

# Seed Germination and Life History Syndromes in the California Chaparral

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## Abstract

Syndromes are life history responses that are correlated to environmental regimes and are shared by a group of species (Stebbins, 1974). In the California chaparral there are two syndromes contrasted by the timing of seedling recruitment relative to wildfires. One syndrome, here called the fire-recruiter or refractory seed syndrome, includes species (both resprouting and non-resprouting) which share the feature that

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the timing of seedling establishment is specialized to the first rainy season after fire. Included are woody, suffrutescent and annual life forms but no geophytes have this syndrome. These species are linked by the characteristic that their seeds have a dormancy which is readily broken by environmental stimuli such as intense heat shock or chemicals leached from charred wood. Such seeds are referred to as "refractory" and dormancy, in some cases, is due to seed coat impermeability (such seeds are commonly called hardseeded), but in other cases the mechanism is unknown. Seeds of some may require cold stratification and/or light in addition to fire related stimuli. In the absence of fire related cues, a portion or all of a species' seed pool remains dormant. Most have locally dispersed seeds that persist in the soil seed bank until the site burns. Dispersal of propagules is largely during spring and summer which facilitates the avoidance of flowering and fruiting during the summer and fall drought. Within a life form (e.g., shrub, suffrutescent, etc.), the seeds of these species have less mass than those of species with non-refractory seeds and this possibly reflects the environmental favorableness of the postfire environment for seedling establishment. Regardless of when fire occurs, germination is normally delayed until late winter or early spring. In the absence of fire, or other disturbance, opportunities for population expansion are largely lacking for species with this syndrome.

The other syndrome, here called the fire-resister or non-refractory seed syndrome, includes species that are resilient to frequent fires (mostly by vegetative resprouting), but require fire-free periods for recruiting new seedlings. Included are shrubs, subshrubs, suffrutescents, lianas, geophytes and annuals. All are linked by the characteristic that their seeds germinate in the absence of cues related to wildfires. In many cases no form of seed dormancy is present and the seeds germinate soon after dispersal; consequently these species do not accumulate a persistent seed bank. Germination and seedling establishment is independent of fire and thus opportunities for population expansion are also independent of fire. The demographic pattern of seedling recruitment varies with the life form. For shrubs, seedling recruitment may be restricted to sites free of fire for periods of a hundred years or more. Recruitment appears to require relatively mesic conditions and this may account for the patchy distribution of these species within the matrix of relatively arid sites. Finding such sites has selected for propagules specialized for wind or animal dispersal; the majority are bird dispersed. These shrub species all disperse fruits in fall and winter and this may have been selected to take advantage of migratory birds as well as to time dispersal to the winter rains typical of the mediterranean-climate. Germination typically occurs within several weeks of the first fall or winter rains. Maturation of flowers and fruits during the summer and fall drought may account for the distribution of these species on more mesic sites. Seed mass of these species is large and this may have been selected to provide an advantage to seedlings establishing under the canopy of this dense shrub community.

### Resumen

Síndromes son las respuestas de ciclos biológicos correlacionados con regímenes ambientales y compartidos por un grupo de especies (Stebbins, 1974). En el Chaparral de California se encuentran dos síndromes, los cuales contrastan por el tiempo requerido para el restablecimiento de retoños en relación con los incendios forestales. Uno de estos síndromes, aquí denominado "síndrome fuego-restablecedor" o "se-

milla refractaria,” incluye especies (tanto retoñantes como no retoñantes) que comparten la característica de que el tiempo para el establecimiento de plántulas está especializado en la primera estación de lluvias después del incendio. Incluidas se encuentran formas de vida anuales, sufrutescentes y leñosas, sin embargo ninguna hierba perenne presenta este síndrome. Estas especies están unidas por la característica de poseer semillas con una latencia fácilmente interrumpida por estímulos ambientales, tales como un intenso shock de calor o productos químicos lixiviados de madera carbonizada. A este tipo de semillas se les conoce como refractarias. En ocasiones, su latencia se debe a la impermeabilidad de la capa de la semilla. En otros casos, el mecanismo es desconocido. Además de los estímulos relacionados con el fuego, las semillas de algunas especies pueden requerir de una estratificación fría y/o de luz. En ausencia de indicadores relacionados con el fuego, una parte o todo el grupo de semillas de una especie permanece latente. La mayoría cuenta con semillas dispersadas localmente, las cuales permanecen en el banco de semillas en el suelo, hasta que el lugar sufre de un incendio. La dispersión de semillas ocurre principalmente durante la primavera y el verano, lo cual impide el florecimiento y producción de frutos durante la sequía del verano y otoño. Dentro de una forma de vida, las semillas de estas especies tienen una masa menor a la de aquellas especies con semillas no refractarias, lo cual refleja posiblemente el favorecimiento ambiental del ambiente posterior a un incendio en cuanto al establecimiento de plántulas. Sin tomar en cuenta cuando ocurre el incendio, la germinación se retrasa normalmente hasta finales del invierno o principios de la primavera. En ausencia de incendios o cualquier otra alteración, las oportunidades de expansión de la población son casi nulas para las especies con este síndrome.

El otro síndrome, aquí denominado “resistidor de fuego” o “semilla no refractaria,” incluye especies resistentes a incendios frecuentes (por retoño vegetativo en su mayoría), las cuales requieren, sin embargo, períodos libres de incendios para restablecer nuevas plántulas. Entre las especies incluidas se encuentran arbustos, subarbustos, sufrutescentes, lianas, hierbas perennes y anuales. Todas están unidas por la característica de tener semillas que germinan en ausencia de indicadores relacionados con incendios. En muchas ocasiones, las semillas no presentan latencia alguna y germinan poco después de su dispersión. Por consiguiente, estas especies no acumulan un banco de semillas persistente. La germinación y establecimiento de plántulas es independiente del fuego y, por lo tanto, las oportunidades de expansión para la población son asimismo independientes del fuego. El patrón demográfico de restablecimiento de plántulas varía de acuerdo a la forma de vida. En el caso de los arbustos, el restablecimiento de plántulas puede estar restringido a sitios libres de incendios por períodos de cien años o más. El restablecimiento parece requerir condiciones relativamente mésicas, lo cual puede ser la causa de la distribución desigual de estas especies dentro de una matriz de sitios relativamente áridos. El encontrar estos sitios ha seleccionado en favor de las semillas especializadas en dispersión por viento o a través de animales. La mayoría son dispersadas por aves. Todas estas especies de arbustos dispersan sus frutos durante el otoño e invierno, lo cual puede haber sido seleccionado para obtener ventaja de las aves migratorias, así como para programar la dispersión de acuerdo con las lluvias de invierno, típicas del clima mediterráneo. La germinación ocurre típicamente por varias semanas durante las primeras lluvias de otoño o invierno. La maduración de las flores y frutos durante la sequía del verano y otoño puede explicar la distribución de estas especies en sitios más mésicos. Las

semillas de estas especies son de masa considerable, lo cual puede haber sido seleccionado para proporcionar una ventaja al establecimiento de plántulas bajo el follaje de esta densa comunidad de arbustos.

## I. Introduction

California chaparral is often characterized as an evergreen shrub vegetation well adapted to recurrent wildfires. While it is true that evergreen shrubs dominate, and many exhibit characteristics best interpreted as evolutionary responses to wildfire, the chaparral community exhibits considerably more diversity than the above statement conveys (Keeley & Keeley, 1988). Not all shrub species show evidence of fire adaptation and in addition to shrubs, chaparral is comprised of semi-deciduous subshrubs, suffrutescents, lianas, geophytes and annuals. Seed germination patterns are also diverse in the chaparral flora. Here I will relate what is presently known of seed germination modes to other reproductive characteristics and discuss how these traits are correlated to produce different life history syndromes.

## II. Wildfires and Life History Modes

Wildfires are a common feature of the chaparral environment and the community is resilient to such perturbations; community structure is altered only briefly and, under most burning regimes (but cf. Zedler et al., 1983), the species composition at a given time after fire does not change noticeably from one fire cycle to the next. However, resilience to a perturbation such as wildfire does not imply that resilient species have evolved traits adapted to such disturbance. This is particularly true in chaparral. Part of the woody and herbaceous flora recover after wildfires by resprouting from belowground vegetative structures; a very widespread trait in the plant kingdom best interpreted as a preadaptation to surviving fires (Wells, 1969). Thus, some species persist in the fire-prone chaparral but do not seem to benefit from fires, and very little about their life history can be interpreted as an adaptation to fire (Zedler, 1981; Keeley & Keeley, 1988). Those chaparral species that most clearly illustrate adaptation to fire are ones that have adapted their seed germination physiology to cue timing of seedling establishment to the post-fire environment.

In summary, within the chaparral flora one can delineate taxa that are resilient to periodic wildfires but show no specialized adaptations to such perturbations. Seedling recruitment does not occur after fires and seedling establishment and potential population expansion occur only under fire-free conditions. These taxa are referred to as "fire-persisters" or "obligate-resprouters." In contrast, other taxa are not only resilient to fires but have specialized the timing of seedling recruitment to coincide with postfire conditions. In these species opportunities for population expansion are restricted to postfire environments. These taxa are referred to as "fire-recruiters" or "seeders" (both facultative- and obligate-seeders). An example of the demographic patterns generated by these two modes is shown in Figure 1. Not surprisingly, fire-persisters and fire-recruiters have evolved markedly different seed germination characteristics and these are correlated with other reproductive and demographic characteristics to produce two life history syndromes.

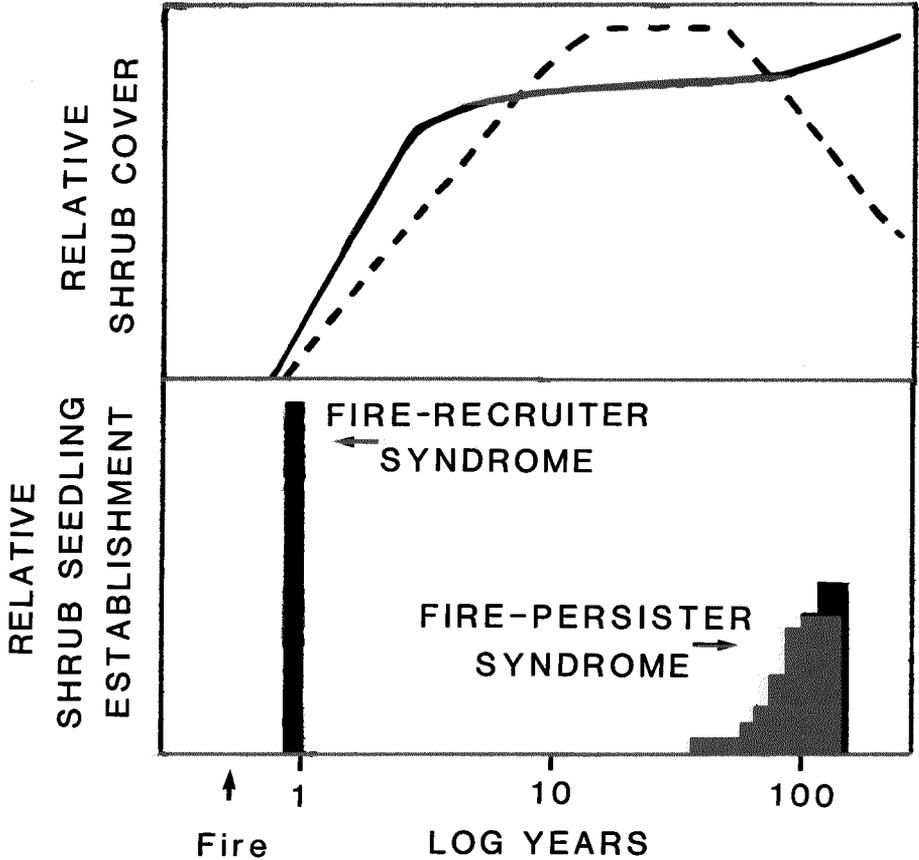


Fig. 1. Changes in shrub cover and seedling recruitment after fire for refractory seeded 'fire-recruiter' species (dashed line) (see Tables I and II) and non-refractory seeded 'fire-persister' species (solid line) (Table VIII) in the California chaparral (Keeley & Keeley, 1988).

