

ALLELOPATHY AND THE FIRE-INDUCED HERB CYCLE

Jon E. Keeley and Sterling C. Keeley

ABSTRACT. Hypotheses accounting for the fire cycle of few herbs under the chaparral canopy but abundant herbaceous growth after fire are reviewed. Allelopathy, or chemical inhibition by the shrub canopy, is an unlikely explanation for this phenomenon. Two critical observations call into question the validity of this hypothesis. Soils that are heated, produce an herb flush comparable to postfire conditions, but the temperatures sufficient to produce this response are far lower than the temperatures required to degrade "toxic" compounds in the shrub foliage and litter. Also the putative toxic compounds isolated from aqueous extracts of shrub foliage are more abundant in burned soils than in unburned soils. Other evidence bearing on this hypothesis is examined. It is concluded that for many of the postfire species, biotic and abiotic conditions in mature chaparral have selected for seed dormancy mechanisms that delay germination until the first spring after fire.

INTRODUCTION

One noteworthy characteristic of chaparral is the depauperate herbaceous vegetation under the canopy. This near lack of herbs occurs even in relatively open stands and, when chaparral is juxtaposed with herbaceous vegetation such as grassland, this near lack of herbaceous vegetation often extends into a zone 1–2 m around the shrub boundary. In contrast, there is an abundant and diverse herbaceous flora in the first spring after a wildfire (Horton and Krabel 1955, Sweeney 1956, Keeley et al. 1981). The vast majority of this postfire flora are annual species that arise from soil-stored seed.

One explanation for this phenomenon that has received wide attention is the theory that the shrubs produce chemicals that are leached out of the foliage and allelopathically inhibit the germination of herb seeds (Muller 1968). When fire removes the shrub canopy, the seeds are released from the in-

hibitory effects of the allelopathic chemicals. However, other hypotheses have been proposed to account for the fire cycle of depauperate herb growth under chaparral followed by abundant herb establishment after fire. These hypotheses are summarized in Table 1 and this paper will review evidence bearing on each of them.

HO 1: CHEMICAL INHIBITION BY SHRUBS (ALLELOPATHY)

This hypothesis is best summarized by McPherson and Muller (1969) who concluded: "The leaves of mature *Adenostoma fasciculatum* shrubs accumulate toxin on their surfaces during the dry summer months. This toxin is produced as a result of normal metabolism and is water soluble. When the rains of each new growing season commence, the toxin is dissolved and carried to the soil Nearly all seeds in the soil of mature *A. fasciculatum* stands are prevented from germinating by the toxin which is most abundantly present during the normal germination period Under natural circumstances these processes continue until a fire consumes the aerial parts of the shrubs and initiates the fire cycle characteristic of chaparral The fire cycle within *A. fasciculatum* stands is clearly under the control of the allelopathic activities of the shrubs. The fire cycle, furthermore, is not limited to *A. fasciculatum* but occurs in all parts of the chaparral."

Below is a discussion of the evidence for allelopathic suppression of herbs based on field studies, laboratory bioassays, and attempts to isolate allelopathic compounds.

FIELD STUDIES

McPherson and Muller (1969) noted that if the *Adenostoma fasciculatum* canopy were removed,

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1989



NO. 34
SCIENCE SERIES
NATURAL HISTORY MUSEUM
OF LOS ANGELES COUNTY

Table 1. Hypotheses proposed to explain the depauperate herb growth under mature chaparral and luxuriant herb growth after fire.

- Ho 1: Chemical inhibition by shrubs (allelopathy).
Ho 2: Abiotic conditions under shrubs inhibit herb establishment.
Ho 3: Animal predation under the canopy reduces herb survival.
Ho 4: Microbial inhibition in unburned soil.
Ho 5: Seeds fail to germinate in the absence of fire-related cues.

without disturbing the soil, seedling establishment could be increased from 40/m² under the canopy to over 1,000/m² in openings. One conclusion to be drawn from this experiment is that removal of the shrub canopy eliminated the source of chemical inhibitors just as fire would do under natural conditions. However, the herb species making up the bulk of the seedling density in these field trials were not the species most common and characteristic of postburn conditions; rather more than half of the seedling density was due to *Filago californica*, a weedy species found in many different types of disturbances. Typical postfire species were rare or absent in these clearings.

