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Seed germination patterns of *Salvia mellifera* in fire-prone environments

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Summary. *Salvia mellifera* seeds from coastal sage, chaparral and desert scrub in southern California failed to germinate in the dark unless exposed to powdered charred wood. This pattern was observed for seeds given a one month stratification at 5 C and for ones not stratified and also for seeds incubated under continuous 23 C or a diurnal alternation of 13 C/23 C. Dark inhibition of germination was also overcome, but only in seeds from chaparral populations, if seeds were incubated on commerical potting soil under alternating 13 C/23 C. Seeds in the light germinated readily in all but one population from desert scrub vegetation. Germination of seeds from this population was markedly stimulated by dry heating of the seeds at either 70 C for 5 h or 115 C for 5 min. For all populations there were numerous significant interactions between incubation temperature, pre-chilling stratification, light, and heating/charred wood treatments. Timing of germination was remarkably consistent between populations; the vast majority of seeds germinated within the first week at 23 C (or 13 C/23 C) regardless of whether or not they had received a pre-chilling treatment.

Key words: Chaparral – Ecotypes, fire – Germination

Salvia mellifera Greene (Lamiaceae) is a small summer-deciduous shrub widely distributed throughout the semi-arid parts of southern California. Along the coast it often dominates the subligneous aromatic coastal sage vegetation, but on arid slopes in the interior it often is successional to chaparral vegetation. On the leeward slopes of the coastal ranges it often extends into desert scrub vegetation.

Wildfires are an integral part of the ecology of coastal sage and chaparral vegetation. *Salvia mellifera* is able to exist in fire-prone environments through resprouting and seedling establishment after fire. However, the predominant mode of reestablishment after fire varies geographically. On coastal sites it recovers quite rapidly by resprouts from the rootcrown and seedling establishment may or may not be important dependent upon the site (Westman et al. 1981; Malanson and O'leary 1982; Keeley and Keeley 1984). In the interior, particularly when associated with chaparral vegetation, shrubs are killed by fire but seedling establishment is abundant from the previously dormant seed bank (Hanes and Jones 1967). Fires are uncommon in desert scrub vegetation due to the much sparser vegetation.

Many species that recruit seedlings after fire have specialized seed germination syndromes that require a specific cue from fire to stimulate germination. Chaparral shrubs such as *Adenostoma fasciculatum, Rhus ovata* and *Ceanothus* species have seeds which lie dormant in the soil until heat shock from fire melts the cuticle or otherwise scarifies the seed coat (Hanes 1977). This is also true of many herbaceous species that are rare in mature chaparral but dominate burned sites. An alternative mechanism for cueing germination to the postfire environment is a dependence upon a chemical stimulus from charred wood as documented for *Emmenanthe penduliflora* (Hydrophyllaceae) (Wicklow 1977; Jones and Schlesinger 1980) and many other postfire herbs (Keeley et al. 1985). In some chaparral species light plays an important role in stimulating germination (Keeley 1984).

The purpose of the present study was to examine seed germination characteristics of *Salvia mellifera*. Due to the fact that many populations exist in fire-prone vegetations, it was hypothesized that germination would be stimulated by either heat or charred wood as cues to the postfire environment. However, since recruitment in some populations is known to occur in the absence of fire, the role of other factors was also examined.

Material and methods

Seeds were collected in summer from populations distributed from the coast to the desert (Table 1). These sites represent the range of environments for *Salvia mellifera* in southern California. Seeds were stored in paper bags under room conditions for 18 months. Longevity of *Salvia mellifera* seeds is unknown although circumstantial evidence suggests they survive in the soil for many years and the closely related species, *Salvia columbariae* Benth., can survive more than a decade of laboratory storage (Went 1969).

