

10. Seed-Germination Patterns in Fire-Prone Mediterranean-Climate Regions

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Wildfires are a known feature of mediterranean ecosystems and most plant communities are resilient to such perturbations; many species have evolved adaptations to periodic fires (Keeley 1986). Resilience to a perturbation such as wildfire does not, however, imply that resilient species have evolved traits adapted to such disturbance. In all mediterranean ecosystems many woody and herbaceous species recover after wildfires by resprouting from below-ground vegetative structures, but resprouting is a widespread trait in plants and is probably a preadaptation to surviving fires (Wells 1969).

In mediterranean ecosystems three modes of plant life history are recognizable:

1. Species that resprout after fire but fail to recruit seedlings in the postfire environment. Such taxa are resilient to fires and may require extended fire-free periods for seedling recruitment (Keeley 1992a). With respect to fire, such species are described in the literature as obligate resprouters or fire persisters. For seedling recruitment, these taxa are best described as having "disturbance-free recruitment," because opportunities for recruitment and population expansion occur in the absence of disturbance.
2. Species that restrict seedling recruitment to the immediate postfire environment. Depending on whether or not these species resprout after fire, they have been described as obligate seeders or facultative seeders. Unlike the first group of plants, these taxa have "disturbance-dependent re-

recruitment." For these species, opportunities for recruitment and population expansion are restricted to a short time immediately after fire.

3. Species that do not recruit seedlings immediately after fire but potentially exploit subsequent postfire years for seedling recruitment. Some of these species resprout and flower in the first year after fire. Others may disperse into burned sites. I describe these species as having "disturbance-dependent recruitment" but in later postfire years.

My focus in this chapter is to compare the seed germination behavior of "disturbance-dependent" and "disturbance-free" modes of life history. As has been demonstrated for California chaparral (Keeley 1991), many other characteristics are correlated with these two life history syndromes.

Seed Dormancy and Germination

If a viable seed does not germinate when incubated under appropriate moisture and temperature ranges, it is considered dormant. Different forms of dormancy are possible (Harper 1977). "Induced" dormancy is acquired inability to germinate, due to an environmental condition experienced by the seed after dispersal from the parent, and may persist even after that condition disappears. Many authors call this state 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 primary dormancy.

Little is known about induced seed dormancy in seeds of mediterranean species. One observation that suggests its presence is the report that for some California chaparral species, fresh seeds germinate readily whereas older seeds require treatment to break dormancy (e.g., Emery 1988).

Enforced seed dormancy imposed by allelopathic compounds has been suggested as an important factor controlling germination in many mediterranean plants. The role of this factor in most ecosystems is a matter of much controversy.

Innate dormancy describes embryos that require an after-ripening period for development, or embryos that require some biochemical transformation that is cued by: (1) an environmental stimulus, (2) an inhibitor in the seed coat that needs to be leached from the seed, or (3) the seed coat, which acts as a barrier to water or oxygen uptake and requires scarification.

Most studies of seed germination of mediterranean species have focused on delineating not the mechanisms responsible for dormancy, but rather the extent to which dormancy could be broken by fire. Refractory seeds are those in which germination depends upon the stimulus of either intense heat shock or chemicals leached from charred wood (Keeley 1991). Thus, my primary focus in this review will be to evaluate the distribution of refractory and nonrefractory seeds in mediterranean ecosystems and the life-history characteristics associated with these two patterns of germination.

California Chaparral

Table 10.1 gives examples of chaparral taxa that illustrate the patterns of germination response evident in the California flora. These germination responses, as we would expect, correlate well with whether the species has disturbance-free or disturbance-dependent seedling recruitment.

Disturbance-Free Recruitment

Species present after fire strictly from resprouts fail to recruit seedlings because they lack a persistent seed bank (Parker and Kelly 1989). The transiency of the seed banks of such species derives from the nonrefractory nature of these seeds and thus do not require fire-related stimuli, e.g., *Quercus dumosa* (Fagaceae) (Table 10.2). Seeds germinate readily at maturity and are

Table 10.1. Representative examples of species exhibiting different germination characteristics from the chaparral. Apparently all herbaceous perennials, including geophytes, have nonrefractory seeds

Nonrefractory seeds	Heat-stimulated seeds	Charred-wood-stimulated seeds
Shrubs		
Fagaceae <i>Quercus dumosa</i>	Anacardiaceae <i>Rhus</i> spp.	Ericaceae <i>Arctostaphylos</i> spp.
Rhamnaceae <i>Rhamnus</i> spp.	Rhamnaceae <i>Ceanothus</i> spp.	Garryaceae <i>Garrya flavescens</i>
Rosaceae <i>Prunus ilicifolia</i>	Sterculiaceae <i>Fremontodendron</i> spp.	Rosaceae <i>Adenostoma fasciculatum</i>
Subshrubs		
Agavaceae <i>Yucca whipplei</i>	Cistaceae <i>Helianthemum scoparium</i>	Papaveraceae <i>Romneya</i> spp.
Polygonaceae <i>Eriogonum fasciculatum</i>	Fabaceae <i>Lotus scoparius</i>	Lamiaceae <i>Salvia mellifera</i>
Scrophulariaceae <i>Keckiella</i> spp.	Lamiaceae <i>Salvia apiana</i>	Hydrophyllaceae <i>Eriodictyon crassifolium</i>
Herbaceous perennials		
Amaryllidaceae <i>Allium</i> spp.		
Liliaceae <i>Zigadenus fremontii</i>		
Paeoniaceae <i>Paeonia californica</i>		
Annuals		
Asteraceae <i>Microseris heterocarpa</i>	Apiaceae <i>Apiastrum angustifolium</i>	Papaveraceae <i>Papaver californica</i>
Polygonaceae <i>Chorizanthe</i> spp.	Fabaceae <i>Lotus salsuginosus</i>	Caryophyllaceae <i>Silene multinervia</i>
Scrophulariaceae <i>Cordylanthus</i> spp.	Onagraceae <i>Camissonia hirtella</i>	Hydrophyllaceae <i>Emmenanthe penduliflora</i>

Table 10.2. Germination patterns of species with nonrefractory seeds, heat-shock-stimulated germination and charred-wood-stimulated germination (data from Keeley 1987 and Keeley et al. 1985)

Temperature (C) Time (min)	Percentage germination									
	Light						Dark			
	Control	70 120	80 60	100 5	120 5	150 5	Control	70 120	100 5	120 5
<i>Quercus dumosa</i> (shrub)										
Control	77	0	—	57	55	—	66	0	60	47
Charred wood	68	0	—	53	27	—	70	0	40	50
<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>Ceanothus megacarpus</i> (shrub)										
Control	11	41	—	48	80	—	6	54	53	88
Charred wood	2	40	—	40	61	—	3	40	56	67
<i>Camissonia hirtella</i> (annual)										
Control	30	—	49	—	66	69	—	—	—	—
Charred wood	26	—	33	—	22	20	—	—	—	—
<i>Romneya trichocalyx</i> (suffrutescent)										
Control	0	0	—	0	0	—	0	0	0	1
Charred wood	24	33	—	34	24	—	17	11	13	10

short-lived; probably none survive beyond nine months in the soil. Examples of other such species, all long-lived evergreen shrubs, with this syndrome include *Heteromeles arbutifolia* (Rosaceae), *Rhamnus* spp. (Rhamnaceae), and *Prunus* spp. (Rosaceae).

Shrub species with nonrefractory seeds produce fleshy fruits or acorns that mature in autumn and winter and are animal dispersed. Germination typically occurs within weeks of the first autumn or winter rains, although seedling establishment is generally rare. The only reports of seedling recruitment come from stands free of fire for more than fifty years (Patric and Hanes 1964, Zedler 1981, Keeley et al. 1986, Keeley 1992a, 1992b).

Physiologically, these "disturbance-free recruiters" are the least drought tolerant of the shrub species in chaparral (Keeley 1992b, 1992d). Adults survive because the established root crowns maintain a root system that allows the plant to avoid extreme stress from summer drought. Seedling recruitment, however, is vulnerable and their recruitment pattern is viewed as a mechanism for escaping the extreme aridity of open disturbed sites. It is argued (Keeley 1992d) that animal dispersal is a necessary correlate of this recruitment syndrome because safe sites for seedlings are a relatively small portion of this arid landscape. Autumn and winter dispersal would take advantage of migrating birds as well as provide for dispersal of these short-lived seeds during the appropriate season for successful seedling establishment.

