b #				

TABLE 1. Continued.

	Percentage germination								Significance of <i>F</i>			
	Light				Dark				Medi- um	Light	Charate	Tem- per- ature
	Control	70°C 1 h	100°C 5 min	120°C 5 min	Control	70°C 1 h	100°C 5 min	120°C 5 min				
Rosaceae												
<i>Adenostoma fasciculatum</i> (30, paper)												
Control	4 ^a	8 ^a	10 ^{a#}	6 ^{a#}	3 ^{a#}	6 ^{a#}	7 ^{a#}	2 ^{a#}	***	*	***	NS
Charate	11	18	9#	6#	4 ^{a#}	9 ^{a#}	9 ^{a#}	11 ^{a#}				
<i>Cercocarpus betuloides</i> (20, paper)												
Control	55 ^{a#}	52 ^{a#}	50 ^{a#}	17#	55 ^{a#}	50 ^{a#}	22#	2#	*	NS	NS	***
Charate	57 ^{a#}	55 ^{a#}	50 ^{a#}	12#	50 ^{a#}	57 ^{a#}	40 ^{a#}	15#				
<i>Heteromeles arbutifolia</i> (20, soil)												
Control	99#	43 ^{a#}	54 ^{a#}	15#	89#	34 ^{a#}	44 ^{a#}	0#	NS	NS	NS	***
Charate	99#	23#	44#	0#	79#	13 ^{a#}	22 ^{a#}	5#				
Scrophulariaceae												
<i>Keckiella antirrhinoides</i> (20, soil)												
Control	67 ^a	67 ^a	48 ^{b#}	40 ^b	15 ^a	25 ^a	12 ^{a#}	12 ^a	NS	***	NS	***
Charate	47	32	55#	10	32 ^a	40 ^a	18#	0				
<i>Keckiella cordifolia</i> (30, paper)												
Control	72 ^{a#}	71 ^{a#}	28	79 ^{a#}	70 ^{a#}	75 ^{a#}	61 ^{a#}	48 ^a	NS	***	*	NS
Charate	75 ^{a#}	69 ^{a#}	73 ^a	78 ^{a#}	67 ^{a#}	63 ^{a#}	64 ^{a#}	60 ^a				
<i>Keckiella ternata</i> (20, paper)												
Control	77 ^{a#}	60#	75 ^{a#}	3	20 ^{a#}	12 ^{a#}	10 ^{a#}	0#	NS	***	*	***
Charate	52 ^{a#}	40 ^{a#}	95 ^{a#}	32 ^a	10 ^{a#}	12 ^{a#}	8 ^{a#}	0#				
<i>Mimulus aurantiacus</i> (30, soil)												
Control	73 ^{a#}	90 ^{a#}	72 ^{a#}	95 ^{a#}	6 ^a	4 ^a	4 ^a	3 ^a	*	***	***	NS
Charate	79 ^{a#}	85 ^{a#}	92 ^{a#}	83 ^{a#}	18 ^a	32	16 ^a	12 ^a				
Sterculiaceae												
<i>Fremontodendron californicum</i> (20, soil)												
Control	2 ^{a#}	0 ^{a#}	0 ^a	2 ^a	3#	2 ^{a#}	0 ^{a#}	2 ^a	**	NS	**	*
Charate	2 ^{a#}	3 ^a	8 ^b	10 ^b	0 ^{a#}	3 ^{a#}	3 ^{a#}	8				

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = not significant.

† Seeds of each species were germinated on both potting soil and filter paper, but only results for that medium with the highest germination (indicated in parentheses) are presented. Significance values are presented for the main effects in a multiway ANOVA performed on arcsine-transformed data. Temperature treatment cell means (light and dark experiments considered separately) with the same superscript letter were not significantly different ($P > .05$ with Duncan's multiple range test). For a given species and temperature treatment, charate and non-charate treatment cell means that were not significantly different ($P > .05$ with two-tailed *t*-test) are indicated with the superscript symbol #.

level of germination varied with the medium, the response to light, charate, and heat remained the same in most cases.

Light had a significant effect on germination of over half of the species (Table 1). For most of these species, germination was light stimulated, but in a few cases, e.g., the montane chaparral shrubs *Arctostaphylos patula* and *Ceanothus integerrimus*, light was inhibitory.