Fifty seeds were sown in 60 × 15 mm petri dishes fitted with two sheets of #42 Whatman filter paper for the control and all treatments. An additional set of controls on commercial potting soil (Gro-lite, see Keeley 1984 for chemical analysis of this soil) were included. Heat treatments of seeds were applied prior to sowing. These treatments were selected to cover a range of conditions potentially encountered by seeds in the soil on open sites or during fire; 70 C for 1 h, 70 C for 5 h and 115 C for 5 min applied to air-dry seeds in a forced convection oven. Powdered charred wood was prepared by charring, but not ashing, stems of the chaparral shrub *Adenostoma fasciculatum* and grinding

Table 1. Source of *Salvia mellifera* seed populations

Population and locality	Distance from coast (km)	Elevation (m)	Precipitation (mm)	Vegetation	Associated species
Leo Carrillo					
Leo Carrillo State Beach, Ventura Co.	2	50	314	Coastal sage	*Salvia leucophylla* *Artemisia californica*
Westlake					
Westlake Blvd, 1 km north of Hwy 101, Thousand Oaks, Ventury Co.	17	250	388	Coastal sage	*Salvia leucophylla*
Del Mar					
Del Mar Heights Rd., 0.5 km east of Hwy 5, Del Mar, San Diego Co.	3	60	280	Mixed coastal sage/chaparral	*Quercus dumosa Encelia californica*
Alberhill					
Lake St, 2 km south of Alberhill, Riverside Co.	35	300	273	Chaparral	*Adenostoma fasciculatum*
Angeles Crest					
Angeles Crest Hwy, 1 km north of La Canada, Los Angeles Co.	38	500	660	Chaparral	*Adenostoma fasciculatum*
Vasquez Rocks					
Vasquez Rocks County Park, Los Angeles Co.	55	690	258	Desert scrub	*Juniperus californica Lycium* spp. *Opuntia basilaris*

Annual precipitation from >40 yr average for the nearest station at the same elevation, from Climatological Data Annual Summary, National Climatic Center, Asheville, North Carolina

Table 2. Significance values for main effects in four-way ANOVA of germination (on arcsin transformed data). Incubation = continuous 23 C or alternating 23 C/13 C; Pre-chilling = with or without 1 month at 5 C; Light = light or dark; treatments are as described in Table 3. ns = $P > 0.05$

Source of variation	Population					
	Leo Carrillo	Westlake	Del Mar	Alberhill	Angeles Crest	Vasquez Rocks
Main effects						
Incubation	ns	<0.004	<0.001	ns	<0.001	<0.006
Pre-chilling	ns	<0.002	<0.001	<0.004	ns	<0.013
Light	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Treatments	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
2-way interactions						
Incubation × light	<0.0016	<0.001	<0.004	<0.006	ns	ns
Incubation × chilling	ns	ns	<0.001	ns	ns	ns
Incubation × treat.	<0.038	<0.001	ns	<0.001	<0.001	<0.001
Light × chilling	<0.001	ns	<0.001	<0.001	<0.001	<0.010
Light × treat.	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Chilling × treat.	<0.001	<0.001	<0.001	<0.001	<0.011	<0.001

these in a Wiley mill to pass a 1-mm screen. Charred wood treatments received 0.25 g of this charate. All treatments were replicated three times.

Experiments were initiated by adding 3.0 ml of distilled water to dishes with filter paper, 6.0 ml to dishes with powdered charred wood and 10.0 ml to potting soil dishes. After adding water, one set of dishes was pre-chilled (stratified) at 5 C. After 1 month, water was added to another set of treatments that were not pre-chilled, and both sets were incubated together in a biological incubator (Percival I-35L) maintained at 65% relative humidity under either a continuous thermoperiod of 23 C or alternating 13 C for 12 h and 23 C for 12 h. This entire experiment was replicated in the light and in the dark. Germination was scored every week and seedlings removed. Seeds in the dark were scored under indirect green light. Most germination occurred within the first week at 23 C, but the experiment continued for 2 months.