Disturbance-Dependent Recruitment: Immediate Postfire

For many chaparral species, seedling establishment is restricted to the first spring after fire. In all but a few species, seeds are refractory and seedlings arise from a persistent seed bank. Correlated with this syndrome must be great seed longevity and a germination mechanism for sensing fire. Two mechanisms have evolved in chaparral species for detecting when a fire has passed through a site. One involves germination stimulated by intense heat shock, and the other involves germination stimulated by chemicals produced by combustion of wood. Examples of species with dormant seeds that germinate in response to one or the other of these two stimuli are shown in Table 10.2. Under natural conditions refractory seeds "require" a fire-related stimulus, either alone or coupled with other conditions such as a cold stratification period.

Shrubs in the genus *Ceanothus* (Rhamnaceae) have been known for many years to be highly refractory and to germinate only after exposure to intense heat (Table 10.2). *Ceanothus* typically have a very small percentage of nonrefractory seeds, whereas in other taxa such as *Camissonia hirtella* (Onagraceae), a significant fraction of the seed pool is nonrefractory and germinates readily upon wetting (Table 10.2). In species with heat-stimulated germination, dormancy is imposed by the seed coat, which prevents uptake of water and gases (Stone and Juhren 1951). These seeds are commonly referred to as "hard" and typically are covered with an unbroken cuticle that prevents imbibition (Fig. 10.1A). Heat shock melts or cracks the cuticle or integuments and allows imbibition (Fig. 10.1B). Such "hard-seeded" species with disturbance-dependent seedling recruitment are not unique to mediterranean ecosystems. For example, Martin and Cushwa (1966) describe species from the southeastern United States with "hard" seeds that lie dormant in soil until germination is stimulated by heat shock from fire.

Many chaparral species have dormant seeds that are stimulated to germinate after fire by the presence of charred wood (Table 10.1). *Romneya trichocalyx* (Papaveraceae) is one example of a species that exhibits nearly obligatory dependence upon charred wood to overcome dormancy (Table 10.2). More than 40 chaparral species have been reported to have refractory seeds that germinate in response to incubation in the presence of charred wood (Wicklowsky 1977, Jones and Schlesinger 1980, Keeley et al. 1985, Keeley 1987, 1991, Keeley and Keeley 1987). Heat shock is ineffective in stimulating germination in most of these species. As with heat shock-stimulated germination, some species have polymorphic seed pools in which some seeds are nonrefractory and germinate readily and others are refractory and germinate only in the presence of charred wood.

The mechanism behind germination stimulated by charred wood is unknown. Experiments thus far have revealed that the chemical is a water-soluble organic compound present in soils of recently burned chaparral (Keeley and Nitzberg 1984, Keeley et al. 1985). Most experiments have been

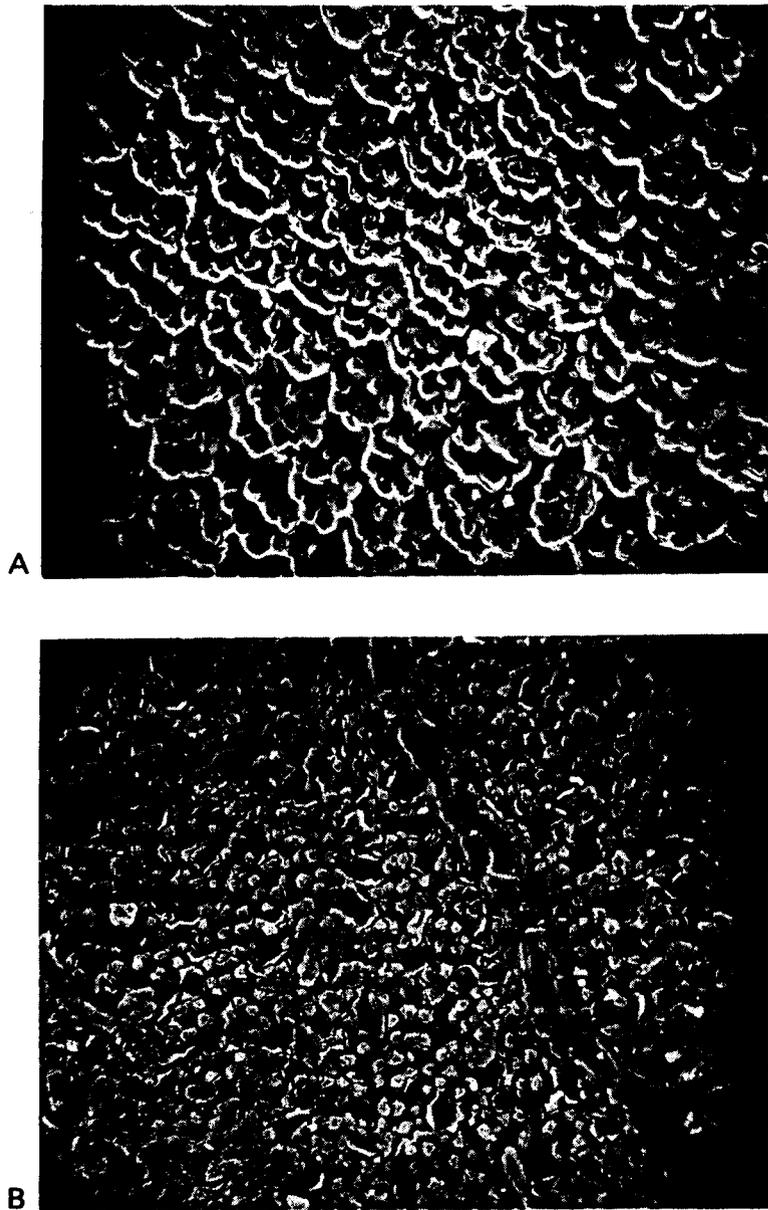


Figure 10.1. SEM (2000x) of *Lotus scoparius* seed coats (A) before, and (B) after heat treatment (120°C for 5 minutes) (from Keeley unpub. data). This species has heat shock-stimulated germination (Keeley 1991).

unsuccessful at pinpointing the precise chemical involved, despite tests of more than twenty potential breakdown products of lignin and cellulose (S. Keeley and Pizzorno 1986, Keeley unpub. data). Recent experiments, however, reveal that for one species, *Romneya coulteri*, the charred wood-stimulated germination response can be duplicated by using either smoke or gibberellic acid (Keeley unpub. data).

For species with heat-stimulated seeds and species with charred-wood-stimulated seeds, sometimes an additional environmental cue other than fire

is required for germination. For example, some of these species require a cold stratification period of several months to overcome innate dormancy of the embryo. In the genus *Ceanothus*, high elevation species require this cold treatment, but low elevation species do not (Quick 1935). Some montane chaparral species of *Arctostaphylos* (Ericaceae) require a cold stratification period (Mirov 1936, Carlson and Sharp 1975), in addition to charred wood (Keeley 1991), to overcome dormancy. Populations of *Salvia mellifera* (Lamiaceae) from the coast, mountains, and desert, however, have no stratification requirement (Keeley 1986).

Shrub species with refractory seeds have similar demographic patterns, regardless of whether germination is stimulated by heat or charred wood. All such species establish seedlings in the first growing season after fire from a persistent soil-stored seed bank. Successful seedling establishment after the first postfire year is rare (Horton and Kraebel 1955, Keeley and Zedler 1978, Mills and Kummerow 1989). Many of these species are incapable of resprouting and thus populations are even aged (Keeley 1992a).

Many annual species with refractory seeds are highly specialized "fire followers," and seedling recruitment is mostly if not entirely restricted to the first year after fire (Sweeney 1956, S. Keeley et al. 1981).

