

The Role of Allelopathy, Heat, and Charred Wood in the Germination of Chaparral Herbs¹

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The southern California chaparral is dominated by woody sclerophyllous-leaved shrubs which are drought tolerant and fire-adapted. Shrubs resprout from root crowns or appear from seedlings once fire has removed the adult plants and provided proper conditions for seed germination. There is also an herbaceous component to the chaparral, the most well known herbs being "fire annuals" which appear in great numbers after the chaparral shrubs have burned. The germination responses of these herbaceous species has been tied to two major effects: the allelopathic properties of shrubs which inhibit herb germination in the mature chaparral, and/or the stimulating effects of the burning process; heat, scarification and chemical changes. Herbs are generally inconspicuous under the mature shrub canopy.

Annual and perennial herbaceous species are associated with chaparral, both before and after fire. It has been suggested that these herbs can be divided into 4 groups on the basis of life form and time of appearance (Table 1; Keeley and Keeley 1981, Keeley et. al. 1981). The perennial herbs form two groups (Table 1), those present within the mature chaparral, but rarely flowering at this time & those which appear abundantly after fire. This second group is composed of suffrutescent species such as Helianthemum scoparium and Eriophyllum confertiflorum which become prominent the second through fifth years after fire (Keeley et. al. 1981), or until they are shaded out by the reestablishing shrubs. Annual species can be similarly divided into those which appear in openings within the mature chaparral, and those annuals which are strict fire followers (Table 1). This diversity in life history suggests differences in seed germination cues.

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Abstract: The herbaceous flora of the chaparral includes annual and perennial species which differ in their temporal relationship to fire. Germination cues for these herb groups could be expected to reflect these temporal differences. Thirty species of herbs were tested for germination in response to Adenostoma leachate and charred stems, direct heat, and their combinations. For herbs present pre- and post-fire, germination was best under control conditions, or with leachate. Fire following herbs germinated best with a combination of charred stems and low heat. The enhancement effect of burned Adenostoma stems was found to be generalizable to other woody plants and was not a fertilizer effect.

The development of hypotheses on seed germination has resulted primarily from the pioneering work of Sweeney (1956). Sweeney (ibid.) investigated the possibility of inhibitory substances which might be produced by the shrubs and retard or prevent herb germination. He also investigated the possible stimulatory role of heat and ash on herb germination. Sweeney (1956) found no effect due to Adenostoma leachate on the germination of several chaparral herb species or on the cultivated radish, under normal aerated conditions. He obtained stimulated germination of refractory herb species, such as Emmenanthe penduliflora, when wood excelsior was burned over the top of seeds planted in soil. Separate tests on the effect of heating, at temperatures similar to those found in fire, and tests with wood ash alone failed to reproduce the result obtained with burned excelsior. Heating for extended periods did increase germination in one species (Oenothera micrantha) but had no effect on other herbs tested. Wood ash generally decreased germination for both scarified and non-scarified herb seeds.

Muller, Hanawalt & McPherson (1968) and McPherson and Muller (1969) pursued the possibility of an inhibitory substance present in mature shrubs which could prevent herb germination. In tests of germination using rainwash and concentrated Adenostoma leachate they recorded some decrease in germination at the highest concentrations, although this was not uniform. These findings were partially confirmed by later tests with 11 annual species (Christensen and Muller, 1975). Germination of herbs from samples of chaparral soil, which may have contained leached compounds, was higher when the soil was heated at temperatures of 80-100°C. Christensen and Muller (1975) found no significant increase in germination when herb seeds were heated directly.

Wicklow (1977) tested the effect of ashed and partially burned (charred) stems of Adenostoma on the germination of Emmenanthe penduliflora, a fire annual. Like Sweeney (1956) he obtained no results with completely ashed stems, but he found that charred stems significantly promoted germination. The effect of charred, but not ashed stems on Emmenanthe germination was confirmed by Jones and Schlesinger (1980).