Christensen and Muller (1975a) did further clearing experiments in *Adenostoma* chaparral and reported 6–132 seedlings/m² in fenced artificial clearings in contrast to 1–11 in fenced control plots, and on burned sites they reported densities of 204–238 seedlings/m². However, Christensen (personal communication) reports that not all clearings in his and Muller's study responded with increased herb growth.

Chou and Muller (1972) did similar clearing experiments in *Arctostaphylos glandulosa* chaparral, but after three years observed only 15 seedlings/m².

McPherson and Muller (1969) also showed that if plots of soil, within openings in the *Adenostoma* canopy, were heated to 70°C for a few minutes, and fenced to prevent animal predation, seedling establishment increased an order of magnitude (>700/m²) over fenced unheated control plots. In these soil heating experiments the herb composition was more typical of the postfire species. They suggested two explanations: 1) Soil heating directly stimulated germination of seeds in the soil, or 2) soil heating degraded toxins in the soil that were inhibiting germination. Further experiments in their lab showed no evidence that seeds of species typical of moist burned sites are stimulated to germinate by heat (discussed further under Ho 5) and therefore the second hypothesis would seem to be favored.

However, Christensen and Muller (1975b) took soil samples from beneath *Adenostoma fasciculatum* shrubs, heated them to 100°C for 1 hr, and

returned them to beneath the shrub canopy. These heated (and fenced) plots produced 608 seedlings/m² (mostly postfire type species), and this was an order of magnitude more than in fenced control plots. Since the heated soil had been returned to beneath the shrub canopy, and thus exposure to allelopathic toxins, it was concluded that heating of the soil acted directly on the seeds in stimulating germination.

LABORATORY BIOASSAYS

Sweeney (1956) investigated the hypothesis of allelopathic herb suppression by soaking an unspecified quantity of litter from beneath the *Adenostoma* canopy in water. The inhibitory effects of this leachate were tested on seed germination of native herb species in Petri dishes and in pots of soil. He found no evidence of chemical inhibition. Landers (1962) performed similar trials on annual grassland species and found that in some species, root growth was inhibited by leachate from *A. fasciculatum*, however, the differences in species sensitivity did not correlate with the differences in abundance along a gradient from the shrubs to the grassland.

McPherson and Muller (1969) used bioassays to test the inhibitory properties of aqueous *Adenostoma fasciculatum* leachate. Extracts were derived by soaking 10 g of roots or leaves in 100 ml water for 3 hr with stirring (or 200 g of stems in 500 ml for 6 hr, and concentrated twofold). After filtering, these extracts were soaked up on sponges, placed in Petri dishes, the sponges were covered by filter paper and seeds were sown on top, and the dishes were sealed with parafilm. These extracts showed no significant inhibitory effect on the germination or growth of the non-native grass *Bromus rigidus*. Significant reductions in radical growth of germinating *B. rigidus* could be obtained, however, if leaves were placed directly against the seeds or if an extract was made from leaves homogenized in a Waring blender. A more natural leachate was obtained by collecting throughfall beneath the shrub canopy during rain or by spraying intact foliage with 3 liters of deionized water in a fine mist over a period of 2 hr. Neither of these leachates had any effect on the germination or radical growth of *Bromus rigidus*. If either of these extracts were concentrated 4–10 times by flash evaporation, germination was still unaffected but growth could be significantly inhibited. Similar experiments were attempted on native species. Germination of three species, *Calandrinia ciliata*, *Helianthemum scoparium*, and *Silene multinervia*, was significantly inhibited by a 10× concentrate of leachate, if the seeds were first scarified with a knife.