Disturbance-dependent recruiters typically disperse their seeds in spring and summer, but often decades pass before germination occurs. Most of these species do not have propagules specialized for dispersal and illustrate the "temporal disperser syndrome" described by Angevine and Chabot (1979). In such species, dispersal is localized and persistent seed banks lie dormant until a disturbance occurs.

Once the chaparral canopy is regrown, seedling establishment by species with refractory seeds (Table 10.1) is seldom successful, except occasionally in gaps (Keeley 1992a, 1992b). Species that produce refractory seeds have polymorphic seed pools of both refractory and nonrefractory seeds. The ratio of refractory to nonrefractory seeds varies with the species. Even within a species there may be ecotypic differences in the ratio, and following dispersal, induced or enforced dormancy may cause changes in this ratio with time.

The role of polymorphic seed pools may be to take advantage of gaps in the chaparral canopy as well as store seeds until fire. Another strategy is illustrated by the germination behavior of *Artemisia californica* (Asteraceae) (Table 10.2). Seeds on the soil surface in gaps would germinate readily following the first autumn rains. Buried seeds, however, remain dormant and persist in the seed bank until charred wood overcomes the dark-enforced dormancy.

Great seed longevity is necessary for refractory seeds that make up the persistent seed banks. *Ceanothus* seeds are known to survive twenty years in laboratory storage (Quick 1935). Longevity is inferred for many other chaparral taxa that may die out on a site, but many years later reestablish seedlings following fire (Keeley 1991).

Enforced seed dormancy has been proposed as a major factor in Califor-

nia chaparral. McPherson and Muller (1969) concluded that nearly all seeds in the soil beneath *Adenostoma fasciculatum* (Rosaceae) are prevented from germinating by a toxin leached from the overstory shrubs; i.e., these allelopathic compounds enforced dormancy on the seeds. Other authors however, have not been able to demonstrate such an effect on the seeds of the most common chaparral shrubs or herbs (Christensen and Muller 1975a, 1975b, Kaminsky 1981, Keeley et al. 1985, Keeley and Keeley 1989). For refractory seeds, allelopathy is not a relevant factor because the seeds remain dormant in the absence of such chemicals. For species with polymorphic seed pools, allelopathic chemicals may suppress germination of the nonrefractory portion of the seed bank. Theoretically such a mechanism would be effective in preventing germination of seeds in such unfavorable sites as under the shrub canopy (Keeley 1991).

A few coniferous taxa, with widely disjunct populations in chaparral, have serotinous cones. These taxa, in genera such as *Cupressus* (Cupressaceae) and *Pinus* (Pinaceae) form even-aged stands with recruitment restricted to the first postfire year (Vogl et al. 1977, Zedler 1977). In these species seeds are not refractory; instead a persistent seed bank accumulates in the canopy because of dormancy imposed by retention within the fruit.

Disturbance-Dependent Recruitment: Later Postfire

All herbaceous perennials in chaparral are abundant on recently burned sites because they resprout from deeply buried rhizomes, corms, or bulbs, but seedlings are not produced in the first postfire year (Keeley and Keeley 1984, unpub. data). All these species flower in the first postfire season and produce nonrefractory seeds (Keeley 1991). Therefore, it is likely that seedling establishment occurs in the second or later postfire years. As the chaparral canopy closes, most of the geophytes are dormant and rarely flower and the few leaves that are produced are consumed by rodents (Stone 1951, Sweeney 1956, Christensen and Muller 1975a). Other herbaceous perennials may persist and flower in gaps in the canopy, and these also have nonrefractory seeds.

Certain resprouting subshrubs, typical of the coastal sage vegetation, do not maintain persistent seed banks and, because they are subliguous, persistence on a site is a function of fire intensity. Examples include *Encelia californica* (Asteraceae) *Eriogonum* spp. (Polygonaceae), and *Haplopappus* spp. (Asteraceae). On coastal sites, where fires are commonly of moderate intensity, these subshrubs resprout and flower profusely in the first year. Because the seeds are nonrefractory, seedling establishment is abundant in the second year (Keeley and Keeley 1984). These same species often do not resprout on the more arid interior sites, possibly because of greater fire intensity, and thus fires may result in localized extinction (Westman and O'Leary 1986).

Many nonnative and a few native annual species disperse into and colo-

nize burned sites in years subsequent to fire. These species have nonrefractory seeds (Keeley and Keeley 1987), although other factors such as light quality and soil-nutrient status may affect germination.

In summary, refractory seeds, which require a fire-related stimulus, are not typical of species that recruit seedlings in the second or subsequent post-fire years.

Mediterranean Basin

Wildfires are a natural feature of the garrigue, maquis, and phrygana vegetation in Europe (Naveh 1974). As in the California chaparral, many taxa are obligate resprouters after fire and seedling establishment occurs if not disturbed. Other taxa depend upon fires for establishing seedlings from a soil-stored seed bank.

Disturbance-Free Recruitment

Postfire obligate resprouting shrubs and lianas include all *Quercus* spp. (Fagaceae), *Pistacia* spp. (Anacardiaceae), *Rhamnus* spp. (Rhamnaceae), *Phillyrea latifolia* (Oleaceae), *Sorbus* spp. (Rosaceae), *Olea europaea* (Oleaceae), *Osyris alba* (Santalaceae), *Crataegus aronia* (Rosaceae), *Erica arborea* (Ericaceae), *Myrtus communis* (Myrtaceae), *Nerium oleander* (Apocynaceae), *Juniperus phoenicea*, *J. oxycedrus* (Cupressaceae), *Smilax* spp. (Liliaceae), and *Rubia* spp. (Rubiaceae) (Le Houerou 1974, Naveh 1975, Gratani and Amadori 1991). None of these species is known to produce refractory seeds and many have been shown to germinate readily under appropriate moisture and temperatures (Mitrakos 1981, Mesleard and Lepart 1991, Izhaki and Safriel 1990, J. Herrera 1991, Keeley unpub. data). Lack of refractory seeds would result in a transient seed bank (Harif 1978), which would account for the lack of seedling establishment after fire.

Results of detailed studies of *Arbutus unedo* are probably typical of others with this syndrome. Fleshy fruits are dispersed by birds in winter but no evidence shows that passage through the gut enhances germination beyond removal of the pericarp (Debussche 1985, Keeley 1987). Seeds are nonrefractory and germinate readily on moist substrate at temperatures below 15°C (Ricardo and Veloso 1987, Mazzoleni 1989, Mesleard and Lepart 1991). Seeds retained within fruits may survive in the soil until the following rainy season, although other seeds that fail to germinate may not survive long in the soil. Seedlings do not tolerate summer drought stress on exposed sites and thus seedling establishment is restricted to dense vegetation (Mesleard and Lepart 1991).

The life history characteristics of these postfire obligate resprouters is remarkably similar to characteristics of obligate resprouters in the California chaparral, many of which are in the same genera—e.g., *Quercus*, *Rhamnus*,

and *Prunus*. As with the California taxa, all these Mediterranean species produce fruits that are animal dispersed. Dispersal is in the autumn and winter, taking advantage of migrating bird populations (C. Herrera 1984a, 1984b, 1987, Izhaki and Safriel 1985, Debussche et al. 1980, Izhaki et al. 1991, J. Herrera 1991). Winter dispersal is a further advantage because seeds are nonrefractory and germination occurs soon after they encounter moist substrates. Successful seedling recruitment appears to require disturbance-free conditions under the vegetation canopy.

This "disturbance-free recruitment" syndrome is apparently quite old and seems to predate the present mediterranean climate. C. Herrera (1992a, 1992b) points out that many species with this character syndrome represent old phylogenetic lines. This observation is supported by the remarkable similarity in seed germination, dispersal, and seedling recruitment patterns observed in Californian and Mediterranean species of *Quercus*, *Rhamnus*, and *Prunus*. Herrera (1992b) suggests there is little reason to accept an "adaptationist" interpretation of this syndrome when it is clearly a result of historical effects.

Much about the seedling recruitment patterns of these taxa suggests that they are best adapted to moist microsites and consequently are not able to fully exploit much of the mediterranean-climate landscape. Under a former summer-rain climate, these taxa would undoubtedly have flourished. Today they persist because (1) they are long lived, (2) they resist destruction by wildfires by resprouting, and (3) older undisturbed vegetation generates sufficient moist microsites to allow occasional seedling recruitment. I suggest that the coevolved life history characteristics of seed germination, seed dispersal, and seedling physiology are just as adaptive in such microsites as they were under former climates, albeit on a far more limited scale.