EXPERIMENTAL DESIGN AND METHODS

Experiments were conducted to test both the effect of possible inhibitors such as Adenostoma leachate, and possible stimulants to herb germination such as heating and charred stem material. Since several agents could be acting in concert interaction effects were also tested.

Our initial experiment was a multifactorial test of the effects of heat, Adenostoma leachate charred Adenostoma stems and combinations of these, using 30 species of chaparral herbs (Table 2-5 & Appendix). Follow up experiments were undertaken to further test those factors which significantly affected germination.

Seeds were collected from burned and unburned chaparral of all ages from throughout southern California during June and July 1980. Seeds were collected in paper bags, returned to the lab and sorted free of debris. Cleaned seed was placed in glass jars and stored at room temperature. Seeds of Emmenanthe penduliflora collected in 1st year burns proved inviable so seeds of this species were obtained from C. Jones (Jones and Schlesinger 1980). Only their Santa Monica Mt. population was used.

For heat treatments seeds were counted into lots, placed in glass petri dishes and put in the oven for varying periods as shown in Tables 2-5.

Leachate was prepared according to the technique of McPherson and Muller (1969). Concentrated leachate (4X) was made by evaporating standard leachate and reducing the volume.

Charate was prepared by burning Adenostoma stems of < 1 cm diameter with a propane torch until they were blackened throughout, and then grinding the stems in a Wiley mill to produce a uniform powder. 2.4 ± 0.2 gms of charate were applied to each seed lot to be tested.

Seeds of all treatments were planted in petri dishes on sterilized, screened potting soil, and watered with 25 ml ± 2 of deionized water. The plates were then placed on trays, covered with plastic to retard evaporation and given a cycle of 20 days cold (10°C) and 15 days at room temperature (23°C). All plates were run for three cycles. Scoring took place at 10 days into the first cold treatment and at 5 day intervals after that.

For follow up experiments sorting, handling and planting procedures were the same. A cold treatment of 30 days was applied in some experiments as indicated, with 12 hour light/dark periods at room temperature.

For tests on other shrub species charate was prepared identically. Partial charate was made by burning the stems to the point that some unblackened material remained in the center.

Table 1. Perennial and Annual herbs by groups, in mature and post-fire chaparral (from Keeley et. al. 1981)

Group	Mature Chaparral	Post-fire Chaparral
1-Perennial	Adults and Seedlings, Flowering Rare	Resprouts, Few Seedlings Flowering 1st yr.
2-Perennial	Rare, In Openings	Abundant from Seedlings (1st yr.)
3-Annual	Infrequent, In openings	Abundant for first several years
3-Annual	Rare	Abundant- First Year Only

Grinding was done as described above. Baked stem material was prepared by cutting small segments of branches, less than 1 cm diameter, placing them in foil packages (open) on a metal sheet. These were baked for selected intervals, cooled and ground in the Wiley mill. Quantities applied were 2.4 ± 0.5 gms of charate.

A water extract of fully charred, but not ground Adenostoma stems was prepared by pouring deionized water over the stem sections and watering as described above. Filter paper as well as soil was utilized in this experiment.

For a test of fertilization on germination half-strength and 2X strength Hoagland's solution was used (as determined by package directions). This solution was used instead of deionized water for the experiment. Normally watered plates were used as a control. Cold/warm cycles were as described for the multifactorial experiment.

RESULTS AND DISCUSSION

Results of the multifactorial experiment will be presented using a representative member of each of the four herb groups (Table 1). These species are: Paeonia californica, Group 1; Eriophyllum confertiflorum, Group 2; Oenothera micrantha, Group 3; and Phacelia cicutaria, Group 4. Since several factors were tested singly and in combination, the individual factor responses will be considered first, with selected follow up experiments and then their interactions.

Effect of Leachate

The responses of members of all four groups of herbs to single strength Adenostoma leachate was not significantly different from the control in most cases. Germination was stimulated in some species, no inhibitory effects were seen (Table 2-5).