Table 3. Germination of *Salvia mellifera* populations under heating and charred wood treatments, in light or dark, with or without pre-chilling and with incubation continuously at 23 C or alternating 13 C/23 C. Treatments were heating prior to sowing or application of powdered charred wood to the germination medium which was filter paper for all except one set of controls on potting soil, n = 3 petri dishes of 50 seeds each

	Percentage germination											
	Light						Dark					
	Control		70 C 1 h	70 C 5 h	115 C 5 min	Charred wood	Control		70 C 1 h	70 C 5 h	115 C 5 min	Charred wood
	Soil	Paper					Soil	Paper				
Continuous 23 C (Leo Carillo)												
Not chilled	32	25	31	33	33	49	1	0	0	1	0	41
Pre-chilled	13	37	18	25	44	14	1	1	1	1	3	31
13 C/23 C												
Not chilled	20	28	20	23	28	57	2	1	1	0	0	49
Pre-chilled	16	20	18	23	25	44	7	5	3	3	3	30
Continuous 23 C (Westlake)												
Not chilled	20	15	39	25	31	20	0	0	1	1	1	45
Pre-chilled	21	35	52	47	53	19	1	0	3	5	9	29
13 C/23 C												
Not chilled	37	27	21	24	21	59	7	0	2	3	2	72
Pre-chilled	14	35	46	40	28	29	4	1	11	9	5	61
Continuous 23 C (Del Mar)												
Not chilled	17	9	11	16	7	13	9	0	1	1	0	12
Pre-chilled	21	23	25	17	25	25	2	1	2	5	1	24
13 C/23 C												
Not chilled	19	6	22	21	29	23	15	0	1	0	0	16
Pre-chilled	23	50	55	55	50	55	14	4	5	9	3	37
Continuous 23 C (Alberhill)												
Not chilled	23	1	22	15	11	55	7	0	0	1	0	37
Pre-chilled	16	17	39	25	31	36	5	0	1	0	0	35
13 C/23 C												
Not chilled	15	17	12	8	13	30	21	0	0	0	0	53
Pre-chilled	34	15	27	16	24	28	24	1	0	1	0	27
Continuous 23 C (Angeles Crest)												
Not chilled	41	42	39	39	43	77	6	1	2	2	0	43
Pre-chilled	34	47	35	34	25	49	7	5	4	5	8	29
13 C/23 C												
Not chilled	71	46	48	52	64	55	43	1	2	3	3	57
Pre-chilled	51	45	51	60	53	55	42	11	5	9	13	68
Continuous 23 C (Vasquez Rocks)												
Not chilled	7	5	21	11	23	21	0	0	0	1	0	30
Pre-chilled	6	8	15	13	47	5	1	2	2	3	7	10
13 C/23 C												
Not chilled	3	11	14	20	41	23	3	1	0	0	0	37
Pre-chilled	2	5	6	28	41	27	1	3	4	7	5	45

Results

Two main effects, light/dark conditions and heating/charred wood treatments, were highly significant for all six *Salvia mellifera* populations (Table 2). Germination was markedly inhibited in the dark but this dark inhibition was readily reversed by the addition of charred wood (Table 3).

With respect to incubation and pre-chilling effects, the two coastal sage populations did not respond the same and this was true of the two chaparral populations (Table 2).

There were many significant interactions between incubation, pre-chilling, light and heating/charred wood treatments indicating that subtle changes in conditions and combinations of factors produced different germination responses (Table 2).

For the coastal sage populations in the light, control germination was between 20 and 30% and in most cases certain heat treatments and charred wood stimulated germination (Table 3). For the Leo Carrillo population, neither incubation regime nor pre-chilling affected germination, whereas for seeds from Westlake, an alternating incubation regime and pre-chilling greatly enhanced germination for certain treatments.

The mixed coastal sage/chaparral population at Del Mar showed significantly increased germination with alternating incubation temperatures and with pre-chilling (Table 2). Highest germination was observed when these conditions were combined in the light (Table 3). Except in the dark, heat or charred wood produced no significant enhancement. This population exhibited a characteristic shared with the two chaparral populations. In the dark, control germination on potting soil, under alternating incubation temperatures, was markedly higher than controls on filter paper. In all three populations this effect was not observed under the continuous 23 C incubation regime.