### III. Seed Germination Physiology

Following dispersal, seeds are quiescent until placed under "adequate" moisture and temperature conditions. Viable seeds that fail to germinate under such conditions are considered dormant (Bewley & Black, 1982). Dormancy is imposed by a block to germination that may be eliminated by time (i.e., an after-ripening period) or by some environmental factor. It should be noted that the conditions necessary for eliminating dormancy may not be conditions conducive to the germination process itself. Also a state of dormancy is not always a static condition but some seeds may go through cycles of dormancy and non-dormancy, often induced by environmental conditions. Likewise the conditions suitable for germination may change with time or with changes in the environment. Finally, the requirements for germination or for overcoming dormancy are not necessarily identical for all seeds from the same parent; i.e., there may be genetic or somatic differences.

To clarify this rather complicated phenomenon, authors have proposed different categories of seed dormancy. Harper (1977) delineates "induced," "enforced" and "innate" dormancy. Induced dormancy is an acquired inability to germinate, due to some environmental condition experienced by the seed after being shed from the parent, and is what most other authors refer to as secondary dormancy. Enforced dormancy is imposed by an environmental restraint such as lack of light or presence of an ambient inhibitor to germination. Innate dormancy is what most other authors call simply dormancy or primary dormancy.

Although induced (secondary) seed dormancy may operate in chaparral taxa, relatively little is documented on this phenomenon. Potential examples are mentioned in Emery (1988) who notes that in some Californian plants fresh seeds germinate readily whereas older seeds require a treatment to break dormancy.

Enforced seed dormancy has been proposed as a major factor in chaparral. McPherson and Muller (1969) concluded that "Nearly all seeds in the soil of mature *A[denostoma] fasciculatum* stands are prevented from germinating by the toxin" which is continually leached from the shrubs. They contended that dormancy was enforced by this allelopathic effect "until a fire consumes the aerial parts of the shrubs." Early studies that supported this hypothesis investigated the allelopathic inhibition of seedling growth. More recent studies that have focused on seed germination, have demonstrated that allelopathic toxins are not likely to play a role in enforcing dormancy of chaparral seeds (Christensen & Muller, 1975a, 1975b; Kaminsky, 1981; Keeley & Keeley, 1989; Keeley et al. 1985). Christensen and Muller (1975b) "concluded 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." While not discounting a possible role for allelopathy in chaparral, it clearly is not a major factor in the germination of chaparral seeds.

Innate dormancy can be subdivided into four types (Harper, 1977). (1) Embryos may be rudimentary at dispersal and breaking of dormancy requires an after-ripening period of development. (2) A biochemical "trigger" within the embryo is needed to initiate the germination process and this trigger is switched on by an environmental stimulus such as a period of cold weather; a process known as stratification. (3) Seeds may contain an inhibitor that needs to be leached from the seed; for example, seeds of fleshy fruited species typically require the removal of the fruit pulp before germination will proceed. (4) The seed coat (or membranes beneath the testa or tissues such as an endocarp or pericarp that surround the seed) may act as a physical barrier to water and gases. The physical or chemical breaking of one or more of these barriers may be required before dormancy is removed; a process known as scarification.

There is evidence that all four of these modes of dormancy are present in the Californian flora (Atwater, 1980; Emery, 1988). However, in the literature on seed germination characteristics of chaparral taxa these mechanisms have not been the focus of study. For obvious reasons the primary focus has been the degree to which breaking of dormancy requires a stimulus that would cue germination to postfire conditions. In this regard, we know that seeds of some species fail to germinate when incubated under a wide variety of moisture and temperature conditions. However, if such seeds are subjected to a stimulus that simulates a fire, dormancy will be

broken. Sweeney (1956) and others have referred to seeds of these species as "refractory" and two stimuli, intense heat shock and chemical(s) from charred wood, are known to overcome dormancy of such refractory seeds (Keeley & Keeley, 1989). However, not all chaparral species have refractory seeds.

#### IV. Seed Germination, Fire and Life History Modes in Chaparral

Here I will attempt to categorize chaparral taxa as to whether or not they have refractory or non-refractory seeds. Several caveats are in order. Refractory seeds, in nature, "require" a fire related stimulus, alone, or in conjunction with other conditions such as a cold stratification period. Species categorized as having refractory seeds may have polymorphic seed pools of both refractory and non-refractory seeds. Classification of a species is based on the observation that the percentage of seeds that germinate increases significantly after intense heat shock or incubation with charred wood (the only known fire related stimuli). Non-refractory seeds are ones that germinate in the absence of fire related stimuli; they may germinate readily upon wetting or they may have a dormancy that is overcome by some factor unrelated to fire, for example stratification. Finally, the germination of many chaparral taxa has not been studied and these are not included.

##### A. REFRACTORY SEEDS

Species with dormant seed that can be stimulated to germinate by intense heat shock or charred wood are listed in Tables I and II, respectively. In a few cases a species may show stimulated germination in response to both heat and charred wood; such species are listed only in Table II. Represented in these groups are woody taxa as well as annuals. Curiously, geophyte species with refractory seeds are absent from the chaparral flora; this appears to be true of other mediterranean-climate ecosystems as well.

##### i. Heat Stimulated Germination

The chaparral species in the genus *Ceanothus* all have refractory seeds that germinate after exposure to intense heat (Table I). Germination of *Ceanothus leucodermis* and *C. megacarpus* are rather typical; a few percent of the seeds are not refractory whereas the vast majority are stimulated by a particular degree of heat shock (Table III). Germination of *Ceanothus* seeds is not sensitive to light.

In other species, such as *Helianthemum scoparium* and *Camissonia hirtella*, a substantial fraction of the seed pool may be non-refractory and germinate readily upon wetting, whereas an equally large fraction of the seeds require heat shock to overcome dormancy (Table III).

It is clear that the temperature that is effective in stimulating the largest fraction of seeds differs with the species (Table III). Possibly, seeds from the same parent also have slight differences with respect to the most effective temperature for breaking dormancy, although this has not been investigated. For seeds of most species, a few minutes at temperatures above 120°C results in decreased germination and temperatures greater than 150°C for more than a few minutes are usually lethal (Keeley et al., 1985; Parker, 1987; Stone & Juhren, 1953; Sweeney, 1956; Went et al., 1952). Bullock (1982) buried *Ceanothus cordulatus* seeds in soils and conducted experi-

Table I

Woody, suffrutescent and herbaceous species with refractory seeds which are stimulated to germinate by intense heat shock. Treatments were either conducted by heating seeds in an oven or submerging seeds in boiling water

Species	Family	Source of information	Mode of dispersal	"Seed" mass (mg)
<b>Shrubs:</b>				
<i>Ceanothus arboreus</i> *	(Rhamnaceae)	3, 21 <sup>b</sup>	Auto <sup>c</sup>	—
<i>C. cordulatus</i>	(Rhamnaceae)	21	Auto	5.3
<i>C. crassifolius</i>	(Rhamnaceae)	21	Auto	1.1 × 10
<i>C. cuneatus</i>	(Rhamnaceae)	11, 21	Auto	1.0 × 10
<i>C. dentatus</i>	(Rhamnaceae)	21	Auto	—
<i>C. foliosus</i>	(Rhamnaceae)	21	Auto	—
<i>C. greggii</i>	(Rhamnaceae)	4, 5	Auto	6.2
<i>C. griseus</i>	(Rhamnaceae)	4	Auto	4.3
<i>C. impressus</i>	(Rhamnaceae)	4, 5	Auto	6.9
<i>C. incanus</i>	(Rhamnaceae)	21	Auto	—
<i>C. integerrimus</i>	(Rhamnaceae)	11, 21	Auto	7.5
<i>C. leucodermis</i>	(Rhamnaceae)	11, 21, 22, 32	Auto	8.7
<i>C. megacarpus</i>	(Rhamnaceae)	3, 7, 11, 22	Auto	2.4 × 10
<i>C. oliganthus</i>	(Rhamnaceae)	11	Auto	6.0
<i>C. papillosus</i>	(Rhamnaceae)	21	Auto	—
<i>C. purpureus</i>	(Rhamnaceae)	21	Auto	—
<i>C. ramulosus</i>	(Rhamnaceae)	19	Auto	—
<i>C. rigidus</i>	(Rhamnaceae)	21	Auto	—
<i>C. sorediatus</i>	(Rhamnaceae)	21	Auto	—
<i>C. spinosus</i>	(Rhamnaceae)	21	Auto	1.1 × 10
<i>C. thyrsiflorus</i>	(Rhamnaceae)	21	Auto	1.3 × 1.0 <sup>-1</sup>
<i>C. tomentosus</i>	(Rhamnaceae)	11	Auto	4.0
<i>C. velutinus</i>	(Rhamnaceae)	21	Auto	—
<i>C. verrucosus</i>	(Rhamnaceae)	11	Auto	9.1
<i>Fremontodendron californicum</i>	(Sterculiaceae)	23	[Zoo]!	3.3 × 1.0
<i>F. decumbens</i>	(Sterculiaceae)	1	[Zoo]!	—
<i>F. mexicanum</i>	(Sterculiaceae)	23	[Zoo]!	2.3 × 10
<i>Malosma (Rhus) laurina</i> Nutt.	(Anacardiaceae)	22, 32	?Zoo!	2.8*
<i>Rhus integrifolia</i>	(Anacardiaceae)	4, 5, cf. 11	Zoo!	5.5 × 10*
<i>R. ovata</i>	(Anacardiaceae)	22, 26, 32	Zoo!	2.6 × 10 <sup>2*</sup>
<b>Subshrubs and suffrutescents:</b>				
<i>Calystegia macrostegia</i>	(Convolvulaceae)	19	Auto	8.1
<i>Helianthemum scoparium</i>	(Cistaceae)	14	Auto	5.7 × 10 <sup>-1</sup>
<i>Lotus scoparius</i>	(Fabaceae)	11	Auto	2.3*
<i>Malachothamnus fasciculatus</i>	(Malvaceae)	11	Auto	1.6
<i>Salvia apiana</i>	(Lamiaceae)	11	Auto	1.4
<b>Annuals:</b>				
<i>Apiastrum angustifolium</i>	(Apiaceae)	14	Auto	2.5 × 1.0 <sup>-1*</sup>
<i>Calyptidium monandrum</i>	(Portulacaceae)	14	Auto	1.2 × 10 <sup>-1</sup>
<i>Camissonia hirtella</i>	(Onagraceae)	14	Auto	6.0 × 10 <sup>-2</sup>
<i>Lotus salsuginosus</i>	(Fabaceae)	13, 14	Auto	1.1 × 10 <sup>-1</sup>
<i>L. strigosus</i>	(Fabaceae)	29, cf. 13	Auto	1.1 × 10 <sup>-1</sup>
<i>Lupinus excubitus</i>	(Fabaceae)	29	Auto	1.1 × 10 <sup>-1</sup>

mental burns and showed that some burns generated temperatures hot enough to kill nearly all seeds, and Wright (1931) noted that lethal temperature was inversely related to seed coat thickness. Generalizations about the temperatures soil-stored seeds are exposed to during fires are difficult because temperatures vary greatly; depth of burial, stand age, and burning conditions are just a few of the factors that determine the temperature seeds in the soil will experience (DeBano et al., 1977).