Disturbance-Dependent Recruitment: Immediate Postfire

Although subshrubs such as *Cistus* spp. (Cistaceae) are capable of resprouting under moderately intense burning, they also establish seedlings in the first year after fire from soil-stored seeds (Martin and Juhren 1954, Naveh 1975, Troumbis and Trabaud 1986, Alonso et al. 1992). It is interesting that these *Cistus* spp. germinate in the autumn following fire, and poor survival is predicted for spring-germinating seeds (Troumbis and Trabaud 1986). This pattern is apparently true for other mediterranean species and contrasts markedly to the chaparral, where postfire seeding species establish in spring following fire.

Seeds of Cistaceae are known to be "hard-seeded"—i.e., dormancy is imposed by an impervious seed coat that prevents imbibition, and heat shock from fire is sufficient to overcome this seed coat imposed dormancy. Traubaud and Oustric (1989) report that germination of the refractory seeds of *Cistus albidus*, *C. monspeliensis*, *C. salvifolius* was increased from a few

percent for controls to >70% with certain heat treatments. They mention too that species differed in the optimal temperature treatment.

Thanos and Georghiou (1988) also report heat-shock-stimulated germination in the eastern Mediterranean *Cistus incanus* and *C. salvifolius*. They demonstrated that light and incubation temperature were unimportant factors in germination. These authors noted that the seed pools of these *Cistus* spp. were polymorphic. Some germinate readily and are capable of establishing on open sites. Others have water-impermeable seed coats and are stimulated to germinate by intense heat shock. They suggest that seed coat hardness was variable in the seed pool and would allow for germination under many conditions. Similar seed-pool polymorphism has also been seen in *C. ladanifer* from the western Mediterranean, where it was demonstrated that nearly 60% of the seeds were nonrefractory (Valbuena et al. 1992). Germination of this species, as well as *C. laurifolius*, was significantly increased, however, with heat shock.

Aronne and Mazzoleni (1989) used microscopic examination of seeds to study the effect of heat shock on seed coat integuments of *Cistus incanus* and *C. monspeliensis*. They demonstrated exposure to 120°C for 90 seconds was sufficient to form cracks on the inner layer of the seed coat, and this was necessary for imbibition and subsequent germination.

Other shrubs that recruit seedlings immediately after fire from persistent soil-stored seed banks include taxa in the Fabaceae (*Ulex* spp., *Cytisus* spp., *Calicotome* spp., and *Genista* spp.), Lamiaceae (*Rosmarinus officinalis*, *Satureja thymbra*, *Teucrium* spp., *Thymus* spp., and *Salvia* spp.), Rosaceae (*Sarcopoterium spinosum*), and Anacardiaceae (*Rhus coriaria*) (Naveh 1974, 1975, Papanastasis and Romanas 1977, Belhassen et al. 1987, Trabaud 1987, Izhaki et al. 1992).

Based on the patterns observed with California taxa, I predict that the "hard-seeded" Fabaceae species will have heat shock-stimulated germination, and some evidence supports this belief; germination is stimulated by high temperatures in *Calicotome villosa* (Keeley, unpublished data), *Cytisus scoparius* (Bossard 1993), and *Genista florida* (Tarrega et al. 1992). The latter two authors also show temperatures above 150°C are lethal. Other species that exhibit heat shock-stimulated germination include *Phlomis lanata*, *Lavandula stoechas*, and *Sarcopoterium spinosum* (Table 10.3).

Of more than fifty species from the eastern Mediterranean, only one, *Stachys tymihaus*, has tested positive for enhanced germination in the presence of charred wood (Table 10.3).

Sarcopoterium spinosum is a species that germinates prolifically after fire, and yet results from Table 10.3 and other studies (Papanastasis and Romanas 1977) indicate that a very high proportion of seeds germinate without heat shock. Other factors may be involved in controlling germination, such as an increase in the ratio of red:far-red radiation, because of canopy removal by fire, could cue germination (Margaris 1981). That this effect might

Table 10.3. Seed germination response of selected Greek maquis species (from Keeley unpub. data): Seeds were incubated in the light on filter paper in petri dishes at 5°C for 2 months, followed by 20° C/12° C (12 hrs/12 hrs) for 1 month. Values represent the mean of 3 dishes of 50 seeds each; numbers within the same row with the same superscript are not significantly different at $P > 0.05$

Species	Family	Growth form	Percentage germination			
			Control	Heated 80°C/30 min	Heated 115°C/5 min	Charred wood
Nonrefractory seeds						
<i>Allium</i> sp.	(Amaryllidaceae)	Geo-	90 ^a	19	3	72 ^a
<i>Asphodelus aestivus</i>	(Liliaceae)	Geo-	57 ^a	55 ^a	0	32 ^a
Heat-shock-stimulated seeds						
<i>Cistus salvifolius</i>	(Cistaceae)	Phano-	3 ^a	39	80	0 ^a
<i>Phlomis lanata</i>	(Lamiaceae)	Chamae-	8 ^a	72 ^b	62 ^b	8 ^a
<i>Lavandula stoechas</i>	(Lamiaceae)	Chamae-	19 ^a	59	17	21 ^a
<i>Sarcopoterium spinosum</i>	(Lamiaceae)	Chamae-	29 ^a	73	50	39 ^a
Charred-wood-stimulated seeds						
<i>Stachys tymihaus</i>	(Lamiaceae)	Chamae-	0 ^a	0 ^a	0 ^a	13

be a factor controlling the nonrefractory portion in the seed pool of *S. spinosum* is supported by the results of Roy and Arianoutsou-Faraggitaki (1985), who showed that germination was stimulated by an increase in the red:far-red radiation ratio from 0.3 to 1.1. Similar patterns have been observed for *Cistus* species (Roy and Sonie 1992).

The factors controlling the postfire germination of *Rhus coriaria* are unknown, but if comparative analysis is of any value I predict that it may be heat, as it is with its Californian congener, *R. ovata* (Stone and Juhren 1951). An important observation is that these two taxa have fleshy fruits and are exceptions (Izhaki et al. 1992) to the generalization that disturbance-dependent recruiters are not animal-dispersed. Bird dispersal may also be one of the factors accounting for distribution of seedlings after fires. Ne'eman et al. (1992) noted a concentration of seedlings within the shadow of the former canopy of burned pines, but other factors have not been ruled out.

As in California, the Mediterranean has relatively few serotinous species with canopy-stored seed banks. The few that occur are gymnosperms, such as *Pinus brutia* (Thanos et al. 1989). Seed dormancy is imposed by retention in the cone and, once released, the seeds are nondormant and germinate optimally at 20°C in darkness (Thanos and Skordilis 1987).

It is noteworthy that many of the postfire seeder species are drought deciduous malacophyllous subshrubs, which are relatively short lived. Conversely, obligate resprouters that establish seedlings under disturbance-free conditions are long lived, broad-leaf, evergreen sclerophyllous shrubs. The subligneous nature of the disturbance-dependent recruiters probably leads to greater susceptibility to destruction by fire and hence strong selective advantage in evolving a persistent seed bank.

Disturbance-Dependent Recruitment: Later Postfire

Many geophytes are endemic to the Mediterranean Basin, although none have been reported to recruit seedlings after fire from a persistent seed bank. Although relatively little is published on germination, the patterns observed for *Asphodelus aestivus* and a species of *Allium* (Table 10.3) indicate nonrefractory seeds in these geophytes from the eastern Mediterranean. This finding, coupled with the knowledge that geophytes resprout and flower after fire, make it likely that seedling recruitment occurs in later postfire years.

Two phenological types have been described for Mediterranean geophytes: those which flower in autumn and those flowering in spring. Although both have nonrefractory seeds, the former seeds germinate immediately after dispersal whereas for the latter, germination is delayed a year by lack of moisture for germination (Dafni et al. 1981).