Table 2. Percent germination of Paeonia californica in response to heat, leachate and charate (N = 8 dishes/ 20 seeds per dish)

	Control	80°C (2 hr)	120°C (5 min)	150°C	P	LSD
Control	67.5	0.6	5.6	1.9	.01	10.4
Leachate	79.4	5.6	20.6	5.0	.01	21.6
Charate	55.0	0.0	12.5	1.3	.01	13.3
Leachate + Charate	41.9	0.0	12.5	0.6	.01	12.9
P	.01	ns	ns	ns		
LSD	16.5					

Germination of the perennials was slightly, but not significantly enhanced with leachate as shown for Paeonia (Table 2) and Eriophyllum (Table 3). Stipa coronata, a group 1 perennial, was significantly enhanced ($P < .01$); no perennial was negatively affected.

The annual species showed a more varied pattern of responses, but none were negative. Group 3 annuals, such as Oenothera micrantha (Table 4) and Cryptantha muricata, Apiastrum angustifolium, Descuriana pinnata, and the generalized exotic Brassica nigra were significantly enhanced by leachate; germination was double that of controls. Fire annuals (Group 4) showed a mixed response to leachate, however. Phacelia cicutaria (Table 5) and P. grandiflora showed significantly enhanced germination, but P. brachyloba, P. fremontii, and Emmenanthe penduliflora showed no effect with germination percentages remaining low ($< 15\%$) in all cases.

The lack of inhibition in herb germination with single strength Adenostoma leachate seen here is similar to the findings of Sweeney (1956),

Table 3. Percent germination of Eriophyllum confertiflorum in response to heat, leachate and charate (N = 8 dishes/ 50 seeds per dish)

	Control	80°C (2 hrs)	120°C (5 min)	150°C	P	LSD
Control	3.8	5.5	3.8	1.0	.05	2.7
Leachate	7.8	5.5	5.5	0.5	ns	
Charate	51.5	58.2	65.7	1.8	.01	11.7
Charate + Leachate	58.3	63.2	65.2	2.8	.01	10.6
P	.01	.01	.01	.01	ns	
LSD	11.8	8.7	9.6			

Table 4. Percent germination of Oenothera micrantha in response to heat, leachate and charate (N = 8 dishes/50 seeds per dish)

	Control	80°C (2 hr)	120°C (5 min)	150°C	P	LSD
Control	30.0	48.5	65.5	69.0	.01	10.2
Leachate	51.7	58.9	58.7	80.0	.01	19.3
Charate	26.0	33.0	22.0	20.0	ns	
Leachate + Charate	45.4	50.7	29.8	58.2	.05	17.8
P	.01	.05	.01	.01		
LSD	20.3	17.8	19.8	17.9		

Muller, McPherson and Hanawalt (1968) and McPherson and Muller (1969). Sweeney (ibid., p. 190) also observed a slight, but non-significant increase in germination in some species. However, McPherson and Muller (1969) did report decreased germination with concentrated leachate, at least for one perennial species, Helianthemum scoparium, and Christensen and Muller (1975) also detected some inhibition with leachate. A follow up experiment was undertaken using 4X concentrated Adenostoma leachate.

Concentrated leachate enhanced the germination of both perennial and annual herb species found within the mature chaparral (Groups 1 & 3, Table 1). The degree of this increased germination varied from a statistically non-significant increase in the case of Paeonia, (control 36.6 pct. germ; 4X leachate, 46.9 pct. germ) or Salvia columbariae (control 6.8 pct. germ; 4X leachate, 14.3 pct. germ, $p < .01$, LSD 15.7) to strongly and significantly enhanced germination in Convolvulus cyclostegius (Control, 5.8 pct. germ; 4 X leachate 12.0 pct. germ, $p < .01$, LSD 5.2) or Descuriana pinnata (Control 19.8 pct. germ; 4X L. 38.0, $p < .01$, LSD 15.4).