Atwater (1980) has proposed that seed structure, which is broadly similar across related plant families, is correlated with similar dormancy and germination patterns. For example, she notes that families such as the Anacardiaceae, Convolvulaceae, Fabaceae and Rhamnaceae are structurally similar in having little endosperm, independent embryos and a hard water-impervious seed coat and this is correlated with a requirement for scarification of the seed coat. In chaparral, heat stimulated seeds are largely in families (the same ones listed in the previous sentence) with structurally similar seeds and thus we might expect the mechanism of heat stimulated germination to be similar in all species listed in Table I.

It appears that species with heat-shock stimulated germination fall within the category of type 4 mode of innate dormancy listed above. In these species dormancy is imposed by a physical barrier, apparently the seed coat in *Ceanothus* or seed coat plus endocarp in *Rhus ovata* (Stone & Juhren, 1951), that prevents uptake of water and gases. Scarification, which breaks through this barrier, is sufficient to overcome seedcoat dormancy. Heat shock plays the role of breaking the barrier, perhaps by melting an impervious cuticle or weakening a portion of the seed coat, possibly the micropyle or hilum. Species listed in Table I are commonly referred to as "hard-seeded."

In some cases this seed coat-imposed dormancy is coupled with other forms of dormancy. For example, Quick (1935) has shown that some species of *Ceanothus* require 2.5°C stratification to overcome dormancy imposed by the embryo, in addition to heat to overcome dormancy imposed by the seed coat. He also demonstrated that such a stratification requirement was present in high elevation species but lacking in coastal species. A similar elevational pattern has been observed in other species (Mirov, 1936; Quick, 1947). Bullock (1982) has shown that for the montane chaparral *C. cordulatus*, germination requires heat shock of 100°C for 1 minute plus an extended period of 2°C stratification; 0, 1, 2, 3, and 5 months of stratification resulted in 0%,

←

<sup>a</sup> Nomenclature according to Munz (1968) except where author is included.

<sup>b</sup> Sources of information: 1. Boyd, 1985; 2. Capon et al., 1978; 3. Carroll et al., in press; 4. Emery, 1988; 5. Everett, 1957; 6. Flint and Palmbad, 1978; 7. Hadley, 1961; 8. Jones and Schlesinger, 1980; 9. Keeley, 1984; 10. Keeley, 1986; 11. Keeley, unpublished data; 13. Keeley and Keeley, 1987; 14. Keeley et al., 1985; 15. Keeley and Tufenkian, 1984; 16. Kruse, 1970; 17. Matsuda and McBride, 1989; 18. Parrish, 1927; 19. Parker, 1987; 20. Plumb, 1982; 21. Quick, 1935; 22. Sampson, 1944; 23. Schopmeyer, 1974; 24. Smith-Huerta, 1984; 25. Stocking, 1966; 26. Stone and Juhren, 1951; 27. Stone and Juhren, 1953; 28. Sweeney, 1956; 29. Westermeier, 1978; 30. Wicklow, 1966; 31. Wicklow, 1977; 32. Wright, 1931; 33. Zammit and Zedler, 1988.

<sup>c</sup> Mode of dispersal: anemo = anemochory, specialized for wind dispersal; zoo = zoochory, specialized for animal dispersal, [zoo] see text for discussion; auto = autochory, dispersal by the plant itself.

! Indicates accessory structures that aid in dispersal; not included in "seed" mass.

\* = "Seed" includes ovary tissues, e.g., as in an achene.

Table II

Woody, suffrutescent and herbaceous species with refractory seeds which are stimulated to germinate by incubation with charred wood. Charred, but not ashed, wood was ground to pass a #20 screen and applied to the incubation medium, either potting soil or filter paper (except sources #8 and 31 used intact charred stems)

Species	Family	Source of information	Mode of dispersal	"Seed" mass (mg)
<b>Shrubs:</b>				
<i>Adenostoma fasciculatum</i> <sup>a</sup>	(Rosaceae)	11, 19, cf. 27 <sup>b</sup>	Auto <sup>c</sup>	1.5*
<i>Arctostaphylos canescens</i>	(Ericaceae)	11, 19	Auto [Zoo]!	—
<i>A. glandulosa</i>	(Ericaceae)	11	Auto [Zoo]!	1.8 × 10*
<i>A. patula</i>	(Ericaceae)	11	Auto [Zoo]!	1.8 × 10*
<i>Fremontodendron californicum</i>	(Sterculiaceae)	11, cf. 23	[Zoo]!	3.3 × 10
<i>Garrya flavescens</i>	(Garryaceae)	11	Zoo!	3.0 × 10
<b>Subshrubs, suffrutescents and lianas:</b>				
<i>Artemisia californica</i>	(Asteraceae)	11	Auto	6.0 × 10 <sup>-2*</sup>
<i>Clematis lasiantha</i>	(Ranunculaceae)	11	Anemo!	4.2
<i>Eriodictyon crassifolium</i>	(Hydrophyllaceae)	11	Auto	1.6
<i>Eriophyllum confertiflorum</i>	(Asteraceae)	14	Auto	1.9 × 10 <sup>-1*</sup>
<i>Galium angustifolium</i>	(Rubiaceae)	13	Zoo?	3.7 × 10 <sup>-1</sup>
<i>Penstemon centranthifolius</i>	(Scrophulariaceae)	13	Auto	1.8
<i>P. heterophyllus</i>	(Scrophulariaceae)	13	Auto	4.0 × 10 <sup>-1</sup>
<i>P. spectabilis</i>	(Scrophulariaceae)	13	Auto	5.5
<i>Rhus trilobata</i>	(Anacardiaceae)	11	Zoo!	2.8 × 10*
<i>Romneya coulteri</i>	(Papaveraceae)	13	Auto	1.1
<i>R. trichocalyx</i>	(Papaveraceae)	11	Auto	6.7 × 10 <sup>-1</sup>
<i>Sabia mellifera</i>	(Lamiaceae)	10, 11	Auto [Zoo]	1.1
<i>Toxicodendron diversifolia</i>	(Anacardiaceae)	11	Zoo!	3.3 × 10*
<b>Annuals:</b>				
<i>Antirrhinum coulterianum</i>	(Scrophulariaceae)	13	Auto	1.3 × 10 <sup>-1</sup>
<i>A. kelloggii</i>	(Scrophulariaceae)	13	Auto	7.0 × 10 <sup>-1</sup>

Table II  
Continued

Species	Family	Source of information	Mode of dispersal	"Seed" mass (mg)
<i>Camissonia californica</i>	(Onagraceae)	13	Auto	$1.6 \times 10^{-1}$
<i>Chaenactis artemisiifolia</i>	(Asteraceae)	14	Auto	$7.4 \times 10^{-1*}$
<i>Clarkia epilobioides</i>	(Onagraceae)	13, cf. 24	Auto	$8.0 \times 10^{-2}$
<i>C. purpurea</i>	(Onagraceae)	13	Auto	$1.2 \times 10^{-1}$
<i>Collinsia parryi</i>	(Scrophulariaceae)	13	Auto	$9.2 \times 10^{-1}$
<i>Cryptantha intermedia</i>	(Boraginaceae)	13	?Zoo	$4.7 \times 10^{-1*}$
<i>C. muricata</i>	(Boraginaceae)	14	?Zoo	$3.8 \times 10^{-1*}$
<i>Emmenanthe penduliflora</i>	(Hydrophyllaceae)	8, 14, 31	Auto	$5.7 \times 10^{-1}$
<i>Gilia australis</i>	(Polemoniaceae)	13	Auto	$9.0 \times 10^{-2}$
<i>G. capitata</i>	(Polemoniaceae)	13	Auto	$6.7 \times 10^{-1}$
<i>Gnaphalium californica</i>	(Asteraceae)	13	Auto	$1.0 \times 10^{-2*}$
<i>Lepidium nitidum</i>	(Brassicaceae)	13	Auto	$5.6 \times 10^{-1}$
<i>Malacothrix clevelandii</i>	(Asteraceae)	13	Auto	$5.0 \times 10^{-2*}$
<i>Papaver californicum</i>	(Papaveraceae)	13	Auto	$1.0 \times 10^{-1}$
<i>Phacelia cicutaria</i>	(Hydrophyllaceae)	14	Auto	$7.6 \times 10^{-1}$
<i>P. grandiflora</i>	(Hydrophyllaceae)	14	Auto	$1.4 \times 10^{-1}$
<i>P. fremontii</i>	(Hydrophyllaceae)	14	Auto	$1.7 \times 10^{-1}$
<i>P. minor</i>	(Hydrophyllaceae)	13	Auto	$1.3 \times 10^{-1}$
<i>P. parryi</i>	(Hydrophyllaceae)	14	Auto	$2.2 \times 10^{-1}$
<i>P. viscida</i>	(Hydrophyllaceae)	14	Auto	$9.0 \times 10^{-2}$
<i>Rafinesquia californica</i>	(Asteraceae)	13	Anemo!	$9.1 \times 10^{-1*}$
<i>Silene multinervia</i>	(Caryophyllaceae)	13	Auto	$1.8 \times 10^{-1}$
<i>Stephanomeria virgata</i>	(Asteraceae)	13	Anemo!	$1.2 \times 10^{-1*}$
<i>Streptanthus heterophyllus</i>	(Brassicaceae)	13	Auto	$1.0 \times 10^{-1}$

See footnotes to Table I.

Table III

Germination patterns of selected species with heat shock stimulated germination. Seeds were heated dry and incubated with or without ground charred wood on potting soil (data from Keeley, 1987 and Keeley et al., 1985)

		Percentage germination									
		Light					Dark				
Temperature (C):	Con- trol	70	80	100	120	150	Con- trol	70	100	120	
Time (min):		120	60	5	5	5		120	5	5	
<i>Ceanothus leucodermis</i> (shrub)											
Control	3	29	—	48	64	—	7	47	50	68	
Charred wood	7	27	—	62	46	—	2	20	58	58	
<i>Ceanothus megacarpus</i> (shrub)											
Control	11	41	—	48	80	—	6	54	53	88	
Charred wood	2	40	—	40	61	—	3	40	56	67	
<i>Helianthemum scoparium</i> (suffrutescent)											
Control	23	—	15	—	43	3	—	—	—	—	
Charred wood	23	—	16	—	37	4	—	—	—	—	
<i>Camissonia hirtella</i> (annual)											
Control	30	—	49	—	66	69	—	—	—	—	
Charred wood	26	—	33	—	22	20	—	—	—	—	

26%, 44%, 81%, and 87% germination, respectively. A similar pattern of increasing germination with up to 4 months stratification has been reported for several species of *Eriodictyon* (Roof, 1988).