Many annual species are mainly opportunistic colonizers that disperse into burned areas (Papio 1988). Examples of such species shown to have non-

refractory seeds include *Daucus carota* (Apiaceae), *Crepis* spp. (Asteraceae), *Linaria* sp. (Scrophulariaceae), *Anagallis arvensis* (Primulaceae), *Filago* sp. (Asteraceae), and *Hedypnois cretica* (Asteraceae) (Keeley unpub. data).

Central Chile

Wildfires are not presently widespread in Chilean matorral vegetation. Because convective thunderstorms and associated lightning are rare, a frequent natural ignition source is lacking (Aschmann and Bahre 1977, Rundel 1981), although vulcanism has been suggested as a natural source of wildfire ignitions (Fuentes and Espinosa 1986). Overall it does not appear that fire has had a major part in shaping the vegetation characteristics of Chile.

Disturbance-Free Recruitment

All Chilean woody species resprout from root crowns or lignotubers (Mooney et al. 1977, Montenegro et al. 1983) and thus are resilient to fires ignited by local residents. One study of a burned matorral site revealed very little cover by native annual species and no seedling regeneration by the shrub flora, with the one exception of *Trevoa trinervis* (Rhamnaceae) (S. Keeley and Johnson 1977). Herbaceous perennials in Liliaceae, Amaryllidaceae, Alstroemeriaceae, and Iridaceae are common components of unburned matorral (Rundel 1981) and are present as resprouts after fire.

Most of the common matorral shrubs such as *Lithrea caustica* (Anacardiaceae), *Quillaja saponaria* (Rosaceae), *Colliguaja odorifera* (Euphorbiaceae), *Kageneckia oblonga* (Rosaceae), and *Muehlenbeckia hastulata* (Polygonaceae) establish seedlings in undisturbed vegetation (Fuentes et al. 1984, 1986, Del Pozo et al. 1989). Seedling recruitment tends to occur under the canopy of shrubs, although survival is precarious and those not preyed upon typically succumb to summer drought (Jaksic and Fuentes 1980).

The demographic pattern of seedling establishment without fire suggests that these species have transient soil-stored seed banks of nonrefractory seeds. *Colliguaja* spp. and *Quillaja saponaria* are known to germinate readily without treatment, but *Lithrea caustica* seeds are reportedly refractory and may require scarification in concentrated sulfuric acid (Montenegro et al. 1983, Muñoz and Fuentes 1989, but cf. Jimenez and Armesto 1992). In nature, *Lithrea* seeds seem to germinate readily after passage through the gut of bird dispersers (Fuentes et al. 1984). As in California, many of these species are fleshy fruited and most tend to be more important on mesic sites (Hoffmann et al. 1989, Jimenez and Armesto 1992).

Enforced dormancy imposed by allelopathic chemicals is not present in evergreen matorral (Montenegro et al. 1978) but may be a factor in certain drought-deciduous vegetation (Fuentes et al. 1987).

Disturbance-Dependent Recruitment

Other than the report mentioned above of postfire seedling recruitment by *Trevoa trinervia*, this mode seems to be poorly represented in Chile. *Baccharis* spp. and other Asteraceae taxa are capable of dispersing in and establishing after fires and other disturbances, but nothing is known of their germination biology.

South Africa

Wildfires are at least as frequent in South African fynbos as in the Californian chaparral, and the vegetation responses show many similarities (Keeley 1992c, Versfeld et al. 1992).

Disturbance-Free Recruitment

Species that are present immediately after fire from resprouts, but have no seedling recruitment, are found in all life forms: shrubs, suffrutescents, and herbaceous perennials (van Wilgen and Forsyth 1992). Such shrubs include members of the Anacardiaceae (*Rhus* spp. and *Heeria*) and *Olea europaea* (Oleaceae) and a number of evergreen tree species restricted to moist ravines, e.g., *Cunonia capensis* (Cunoniaceae), *Kiggelaria africana* (Flacourtiaceae).

The few data available on seed germination indicate nonrefractory seeds, and some of these species are known to establish seedlings in unburned fynbos (Manders et al. 1992). As with the California obligate resprouters, these species have fleshy fruits dispersed in the autumn and winter by birds, strongly affecting distribution of seedlings. This strategy may explain why, as in the California chaparral, these obligate resprouting species tend to be distributed patchily within a matrix of seeding species (Kruger 1979).

Other evergreen shrubs, which persist on burned sites strictly as obligate resprouters, include species of *Protea*, *Leucospermum* and *Leucadendron* in the Proteaceae, *Widdringtonia* spp. in the Cupressaceae, species in the Rhamnaceae, Asteraceae, Anacardiaceae, Fabaceae, and Restionaceae (Wicht 1948, Scriba 1976, Bond 1980, 1985, Hoffmann et al. 1987, Higgins et al. 1987). Some, such as *Protea grandiflora*, *Widdringtonia cedarbergensis*, and *Gymnosporia laurina*, survive fires in protected locations and because of their thick bark and self-pruning (Wicht 1948, Manders 1987). Many of these taxa have nonrefractory seeds, but little is known about patterns of seedling recruitment. One exception is the observation by Taylor (1978b) that in an area protected from fire for thirty-five years, *Protea neriifolia* seedlings established in gaps created by the death of shrubs, along with some recruitment of woody shrubs and small tree species derived from the forest flora. Other *Protea* species routinely establish seedlings without fire. These taxa occur on more arid sites and probably experience a longer fire-return

interval than most fynbos sites. *Widdringtonia cedarbergensis* is not serotinous, and the nonrefractory seeds germinate within a few weeks of the first autumn rains (Manders 1987). Germination, however, is inhibited by litter from the parent plant and thus little is known about the exact patterns of seedling recruitment for this species.

Disturbance-Dependent Recruitment: Immediate Postfire

Many shrubs establish seedlings after fire from persistent seed banks in the soil or canopy (Le Maitre and Midgley 1992). Seed-germination behaviors are quite different, depending upon the mode of seed storage.

Soil-Stored Seeds

The proteaceous genus *Leucadendron* includes some species that have soil-stored seed, along with the serotinous taxa discussed below (Bond 1985). Other taxa with soil-stored seed include *Leucospermum* spp., *Mimetes stokoei* and *Orothamnus zeyheri* (Proteaceae), *Cliffortia* spp. (Rosaceae), *Phyllica* spp. (Rhamnaceae), *Euryops abrotanifolius*, *Metalasia muricata* and *Elytropappus rhinocerotis* (Asteraceae), *Selago corymbosa* (Selaginaceae), *Passerina* spp. (Thymelaceae), *Aspalathus* spp. (Fabaceae), and *Anthospermum aethiopicum* (Rubiaceae) (Adamson 1935, Levyns 1935, Martin 1966, Kruger 1979, Bond 1985, Higgins et al. 1987, Kilian and Cowling 1992).

Refractory seeds of *Leucadendron* may be stimulated to germinate by temperatures of 100°C (Williams 1972). Heat-stimulated germination has also been shown for *Elytropappus rhinocerotis* (Levyns 1927) and *Agathosma* spp. (Rutaceae) (Blommaert 1972). *Erica hebecalyx* (Ericaceae) germination is greatly stimulated by a 3-min treatment at 96.5°C, and this treatment is capable of overcoming the almost total inhibition imposed by darkness (van de Venter and Esterhuizen 1988). *Podalyria calyptrata* (Fabaceae) germination is increased from 9% (control) to 72% when seeds are exposed for just 1 min at 60°C (Jeffery et al. 1988). Other species with heat shock-stimulated germination include *Phyllica ericoides* (Rhamnaceae) and *Hermania* spp. (Sterculiaceae) (Table 10.4).