The response of fire following perennials and annuals was more heterogenous and included one case of clear inhibition. Helianthemum scoparium was significantly inhibited by high leachate concentrations (Control 16.0 pct. germ., 4X leachate 10.3 pct. germ., $p < .05$, LSD 4.6). This is the same species shown to be inhibited by leachate by McPherson and Muller (1969). Eriophyllum confertiflorum was not significantly affected. None of the fire annuals tested showed a significant effect due to concentrated leachate.

On the basis of both sets of experiments reported here leachate cannot be regarded as a strong deterrent to growth by chaparral herbs. It may actually stimulate growth of those species

tolerant of sub-canopy conditions. The effect of any toxic substances found within leachate, if they are present, may be exerted on the growth and development of herbs once they germinate. This was not tested here.

Effect of Heat

Heat treatments produced variable effects within and between herb groups. In only a few cases did it stimulate germination above control conditions.

For the perennials like Paeonia which appear both before and after fire (Table 2) heating the seeds resulted in decreased germination from the non-heated control. The highest temperature tested, 150°C reduced germination of all species, and was lethal in the case of Zigadenus fremontii and Stipa coronata.

Fire following perennials such as Eriophyllum (Table 3) germinated at low levels under control conditions and with heat. However, Helianthemum scoparium was stimulated at 120°C (Control 23 pct. germ.; 120°C, 43 pct. germ; $P < .01$, LSD 9.6). High temperatures reduced germination to less than 5 percent in both species.

Annuals of Group 3, present before and after fire, showed both strong positive and strong negative responses to heating. Oenothera (Table 4), Lotus salsuginosus, Apiastrum angustifolium and Brassica nigra were significantly enhanced by heating at either 80°C or 120°C, but not at 150°C. In contrast, Salvia columbariae, and Avena barbata were inhibited by heating at even low temperatures (Salvia, Control 29.5 pct. germ.; 80°C 8.8 pct. germ.); other species were not affected except at the highest temperature.

The fire annuals were not affected by heating at moderate temperatures with the exception of Phacelia cicutaria (Table 5). In this species moderate heat stimulated germination above the level of the control. For most other species there was no significant difference at lower temperatures; 150°C was lethal.

Sweeney (1956), Christensen and Muller (1975) and McPherson and Muller (1969) also found that direct heat resulted in little stimulation of germination except in a few species, including Oenothera micrantha and Helianthemum scoparium. For the majority of species they tested germination remained low under heat treatments.

It appears that moderate heat may have some stimulative effect on germination of chaparral herbs, but that this is probably not the major factor promoting germination either before or after fire. Soil heating by sun (Christensen and Muller 1975) and during fire may serve in concert with other factors to promote germination of herbs away from the shrub canopy.

Table 5. Percent germination of Phacelia cicutaria seeds in response to heat, leachate and charate (N = 8 dishes/ 50 seeds per dish)

	Control	80°C (2 hr)	120°C (5 min)	150°C	P	LSD
Control	4.8	10.8	5.8	0.0	.01	6.0
Leachate	12.8	20.3	12.5	0.5	.01	8.7
Charate	32.0	45.2	56.7	0.0	.01	16.2
Leachate + Charate	38.0	51.2	33.2	0.0	.01	12.6
P	.01	.01	.01	.01	ns	
LSD	14.6	10.2	14.6			

Effect of Charate

Charred Adenostoma stems produced significantly enhanced germination in fire following perennials and annuals, but had mixed effects on those species present both before and after fire. Germination of fire preceding perennials like Paeonia did not differ significantly between controls and charate treated seeds (Table 2). For all species tested in this group germination remained within 15 percent of control. Germination of annuals species found before as well as after fire varied. It was similar to control conditions for a number of species: Oenothera (Table 4), Lotus salsuginosus, Apiastrum angustifolium and Descuriana pinnata, and the adventive grass Avena barbata. Brassica nigra was strongly and negatively affected (Control, 24.3 pct. germ. vs 4.0 pct. germ. with Charate). Cryptantha muricata showed significantly enhanced germination with charate (Control, 24.3 pct. germ. vs 66.7 pct. germ. With Charate) as did Salvia columbariae (Control, 29.5 pct. germ., vs. 40.0 pct. germ With Charate).