A different example is *Malosma laurina* which seems to require the leaching of the pericarp, in addition to heat shock, to overcome dormancy (Keeley, 1987a).

### ii. Charred Wood Stimulated Germination

Species that have been demonstrated to respond to charred wood (Table II) illustrate various patterns (Table IV). dormancy of *Arctostaphylos glandulosa* is eliminated in some seeds by the presence of charred wood. Darkness may also promote germination. *Arctostaphylos* seeds in general are highly refractory, and few studies have demonstrated conditions that generate high percentages of germination (e.g., Berg, 1974; Geirsbach, 1937; Rogers, 1949). Parker (1987) reported 14% germination for *A. canescens* seeds incubated with an aqueous leachate of charred wood (over 0% for controls), but only for older seeds extracted from the soil; charred wood did not stimulate the germination of fresh seed, unless it was coupled with gibberellic acid.

*Romneya trichocalyx* exhibits a nearly obligatory dependence upon charred wood to overcome dormancy (Table IV). Other species listed in Table II that demonstrate large increases in germination in the presence of charred wood include: *Antirrhinum coulterianum*, *Camissonia californica*, *Garrya flavescens*, *Gilia capitata*, *Malacothrix clevelandii*, *Silene multinervia*, *Papaver californicum*, *Penstemon spectabilis*, and *Romneya coulteri*. In these species heat shock plays no role in stimulating germination.

The widely distributed chaparral shrub *Adenostoma fasciculatum* has been shown

**Table IV**

Germination patterns of selected species with charred wood stimulated germination. Seeds were heated dry and incubated with or without ground charred wood on potting soil (data from Keeley, 1987 and Keeley et al., 1985)

Temperature (C): Time (min):	Percentage germination									
	Light						Dark			
	Con- trol	70 120	80 60	100 5	120 5	150 5	Con- trol	70 120	100 5	120 5
<i>Arctostaphylos glandulosa</i> (shrub)										
Control	0	0	—	0	0	—	0	0	0	0
Charred wood	5	3	—	2	3	—	8	13	3	7
<i>Garrya flavescens</i> (shrub)										
Control	4	12	—	10	6	—	24	1	4	0
Charred wood	65	34	—	54	19	—	17	47	57	28
<i>Artemisia californica</i> (subshrub)										
Control	73	56	—	47	56	—	0	10	3	0
Charred wood	78	80	—	81	87	—	62	49	64	50
<i>Rhus trilobata</i> (subshrub)										
Control	38	45	—	37	72	—	17	5	3	13
Charred wood	65	62	—	53	62	—	28	25	12	12
<i>Romneya trichocalyx</i> (suffrutescent)										
Control	0	0	—	0	0	—	0	0	0	1
Charred wood	24	33	—	34	24	—	17	11	13	10
<i>Cryptantha muricata</i> (annual)										
Control	24	—	20	—	37	7	—	—	—	—
Charred wood	67	—	85	—	64	10	—	—	—	—
<i>Phacelia cicutaria</i> (annual)										
Control	5	—	11	—	6	0	—	—	—	—
Charred wood	32	—	45	—	57	0	—	—	—	—

in two studies to have germination stimulated by charred wood (Keeley, 1987a; Parker, 1987). Earlier studies by Stone and Juhren (1951) indicated that heat alone would stimulate germination, however, most studies have found heat alone is ineffective in stimulating germination of the species (Christensen & Muller, 1975a; Parker, 1987; Wright, 1931). One study, though, reported that heat plus charred wood had a synergistic effect on percentage germination, over charred wood alone (Keeley, 1987a). A similar pattern is observed for *Phacelia cicutaria* (Table IV); maximum germination with a combination of heat plus charred wood. On the other hand, germination of *Rhus trilobata* is doubled by either heating or charred wood (Table IV).

Many of the other species listed in Table II respond to charred wood in a manner similar to the pattern observed for *Cryptantha muricata* in Table IV. A substantial fraction of the seeds are non-refractory and germinate readily upon wetting, but a large fraction of the seeds are dormant and this dormancy can be broken by incubation with charred wood.

*Artemisia californica* illustrates an interesting interaction between light and charred wood (Table IV). Seeds show a positive photoblastic response; they germinate readily in the light but are dormant in the dark. However, this dark-induced dormancy is readily broken by charred wood. This pattern may be widespread in subligneous shrubs; a similar response is observed in *Salvia mellifera* and to a limited extent in *Diplacus aurantiacus* (Keeley, 1987a). The closely related *D. longiflorus* has also been reported to exhibit dormancy in the dark (Schroeder & Barton, 1939), although the effect of charred wood has not been tested on this species. There is some evidence that a similar pattern may operate in the widespread, almost weedy, *Salvia columbariae* (Keeley, 1984). In this latter species, Newton (1979) has provided evidence that dormancy in the dark is induced by the ratio of red : far-red light.

Most species of *Arctostaphylos* have a requirement for a cold stratification period (Carlson & Sharp, 1975; Geirsbach, 1937; Mirov, 1936), in addition to charred wood, to overcome dormancy. However, populations of *Salvia mellifera* from the coast, mountains and desert have no stratification requirement (Keeley, 1986).

In addition to factors involved in overcoming dormancy, some species may respond quite differently to constant vs. alternating temperature regimes during germination (Bewley & Black, 1982). This has been largely unexplored in studies of chaparral seed germination. In a study of *Salvia mellifera*, germination under a diurnal regime of 13°C/23°C was similar to the level of germination under a constant 23°C regime for low elevation populations, in the light or dark (Keeley, 1986). However, for one higher elevation population from chaparral, alternating temperatures nearly doubled germination in the light (41% vs. 71%), and in the dark, produced an even more profound increase in germination (6% vs. 43%). This experiment also revealed an interesting interaction with charred wood; under constant temperature, both in the light and the dark, charred wood produced a substantial increase in germination, but not under alternating temperatures.

The mechanism behind charred wood stimulated germination is unknown. Experiments on a few species have revealed several characteristics of this phenomenon. The active ingredient in charred wood is soluble in water and capable of passing a 0.2 µm nitrocellulose filter (Table V). Also a similar stimulatory response can be produced by application of sterile extracts made from soils collected on recently burned sites but not from soils collected on unburned sites (Table V).

Experiments with *Emmenanthe penduliflora* have shown that neither completely ashed wood (Jones & Schlesinger, 1980; Wicklow, 1977) nor Hoaglands solution (Keeley et al., 1985) can simulate the stimulatory effect of charred wood in overcoming seed dormancy. This suggests that the active ingredient is an organic compound. Also, heating for 30 minutes at 175°C the wood of many ligneous species will produce the same stimulatory effect on germination as observed with charred wood (S. Keeley & Pizzorno, 1986).

Some progress has been made in identifying the organic breakdown products of heated wood that are responsible for the stimulated germination of *Emmenanthe penduliflora* seeds (S. Keeley & Pizzorno, 1986). This study tested several sugars, acids, hemicelluloses and PEG, none of which stimulated germination. However, heating the hemicellulose xylan to 175°C for 10 minutes, did stimulate germination, suggesting that the stimulatory product may be an oligosaccharide or other carbohydrate. Recent studies (Lindquist & Keeley, unpubl.) have found that the compound in charred wood that stimulates germination of *E. penduliflora*, *Silene multinervia* and *Romneya coulteri* is extractable in the solvents methane, acetone, and hexane.

Table V

Germination of *Eriophyllum confertiflorum* seeds in sterile extracts of charred wood and of soils from recently burned or unburned chaparral sites (data from Pack & Keeley, unpublished)

Sterile extract of:	Percentage germination
Distilled water	13
Distilled water + charred wood	63
Distilled water + soil from:	
Mature chaparral site 1	16
Mature chaparral site 2	28
Mature chaparral site 3	18
Mature chaparral site 4	29
Burned chaparral site 5	61
Burned chaparral site 6	69
Burned chaparral site 7	80
Burned chaparral site 8	73

Thus, activity from both polar and non-polar solvents suggests the possibility that more than a single compound may be involved.

The mode of action of this charred wood compound may be: (1) to trigger a biochemical change in the embryo, (2) to leach out or inactivate an inhibitor in the seed coat or within the seed itself, or (3) to chemically break the seed coat or membranes beneath. The last of these three hypotheses seem unlikely, at least for *E. penduliflora*, since Sweeney (1956) reported a solution of eosin dye could pass through the seed coat of dormant seeds. He concluded that these seeds could imbibe water and yet remain dormant. In other words, the refractory character of these seeds is not because they are "hard-seeded." This is consistent with the report by Parker (1987) that dormant seeds of this species can absorb moisture up to 45% of their dry weight, and yet remain dormant. Inconsistent with the conclusion that these seeds are not hard-seeded, is the repeated observation that scarification of the "seed coat" is sufficient to overcome dormancy in many of the charred wood stimulated species listed in Table II (e.g., Ammirati, 1967; Christensen & Muller, 1975a; Jones & Schlesinger, 1980; Sweeney, 1956; Wicklow, 1977).

A model compatible with these observations would be one in which membranes beneath the seed coat act as a barrier to oxygen uptake, but not water uptake. Scarification could disrupt this barrier. The only evidence bearing on this hypothesis is negative. *Emmenanthe penduliflora* seeds incubated in atmospheres of >90% oxygen remained dormant (Keeley, unpubl.).

Distinguishing between the other two modes is not possible at this point, although if there is a seed coat inhibitor it is not removed by activated charcoal or leaching with water (Keeley et al., 1985). One piece of evidence that would support hypothesis number 1 is that gibberellic acid can produce the same stimulatory action as charred wood in several species. Harrington (1975) reported 42% germination for *Romneya coulteri* seeds when treated with 100 ppm GA<sub>3</sub>, compared to 0% for controls and most other treatments including heating and cold stratification. This mirrors the 40% germination reported for this species when incubated with charred wood over 0% for controls (Keeley & Keeley, 1987). Another example is *Penstemon spectabilis*; 1% germination for controls was increased to 61% with charred wood (Keeley & Keeley, 1987) and Atwater (1980) reported 2% for controls but 70% with 400 ppm GA<sub>3</sub>.

In light of the diversity of plant families represented by species reported to respond to charred wood (Table II), it seems likely that this phenomenon is polyphyletic. The taxa listed in Table II represent a diversity of seed structures (e.g., Martin, 1946). If Atwater's (1980) proposition that seed structure is correlated with the mechanism of dormancy is generally applicable, then future studies should consider the possibility that the mechanism of action of charred wood may not be the same in all species.

A number of species with refractory seeds can not be categorized as to whether heat shock or charred wood (or other factor) is responsible for overcoming dormancy (Table VI). Many of these, e.g., *Dendromecon rigida*, *Dicentra* spp., *Turricula parryi*, *Eucrypta chrysanthemifolia* and *Phacelia brachyloba* exhibit massive germination only in the first season after fire (Bullock, 1989; Christensen & Muller, 1975a; Horton & Kraebel, 1955; S. Keeley et al., 1981; Stocking, 1966; Zammit & Zedler, 1988). In several studies, germination has been stimulated by burning wood over the seed bed, but this does not clarify whether heat or a chemical from charred wood is the responsible agent. In the case of the species mentioned above, heat and charred wood have been tested but neither treatment induced germination (Keeley et al., 1985; Keeley & Keeley, 1987).