It is often assumed that the mechanism for heat-stimulated germination lies in breaking the seed coat (or pericarp), which in most hard seeds imposes dormancy by inhibiting entry of water or movement of gases. This description is very likely to apply to the refractory seeds of *Protea*, *Leucodendron*, and *Leucospermum*, which have been shown to lack leachable chemical inhibitors (van Staden and Brown 1977). In some cases when the hard outer pericarp inhibits gaseous exchange, scarification greatly improves germination, and incubation of unscarified seeds under pure oxygen may overcome the pericarp-imposed dormancy (van Staden and Brown 1977, Deall and Brown 1981). Brits (1986b) and Brits and van Niekerk (1986) show that refractory seeds of *Leucadendron* species and *Leucospermum* species can be stimulated to germinate by soaking them 24 hr in 1% H₂O₂, and they sug-

Table 10.4. Seed germination response of selected South African fynbos species (from Keeley and Bond, unpub. data): Seeds were incubated in the light on filter paper in petri dishes at 5°C for 2 months, followed by 20°C/12°C (12 hrs/12 hrs) for 1 month. Values represent the mean of 3 dishes of 50 seeds each; numbers within the same row with the same superscript are not significantly different at $P > 0.05$

Species	Family	Growth form	Percentage germination			
			Control	Heated 80°C/30 min	Heated 115°C/5 min	Charred wood
Nonrefractory seeds						
<i>Wachendorfia paniculata</i>	(Hyacinthaceae)	Geo-	80 ^a	72 ^a	0	80 ^a
<i>Moraea</i> sp.	(Iridaceae)	Geo-	74 ^a	77 ^a	0	60 ^a
Heat-shock-stimulated seeds						
<i>Phyllica ericoides</i>	(Rhamnaceae)	Phano-	9 ^a	44	84	11 ^a
<i>Hermannia alnifolia</i>	(Sterculiaceae)	Chamae-	0 ^a	17	67	1 ^a
Charred-wood-stimulated seeds						
<i>Pharnaceum elongatum</i>	(Aizoaceae)	Chamae-	0 ^a	4 ^a	1 ^a	47
<i>Nemesia</i> cf. <i>lucida</i>	(Scrophulariaceae)	Thero-	7 ^a	9 ^a	2 ^a	84

gest that dormancy is imposed by barriers to oxygen uptake. In other species the pericarp physically restricts growth of the embryo and elevated oxygen does not improve germination (Brown and Dix 1985).

Other temperature regimes that stimulate germination include fluctuating soil temperatures, as on recently burned sites (Brits 1986a, 1987). Most seeds sown in summer remain dormant until fall (Brits and van Niekerk 1986). Whether they do so because of dormancy induced by high temperatures or a germination requirement for cool temperatures is unknown. Tests with *Elytropappus rhinocerotis* indicate that an afterripening may be required following dispersal of seeds (Levyns 1927).

The seeds of some fynbos species are stimulated to germinate by the presence of charred wood (Table 10.4). Along with species reported in Table 10.4, at least five other fynbos taxa have charred-wood-stimulated germination (Keeley and Bond unpub. data). Other studies, however, have not found a stimulatory effect for charred wood. Pierce (1990) reported no such effect on germination of various coastal fynbos species, but these species had non-refractory seeds that germinated readily under alternating temperatures. Van de Venter and Esterhuizen (1988) demonstrated that gases such as ethylene and ammonia, which are products of combustion, can stimulate germination of *Erica hebecalyx*. This species, however, seems also to be stimulated by heat shock, though it showed no response to charred wood (Keeley and Bond unpub.). Germination of *Audouinia capitata* (Bruniaceae) is stimulated by exposure to smoke (de Lange and Boucher 1990) although it is unknown whether this reaction is caused by gases produced by the smoke or particulate matter suspended in the smoke (Le Maitre and Midgley 1992).

Soil-stored seeds are often dispersed by ants, whereas serotinous species of both *Protea* and *Leucodendron* are more often wind dispersed (Bond 1985). For both genera, dispersal is relatively localized (Kruger 1983, Slingsby and Bond 1985, Manders 1986). Unlike canopy-stored seeds, which are generally short-lived once they are dispersed, soil-stored seeds are thought to have great longevity.

In many species the controls on seed germination are not clearly worked out. For example, in coastal dune fynbos, species such as *Muraltia squarrosa* (Polygalaceae) and *Passerina vulgaris* have few or no seedlings on unburned sites but abundant recruitment immediately after fire (Pierce and Cowling 1991). Seeds, however, appear to germinate readily without fire-related stimulus. *Passerina paleaceae* is another species with strict postfire seedling recruitment. Seeds are highly refractory, but various heat treatments and charred wood have not been successful in stimulating germination (Kilian and Cowling 1992, Keeley and Bond unpub. data).

Canopy-Stored Seeds

Serotinous fruits are produced by species of *Protea*, *Leucadendron*, *Aulax* (Proteaceae), *Widdringtonia* (Cupressaceae), *Nebelia* (Bruniaceae), *Phaeno-*

coma, *Helipterum* (Asteraceae), *Brunia*, *Berzelia* (Bruniaceae), *Cliffortia* (Rosaceae), and *Erica sessiliflora* (Ericaceae) (Wicht 1948, Gill 1975, Frost 1984, Bond 1985, E. Oliver pers. comm.). Seeds are retained for variable lengths of time, and all these species disperse some seeds before as well as after fire. Thus, these species have both a transient and persistent seed bank. In the absence of fire, fruits often open after several years and release seed that is nonrefractory and germinates in the first rainy season after being shed (Bond 1984, Le Maitre 1990).

Although seeds may be dispersed both before and after fire, in mature fynbos, seedling establishment is rare (Bond 1980). Strictly speaking, *Protea arborea* does not produce serotinous cones and most germination occurs before fire. But only the seeds retained in the fruits until fire result in successful seedlings (Kruger 1977). In older stands, predation of seedlings appears to be a major factor limiting establishment (Bond 1983, Breytenbach 1984). *Protea laurifolia* (Manders 1986) has seedling regeneration mostly restricted to the first year after fire, but some seedlings may establish in the second or third year (Bond 1984, Bond et al. 1984). Seeds released after spring burns seem less successful because of predation than seeds released after fall burns (van Wilgen and Viviers 1985).

Seeds in serotinous cones are nonrefractory, but are maintained in a quiescent state by enclosure in the fruit. If seeds are dispersed in summer, most do not germinate until fall (Bond 1984). It is unclear if this delay is caused by dormancy induced by high temperature or a germination requirement for low temperature. It appears that some *Leucadendron* species require cold stratification (Deall and Brown 1981). This characteristic prevents germination during the summer drought and it is noteworthy that *Protea roupelliae* from the summer-rain eastern Cape region does germinate in summer (Bond 1984). Although seeds do not appear to survive in the soil for more than one season, *Leucadendron xanthoconus*, a weakly serotinous nonsprouter, is perhaps an exception to this generalization (Davis 1992).

Disturbance-Dependent Recruitment: Later Postfire

Apparently geophytes in the South African flora share with their chaparral counterparts the characteristic of being obligate resprouters after fire. Included are taxa of Geraniaceae, Oxalidaceae, Poaceae, Orchidaceae, Liliaceae, Iridaceae, Amaryllidaceae and related families (Adamson 1935, Hoffmann et al. 1987). These species flower profusely in the first year after fire, and some in fact flower "only" after fire and have gained the name "fire-lilies." One of these, *Cyrtanthus angustifolius* (Amaryllidaceae) produces flower heads almost immediately after burning, prior to vegetative growth (Bond 1980, Le Maitre and Brown 1992). Other geophytes observed to have flowering mainly restricted to the first postfire season include *Brunsvigia orientalis* (Amaryllidaceae) (Taylor 1978a), *Androsymbirium leucanthum* (Liliaceae) (Wicht 1948), *Haemanthus canaliculatus* (Amaryllidaceae) (Levyns

1966), *Bobartia spathacea* (Iridaceae) (Adamson 1935) and *Watsonia pyramidata* (Iridaceae) (Kruger 1977). It has been suggested that the stimulus for postfire flowering comes from the changed rhythm in diurnal fluctuations in soil temperature (Martin 1966) or higher soil temperatures (Frost 1984). One experiment with the strict fire-lily *Cyrtanthus ventricosus*, however, induced flowering by treating planted bulbs with smoke from burning wood (Keeley 1993).