Charate had a significant effect on germination of more than two-thirds of the species, and in nearly all cases germination was stimulated (Table 1). Particularly striking in this regard were *Arctostaphylos glandulosa*, *Clematis lasiantha*, *Eriodictyon crassifolium*, *Garrya flavescens*, and *Romneya trichocalyx*, all species from chaparral.

Heat treatment of seeds had a significant effect on the majority of species (Table 1). In some (e.g., all species of *Ceanothus*), heat treatment was highly stim-

ulatory, whereas in others (e.g., *Cercocarpus betuloides*, *Heteromeles arbutifolia*, and *Quercus dumosa*) certain heat treatments reduced germination and were apparently lethal, as indicated by the fact that these seeds had rotted by the end of the experiment. For the large acorns of *Q. dumosa*, longer heating at low temperature was more detrimental than short bursts of high temperature, whereas the opposite applied to the smaller seeds of the other two shrubs. For those seeds with heat-stimulated germination, the most stimulatory treatment varied with the species. For instance, *Salvia apiana* was stimulated by 70°C for 1 h, but 5 min at higher temperatures was not stimulatory; the opposite applied to most *Ceanothus* species. For *Eriodictyon crassifolium*, germination was significantly higher when heat treatment was combined with charate than for heat or charate alone.

Particularly striking is the fact that, in the light, a

substantial number of species germinated readily without any treatment of heat or charate (Table 1). This was true for most coastal sage scrub species and a significant number of chaparral shrubs.

Significant interactions between certain main effects were observed for nearly all species, although there was no obvious pattern between the types of interactions and the responses to treatments. In most instances the interactions were not clearly interpretable. One exception was an interaction between light and charate observed for *Rhus integrifolia*, *Artemisia californica*, *Salvia mellifera*, *Rhamnus crocea*, *Keckiella antirrhinoides*, and *Mimulus aurantiacus*: these species germinated readily in the light and were significantly inhibited in the dark, but this dark inhibition was overcome by charate.

Some species had very low germination under all conditions. In *Adenostoma fasciculatum*, this was due in large part to a high percentage of achenes being "empty," but not readily distinguishable from "good" achenes. For several other species, there was low germination despite the fact that the seeds appeared filled and viable (tetrazolium tests for viability were not done on any species, since many had such small seeds or tiny embryos that the results would have been questionable). For some species, part of the explanation for low germination is apparently due to inhibitors in or on the seed coat, which must be leached away. For example, *Malosma laurina* and *Toxicodendron diversiloba* produce a gummy pericarp over the seed that leaches off only very slowly. The germination response shown in Table 1 for these two species is from the second of two experiments. In the first, seeds were sown without prior leaching and very few germinated. Prior to the second experiment, seeds were soaked for 1 mo in buckets of water, which was changed daily. These two species were also among the slowest of all species in rate of germination.

Rate of germination varied markedly. For approximately a third of the species, >75% of the total germination occurred by the 1st wk at 23° (after 1 mo stratification). These included many that germinated readily under control conditions—subshrubs *Artemisia californica*, *Haplopappus squarrosus*, *Mimulus aurantiacus*, *Keckiella* spp., and shrubs *Cercocarpus betuloides* and *Rhamnus californica*—and the heat-stimulated species *Ceanothus megacarpus*, *C. oliganthus*, and *Salvia apiana*. Another third of the species germinated slowly, with >75% of the total germination delayed until the second stratification treatment (more than 2 mo after the experiment started). These included *Viguiera laciniata*, *Rhamnus crocea*, all species in the Anacardiaceae, and the charate-stimulated species *Clematis lasiantha*, both *Arctostaphylos* species, and *Garrya flavescens*.

For the nine species with limited seed stocks, results were mixed. The coastal sage subshrub *Haplopappus venetus* responded similarly to its congener reported in

Table 1: highest germination with no treatment. *Romneya coulteri* exhibited a highly significant enhancement in the presence of charate, similar to the response of *R. trichocalyx* (Table 1). *Ceanothus tomentosus* and *C. verrucosus* were heat-stimulated, as observed for other *Ceanothus* tested. *Prunus ilicifolia* (Rosaceae) and hardwood trees often associated with chaparral, including *Juglans californica* (Juglandaceae), *Quercus agrifolia*, *Q. chrysolepis*, and *Umbellularia californica* (Lauraceae), all germinated readily without treatment. Germination of all nine species was significantly inhibited in the dark.