If the information on germination patterns presented in Tables I and II are of any predictive value, one would expect that the hard-seeded species in the Fabaceae listed in Table VI are stimulated by heat shock. In light of the representation of charred wood stimulated germination in the Hydrophyllaceae and Papaveraceae (Table II), I expect that charred wood may play a role in the germination of the species in those two families (listed in Table VI). In support of this, as with known charred wood stimulated species, Atwater (1980) reported that 400 ppm GA<sub>3</sub> would stimulate germination of *Dicentra chrysantha* and *D. ochroleuca*.

Atwater (1980) also noted that these *Dicentra* species, as well as *Dendromecon rigida* and *Romneya coulteri*, have rudimentary embryos that require an after-ripening period for development. Anatomical studies on the rate of after-ripening are lacking, but would be helpful in evaluating the period of imbibition required for germination.

### iii. Demography of Species With Refractory Seeds

The demographic consequences of having refractory seeds are broadly similar for species with heat stimulated (Table I) and charred wood stimulated (Table II) germination, and for all life forms (and those species listed in Table VI). Most species establish seedlings in the first growing season after fire from a persistent seed bank (Fig. 1). For shrub species, dominants at a site may recruit on the order of 10–100 seedlings m<sup>-2</sup> (e.g., Horton & Kraebel, 1955; Keeley & Zedler, 1978; Mills & Kummerow, 1989). *Adenostoma fasciculatum*, *Arctostaphylos* spp. and *Ceanothus* spp. are prolific postfire seedling producers. In isolated instances certain of the shrub species have been reported to establish seedlings in the second year after fire (S. Keeley et al., 1981), but in general, the shrubs listed in Tables I and II do not have successful seedling establishment after the first postfire year.

*Rhus* spp. (including *Malosma*) are seldom reported to successfully recruit many seedlings after fire, despite having highly refractory seeds noted for their requirement for scarification. Studies with *Malosma laurina* indicate that postfire germination is not uncommon, but seedlings succumb to water stress during the first summer drought (Davis, 1989). The only sites I have observed successful *Rhus ovata* seedling establish-

Table VI

Woody, suffrutescent and herbaceous species with refractory seeds but the cue has not been elucidated. For most of these species seedlings are present in abundance only after fire

Species	Family	Source of information	Mode of dispersal	"Seed" mass ( $\mu\text{g}$ )
<b>Shrubs:</b>				
<i>Xylococcus bicolor</i> <sup>a</sup>	(Ericaceae)	3, 4, 10 <sup>b</sup>	Auto! <sup>c</sup>	$1.1 \times 10^{2*}$
<b>Subshrubs and suffrutescents:</b>				
<i>Dendromecon rigida</i>	(Papaveraceae)	3, 4, 10	[Zoo]!	$1.2 \times 10$
<i>Dicentra chrysantha</i>	(Papaveraceae)	3, 4, 11	Auto	1.2
<i>D. ochroleuca</i>	(Papaveraceae)	3, 4, 11	Auto	$7.5 \times 10^{-1}$
<i>Turricula parryi</i>	(Hydrophyllaceae)	10	Auto	$1.3 \times 10^{-1}$
<b>Annuals:</b>				
<i>Astragalus congdonii</i>	(Fabaceae)	24	Auto	
<i>Eucrypta chrysanthemifolia</i>	(Hydrophyllaceae)	11	Auto	$4.0 \times 10^{-1}$
<i>Gilia gilioides</i>	(Polemoniaceae)	27	Auto	
<i>G. splendens</i>	(Polemoniaceae)	27	Auto	$4.0 \times 10^{-2}$
<i>Lupinus hirsutissimus</i>	(Fabaceae)	3, 4	Auto	$2.3 \times 10$
<i>L. succulentus</i>	(Fabaceae)	3, 4	Auto	$2.1 \times 10$
<i>Phacelia brachyloba</i>	(Hydrophyllaceae)	12, 31	Auto	$1.3 \times 10^{-1}$
<i>P. heterophylla</i>	(Hydrophyllaceae)	27	Auto	
<i>Trifolium ciliolatum</i>	(Fabaceae)	24	Auto	

See footnotes to Table I.

ment are in chaparral burns in Arizona; distinct from California in the predictability of summer rains (Vankat, 1989). *Xylococcus bicolor* is another shrub noted for its refractory seeds, yet it seldom is observed to establish seedlings after fire (Zedler, 1982).

Subligneous species, with few exceptions, recruit most seedlings in the first year after fire, although low levels of seedling recruitment occur in subsequent years. Some species such as *Artemisia californica* and *Salvia mellifera* readily establish seedlings in gaps within the chaparral. As described above, these species have seeds that germinate readily in the light. However, buried seeds may remain dormant until after fire when water leaching through charred wood could stimulate germination (Table IV).

Certain annual species, often called "fire-annuals," establish seedlings "only" in the first season after fire and then remain dormant until the next fire (Ammirati, 1967; Horton & Kraebel, 1955; S. Keeley et al., 1981; Sweeney, 1956). These "fire-annuals" include *Emmenanthe penduliflora*, *Papaver californica* and certain species of *Phacelia*. These species are charred wood-stimulated taxa. This is not surprising since charred wood is a more specific cue to the postfire environment, in contrast to heat stimulated germination, which is potentially simulated by high soil temperatures on exposed sites; for example, 12 hours at 60°C can stimulate the same level of germination in *Convolvulus cyclostegius* as 10 min at 100°C (Christensen & Muller, 1975a). Occasionally, fire-annual species may be observed in subsequent postfire years (Mills, 1986; O'Leary & Westman, 1988) but typically they will concentrate near the remains of charred stems (Keeley, pers. obs.). Other annuals listed in Tables I and II produce massive populations in the first year after fire and progressively

smaller populations in subsequent years, although precipitation levels can profoundly affect the size of populations in subsequent years (S. Keeley, 1977).

In mature chaparral, shrub species with refractory seeds produce seed crops on an annual or biennial basis adding to a persistent seed bank (Parker & Kelly, 1989). For many species, however, a portion of the seed crop is non-refractory and possibly these seeds are transient in the soil.

The common chaparral shrub *Adenostoma fasciculatum* is an example of such a plant. Stone and Juhren (1953) reported that for seeds taken directly from the plant, 70% were non-refractory and germinated readily upon dispersal whereas 23% were dormant; a condition that could be overcome by burning wood over the seed bed. These authors also noted that of the seeds collected from the soil, only 11% were non-refractory and 89% were refractory. Parker (1987) has reported similar findings for soil-stored *A. fasciculatum* seed, where little or no germination occurred without charred wood. The difference in percentage of dormant seeds between fresh seed and soil-stored seed is probably because non-refractory seeds germinate and thus do not accumulate in the seed bank, although the possibility can not be ruled out that some seed undergoes a secondary dormancy following dispersal. Stone and Juhren (1953) concluded that this species produced polymorphic seeds, and refractory seeds should accumulate in the soil with time. They predicted that total germination would be higher after fire in an old stand than after fire in a young stand. Studies by Zammit and Zedler (1988) support this conclusion; soil samples from beneath *Adenostoma* chaparral yielded substantially more *A. fasciculatum* seedlings after fire treatment of the soil and the highest germination occurred in soil taken from the oldest stand of 85 years (Table VII).

A similar relationship between seed bank size and stand age has been reported for *Ceanothus cordulatus* (Bullock, 1982). In one study, though, the persistent seed banks of *Arctostaphylos glauca* and *A. glandulosa* did not change significantly over the period of 10 years, despite continual seed production (Keeley, 1987b). Others have suggested that continued seed production may be necessary to sustain seed banks of species specialized for postfire seedling recruitment (Schlesinger et al., 1982).

Germination of *Adenostoma fasciculatum* seeds under the mature chaparral canopy has been noted by numerous investigators but invariably they succumb within the first growing season (Christensen & Muller, 1975b; J. Kummerow, pers. comm.; T. Parker, pers. comm.). This species never successfully recruits new seedlings under the chaparral canopy but seedlings will occasionally establish in disturbances other than burns.

Apparently, many other species disperse polymorphic seed pools, in which a fraction of the seeds are non-refractory and germinate readily and another fraction germinate only in the presence of charred wood or after experiencing heat shock. Such physiological polymorphism is usually not correlated with morphological variation. *Platystemon californicus* is an annual that produces two seed types that are morphologically and physiologically different. Most seeds are enclosed in a persistent pericarp, but some are naked. Hannan (1980) has documented that the naked seeds have an innate dormancy when they are dispersed (in mid-summer), but germinate readily in the fall. This behavior would delay germination until a season of more predictable rainfall. The seeds enclosed in the pericarp do not germinate readily in the fall and may persist in the soil seed bank. This polymorphism accounts for the annual occurrence of this species in grasslands and periodic abundance after wildfires.

**Table VII**

Germination of seeds in soils collected from beneath different aged stands of chaparral; untreated soil (control) and fire stimulated soil (treated by burning straw over soil,  $n = 72$ ) (data from Zammit & Zedler, 1988)

Stand age (years after fire): Species	Seedlings $\text{dm}^{-2}$ of surface		
	9 $\bar{x} \pm \text{SD}$	35 $\bar{x} \pm \text{SD}$	85 $\bar{x} \pm \text{SD}$
<i>Adenostoma fasciculatum</i>			
Control	13.8 $\pm$ 11.6	40.3 $\pm$ 21.1	94.7 $\pm$ 51.4
Fire	19.3 $\pm$ 16.0	63.0 $\pm$ 54.7	206.5 $\pm$ 169.5
<i>Camissonia hirtella</i>			
Control	24.4 $\pm$ 19.4	7.1 $\pm$ 9.4	8.9 $\pm$ 10.8
Fire	17.0 $\pm$ 11.5	6.6 $\pm$ 7.2	7.0 $\pm$ 8.8
<i>Ceanothus greggii</i>			
Control	0	0.7 $\pm$ 1.2	0.4 $\pm$ 0.9
Fire	0.9 $\pm$ 1.0	12.7 $\pm$ 6.4	4.3 $\pm$ 3.4
<i>Malacothrix clevelandii</i>			
Control	3.8 $\pm$ 1.3	0.9 $\pm$ 1.3	3.5 $\pm$ 3.0
Fire	1.9 $\pm$ 3.4	0.1 $\pm$ 0.5	3.0 $\pm$ 2.7
<i>Phacelia brachyloba</i>			
Control	0	1.3 $\pm$ 2.1	0.2 $\pm$ 0.5
Fire	0.3 $\pm$ 0.8	3.9 $\pm$ 2.9	0.2 $\pm$ 0.8

There is the potential for much ecotypic variation which could fine tune ratios of refractory and non-refractory seeds, and thus optimize reproduction across the diversity of environments occupied by a species (Cohen, 1967). One example of this is that of *Ceanothus* spp. that have substantially higher percentages of non-refractory seeds on the less fire-prone Santa Cruz Island, than on nearby mainland sites (Carroll et al., in press). There are also examples of ecotypic variation in charred wood stimulated germination (Jones & Schlesinger, 1980; Keeley, 1986).