Fire following perennials like Eriophyllum (Table 3) were strongly enhanced by the addition of charate as were most fire annuals. Germination was strongly stimulated in Phacelia species (Table 5) and P. grandiflora and P. fremontii, in Emmenanthe penduliflora (Table 7), Antirrhinum coulterianum and Chaenactis artemisaefolia. Germination was often less than 10 percent under control conditions for these species and was greatly increased by charate. The magnitude of this response was greater than that observed with leachate or heat for most species.

Given the magnitude of the germination enhancement shown in fire following annuals and perennials further experiments were undertaken to determine the nature of this effect. Charred wood of other chaparral, and non-chaparral species was tested on

Table 6. Effect of charate of chaparral and desert shrubs, and pine on the germination of *Eriophyllum confertiflorum* and *Emmenanthe penduliflora* (N = 5 dishes/ 50 seeds per dish; seeds given 30 day cold treatment, 12 hr lt/dk at room temperature)

	PERCENT GERMINATION	
	<i>Emmenanthe</i>	<i>Eriophyllum</i>
Control	0.0	19.2
CHARATE:		
<u>Species</u>		
<i>Arctostaphylos glauca</i>	6.4	70.0
<i>Ceanothus crassifolius</i>	5.6	71.2
<i>Quercus dumosa</i>	11.6	78.0
<i>Rhus laurina</i>	8.4	77.6
<i>Larrea divaricata</i>	54.8	74.0
<i>Artemisia tridentata</i>	10.0	71.6
<i>Pinus coulteri</i>	13.6	98.0
P	.01	.01
LSD	9.8	20.7

two herbs which had shown significant enhancement with *Adenostoma* charate (Table 6). The results of this experiment indicated that charred wood from other shrubs and Pine also stimulated the germination of these herbs at levels similar to that of *Adenostoma*. (Compare Tables 3 & 5).

A second experiment was conducted to determine if stem material would be effective in stimulating germination if it were only heated, or partially burned. Results of this experiment are shown in Table 7. These results indicated that complete burning was not necessary to produce significant improvement in germination. There was no significant difference between the enhancement of germination observed with partially charred or baked stems. Evidently, whatever the factor responsible for stimulating germination it is produced prior to combustion. The difference in effect of completely and partially charred stems seen here (Table 7) was not confirmed in other tests (unpublished data) using *Emmenanthe* and three other chaparral herb species.

Table 7. Effect of heated, partially and fully charred *Adenostoma* stem material on germination of *Emmenanthe penduliflora* seeds (N = 5 dishes/ 50 seeds per dish; 30 day cold treatment; 12 hr lt/dk at room temperature)

	PERCENT GERMINATION
Control	0.0
Charate	37.3
Partial Charate	68.0
Baked, 260° C (10 minutes)	68.0
Baked, 175° C (30 minutes)	66.0
P	.01
LSD	14.5

An aqueous extract of charred stems was also found to enhance germination of *Eriophyllum*. The effect of this water extract varied with the substrate on which germination trials were conducted. Germination was highest on filter paper (64 pct.) and lowest on soil (12 pct.) with intermediate values for the control (deionized water) on filter paper (40%). Good germination was obtained when charate was applied directly to soil and then watered as usual.

The stimulation of germination by charate, and charate extract, and perhaps by filter paper may reflect some common substance found in treated or processed wood, or it may reflect some property of soil that binds water soluble wood-derived compounds, at least in low concentrations. Further experiments are being conducted to determine if the same results can be obtained on glass filters and/or with other wood products.

Another possible effect of charate might be that of a general fertilizer since nutrients would be released from structural compounds during the burning process. To test this effect, which would be common to any woody species, we applied Hoagland's solution in two concentrations (Table 8). Levels of germination with fertilization were similar to that of controls and significantly lower than with charate and water. Apparently the effect of charred stems is not due to increased nutrients.