Christensen and Muller (1975a) performed further bioassay experiments with *Adenostoma* leachate applied on sponges, sand, or glass wool as the incubation media. They found that *Adenostoma* leachate, prepared as in the previous study, inhibited the radical growth of all native species, and to

a greater degree than in *Bromus rigidus*. Germination of the native *Cryptantha intermedia* and *Erigeron divergens*, and the non-native ruderal species *Lactuca serriola* and *Centaurea melitensis* was strongly inhibited by leachate. This inhibition was shown to be reversible upon removal of the plant extract. Germination, however, was not inhibited in the more typical fire-following chaparral species, *Lotus scoparius*, *Convolvulus cyclostegius*, *Allophylum glutinosum*, *Emmenanthe penduliflora*, *Eucrypta chrysanthemifolia*, and *Phacelia grandiflora*.

Bioassays of *Arctostaphylos glauca* leaf extracts, using techniques similar to McPherson and Muller (1969), showed inhibition of radical growth of 11 herb species (Hanawalt 1971). Germination was also inhibited in most species; these, however, were grassland species that are seldom found on recently burned sites.

Chou and Muller (1972) did bioassays of *Arctostaphylos glandulosa* leaves. They found that a 5% aqueous extract (5 g powdered leaves, roots, or bark, to 95 ml distilled water, shaken for 2 hr) applied to seeds on sponges or in sand, significantly reduced radical growth in the non-native *Avena fatua*, *Bromus mollis*, *B. rigidus*, *Raphanus sativus*, and the native *Festuca megalura*. Leachate, prepared by spraying branches, was also shown to inhibit radical growth of *Bromus rigidus*, and inhibition increased with increasing concentration of the extract.

Keeley et al. (1985) surveyed typical postfire chaparral herbs for inhibitory effects of *Adenostoma fasciculatum* leachate on seed germination. Leachate was prepared by spraying branches as described in Christensen and Muller (1975a), but was applied to seeds in soil. Significant inhibition was observed for only three of 30 species tested, *Apiastrum angustifolium*, *Cryptantha muricata*, and *Helianthemum scoparium*, and only if the leachate was concentrated fourfold. Surprisingly, in eight other species, concentrated leachate stimulated higher germination, possibly due to the high NO_3^- levels present in leachate.

Soil collected from beneath *Arctostaphylos glandulosa* shrubs inhibited radical growth of test species (Chou and Muller 1972), but soil collected from beneath *Adenostoma fasciculatum* shrubs did not unless 4 \times -concentrated leachate was added (McPherson and Muller 1969).

Chou and Muller (1972) found that *Arctostaphylos* leaf material had to be heat-treated to 180°C for 2 hr before toxicity of water extracts was destroyed. This calls into question the relevance of bioassays to field experiments described above where germination was induced by heating soil to 70°C. Stowe's (1979) conclusion "that perhaps any species can be shown to have allelopathic properties in bioassays, and that bioassays may, for many communities, have no ecological meaning," is supported by studies of Heisey and Delwiche (1983, 1985).

Beyond the obvious problems of attempting to

relate bioassay results to field conditions, the majority of studies on the allelopathic control of the "chaparral herb fire cycle" have had two characteristics that limit their usefulness in evaluating that hypothesis. The primary problem involves the failure to focus on the potential for chemical inhibition of germination. If chemicals leached from the shrubs inhibit the growth of seedlings beneath the canopy, this says something about the hospitableness of that environment. However, unless the seeds are inhibited from germinating, there is no possibility for a flush of herbs after fire. Second, the dependence upon testing non-native species, which seldom are part of the postfire flora, suggests little appreciation for the potential for evolutionary adaptation by the local flora.

ALLELOPATHIC COMPOUNDS

In studies where inhibition of radical growth occurs after application of *Adenostoma* or *Arctostaphylos* leachate, evidence has been presented showing that the inhibitory effect is not due to pH or osmotic effects (McPherson and Muller 1969, McPherson et al. 1971, Chou and Muller 1972, Christensen and Muller 1975a).