Another means by which species could adapt the proportion of polymorphic seeds cued to different environments would be through maternal effects on germination characteristics (Roach & Wulff, 1987). One attempt to test for this in chaparral proved negative; *Gilia capitata* seeds collected from a gap in mature chaparral had a proportion of charred wood stimulated seeds nearly identical to that of a population from a recently burned site (Keeley & Keeley, 1987).

For species with polymorphic seed pools, refractory seeds accumulate in a persistent soil seed bank, however, the fate of non-refractory seeds is uncertain. Three possibilities present themselves: (1) The seeds may germinate during the first growing season and, if in an appropriate "safe site" such as a disturbance or gap, establish themselves. If the seed germinates while under the shrub canopy, in most cases it will succumb; although not always, e.g., *Apiastrum angustifolium* (Ammirati, 1966; Christensen & Muller, 1975a; Shmida & Whittaker, 1981). The factors typically cited for unsuccessful seedling establishment under the chaparral canopy include animal predation (perhaps the most important) as well as light and inorganic nutrient levels (Keeley & Keeley, 1989). (2) Non-dormant seeds may undergo secondary (induced)

dormancy after dispersal and thus non-refractory seeds become refractory seeds. (3) If the seeds land in an unfavorable microsite, such as under the shrub canopy, they may be forced into dormancy by ambient conditions; e.g., by allelopathic compounds.

McPherson and Muller (1969) contend that allelopathic chemicals leached from the overstory shrubs act to enforce the dormancy of seeds in the soil beneath. In much of the literature these allelochemical substances are viewed as inhibitory agents produced by plants to suppress growth of their competitors. However, Koller (1972) and Angevine and Chabot (1979) suggest that such enforced dormancy may act in the best interests of the species being suppressed by transferring it to a state of dormancy. If the non-refractory seeds were sensitive to compounds leached from the overstory it would act to inhibit germination in unsafe sites. Thus, some non-refractory seeds that land under the shrub canopy may be forced into dormancy until disturbance removes the canopy. It is unknown whether or not this takes place, although an experiment by Christensen and Muller (1975a) is consistent with the hypothesis. They found that the putatively allelopathic leachate from *Adenostoma* shrubs did not inhibit germination of scarified seeds of species with refractory seeds (e.g., *Emmenanthe penduliflora*, *Eucrypta chrysanthemifolia* and *Phacelia grandiflora*) but it completely inhibited germination of species with non-refractory seeds (e.g., *Erigeron divergens*, *Cryptantha intermedia* and *Centaurea melitensis*).

Seed longevity of the persistent seed bank of shrubs such as *Ceanothus* spp. is known to exceed 20 years (Quick & Quick, 1961). Circumstantial evidence suggests that these taxa may survive hundreds of years in the soil (e.g., Gratkowski, 1962). Many species that germinate in profusion immediately after fire may lie as dormant seeds in the soil for 50–100 years until after a fire, indicative of great longevity for these species.

## B. NON-REFRACTORY SEEDS

Species with non-refractory seeds may be shrubs, subshrubs, suffrutescents, lianas, geophytes or annuals (Table VIII). Seeds of these species typically germinate readily upon wetting and incubation under moderate temperatures. Many lack any form of dormancy and some germinate immediately upon dispersal. Indeed, acorns of *Quercus dumosa* have been observed to germinate prior to abscission from the parent plant and cotyledons of *Rhamnus californica* seeds may be chlorophyllous at the time of dispersal (Keeley, 1987a). Species listed in Table VIII represent those species for which germination data exist. Undoubtedly, there are many other species that should be included here.

Only limited information is available on seed longevity of species with non-refractory seeds. I have observed that seeds of shrubs such as *Heteromeles arbutifolia*, *Quercus dumosa*, *Prunus ilicifolia* and *Rhamnus californica* have a shelf-life of less than a year at room temperature; it is unknown whether this is due to an inherently short life-span or is a result of drying under laboratory humidity levels (e.g., Plumb, 1982). Regardless, in nature, under summer soil humidity conditions, the consequences would be the same. Some species with non-refractory seeds are capable of retaining viability for more than 8 years under laboratory conditions; e.g., *Cneoridium dumosum*, *Comarostaphylos diversifolia*, *Eriogonum fasciculatum*, *Keckiella cordifolia*, *Marah macrocarpus*, *Melica imperfecti*, *Sisyrinchium bellum*, *Stipa coronata*, *S. lepida* and *Daucus pusillus* (Keeley, unpubl.). Thus, some of these species, if maintained in a quiescent state, may survive a decade or more. Since most of these

seeds lack any form of dormancy, it seems unlikely that they would persist in the soil for more than a year, unless dormancy was enforced on them by some ambient condition.

Non-refractory seeds not only are not stimulated to germinate by high temperature, but the seeds are relatively sensitive to high temperature. Temperatures of 70°C for 1 hour have been shown to be lethal to *Quercus dumosa* seeds (Keeley, 1987a). In general, larger-seeded species ( $\geq 10^2$  mg), such as *Q. dumosa*, *Marah macrocarpus*, or *Paeonia californica* are more sensitive to long durations of temperatures of 70–80°C than short bursts of 120–150°C (Keeley et al., 1985), but this is not true of smaller seeded species. It is possible that for certain of these seeds, summer soil temperatures may be lethal.

### *i. Demography of Shrubs With Non-refractory Seeds*

The demographic consequences of having non-refractory seeds varies with the life form. Considering the shrubs, all are vigorous resprouters and mature individuals are seldom eliminated by fire, but they rarely establish seedlings after fire; these species are fire-resisters. Lack of postfire seedling establishment is primarily because a dormant seed bank does not accumulate during the fire-free period. Parker and Kelly (1989) describe such species as having transient seed banks. Absence of a persistent seed bank is due either to the fact that these seeds lack any dormancy or dormancy is readily overcome by winter stratification; most species probably germinate in the first rainy season following dispersal. Other factors that contribute to a transient seed bank include short-lived seeds, seeds incapable of surviving low summer humidities and seeds with a sensitivity to high soil temperatures.

Although none of the species shown in Table VIII establish seedlings in the first year after fire, the conditions under which successful seedling recruitment occurs may differ with life form. Successful seedling establishment for most of the shrub species listed in Table VIII has been observed in stands free of fire for very long periods (60–120 yr, e.g., Fig. 1) (Keeley et al., 1986; Keeley, unpubl.; Minnich, 1982; Parker & Kelly, 1989; Patric & Hanes, 1964; Zedler, 1981). Observations suggest this is not due to gap formation since these stands, contrary to dogma, are not senescent or lacking in productivity and seedlings are frequently distributed beneath relatively dense canopies. Seedling establishment of these shrubs is correlated with a thick litter layer and high soil organic matter (Keeley, unpubl.). Thus, successful seedling regeneration may be limited by inorganic nutrients and moisture retention ability of the soil. These factors may account for why such species tend to dominate on the more mesic sites in chaparral (Critchfield, 1971; Keeley & Keeley, 1988). Minnich (1982) reported a comparison of historic and modern aerial photographs reveals that the distribution of species such as *Heteromeles arbutifolia*, *Rhus* spp., *Rhamnus crocea* and *Prunus ilicifolia* has expanded on sites unburned for long periods. He estimated a great longevity, in the absence of fire for these taxa he called “fleshy-fruited sprouters.”

### *ii. Demography of Other Life Forms With Non-refractory Seeds*

Seedling recruitment by the more diminutive subshrubs and suffrutescent species shown in Table VIII is variable. Although all are capable of resprouting after fire, this is more tenuous for these lighter-wood species. In dense chaparral these species

Table VIII

Woody, suffrutescent and herbaceous species with non-refractory seeds; most germinate readily upon wetting, but certain ones may require a period of cold stratification to overcome embryo dormancy

Species	Family	Source of information	Mode of dispersal	"Seed" mass (mg)
<b>Shrubs:</b>				
<i>Cercocarpus betuloides</i> <sup>a</sup>	(Rosaceae)	11 <sup>b</sup>	Anemo! <sup>c</sup>	1.8 × 10*
<i>Cneoridium dumosum</i>	(Rutaceae)	12	[Zoo?]	1.4 × 10
<i>Comarostaphylis diversifolia</i>	(Ericaceae)	11	Zoo!	1.4 × 10*
<i>Heteromeles arbutifolia</i>	(Rosaceae)	11, 18, 23	Zoo!	5.5
<i>Quercus dumosa</i>	(Fagaceae)	11, 17, 20, 23	Zoo	1.8 × 10**
<i>Prunus ilicifolia</i>	(Rosaceae)	4, 5, 11, 23	Zoo!	1.2 × 10*
<i>Rhamnus californica</i>	(Rhamnaceae)	11, 22, 32	Zoo!	9.3 × 10*
<i>R. crocea</i>	(Rhamnaceae)	4, 5, 11	Zoo!	9.5
<b>Subshrubs, suffrutescents and lianas:</b>				
<i>Baccharis pilularis</i>	(Asteraceae)	4, 5	Anemo!	—
<i>B. sarothroides</i>	(Asteraceae)	4, 5	Anemo!	7.0 × 10 <sup>-2</sup> *
<i>Encelia californica</i>	(Asteraceae)	12, 18	Anemo	3.6*
<i>Eriogonum fasciculatum</i>	(Polygonaceae)	11	Auto	1.4*
<i>Gutierrezia sarothrae</i>	(Asteraceae)	16	Auto	—
<i>Haplopappus squarrosus</i>	(Asteraceae)	11	Auto	6.8 × 10 <sup>-1</sup> *
<i>H. venetus</i>	(Asteraceae)	11	Anemo!	3.4 × 10 <sup>-1</sup> *
<i>Keckiella anthirrhinoides</i>	(Asteraceae)	11	Auto	2.8 × 10 <sup>-1</sup>
<i>K. cordifolia</i>	(Scrophulariaceae)	11	Auto	1.9 × 10 <sup>-1</sup>
<i>K. ternata</i>	(Scrophulariaceae)	11	Auto	3.0 × 10 <sup>-1</sup>
<i>Lonicera subspicata</i>	(Caprifoliaceae)	11	Zoo!	5.5
<i>Diplacus (Mimulus) aurantiacus</i> Jeps.	(Scrophulariaceae)	11	Auto	2.0 × 10 <sup>-2</sup>
<i>Porophyllum gracile</i>	(Asteraceae)	13	Anemo!	6.1 × 10 <sup>-1</sup> *
<i>Solanum douglasii</i>	(Solanaceae)	13	Zoo!	4.2 × 10 <sup>-1</sup>
<i>Trichostema lanatum</i>	(Lamiaceae)	4, 5	Auto	5.2
<i>Yiguera laciniata</i>	(Asteraceae)	11	Zoo	7.7 × 10 <sup>-1</sup> *
<i>Yucca whipplei</i>	(Agavaceae)	4, 5, 15	Anemo	1.8 × 10