Although geophytes and other herbaceous perennials apparently do not store persistent seed banks until fire, the precise timing of seedling establishment is not known. Kruger (1977) did report that for *Watsonia pyramidata*, seedling establishment occurred in the second growing season after fire. It is quite likely that this delay is typical of other geophytes because flowering is abundant in the first year and most species apparently have nonrefractory seeds; *Wachendorfia paniculata* (Haemodoraceae) and *Geissorhiza Moraea* sp. (Iridaceae) germinate readily and this readiness has been observed for more than a dozen other geophytes from the fynbos (Keeley and Bond unpub. data). Some species, however, are inhibited in the dark, as illustrated by the germination response of *Wachendorfia paniculata* (Fig. 10.2). Others are apparently inhibited by high temperatures. *Watsonia fourcadei* germinates readily at 10°C (in light and dark), but is mostly inhibited at temperatures above 25°C (Esterhuizen et al. 1986).

Other species may be absent on recent burns but disperse on to sites in particular annuals subligneous species of *Erica* (Ericaceae) (Adamson 1935). This species may remain in gaps in broad-leaved Proteaceae dominated fynbos (Wicht 1948; Hoffmann et al. 1987) or form a more heathlike fynbos,

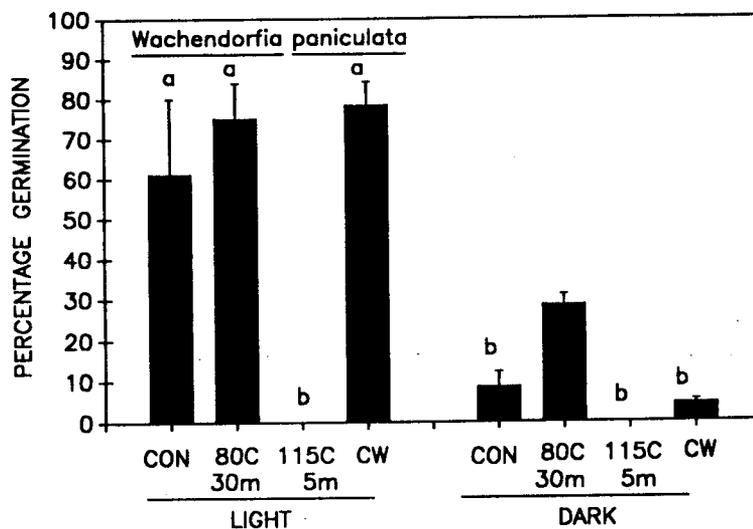


Figure 10.2. Germination of a South African fynbos geophyte in light and darkness (methods as described in Table 10.4) (from Keeley and Bond unpub. data).

as on coastal dunes (Pierce 1990). For some, seed banks are relatively transient because seeds germinate readily under a diurnal temperature range of 10°C to 20°C (Pierce 1990). Seedling recruitment in mature fynbos seems to be rare, although seedlings of *Agathosma* spp. (Rutaceae) have been reported from mature fynbos (Pierce and Cowling 1991).

Australia

After wildfires in heath, mallee, and other sclerophyllous shrublands in Australia, some species reestablish by seed only, some by resprouts and seed, and rarely, strictly by resprouts.

Disturbance-Free Recruitment

It is not apparent from the literature that clear examples of this mode appear in the mediterranean ecosystems in Australia. Most Australian woody plants, whether they resprout or not, seem to establish seedlings after fire.

Disturbance-Dependent Recruitment: Immediate Postfire

Shrubs, suffrutescents, and annual taxa are seeders, many of which establish seedlings only in the first postfire year. Many of the woody taxa both resprout and establish seedlings. As in South Africa, seed banks contributing to this flush of seedlings are either soil-stored or canopy-stored.

Soil-Stored Seeds

Woody taxa with soil-stored seed include many members of the Fabaceae, a family known for its hard-seeded character, such as *Acacia*, *Bossiaea*, *Dillwynia*, *Daviesia*, *Kennedia*, and *Pultenaea* (Floyd 1966, Warcup 1980, Pieterse and Cairns 1986, Bell et al. 1993). *Leptospermum* (Myrtaceae) includes species that are serotinous and others that are nonserotinous; the latter species are hard-seeded and form a persistent seed bank. Circumstantial evidence of seed longevity for soil-stored seed suggests fifty years or more (Mott and Groves 1981). Although annuals are not a highly diverse group in Australia, some species are present after fires from a persistent seed bank (Specht 1981, Bell et al. 1984).

Germination of hard-seeded legumes, such as species of *Acacia*, *Albizzia*, *Chorizema*, *Gompholobium*, *Hardenbergia*, *Kennedia*, *Labichea*, *Mirbelia*, and *Oxylobium* is stimulated after brief heating treatments of 80°C and 100°C or boiling water (Shea et al. 1979; Jeffery et al. 1988; Bell et al. 1993). *Acacia suaveolens* germination is nil without exposure to temperatures above 60°C and is stimulated by temperatures of up to 100°C for durations of a hour (Auld 1986b). Brief exposure to temperatures of 120°C were also stimulatory, but temperatures above 150°C were lethal. Apparently the heat

breaks the seedcoat, allowing imbibition (Cavanagh 1980). There is some evidence that *Acacia aneura* seeds have an afterripening period; with scarification, germination is low immediately after being shed but increases over several months (Preece 1971). Hodgkinson and Oxley (1990) show that the optimal temperature for germination of this species is a function of numerous factors, including depth of seed burial, fuel levels, and soil moisture.

Other families with taxa having persistent seed banks that show heat-stimulated germination included Convolvulaceae, Epacridaceae, Euphorbiaceae, Geraniaceae, Haemodoraceae, Rhamnaceae, Rubiaceae, and Sapindaceae (Warcup 1980) and a fuller description of these species has recently been published by Bell et al. (1993).

Bell et al. (1987) have tested the stimulatory effect of charred wood on germination of forty nonleguminous understory species of the jarrah (*Eucalyptus marginata*) forest. Only one of the species, *Burchardia umbellata* (Liliaceae) increased germination; 9% for controls and 35% with charred wood (heating 2 min at 85°C had no stimulatory effect). This species normally does not establish seedlings in the first season after fire, but, like other geophytes, it flowers from resprouts in the first postfire season. It is unclear what role charred wood-stimulated germination has in the life history of this herb. Tests of species in other vegetation are needed to evaluate the importance of charred wood-stimulated germination in Australia.

Enforced seed dormancy imposed by allelopathic compounds was suggested as an important phenomenon in Californian populations of *Eucalyptus* (del Moral and Muller 1969). Some have questioned whether allelopathy is important in Australia (Mott and Groves 1981), although experimental studies suggest it may be a factor in suppressing understory species in *Eucalyptus* forests (May and Ash 1990) and other vegetation types (Hobbs and Atkins 1991). Many species in the understory of Australian forests, though, are hard-seeded and thus dormancy is imposed by the seed coat.

Although passive dispersal is common, many of the Australian *Acacia* species have seeds with appendages that are attractive to either birds or ants, and thus the seeds are relatively specialized for dispersal (Davidson and Morton 1984, Auld 1986a). Dispersal, however, is fairly localized. Potential advantages of such myrmechochorous seed dispersal include transport of the seed to nutrient-rich sites and burial of the seed, which reduces loss of seed to predation or to intense temperatures during fire. One test did not support the nutrient-enrichment hypothesis (Rice and Westoby 1986). One additional advantage may be to reduce predation by using the elaiosome as a form of bribe so that ants are selected to leave the seed unscathed (Keeley 1992c).

Canopy-Stored Seeds

Taxa with serotinous woody fruits that open after fire include *Eucalyptus* (Myrtaceae), *Casuarina* (Casuarinaceae), *Banksia* (Proteaceae), *Hakea* (Proteaceae), and *Leptospermum* (Myrtaceae) (Specht 1981).

Most species of the shrubby genus *Banksia* produce woody "cones" that retain seeds for several to many years after cones mature, forming a canopy seed bank that persists until fire (Bradstock and Myerscough 1981, Bell et al. 1984, Cowling et al. 1987, Zammit and Westoby 1987a, 1988, Bradstock and O'Connell 1988, Lamont and Barker 1988). Serotinous cones open after exposure to temperatures of 145°C to 390°C (Gill 1976, Enright and Lamont 1989), and disperse seeds over several months (Cowling and Lamont 1985a). Dispersal is relatively localized and subject to intense predation. Consequently, fires in spring provide more time for predation than fires in fall, and thus seasonal effects on seedling regeneration are reported (Cowling and Lamont 1987). It is suggested that successful seedling recruitment may be tied to particular weather patterns following fire (Lamont et al. 1991).