Leachate from *Adenostoma fasciculatum* foliage has been separated chromatographically and components tested separately for toxicity. Several phenolic compounds, vanillic acid, umbelliferone, *p*-hydroxybenzoic acid, ferulic acid, hydroquinone, and *p*-coumaric acid have been shown to produce complete inhibition of *Lactuca sativa* (lettuce) seed germination (McPherson et al. 1971). Most of these phenolics, however, had no effect on radical growth of *Bromus rigidus* (Christensen and Muller 1975a). In both of these studies, toxicity was present in unidentified compounds that separated out in 2% acetic acid solvent at $R_f = 0.8-1.0$.

One phenolic compound, umbelliferone, separated from *Adenostoma* leachate, was shown to inhibit elongation of *Cucumis sativus* (cucumber) roots, and this effect was fully reversible if the toxin was diluted or removed (Jankay 1973).

Chou and Muller (1972) separated compounds from *Arctostaphylos glandulosa* leachate and found that some of the same phenolics isolated from *Adenostoma* leachate were present, and inhibitory to *Lactuca sativa* germination and growth. A number of unidentified compounds were isolated and showed very high toxicity. These may be the same as the unidentified toxic compounds reported for *Adenostoma* as they migrated the same distance in the 2% acetic acid solvent.

Chou and Muller (1972) also demonstrated that some of the phenolic compounds such as hydroquinone, with demonstrable toxicity, were present in *Arctostaphylos glandulosa* leaves and leaf litter, but absent from soils. One explanation is that some of these compounds may be microbially degraded in the soil. If that were true one would predict that the longevity of these phenolic compounds in soils

would be inversely related to carbon substrate content. Experiments by Chou and Muller (1972) showed that, in fact, this is true. Relative to bare mineral soil, most of these phenolic compounds have a relatively short residence time in organic soils collected from beneath the shrubs.

McPherson et al. (1971) and Chou and Muller (1972) found that most of these phenolic compounds had to be present in quantities above 100 ppm and often as high as 400 ppm in order to inhibit radical growth of *Lactuca sativa*. Although many of these phenolic compounds are present in soil beneath *Adenostoma* and *Arctostaphylos* shrubs (McPherson et al. 1971, Chou and Muller 1972), Kaminsky (1981) reported that throughout most of the year, total available phenolics in soil beneath *Adenostoma* are far lower than these levels. Kaminsky (1981) also demonstrated that soil particles had a far greater affinity for adsorption of these compounds than did seed coats of the native herb *Dicentra ochroleuca*.

Christensen and Muller (1975a) noted that on all dates sampled, the "toxic" phenolic compounds extracted from *Adenostoma* leachate, occurred in much greater abundance in soils from recently burned sites than in soils from beneath the mature shrub canopy. This finding calls into question the notion that the abundant herb growth after fire is the result of release from allelopathic inhibition, at least by these toxins.

HO2: ABIOTIC CONDITIONS UNDER SHRUBS INHIBIT HERB ESTABLISHMENT

Levels of light, soil moisture, and inorganic nutrients could potentially inhibit herb growth under the mature chaparral canopy. Herbs may be released from this inhibition by changes in these conditions after fire.

Irradiance at the soil surface is much higher after fire, but before fire it is unclear whether irradiance levels under the shrub canopy are inhibitory to herb growth. McPherson and Muller (1969) reported irradiances along a transect ranged from <30% to >90% of full sunlight with a mean of 65%. Miller et al. (1981) reported that chaparral canopies intercepted 51–88% of the direct solar irradiance, with the higher levels during the winter and early spring, the time of growth for most chaparral herbs. Light compensation points are unknown for the postfire herb species, but some are known to have much higher photosynthetic rates than are found in the dominant shrubs, and this would be consistent with having a high light requirement (Oechel et al. 1981). *Avena fatua*, although not a postfire herb species, but one which is common in California grasslands, has been shown to be excluded from beneath oak canopies due to low light intensities (Mahall et al. 1981). Also McPherson and Muller (1967) provided evidence for light limitations playing a major role in the elimination of *Salvia mellifera* shrubs from beneath the canopy of *Ceanothus* chaparral.