Table VIII  
Continued

Species	Family	Source of information	Mode of dispersal	"Seed" mass (mg)
Geophytes*:				
<i>Allium praecox</i>	(Amaryllidaceae)	13	Auto	4.0
<i>Allium</i> spp.	(Amaryllidaceae)	4, 5	Auto	—
<i>Bloomeria crocea</i>	(Amaryllidaceae)	13	Auto	1.2
<i>Brodiaea ixiodes</i>	(Amaryllidaceae)	18	Auto	—
<i>Brodiaea</i> spp.	(Amaryllidaceae)	4, 5	Auto	—
<i>Calochortus concolor</i>	(Liliaceae)	13	Auto	1.6
<i>C. luteus</i>	(Liliaceae)	18	Auto	—
<i>C. splendens</i>	(Liliaceae)	13	Auto	1.5
<i>C. spp.</i>	(Liliaceae)	4, 5	Auto	—
<i>Chlorogalum parviflorum</i>	(Liliaceae)	13	Auto	1.3 × 10
<i>C. pomeridianum</i>	(Liliaceae)	18	Auto	9.8
<i>Delphinium cardinale</i>	(Ranunculaceae)	13	Auto	1.2
<i>D. parryi</i>	(Ranunculaceae)	13	Auto	5.5 × 10 <sup>-1</sup>
<i>Dichelostemma pulchella</i>	(Amaryllidaceae)	13	Auto	1.9
<i>Elymus condensatus</i>	(Poaceae)	12	Auto	—
<i>E. glaucus</i>	(Poaceae)	22	Auto	—
<i>Heterotheca grandiflora</i>	(Asteraceae)	6, 13	Anemo!	9.1 × 10 <sup>-1*</sup>
<i>Lomatium dasycarpum</i>	(Apiaceae)	13	Anemo	5.0
<i>Marsh macrocarpus</i>	(Cucurbitaceae)	14	Auto [Zoo?]	1.4 × 10 <sup>3</sup>
<i>Melica imperfecta</i>	(Poaceae)	13	Auto	1.1*
<i>Paeonia californica</i>	(Paeoniaceae)	14	Auto	2.5 × 10 <sup>2</sup>
<i>Perezia microcephala</i>	(Asteraceae)	13	Anemo!	1.8
<i>Scrophularia californica</i>	(Scrophulariaceae)	13	Auto	6.0 × 10 <sup>-2</sup>
<i>Sisyrinchium bellum</i>	(Iridaceae)	4, 5	Auto	1.7
<i>Stipa coronata</i>	(Poaceae)	14	Zoo	5.0*
<i>S. lepida</i>	(Poaceae)	13	Zoo	7.5*
<i>S. pulchra</i>	(Poaceae)	22	Zoo	7.3*
<i>Zigadenus fremontii</i>	(Liliaceae)	14	Auto	3.4

Table VIII  
Continued

Species	Family	Source of information	Mode of dispersal	"Seed" mass (mg)
Annuals:				
<i>Agoseris heterophylla</i>	(Asteraceae)	13	Anemo!	$6.1 \times 10^{-1}$
<i>Antirrhinum nuttallianum</i>	(Scrophulariaceae)	13	Auto	$3.0 \times 10^{-2}$
<i>Chorizanthe fimbriata</i>	(Polygonaceae)	13	Auto	2.0*
<i>Clarkia delicata</i>	(Onagraceae)	24	Auto	—
<i>C. unguiculata</i>	(Onagraceae)	13, 24	Auto	$1.7 \times 10^{-1}$
<i>Cordylanthus filifolius</i>	(Scrophulariaceae)	13	Auto	$1.4 \times 10^{-1}$
<i>Cryptantha torreyana</i>	(Boraginaceae)	28	[Zoo?]	$1.7 \times 10^{-1}$
<i>Daucus pusillus</i>	(Apiaceae)	13	Zoo	$5.5 \times 10^{-1}$
<i>Descurainia pinnata</i>	(Brassicaceae)	14	Auto	$1.2 \times 10^{-1}$
<i>Emmenanthe rosea</i>	(Hydrophyllaceae)	30	Auto	—
<i>Eschscholtzia californica</i>	(Papaveraceae)	4, 5	Auto	1.4
<i>Festuca megalura</i>	(Poaceae)	14	Zoo	$3.9 \times 1.0^{-1}$ *
<i>F. reflexa</i>	(Poaceae)	28	Zoo	—
<i>Madia gracilis</i>	(Asteraceae)	13	Zoo	1.6
<i>Microseris heterocarpa</i>	(Asteraceae)	13	Zoo	$6.1 \times 10^{-1}$
<i>Pterostegia drymarioides</i>	(Polygonaceae)	13	Auto	$2.2 \times 10^{-1}$ *
<i>Salvia columbariae</i>	(Lamiaceae)	2, cf. 9	?Zoo	$6.8 \times 10^{-1}$

See footnotes in Table I.

\* Includes cryptophytes and hemicryptophytes.

may survive fire only in gaps or rock outcrops. In older stands of chaparral, subshrubs *Diplacus aurantiacus* and *Keckiella ternata* and the liana *Lonicera subspicata* have been observed to recruit seedlings within gaps (Keeley, unpubl.). *Yucca whipplei* is somewhat different. Technically, it does not resprout after fire; however, due to the harsh sites occupied by this species, rosettes often survive fires and flowering may occur at any time, thus seedlings might be expected in the second and subsequent years after fire.

Although all geophytes in chaparral have non-refractory seeds, they are abundant on burned sites because they sprout from deeply buried rhizomes, corms or bulbs (Keeley & Keeley, 1984, unpubl.). Ammirati (1967) reported this life form was more abundant than annuals on coastal sites but the opposite was true on interior sites. The timing of seedling recruitment by these species is largely unknown. Since all of these species flower in the first postfire season, seedling establishment is possible in subsequent years. A potential model of recruitment by geophytes may be the pattern observed for subshrubs in coastal sage (soft chaparral), which also flower from resprouts. *Encelia californica* and *Haplopappus squarrosus* resprouts are capable of seed production the first year after fire. Since the seeds are non-refractory, these shrubs recruit  $10^4$ – $10^6$  seedlings  $ha^{-1}$  in the second year after fire (Keeley & Keeley, 1984).

As the chaparral canopy closes, geophytes such as species of *Allium*, *Brodiaea*, *Chlorogalum*, and *Zigadenus* may survive for decades as dormant bulbs or corms, occasionally sending up leaves but, due to low light levels, seldom flowering under the shrub canopy (Ammirati, 1967; Christensen & Muller, 1975a; Stocking, 1966; Stone, 1951; Sweeney, 1956). Some of these taxa, e.g., *Elymus* spp., *Paeonia californica*, *Perezia microcephala*, *Scrophularia californica* and *Stipa* spp., persist and flower in gaps between shrubs, and others, e.g., *Marah macrocarpus*, are capable of growing through the canopy and flowering.

Annual species with non-refractory seeds may persist in chaparral burns by having some seeds that survive fire or by dispersal into burned areas. In mature chaparral, these species rarely establish under the shrub canopy, but rather are restricted to gaps created by shallow soils or by disturbance. Personal observations suggest that population size varies directly with annual precipitation level.

## V. Dispersal, Phenology and Seed Mass

Primack (1987) hypothesizes that there are close ecological and evolutionary relationships among seed size, seed dispersal and seedling establishment. Here I will illustrate how seed germination is also correlated with these reproductive characters.

### A. REFRACTORY SEED (FIRE-RECRUITER) SYNDROME

Shrubs with refractory seeds are modally quite different in dispersal mechanisms from species with non-refractory seeds. Most species with refractory seeds have propagules that are unspecialized for widespread dispersal and the average dispersal distance is not great. *Ceanothus* have capsules that eject seeds, but most fall beneath the canopy and, even on open sites, less than 2% reach 9 m (Davey, 1982; Evans et al., 1987). *Adenostoma fasciculatum* achenes are relatively light but have no specialized structures for anemochory (wind dispersal).

*Arctostaphylos* and the closely related *Xylococcus* produce drupes with a dry me-

socarp. These fruits are not specialized to attract animals, at least relative to related taxa such as *Comarostaphylos diversifolia* and *Arbutus menziesii* which have fleshy fruits; these latter taxa also have non-refractory seeds. Observations indicate that the vast majority of *Arctostaphylos* fruits are dispersed within the canopy radius (Keeley, 1977; Kelly, 1986). Rodents are attracted to these fruits, but most are not moved far and many are destroyed (Horton & Wright, 1944; Keeley & Hays, 1976). Coyotes and black bears are known to consume these fruits (Barrett, 1983; Grenfell & Brody, 1983) although in many cases they pass through intact and it is questionable as to how "attractive" they are as a food source. These vectors may be significant factors affecting range expansion of some species, although quantitatively they do not have an impact on the bulk of the fruit crop of most *Arctostaphylos* species in chaparral.

The attractiveness of drupes such as those of *Malosma laurina* are questionable. The fruits of this species have a gummy mesocarp that exudes noxious aromatic compounds, capable of vaporizing polypropylene petri dishes (Keeley, pers. obs.). One effect of this covering is to extend germination of the seed bank over a longer period (Hellmers & Ashby, 1958).

Seeds of *Fremontodendron* spp. and *Dendromecon rigida* are myrmecochores and thus specialized for ant dispersal; the seeds have a fatty appendage that is consumed but the seed is unharmed. Dispersal is relatively localized, usually < 10 m (Bullock, 1989). Also, seeds are highly concentrated at the nest site and few are lost en route. Potential advantages to myrmecochory include the dispersal of seeds uphill and to ridgetops where they may move by gravity into other drainages. Perhaps an even more important advantage is the potential for reducing predation, not only by sequestering the seeds away from other species, but the fatty appendage to the seed may be thought of as a "bribe" to discourage ant predation.

The refractory seeds of annual species are tiny and some are potentially moved by wind. The vast majority have no specialized structures or shapes conducive to anemochory or zoochory. Indeed, many of the Asteraceae have a deciduous or obsolete pappus (e.g., *Chaenactis*, *Malacothrix*), a characteristic designed to encourage localized dispersal.

The refractory seed (or fire-recruiter) syndrome exhibits what Angevine and Chabot (1979) call the "temporal disperser syndrome," where persistent seed banks lie dormant at a site and wait for a disturbance to occur on that spot; that is, rather than dispersing to a safe site, these seeds wait for a safe site (in the form of disturbance) to find them. These authors note that correlated with this syndrome must be great seed longevity and a germination mechanism for sensing and responding to a change in the competitive situation of the site. Both of these are characteristic of the refractory seed syndrome. When fires do occur they are quite extensive and thus safe sites are likewise extensive. This may partly explain why, on many sites, shrubs with this syndrome often dominate, whereas shrubs with the non-refractory seed (fire-resister) syndrome are more often scattered within a matrix of such species (Bullock, 1978).

Phenologically, the refractory seed syndrome contrasts with the non-refractory seed syndrome in that seed dispersal is nearly uniform in the spring and summer, compared to fall and winter for the latter group (Appendix I in Keeley, 1987a). For species with refractory seeds, decades are likely to pass between the time of seed dispersal and seed germination; consequently it is unlikely that the phenology of seed germination will have any selective effect on the timing of dispersal. A more important factor in timing of dispersal is the fact that a portion, or all, of the population of refractory seeded species will be plants which began as seedlings (in contrast to

resprouts) after the last fire. These shrubs will have shallower root systems (Kummerow et al., 1981) and will be subject to great water stress during the summer drought (Poole et al., 1981), putting a premium on completion of fruit maturation prior to the summer drought.