Seeds of *Banksia*, and of the closely related genus *Hakea*, are nonrefractory and germinate readily (Siddiqi et al. 1976, Sonia and Heslehurst 1978, Abbott 1985a, Zammit and Westoby 1987b, Richardson et al. 1987, Lamont and Barker 1988, Lamont et al. 1993), soon after autumn rains. Temperatures above 150°C are lethal and thus the thick woody follicles are important in protecting seeds during fires. Germination is light-insensitive and, as a rule, temperatures below 12°C and above 25°C suppress germination. Seeds in cones 1 to 3 years of age show the highest germination, but substantial germination is still possible from seeds as old as 9 years of age (Cowling and Lamont 1985b). Seeds exposed on the soil surface for 5 months over spring and summer germinated poorly when tested at 15°C. It is unclear whether this failure was caused by an induced dormancy, loss of seed viability, or change in the optimal temperature for germination caused by these storage conditions.

In mature stands, very old cones, or cones on dead branches, open and release their seeds. In most unburned stands, successful seedling establishment is rare (Brown and Hopkins 1984, Abbott 1985b, Cowling and Lamont 1985b, Lamont and Barker 1988), although it has been reported (Specht 1981, Zammit and Westoby 1987a).

Several genera of Myrtaceae are known for congregation of serotinous cones in clusters, and this has been demonstrated to be an important factor in shielding seeds from excessive heating during fires (Judd and Ashton 1991).

Eucalyptus spp. have woody capsules that release seed following maturation, but also retain seed within fire-resistant capsules so that seeds will disperse after fire. As in other serotinous species, seeds of *Eucalyptus* spp. are nonrefractory and germinate readily over a wide range of temperatures (Prescott 1941, Ladiges 1974, Zohar et al. 1975). Some *Eucalyptus* species require light and others require darkness for germination (Clifford 1953, Grose 1963), and an afterripening period has been recorded for others. In nature, germination occurs soon after the first autumn rains following release (Abbott 1984, Wellington and Noble 1985b). Consequently, these weakly serotinous *Eucalyptus* species do not accumulate a persistent soil seed bank (Vlahos and Bell 1986).

In unburned *Eucalyptus* stands, some seedling recruitment occurs, but successful seedling establishment is more likely in burned areas. Wellington and Noble (1985a) reported 7000 *E. incrassata* seedlings/ha in a one-year-old burn, but only 30 seedlings/ha in unburned mallee. Ants are important seed predators in unburned stands, which may be an important factor limiting recruitment (O'Dowd and Gill 1984, Andersen 1987).

Disturbance-Dependent Recruitment: Later Postfire

Geophytes apparently survive fire by resprouting and do not establish seedlings from a persistent seed bank (Purdie and Slatyer 1976, Purdie 1977, Bell et al. 1984). These include taxa in the Orchidaceae (*Caladenia* and *Prasophyllum*), Liliaceae (*Blandfordia*, *Dasypogon*, *Lomandra*, and *Thysanotus*), and Droseraceae (*Drosera*) (Pate and Dixon 1981). These resprouts flower in the first year after fire. From what is known about geophytes in other mediterranean type ecosystems, it is expected that Australian geophytes would have nonrefractory seeds and establish seedlings in subsequent postfire years. Some dependence upon fire is suggested by the observation that some geophyte species may disappear from infrequently burned sites (Nieuwenhuis 1987).

Some shrubs lack abundant seedling establishment after fire, but resprouts (or survivors) flower in the first and second year after fire. Seeds of these species are nonrefractory and seedlings establish in the first rainy season after dispersal, not unlike the coastal sage scrub of California. Examples include *Xanthorrhoea* spp. (Xanthorrhoeaceae), *Telopea speciosissima* (Proteaceae), *Lambertia formosa* (Proteaceae) and *Angophora hispida* (Myrtaceae) (Gill and Ingwersen 1976, Pyke 1983, Auld pers. comm.).

Conclusions

A remarkable degree of convergence appears in seed-germination syndromes in the five mediterranean-climate ecosystems. The main areas of convergence are summarized here, and those statements I believe to be much in need of further study are indicated (*).

1. *Disturbance-free recruitment.* All but the Australian region have shrub species with transient seed banks, and persistence of such species after fire depends entirely on their resprouting capacity. Most of these have fleshy fruits that are dispersed by birds in the autumn and winter. Seeds are nonrefractory and germinate soon after dispersal. In California, successful seedling recruitment seems to depend on long fire-free conditions. *In other regions the conditions required for successful seedling establishment by these taxa needs further study.
2. *Disturbance-dependent recruitment: soil seed banks.* All regions except Chile have diverse flora of species that cue their seedling recruitment to

the immediate postfire environment. Species that establish seedlings after fire must have a persistent seed bank, either in the soil or on the canopy. Soil-stored seeds are refractory. Heat-shock-stimulated germination is found in species of all regions, except possibly Chile. Seeds of such species are usually hard-seeded, meaning that the seed coat or pericarp imposes dormancy by preventing imbibition or gas exchange.

Some taxa with persistent soil seed banks are not hard-seeded, and many of these have charred wood-stimulated germination. This strategy is important in California and South Africa.

3. *Disturbance-dependent recruitment: canopy seed banks.* In South Africa and Australia, many species have persistent seed banks in the canopy (i.e., serotinous fruits) and seed germination is cued by timing of dispersal. Heat stimulates the opening of fruits, and the seeds are usually nonrefractory. For some species, seeds may have innate or induced dormancy mechanisms that prevent germination during summer. Serotinous species are unknown in Chile and uncommon in California and Europe. Why canopy-stored seed banks are more important in South Africa and Australia than elsewhere requires some thought. Seeds of serotinous species are typically much larger than those of soil-stored taxa, possibly because they have the luxury of retaining seeds within the protection of woody fruits.* Perhaps the low nutrient content of the South African and Western Australian soils has selected for large seeds that can store critical elements such as nitrogen and phosphorous.
4. *Polymorphic seed pools.* Postfire seeders, regardless of where the persistent seed bank is stored, have both a transient and a persistent seed bank. For soil-stored seeds this condition arises because of polymorphic seed-germination behavior. For canopy-stored seeds this arises because of incomplete retention of seeds within fruits until fire. Both have the potential for some seed germination without fire, although the most successful recruitment occurs after fire.
5. *Geophytes.* Apparently, in all five regions, geophytes do not recruit seedlings in the immediate postfire environment, and their presence is due to resprouts from bulbs, corms, or rhizomes. Seeds are nonrefractory and * are likely to germinate soon after the first autumn or winter rains following dispersal. For many species, flowering is restricted to, or more profuse in, the first year after fire. *The second year after fire is probably an important time for seedling establishment. One exception may be *Cyrtanthus angustifolius*, a fynbos geophyte that flowers within a few days after fires, and thus may recruit seedlings in the first postfire season.

The uniformity among regions in the response of geophytes to fire suggests that intense selective pressure is acting on this life form. Geophytes are unable to compete with the dominant shrub vegetation, and thus growing conditions are optimal after fire. Corms and bulbs are a reliable mode of establishing after fire; they are deeply buried and thus not subject to damage

by fire or predation between fires. Flowering from stored carbohydrates produces an abundant seed pool in the first postfire year. *The subsequent post-fire years are the optimal time for seedling recruitment and therefore this life form has not evolved refractory seeds. A weakness of the geophyte strategy is that bulbs and corms need to persist in a relative dormant state until fire. If bulbs and corms were not long-lived then infrequent fires would select against this life form. *The very high fire frequency in South Africa and Australia may account for the abundance of geophytes in those regions, relative to other ecosystems of mediterranean type. *Other factors may be involved, for example, the low phosphorus and nitrogen content of soils in these Southern Hemisphere regions may also select for life forms capable of retaining these nutrients in underground corms or bulbs.

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