DISCUSSION

Despite the fact that these species all occur in fire-prone environments, it is clear that not all have germination syndromes specialized to fire. Some woody species have seeds capable of germinating when the winter rains replenish soil moisture. Others have a marked requirement for heat, either from fire or elevated soil temperatures on open sites, or a requirement for charred wood. I suggest that these germination behaviors can be correlated with other life history responses, illustrating the presence of different character syndromes (sensu Angevine and Chabot 1979).

Species that germinate readily without treatment

Included here are the majority of dominants in coastal sage scrub, e.g., *Artemisia californica*, *Haplopappus squarrosus*, *Eriogonum fasciculatum*, *Mimulus aurantiacus*, *Viguiera laciniata* (Table 1), and *Encelia californica* (Keeley and Keeley 1984). One consequence of this germination behavior is that a soil seed bank may not build up between fires. Thus on some sites the predominant mode of reestablishment after fire is by resprouts from the root crown. In a study of postfire recovery that included five of these species (Keeley and Keeley 1984), all were present the first growing season as vigorous resprouters, and seedlings were absent. However, the resprouts flowered and fruited abundantly, and in the second growing season there was a large pulse of seedling recruitment. Often, on sites away from the coast, fires are intense enough so that few coastal sage shrubs survive as resprouts (Westman et al. 1981, Zedler 1981, Zedler et al. 1983), and the result may sometimes be localized extinction. On other sites, seedling populations, particularly of *Artemisia californica* and *Salvia mellifera*, have been observed in the first season after fire. These may arise from either post-fire dispersal onto the site, or the seed crop from the previous season that remained dormant, due to drought, at the time of dispersal in summer and fall. One other factor which could impose dormancy until fire is burial of seeds at sufficient depth in the soil. For example, the response of *Artemisia californica* (Table 1) suggests it will germinate readily upon wetting by winter rains if seeds remain near the soil surface, but they will remain dormant until exposed to charred wood if buried

below the level of light penetration. A nearly identical pattern is evident in two other coastal sage shrubs, *Salvia mellifera* and *Mimulus aurantiacus* (Table 1).

In the absence of fire, coastal sage shrubs flower more or less annually, but successful seedling recruitment is uncommon in mature vegetation due to intense animal predation (Halligan 1974), and possibly due to allelopathic effects (Muller 1966). All of these species have lightweight diaspores (Appendix) which are widely dispersed. Lacking any innate dormancy that requires fire to break it, these species readily colonize other types of disturbance (Zedler 1982) or open grasslands (Freudenberger et al. 1987). Thus this germination syndrome is successful with or without fire.

Some of the most widespread woody dominants of the chaparral also have seeds with no innate germination requirement for fire: *Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Prunus ilicifolia*, and *Quercus dumosa*, or at least most of the seeds germinate readily, as in *Rhus integrifolia*, *Rhamnus crocea*, and *R. californica*. On most sites these species re-establish after fire strictly from resprouts (Zedler 1981, J. E. Keeley 1986). Seedlings are rare in the first growing season after fire for several reasons. A soil seed bank does not build up between fires since the seeds are likely to germinate the winter or spring following dispersal. Indeed, in the case of *Q. dumosa*, germination may occur prior to dispersal from the shrub, and *R. californica* disperses seeds with chlorophyllous cotyledons indicating germination is imminent. Also, in the case of *H. arbutifolia*, *P. ilicifolia*, *Q. dumosa*, and *R. californica*, seeds are relatively short lived (<9 mo if allowed to dry to room conditions; J. E. Keeley, *personal observation*), and thus seeds that fail to germinate the first spring are unlikely to survive through the summer drought. In addition, current-year seed crops are likely to be destroyed by fire, since maturation occurs during late summer and fall. Any seeds in the soil at the time of the fire are also likely to be destroyed due to their sensitivity to high temperatures (Table 1).