For the chaparral population at Alberhill, pre-chilling had a significant effect but it tended to increase germination for some treatments and decrease germination for others (Table 2). The Angeles Crest seeds were insensitive to pre-chilling but alternating 13 C/23 C during incubation enhanced germination for most treatments (Table 3).

The desert scrub population from Vasquez Rocks was distinct from all other populations in that heat treatments markedly stimulated germination over controls (Table 3). Overall germination was higher with pre-chilling and under alternating incubation temperatures.

Timing of germination was similar for all populations (Table 4). The majority of the total germination occurred within the first week at 23 C (or 13 C/23 C). Without a pre-chilling treatment at 5 C, seeds under constant incubation at 23 C germinated more rapidly than seeds under alternating 13 C/23 C incubation. However, in all but one population, after pre-chilling, incubation regime did not affect the rate of germination.

Table 4. Percentage of total germination occurring by the first week of incubation at 23 C or 13 C/23 C. Combined data for heat and charred wood treatments in the light. ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$ with two-tailed t-test

	Not pre-chilled			Pre-chilled		
	23 C incubation		13 C/23 C incubation	23 C incubation		13 C/23 C incubation
Leo Carrillo	86	**	70	96	ns	97
Westlake	94	**	55	90	ns	87
Del Mar	80	*	74	81	ns	85
Alberhill	79	**	61	87	ns	90
Angeles Crest	80	ns	75	72	**	93
Vasquez Rocks	88	**	51	88	ns	97

Discussion

Salvia mellifera seeds buried below the depth of light penetration in the soil remain dormant until exposed to charred wood and thus a portion of the soil seed bank undoubtedly remains dormant until the aboveground vegetation is destroyed by wildfire.

The mechanism behind charred wood stimulated germination is not known, although based on several studies (Keeley and Nitzberg 1984; Keeley and Pizzorno, in press) it appears that a water soluble compound is leached from charred wood and is effective at concentrations far lower than those utilized in this study. The compound can be produced by heating or charring of virtually any type of wood. It is destroyed if the wood is combusted to ash and it is generated by merely heating wood to 170 C without charring. The compound is apparently an oligosaccharide produced by heating of hemicelluloses.

The observation that seeds from chaparral populations overcame dark inhibition when exposed to potting soil and alternating temperatures is not readily explicable. It suggests that seeds buried in the soil may be stimulated to germinate if there is a strong diurnal temperature fluctuation. Although the soil is a good insulator, large temperature fluctuations could be expected on open sites or in gaps in the chaparral canopy.

Seeds exposed to the light germinate much more readily than buried seeds. However, very little germination is likely to occur at the time of dispersal because seeds are dispersed in late spring and summer when soil moisture levels are extremely low. Also, experiments with the very closely related and sympatrically occurring *Salvia columbariae* (with which *S. mellifera* hybridizes, Munz 1968) show that these seeds have an innate dormancy at the time of dispersal, one which is overcome after approximately six months of aging (Capon et al. 1978). In the winter and early spring following dispersal, seeds near the soil surface, particularly in sparse vegetation and on open sites, very likely will be stimulated to germinate by the light.

The only indication of ecotypic differences in germination behavior was the very limited germination (in the light) by the desert scrub population, unless given a heat treatment of 70 C or 115 C. For the coastal sage and chaparral populations 25–50 % of the seeds in the light germinated readily and showed no clear response to heat treatment. This difference between chaparral and desert populations has also been reported for *S. columbariae* populations (Capon et al. 1978). Due to the limited occurrence of fires in desert scrub, it is more likely that temperatures capable of stimulating germination would come about from elevated soil temperatures, which in the summer could exceed 70 C. Such a requirement may further ensure dormancy of seeds until the winter rainy season.

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