Seed mass of most species is shown in Tables I, II and VIII. A comparison of average seed mass for species with refractory and non-refractory seeds is shown in Table IX. Comparing shrubs or annuals of each type shows that species with refractory seeds have lighter seeds. This may reflect the environmental favorableness of the postfire environment for seedling establishment. Also, persistent seed banks result in longer exposure to predation and this would select for small seeds.

After fire, the phenology of seedling establishment is consistently late winter to early spring (Bullock, 1982; Christensen & Muller, 1975b; Keeley & Soderstrom, 1986; Rundel et al., 1987; Sweeney, 1956). While heat shock or charred wood play a dominant role in overcoming dormancy of these refractory seeds, other factors must be involved in delaying germination to this time. As already mentioned, many species of *Arctostaphylos* and *Ceanothus* require various periods of cold stratification to overcome other forms of embryo dormancy. Additional factors that may play a role are specific temperature regimes for germination. For example, Imamura (1971) noted that scarified *Phacelia grandiflora* seeds remained dormant under high (summer) temperatures but germinated after being exposed to alternating high and low temperatures.

## B. NON-REFRACTORY SEED (FIRE-RESISTER) SYNDROME

Chaparral taxa with non-refractory seeds are relatively heterogeneous in their life history characteristics. The term "fire-resister" well describes the shrubs in this group. Although the other life forms do not recruit seedlings in the first postfire year, they may benefit from disturbance by increased opportunity for flowering.

### *i. Shrubs With the Non-refractory Seed Syndrome*

Shrubs with non-refractory seeds (Table VIII) are specialized for animal dispersal. Most produce a fleshy berry or drupe that is attractive to resident as well as migratory birds (Bailey, 1978; Hom, 1984). Scarification by passage through the birds is not a necessity for germination, but this undoubtedly expedites the necessary removal of the fruit pulp (Keeley, 1987a). Oaks that occur in chaparral all have non-refractory seeds and these are widely dispersed by scrub jays (Grinnell, 1936). *Cercocarpus betuloides* is the only chaparral shrub with plumose achenes specialized for wind dispersal.

The selective basis for wide dispersal in these shrubs is that safe sites are very likely highly variable in space. Seedlings not only appear to require the mesic conditions of a thick litter layer (Keeley, unpubl.), possibly coinciding with very wet years (Zedler, 1982), but established shrubs of these species require relatively mesic sites. This group typically requires deeper substrates for development of deep roots (Kummerow et al., 1981) that can tap water during summer drought. These species, e.g., *Quercus* spp., *Rhamnus* spp., *Prunus ilicifolia*, *Heteromeles arbutifolia*, and *Cercocarpus betuloides*, are drought-evaders and are not capable of sustaining water potentials as low as those of other chaparral shrubs, i.e., ones with the refractory seed syndrome such as *Adenostoma fasciculatum*, *Ceanothus* spp., and *Arctostaphylos*

(Burk, 1978; Krause & Kummerow, 1977; Parker, 1984; Poole et al., 1981; Roberts et al., 1981). Finding such mesic sites must be a precarious undertaking, one best accomplished by widespread dispersal and recruitment independent of fire. Bullock (1978) found that individuals of fleshy fruited species are sparsely distributed in the chaparral; he regarded them as interstitial, persisting in cracks in the matrix of other shrubs. Once such a site has been encountered and occupied, continuing exploitation of that site by vigorous resprouting through repeated fire cycles would be selected for.

Associated with the non-refractory seed syndrome is the phenology of fruit dispersal; all disperse in fall and winter (Appendix I in Keeley, 1987a). This may have been selected to take advantage of migratory birds as well as to time the shedding of non-refractory seeds to arrival of winter rains (and avoid the mediterranean-climate summer drought). A consequence of this is that flower and/or fruit maturation must occur during the summer and fall drought. Apparently for deep rooted (resprouting) shrubs this is possible in many years, although fruit maturation is extremely sensitive to drought (Mooney et al., 1977).

The average seed mass for shrub species with non-refractory seeds was significantly greater than the average for heat stimulated or charred wood stimulated seeds (Table IX). This difference in seed mass could be accentuated by inclusion of other non-refractory seeded species (with massive seeds) that were excluded because of their very localized distributions; e.g., *Simmondsia chinensis* and other species of *Quercus* and *Prunus* (Keeley, unpubl.). Baker (1972) noted that in the California flora, shrub seed weight was negatively correlated with light availability in the habitat. He suggested that this may reflect selection for larger seed reserves to enhance establishment under the canopy of closed vegetation. Large seeds would also enhance the speed with which seedlings could develop root systems deep enough to survive the summer drought, a critical feature for seedling establishment by these drought-evading species that require access to summer water (Davis, 1989; DeSouza et al., 1986; Poole et al., 1981).

The phenology of seedling establishment by species with non-refractory seeds is mainly cued to the first rains that occur in fall. This is known to be the case for the shrubs *Quercus dumosa* and *Rhamnus californica* and for geophytes such as *Paenonia californica*, *Marah macrocarpus*, species of *Calochortus* and *Stipa* (Fiedler, 1987; Keeley, 1987a; Matsuda & McBride, 1989; Schlising, 1969, 1976). It is unclear why these species would germinate earlier than species with refractory seeds, which delay germination to late winter or spring. The answer may lie in the fact that many species in this group produce large seeds that are targets for predation or a longer season for seedling establishment (before the summer drought) may be required for these more mesic-adapted species. The disadvantage of early germination is that fall precipitation is less predictable than spring precipitation; e.g., in southern California the coefficient of variation is 325%, 144%, and 111% for September, October and November precipitation but 89%, 83%, and 88% for January, February and March (data from 83 year total at Sweetwater Reservoir, San Diego Co. U.S. Weather Bureau, unpubl. data). This pattern is upheld even in the Arizona chaparral where the *Quercus dumosa* vicariant, *Q. turbinella*, germinates (in unburned chaparral) following summer rains, whereas refractory seeded species *Arctostaphylos* and *Ceanothus* germinate on burned sites in spring (Pase, 1965).

Curiously, the non-refractory seed syndrome described here for certain chaparral shrubs (Table VIII) is identical in most aspects of germination, dispersal mode, large

**Table IX**

Mean "seed" mass of species with different germination response ("seed" may include ovary tissues, e.g., as in an achene or drupe pit)

	"Seed" mass (mg)		
	Non-refractory $\bar{x} \pm SD$ (n)	Heat stimulated $\bar{x} \pm SD$ (n)	Charred wood-stimulated $\bar{x} \pm SD$ (n)
Shrubs	410.00 $\pm$ 693.24 (8)	25.68 <sup>a,1</sup> $\pm$ 58.23 (19)	20.10 <sup>a</sup> $\pm$ 12.44 (5)
Subshrubs and suffrutescents	2.49 <sup>a,1</sup> $\pm$ 34.68 (15)	2.79 <sup>a,1</sup> $\pm$ 3.03 (5)	6.00 <sup>a</sup> $\pm$ 11.04 (13)
Geophytes	81.83 $\pm$ 306.78 (21)	—	—
Annuals	0.62 <sup>1</sup> $\pm$ 0.62 (14)	0.14 <sup>a,1</sup> $\pm$ 0.08 (4)	0.33 <sup>a</sup> $\pm$ 0.30 (26)

<sup>a</sup> Within a row, means with the same superscript letter are not significantly different at  $P < 0.05$ .

<sup>1</sup> Within a column, means with the same superscript number are not significantly different at  $P < 0.05$ .

seed mass and phenology of seed dispersal and seedling establishment, to that of taxa in Californian woodland communities; e.g., *Umbellularia*, *Quercus*, *Acer*, *Arbutus*, and *Juglans* (Keeley, 1987a). In this regard it should be pointed out that many of the non-refractory seeded species, e.g., *Heteromeles arbutifolia*, *Prunus ilicifolia* and *Rhamnus* spp. are regular components of those communities (Campbell, 1980; Griffin, 1977; Pelton, 1962; Sawyer, et al., 1977).

### ii. Other Life Forms With the Non-refractory Seed Syndrome

Half of the subshrubs and suffrutescents in this group have propagules specialized for dispersal (Table VIII). Taxa with anemochory include *Baccharis* with persistent pappus and species such as *Yucca whipplei* with flattened winged seeds. Wind dispersed subshrubs such as *Baccharis* spp. establish in many sorts of disturbances or gaps within the chaparral matrix (Wells, 1962). Others with this life form have no specialized mode of dispersal, e.g., *Keckiella* spp. or *Diplacus* spp. These subliguous forms tend to recruit seedlings within gaps in the chaparral canopy. This life form disperses propagules from spring to fall. Seed mass is, on average, the same as subshrubs with refractory seeds (Table IX).

All geophytes have non-refractory seeds, and most are relatively unspecialized for dispersal and thus depend on factors such as gravity (Bullock, 1976). A few grasses have awns that may attach to animal fur. Species such as *Marah* have seeds that are attractive to rodents, and burial by these animal dispersers may be critical to successful establishment (Schlising, 1969). On average, seed mass of these geophytes is surpassed only by shrubs with non-refractory seeds (Table IX). In order to survive the summer drought these taxa must develop an adequate root system and underground storage organ. A large seed mass may be a prerequisite for this (Schlising, 1976), an idea supported by Baker's (1972) observation of a strong correlation between seed mass and aridity of the habitat in the Californian herbs.

Annuals with non-refractory seeds are a heterogeneous group; some are wind dispersed, some animal dispersed and some relatively unspecialized. Average seed mass is greater than for annuals with refractory seeds (Table IX), although the phenology of dispersal is relatively similar. These species may disperse into burns and gaps

within the chaparral matrix. *Heterotheca grandiflora* is one that has become an invasive weed along roadsides far beyond its original cismontane California range, due in part to its developmental plasticity (Flint & Palmblad, 1978). Baker (1972) notes that annuals in the Californian flora found in unnatural communities have greater seed mass than species indigenous to natural communities. He relates this to greater aridity in unnatural communities. Perhaps gaps within the chaparral matrix are more arid sites than recently burned sites.

## VI. Conclusions and Areas for Future Research

Much remains to be learned of the ecophysiology of seed germination in the California chaparral flora. The summary by Baskin and Baskin (1988) of the extensive studies made on the southeastern U.S. flora illustrate the potential complexity still unstudied for the Californian flora. The detailed examination by Cruden (1974) of the germination of *Nemophila menziesii* illustrates the level of "fine-tuning" of germination to the mediterranean-climate yet to be uncovered for the chaparral flora. The areas in need of focus include:

1. Importance of post-dispersal environments on inducing secondary dormancy in both non-refractory seeds and refractory seeds.
2. Degree to which allelopathic substances play a role in enforced dormancy.
3. The role of after-ripening of rudimentary embryos on maintenance of long term dormancy in the several fire-following species with such seeds.
4. The mechanism behind charred wood stimulated germination.
5. The role of alternating moistening and drying periods, induced by unpredictable patterns of precipitation, on dormancy and germination.

As illustrated here, seed germination modes are correlated with other reproductive and life history characteristics shared by many species. These syndromes have co-evolved to generate very different demographic patterns and responses to the repeated disturbance of wildfires. The life history approach taken here illustrates that opportunities for population expansion increase after fire for some species, but for other species they increase in the absence of fire. It seems evident that equilibrium in species composition is enhanced by variable burning regimes. What impact does the current anthropogenic fire regime have on the demography of these species?

## VII. Acknowledgments

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