Timing of seedling recruitment by these shrubs requires careful analysis. All of the species mentioned above have diaspores that potentially are widely dispersed (Appendix). Acorns are commonly dispersed by Scrub Jays and squirrels (Grinnell 1936), and the long-tailed plume on *Cercocarpus* fruits carries the seeds great distances in the wind. Some other species produce brightly colored berries in fall and winter, and these are readily consumed by migrating birds (Hom 1984). Dispersal onto burned sites is possible, and Zedler (1981) reported seedling recruitment by *Heteromeles arbutifolia* in a 3-yr-old burn, but this is not commonly observed. In most stands of mature chaparral vegetation, successful seedling establishment by any species is rare. However, in very old stands (60–100+ yr) substantial seedling populations (10^3 – 10^4 seedlings/ha) have been reported for all of the shrubs listed above, but not for any of the species discussed in the following

section (Patric and Hanes 1964, Zedler 1981, 1982, Keeley et al. 1986, J. E. Keeley, *personal observation*). It should be noted, however, that stands of California chaparral of this age are uncommon (Keeley 1982), due to increased fire frequency caused by humans. The chaparral species which germinate readily without treatment share this characteristic of germinating without the stimulus of heat or charred wood, as well as others (e.g., relatively large seeds, potential long-distance dispersal, seedling establishment in the absence of fire) with woodland species (Appendix), with which they often associate.

Species with heat-stimulated germination

Heat-stimulated germination has been documented for *Ceanothus* species (Quick 1935, Hadley 1961, and Table 1 above), *Rhus ovata* (Stone and Juhren 1951) and *Adenostoma fasciculatum* (Stone and Juhren 1953, Christensen and Muller 1975). Other heat-stimulated species include *Malacothamnus fasciculatus* and *Salvia apiana* (Table 1). In the first growing season after fire, seedling populations are high, derived from the previously dormant soil seed bank. After this 1st-yr pulse, seedling recruitment is rare until the next fire. Dormancy is imposed by a more or less impermeable seed coat (Stone and Juhren 1953). Heat shock from fire melts or cracks the cuticle or otherwise scarifies the seed coat. In some instances seeds near the soil surface on exposed sites may experience soil temperatures sufficient to stimulate germination, but seedling recruitment is seldom successful in undisturbed chaparral.

Certain of these species, e.g., *Ceanothus cuneatus* and *C. megacarpus*, have life histories that represent extreme specialization to fire. Over evolutionary time these taxa have lost the ability to resprout after fire (Wells 1969), and thus continuance in this fire-prone environment is dependent upon the buildup of a soil seed bank. In the absence of fire, such species are not capable of maintaining their population sizes, nor are they able to colonize new sites. Seed dispersal is limited, as most fall within 2 m of the parent shrub (Davey 1982), and unlike some disturbance-dependent species that disperse to open sites, these taxa are dependent upon fires coming to them. Species with this "temporal dispersal syndrome" (Angevine and Chabot 1979) must necessarily have long-lived seeds, a phenomenon documented for *Ceanothus* (Quick and Quick 1961).

Species with charate-stimulated germination

Germination of *Arctostaphylos glandulosa*, *Romneya trichocalyx*, *R. coulteri*, and *Garrya flavescens* requires a chemical cue from charred wood. The bulk of the soil seed bank thus remains dormant in the absence of fire. In this study some species, such as *Clematis lasiantha* and *Rhus trilobata*, exhibited a pattern in which a third of the seeds germinated readily but charate doubled germination, suggesting polymorphic seed pools as described for other chaparral species (Stone

and Juhren 1953, Keeley et al. 1985). For some species, such as *Eriodictyon crassifolium* and *Adenostoma fasciculatum*, heat shock from fire and charred wood may act synergistically to stimulate germination (Table 1).

The mechanism behind charate-stimulated germination is not known. Based on several studies (Keeley and Nitzberg 1984, Keeley and Pizzorno 1986), it is known that activated charcoal will not produce the same effect. The stimulus is a water-soluble chemical leached from charred or heated (but not ashed) wood. It is apparently an oligosaccharin produced by heating of hemicelluloses. Such a chemical is unlikely to appear in the environment except after fire. In life history characteristics, these species have much in common with species in the previous group. Clearly, there are two different cues available for timing seedling recruitment to postfire environments, although there is a tendency for slower germination in charate-stimulated species relative to heat-stimulated species.