Germination was enhanced to a greater degree in most fire following species with the addition of charate than by any other single factor tested. From our data it is apparent that charred wood from both chaparral and non-chaparral species is equally efficacious. Its effect is probably due to some common, although unknown, property of wood.

Table 8. Effect of fertilization using Hoaglands solution in 2 concentrations and the effect of charate on the germination of Eriophyllum confertiflorum and Chaenactis artemisaefolia (N = 8 dishes/ 50 seeds per dish)

	PERCENT GERMINATION	
	<u>Eriophyllum</u>	<u>Chaenactis</u>
Control	10.5	27.2
½ X Hoaglands	8.8	29.3
2X Hoaglands	2.8	25.8
Charate	60.8	86.5
P	.01	.01
LSD	12.7	9.9

Even though the exact basis for this stimulation of germination is unclear, charate evidently provides a very precise, and in some species, e.g. Emmenanthe an obligate cue to germination. This sort of cue to fire would seem to be highly adaptive to annual species, with high light requirements and low competitive ability. The only time such conditions are readily available in the chaparral is after fire when shrubs are temporarily removed. Such a close tracking of the environment suggests a long association between fire and the flora of the chaparral.

Interactions

Although interactions between heat, charate and leachate are likely to occur at some point in the fire cycle, such combined effects are apparently limited (Tables 2-5). For perennial species present before and after fire such as Paeonia (Table 2), Zigadenus fremontii and Marah macrocarpa germination was best under control conditions. The combination of leachate and low heat did stimulate germination in some cases, but was not significantly different from controls. Charate plus leachate, plus heat produced significantly lower germination than either alone, and again less than the control.

The annual species present before as well as after fire germinated best with the addition of leachate and in some with the combination of leachate and moderate heat (Table 4). Oenothera responded strongly to heating, including heat of 150°C (Table 4), however most other species were negatively affected by this heat. Like Oenothera, Cryptantha muricata, Lotus salsuginosus, Apiastrum angustifolium and Brassica nigra responded significantly to a combination of moderate heat and leachate. For species such as Cryptantha muricata which showed increased

germination with charate, the effect of leachate and charate together was similar to the effect of charate alone. In some cases low heat together with leachate and charate raised the percentage of germination, but this was not significant. In the case of Brassica nigra, which was strongly inhibited by charate alone, the combination of leachate (and heat) and charate significantly increased germination.

The combination of leachate plus moderate heat produced high levels of germination in both annuals and perennials found before fire. These conditions could be expected to occur within the mature canopy and may provide a cue to suitable sites and/or environments. Seeds germinating in response to these factors would provide a low level seedling population in those patches of suitable habitat within the shrub vegetation. The proportion of seeds within each species seed pool which would react to these factors would be expected to be low since the availability of suitable sites would not be great in mature chaparral.

Although these species are present before fire they are also in evidence, and often more abundant after fire. They also germinate well in response to charate. This response would appear to provide a way to track changes in the environment from pre-to post-fire. Conditions for growth of all herbs would be improved when the shrub cover was destroyed and light and nutrients more available. A significant proportion of the seed pool can tolerate, and cue into these conditions. Individual species evidently vary in their responses to combinations such as heat and charate, but a certain number of all species remain, even under the most severe conditions. This may represent the best adaptive compromise to the unpredictable nature of fire within the chaparral.

The responses of fire following annuals and perennials were more strongly cued to charate and the combination of charate plus moderate heat (Tables 3 & 5). Leachate in combination with any of these factors resulted in lower levels of germination than seen with charate alone. For the most part the effect of either leachate and/or high temperatures was ameliorated and enhanced by charate. In Phacelia cicutaria for example (Table 5), germination was greatest with a combination of charate and heat. Such a synergistic effect was observed in other species as well. A positive response to this combination, more than to any single factor would appear to provide a precise way to track fire and the conditions most suitable to growth.