Soil moisture levels in mature chaparral soils are equal to or higher than in soils from recent burns (Christensen and Muller 1975a), thus soil moisture alone cannot account for the herb fire cycle. However, Mahall and Schlesinger (1982) noted that *Ceanothus megacarpus* seedlings had much lower water-use efficiency under low irradiance (similar to beneath the shrub canopy) than under high irradiance (typical of burned sites).

Soil concentrations of inorganic nutrients are quite different between burned and unburned sites. Under the chaparral canopy they potentially are limiting to growth of herbs (Christensen and Muller 1975a, b, Rundel and Parsons 1980, 1984, Gray and Schlesinger 1981). Postfire conditions typically represent nutrient rich sites, at least for the first year or two. As soil nutrient levels decrease after fire, selection should favor herbs with enhanced nutrient-use efficiency. However, this may require compromises such as the tradeoffs Field et al. (1983) showed between nutrient-use efficiency and water-use efficiency in chaparral shrubs.

Taken all together, it would appear that the abiotic conditions under the chaparral canopy are far less conducive to herb growth than on burned sites. It is unlikely that these abiotic factors act directly to inhibit germination. Most chaparral species fail to germinate in the dark, but light levels under the canopy are insufficient to produce this effect (Keeley 1984, 1987). Inorganic nutrients do stimulate germination of some species (Keeley et al. 1985) but failure to germinate due to low soil nutrient levels cannot account for the difference in herb densities between mature chaparral and recently burned sites (Christensen and Muller 1975b).

HO 3: ANIMAL PREDATION UNDER THE CANOPY REDUCES HERB SURVIVAL

Populations of rabbits (*Sylvilagus* sp.), mice (*Peromyscus* sp., *Perognathus* sp.), and woodrats (*Neotoma* sp.) are common in chaparral and have a very marked impact on survival of herbs. McPherson and Muller (1969) recorded seedling densities under chaparral increased from 11/m² in control plots to 70/m² in plots fenced from rodents, and Quinn (1986) reported similar findings: 6–15 seedlings/m² in fenced exclosures vs. 0–3 in unfenced plots. Christensen and Muller (1975b) heat treated soil and produced the abnormally high seedling density of >600/m² under the shrub canopy, but outside of fenced exclosures, none of the seedlings survived through the spring. In the absence of herbaceous species, rodents such as woodrats survive on foliage and fruits from the mature shrub vegetation (Horton and Wright 1944).

The impact of rodents on herbaceous species survival extends beyond the border of chaparral and is one explanation for the typical bare zone that separates chaparral and grassland (Bartholomew 1970, Bradford 1976, Quinn 1986).

Survival of wildfires is precarious for many of the

Table 2. Germination of selected chaparral herbs and suffrutescents in response to 120°C for 5 minutes or application of powdered charred wood to the germination medium (n = 5 dishes of 50 seeds each). Statistical analysis was with ANOVA on arcsine transformed data; ns = no significant difference between treatments (P > 0.05); treatments with the same superscript are not significantly different at P > 0.05 with the Student-Newman-Keuls procedure. Data from Keeley and Keeley (1987).