Other factors

For most species, germination was significantly stimulated by light, and this may increase the chance of seedling establishment in gaps or on other open sites. Two exceptions are *Ceanothus integerrimus* and *Arctostaphylos patula* (Table 1). Both of these species are important components of montane chaparral and are often successional to mixed conifer forest following disturbance. The role of light inhibition in the life history of these shrubs is not clear, but it is consistent with other observations (Adams 1962). Responses not readily explained include the very low total germination observed for several species. In taxa such as *Arctostaphylos glandulosa* and *Fremontodendron californicum*, low germination apparently was not related to poor viability, and thus some additional germination condition may be required. In the case of *Malosma laurina* and *Toxicodendron diversiloba*, germination is apparently slowed due to the gummy covering of the seed coat, and is perhaps a means of extending germination over long periods of time. Seedlings of these species occur both before and after fire.

The striking effect of germination medium, observed for some species, should stand as a warning for future studies of germination behavior. The explanation of how the medium affects germination remains to be explored. In this study it was observed that seeds sown on filter paper almost invariably developed more fungal growth than seeds sown in soil. It may be that the medium affects microbial growth, and thus indirectly seed germination. In some species this may inhibit germination, while in others it may stimulate germination.

Conclusions

Coastal sage scrub and chaparral taxa represent a diversity of seed germination syndromes that can be correlated with different life history responses. Despite

the fact that wildfires are a frequent and predictable part of the environment, fire has not played a role in shaping the germination behavior of all species. Those which do time seedling establishment to occur after fire may use different cues. As a consequence of different character syndromes, opportunities for population expansion increase after fire for some species, but increase in the long absence of fire for others. Equilibrium in species composition is probably enhanced by variable burning regimes.

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APPENDIX

Growth, form, vegetation type, and fruit and seed characteristics for the woody species of coastal sage scrub and chaparral used in the germination studies.

	Growth form*	Vegetation type†	Fruit and diaspore characteristics	Season of dispersal	Seed mass (μg)
Anacardiaceae					
<i>Malosma laurina</i>	esh	cs/ch	drupe with gummy pericarp	fall	$2.8 \times 10^{3\ddagger}$
<i>Rhus integrifolia</i>	esh	cs/ch	fleshy drupe	summer	$5.5 \times 10^{4\ddagger}$
<i>Rhus trilobata</i>	esh	cs/ch/o	fleshy drupe	summer	$2.8 \times 10^{4\ddagger}$
<i>Toxicodendron diversilobium</i>	dl	cs/ch/o	drupe with gummy pericarp	summer	$3.3 \times 10^{4\ddagger}$
Asteraceae					
<i>Artemisia californica</i>	dss	cs	achene with minute pappus	fall	$6.0 \times 10^{\ddagger}$
<i>Haplopappus squarrosus</i>	dss	cs	achene with plumose pappus	fall	$6.8 \times 10^{3\ddagger}$
<i>Haplopappus venetus</i>	dss	cs	achene with plumose pappus	fall	$3.4 \times 10^{2\ddagger}$
<i>Viguiera laciniata</i>	dss	cs	achene with plumose pappus	summer	$7.7 \times 10^{2\ddagger}$
Caprifoliaceae					
<i>Lonicera subspicata</i>	el	cs/ch	fleshy berry	summer	5.5×10^3
Ericaceae					
<i>Arctostaphylos glandulosa</i>	esh	ch	pulpy drupe	summer	$1.8 \times 10^{4\ddagger}$
<i>Arctostaphylos patula</i>	esh	mch	pulpy drupe	summer	$1.8 \times 10^{4\ddagger}$
<i>Comarostaphylis diversifolia</i>	esh	ch	fleshy drupe	summer	$1.4 \times 10^{4\ddagger}$
Fabaceae					
<i>Lotus scoparius</i>	dss	cs/ch	indehiscent legume	spring	$2.3 \times 10^{3\ddagger}$

APPENDIX

Continued.