The germination responses of chaparral herbs appear to vary with differences in life history characteristics and in relation to time of fire. For those species which are present both pre- and post-fire germination and growth activities are at a low level until after fire. These species have the ability to germinate under all conditions,

but respond positively to the post-fire environment. This response was strongest in the annuals, perhaps due to their greater light requirements and lower competitive ability than perennials. The fire following species on the other hand, have apparently adapted to germinate only in response to those factors which are present as a direct result of fire. Burned stem material and moderate heat are the result of burning the mature canopy and these effects would gradually dissipate with time. It may be that given the genetic background of these species, particularly the annuals, that fitness is maximized only under post-fire conditions. Although the exact nature of the germination responses observed is not fully understood, it is apparent that the herbaceous component of the chaparral flora is well adapted to the fire cycle. The variety of responses to different germination cues demonstrates the precision of this adaptation.

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LITERATURE CITED

- Christensen, N.L.; Muller, C. H. Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. *Ecol. Monogr.* 45: 29-55; 1975.
- Jones, C. S.; Schlesinger, W. H. *Emmenanthe penduliflora* (Hydrophyllaceae) further considerations of germination response. *Madrono* 27: 122-125; 1980.
- Keeley, J. E.; Keeley, S.C. Post-fire regeneration of southern California chaparral. *Amer. J. Bot.* 68: 524-530; 1981.
- Keeley, S. C.; Keeley, J. E.; Hutchinson, S.-M.; Johnson, A. W. Post-fire succession of the herbaceous flora in southern California chaparral. *Ecology* (in press, 1981).
- Muller, C. H.; Hanawalt, R.B.; McPherson, J.K. Allelopathic control of herbaceous growth in the fire cycle of California chaparral. *Bull. Torrey Bot. Club* 95: 225-231; 1968.
- McPherson, J. K.; Muller, C.H. Allelopathic effects of *Adenostoma fasciculatum*, "chamise," in the California chaparral. *Ecol. Monogr.* 39: 177-198; 1969.
- Munz, P. A. *A California Flora*: Berkeley, Calif.; University of California Press; 1959.
- Sweeney, J. R. Response of vegetation to fire. *U. C. Pub. in Bot.* 28: 143-250; 1956.
- Wicklow, D. T. Germination response in *Emmenanthe penduliflora* (Hydrophyllaceae). *Ecology* 58: 201-205; 1977.

APPENDIX

Herb species tested multifactorial germination experiments. Nomenclature according to Munz (1959)

- Antirrhinum coulterianum* Benth in DC.
Apiastrum angustifolium Nutt. in T. & G.
Avena barbata Brot.
Brassica nigra (L.) Koch.
Calyptridium monandrum Nutt. in T. & G.
Calystegia macrostegia (Greene) Brummit ssp. *arida* (Greene) Brummit
Chaenactis artemisiaefolia (Harv. & Gray) Gray
Claytonia perfoliata (Donn) Howell
Cryptantha muricata (H. & A.) Nels. & Macbr.
Descuriana pinnata (Walt.) Britton ssp. *menziesii* (DC.) Detl.
Dicentra ochroleuca Engelm.
Emmenanthe penduliflora Benth.
Eriophyllum confertiflorum (DC.) Gray
Festuca megalura Nutt.
Gilia splendens Dougl. ex Lindl.
Helianthemum scoparium Nutt.
Lotus salsuginosus Greene
Marah macrocarpa (Greene) Greene
Nicotiana attenuata Torr.
Oenothera micrantha Hornem ex Spreng.
Paeonia californica Nutt. ex T. & G.
Phacelia brachyloba (Benth.) Gray
Phacelia cicutaria Greene
Phacelia fremontii Torr.
Phacelia grandiflora (Benth.) Gray
Phacelia viscida (Benth.) Torr.
Salvia columbariae Benth.
Sisyrinchium bellum Wats.
Stipa coronata Thurb. in Wats.
Zigadenus fremontii Torr.