		Percentage germination			P
		Control	120°C, 5 min	Charred wood	
<i>Antirrhinum coulterianum</i>	(Scrophulariaceae)	2 ^a	3 ^a	42	<0.001
<i>A. nuttallianum</i>	(Scrophulariaceae)	69 ^a	56 ^a	58 ^a	ns
<i>Camissonia californica</i>	(Onagraceae)	3 ^a	6 ^a	49	<0.001
<i>C. hirtella</i>	(Onagraceae)	30 ^a	66	26 ^a	<0.001
<i>Clarkia unguiculata</i>	(Onagraceae)	61 ^a	65 ^a	68 ^a	ns
<i>Collinsia parryi</i>	(Scrophulariaceae)	24	12	77	<0.001
<i>Cordylanthus filifolius</i>	(Scrophulariaceae)	57 ^a	27	62 ^a	<0.01
<i>Dichelostemma pulchella</i>	(Amaryllidaceae)	100	1	64	<0.001
<i>Gilia australis</i>	(Polemoniaceae)	31 ^a	32 ^a	80	<0.001
<i>Madia gracilis</i>	(Asteraceae)	86 ^a	45	86 ^a	<0.05
<i>Penstemon spectabilis</i>	(Scrophulariaceae)	1 ^a	3 ^a	61	<0.001
<i>Pterostegia drymarioides</i>	(Polygonaceae)	68	30	47	<0.01
<i>Rafinesquia californica</i>	(Asteraceae)	4 ^a	3 ^a	55	<0.01
<i>Romneya trichocalyx</i>	(Papaveraceae)	0 ^a	0 ^a	44	<0.001

small mammals in chaparral. In a bizarre experiment in which caged animals were placed in chaparral prior to a controlled burn, Howard et al. (1959) determined that temperatures >60°C were lethal to most species. Consequently populations of species that live aboveground, e.g., woodrats, but also rabbits, are drastically reduced by fire (Chew et al. 1959, Lawrence 1966, Wirtz 1982). Populations of other species are reduced by fire and are subject to greater predation in the more open conditions after fire. Typically, small mammal populations are greatly reduced in the first spring after fire. However, rabbits and rodents invade recently burned sites, and may account for a significant level of seedling mortality (Mills 1986). Many herbaceous and shrub seedlings, however, survive on burned sites, although exclosures result in greater seedling survival (Quinn 1986).

HO 4: MICROBIAL INHIBITION IN UNBURNED SOIL

Sweeney (1956) noted that inhibition of seed germination by *Adenostoma leachate* was readily overcome by aerating the solutions and he proposed that microbes could be responsible for inhibiting germination in chaparral soil by depleting oxygen levels.

Kaminsky (1981) hypothesized that microbes in the soil beneath chaparral produced chemicals that inhibited germination of the native herbs. He showed that microbes in the soil beneath *Adenostoma fasciculatum* produced chemicals that inhibited the germination of *Lactuca sativa* seeds. Pack (unpublished data) repeated these experiments using native species and found no evidence to support

the theory. It is particularly difficult to accept the conclusion that "microbially produced toxins could account for the lack of an herbaceous understory in stands of mature *Adenostoma* as well as the flush of herbs following a fire" (Kaminsky 1981), since Christensen and Muller (1975a) had previously reported that bacterial and fungal populations were at least one to two orders of magnitude higher in burned soils than in unburned soils.

HO 5: SEEDS FAIL TO GERMINATE IN THE ABSENCE OF FIRE-RELATED CUES

Seeds of herbaceous and shrub species exhibit a range of germination behaviors. Some species germinate readily upon wetting and incubation at spring temperatures. In other species, all or a portion of the seeds will not germinate unless they receive some particular treatment (Table 2).

Heat-stimulated germination has been documented for many species (Quick and Quick 1961, Stone and Juhren 1951, 1953, Christensen and Muller 1975a, b, Keeley et al. 1985, Keeley 1987). Under natural conditions seeds of these species may lie dormant in the soil until exposed to temperatures sufficient to stimulate germination. This may occur on sites devoid of shrubs where soil temperatures can exceed 70°C (Christensen and Muller 1975a) or on burned sites.