	Growth form*	Vegetation type†	Fruit and diaspore characteristics	Season of dispersal	Seed mass (µg)
Fagaceae					
<i>Quercus agrifolia</i>	et	ch/o	acorn	fall	$9.4 \times 10^3 \ddagger$
<i>Quercus chrysolepis</i>	et	ch/o	acorn	fall	$3.8 \times 10^6 \ddagger$
<i>Quercus dumosa</i>	esh	ch	acorn	fall	$1.8 \times 10^6 \ddagger$
Garryaceae					
<i>Garrya flavescens</i>	esh	ch	berry	summer	3.0×10^4
Hydrophyllaceae					
<i>Eriodictyon crassifolium</i>	ess	cs/ch	capsule	summer	1.7×10^2
Juglandaceae					
<i>Juglans californica</i>	dt	ch/o	nut	fall	$4.8 \times 10^6 \ddagger$
Lamiaceae					
<i>Salvia apiana</i>	dss	cs/ch	dehiscent nutlet	summer	$1.4 \times 10^3 \ddagger$
<i>Salvia mellifera</i>	dss	cs/ch	dehiscent nutlet	summer	$1.1 \times 10^3 \ddagger$
Lauraceae					
<i>Umbellularia californica</i>	et	ch/o	fleshy drupe	fall	$1.7 \times 10^6 \ddagger$
Malvaceae					
<i>Malacothamnus fasciculatus</i>	dss	ch	dehiscent follicle	summer	1.6×10^3
Papaveraceae					
<i>Romneya coulteri</i>	ess	ch	capsule	summer	1.1×10^3
<i>Romneya trichocalyx</i>	ess	ch	capsule	summer	6.7×10^2
Polygonaceae					
<i>Eriogonum fasciculatum</i>	ess	cs/ch	achene	summer-fall	$1.4 \times 10^3 \ddagger$
Ranunculaceae					
<i>Clematis lasiantha</i>	dl	ch	plumose-tailed achene	summer	$4.2 \times 10^3 \ddagger$
Rhamnaceae					
<i>Ceanothus cuneatus</i>	esh	ch	exploding capsule	spring	1.0×10^4
<i>Ceanothus integerrimus</i>	esh	mch/o	exploding capsule	summer	7.5×10^3
<i>Ceanothus leucodermis</i>	esh	ch	exploding capsule	summer	8.7×10^3
<i>Ceanothus megacarpus</i>	esh	ch	exploding capsule	spring	2.4×10^4
<i>Ceanothus oliganthus</i>	esh	ch	exploding capsule	spring	6.0×10^3
<i>Ceanothus tomentosus</i>	esh	ch	exploding capsule	spring	4.0×10^3
<i>Ceanothus verrucosus</i>	esh	ch	exploding capsule	spring	9.1×10^3
<i>Rhamnus californica</i>	esh	ch/o	fleshy drupe	fall	$9.3 \times 10^4 \ddagger$
<i>Rhamnus crocea</i>	esh	ch	fleshy drupe with dehiscent endocarp	summer	9.5×10^3
Rosaceae					
<i>Adenostoma fasciculatum</i>	esh	ch	achene coalesced to floral tube	summer	$1.5 \times 10^3 \ddagger$
<i>Cercocarpus betuloides</i>	esh	ch	plumose tailed achene	summer	$1.8 \times 10^4 \ddagger$
<i>Heteromeles arbutifolia</i>	esh	ch/o	fleshy berry	winter	5.3×10^3
<i>Prunus ilicifolia</i>	esh	ch/o	fleshy drupe	fall	$1.2 \times 10^6 \ddagger$
Scrophulariaceae					
<i>Keckiella antirrhinoides</i>	esh	ch	capsule	summer	2.8×10^2
<i>Keckiella cordifolia</i>	el	ch/cs	capsule	summer	1.9×10^2
<i>Keckiella ternata</i>	dl	ch	capsule	summer	3.0×10^2
<i>Mimulus aurantiacus</i>	dss	cs/ch	capsule	summer-fall	2.0×10
Sterculiaceae					
<i>Fremontodendron californicum</i>	esh	ch	capsule (seeds with elaiosome)	summer	3.3×10^4

* Growth forms: dl = deciduous liana, dss = deciduous subshrub, dt = deciduous tree, el = evergreen liana, esh = evergreen shrub, ess = evergreen subshrub, et = evergreen tree.

† Vegetations: cs = coastal sage scrub, ch = chaparral, mch = montane chaparral, o = "other" plant communities.

‡ "Seed" includes endocarp or other fruit parts.