Wicklow (1977) and Jones and Schlesinger (1980) demonstrated that one of the most widespread postfire chaparral herbs, *Emmenanthe penduliflora*, is stimulated to germinate in the presence of charred *Adenostoma* wood. It is now clear that this germination behavior is widespread in chaparral herbs and shrubs, being documented from over two doz-

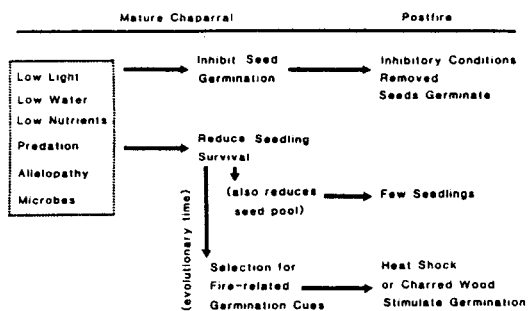


Figure 1. A model relating the effect of biotic and abiotic conditions under the chaparral canopy to germination and survival of postfire herbs.

en species in many different families (Keeley et al. 1985, Keeley 1987, Keeley and Keeley 1987).

An example of the germination response to heat, charred wood, or no treatment at all for a selection of herbaceous species commonly encountered on burned sites is shown in Table 2. It would appear that in nature, a substantial portion of the seed pool of some species is unlikely to germinate in the absence of fire. However, a portion of the seed pool of these species, as well as the bulk of the seed pool for other species is potentially capable of germinating in the absence of fire. Our understanding of the germination physiology of these species, with respect to chemicals in the soil environment and the effect of temporal changes in ambient temperature and moisture, is too premature to predict the fate of these seeds.

CONCLUSIONS

A model relating these hypotheses to the cycle of herbaceous growth before and after fire is shown in Figure 1. We assume some or all of the factors discussed in hypotheses 1-4 produce conditions unfavorable for herbaceous growth under the chaparral canopy. These conditions can have two outcomes; either they 1) inhibit seed germination or 2) reduce seedling survival.

Evidence discussed above suggests the first outcome is not very likely. There are few data showing abiotic conditions under the canopy are sufficient to inhibit the germination of most chaparral species. Also it is difficult to imagine a mechanism by which predation could inhibit germination. Additionally, the evidence that allelochemicals from either plants or microbes play a dominant role in inhibiting germination of the vast majority of chaparral species is weak. At the very least, work to date indicates a range of species-specific tolerances to chemicals produced in the understory environment.

Evidence presented above supports the second outcome, viz., that biotic and abiotic factors under the chaparral canopy may lead to reduced seedling survival. However, if seedlings do not survive to maturity, the seed pool under the canopy will, with

time, be depleted and those species will be poorly represented in the postfire flora. The obvious fate for annual species that germinate, but fail to survive under the canopy, is extinction. We subscribe to the conclusions of Christensen and Muller (1975b) that "numerous ecological factors associated with the chaparral understory result in an extremely low probability of seedling survival. Among these are animal grazing, low soil fertility, plant toxins and, perhaps, low light levels. Following fire, the negative effect of each of these factors is removed or reduced. This has resulted in selection for dormancy mechanisms in some species which minimize seed germination during periods of low survival probability."

Although many chaparral species have such dormancy mechanisms that insure recruitment in the postfire environment, a number of species do not. Germination appears to occur readily upon wetting. Some of these species are common in gaps within the chaparral canopy and on other sorts of open sites. However, if germination occurs under the shrub canopy, these species seldom survive. It is in these particular species that we might expect to see a role for chemical inhibition of germination. In fact in studies by Christensen and Muller (1975a) and Keeley et al. (1985), those species where germination was inhibited by aqueous extracts of shrubs are the species commonly encountered in openings within the chaparral mosaic. While this may represent allelopathic inhibition, it clearly is not of the form Muller (1974) described as allelopathic exclusion of invader species by the dominants. Rather, if allelopathy plays a role in chaparral, it may well be one of selecting for chemical inhibition of germination in gap type herbaceous species.

ACKNOWLEDGMENTS

We thank Norm Christensen and Mary Carroll for helpful comments on these ideas.

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