Chapter 13

Role of Fire in Regeneration from Seed

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Introduction

Fire is a disturbance factor in ecosystems worldwide and affects the reproduction of many plant species. For some species, it is just one of several disturbances that trigger seed germination and subsequent seedling recruitment, whereas in other 'fire-dependent' species, fire may be required for seedling recruitment. Fire may trigger seed regeneration directly, through the opening of serotinous fruits or cones or by inducing the germination of dormant soil-stored seed banks. Fire may also indirectly initiate seedling recruitment by opening gaps in closed vegetation, thus providing conditions suitable for colonization. There is a multitude of mechanisms for capitalizing upon such disturbances and the particular mode is a function of fire regime, climate, growth form, phylogeny and biogeography.

Postfire environments

Fire causes a multitude of changes in the environment that enhance site quality for seedling recruitment and thus provide the selective impetus for fire-dependent germination. Perhaps foremost is the removal of vegetation (formation of gaps), resulting in an increase in irradiance at ground (seedling) level and a reduction in competition for water. In addition, fire accelerates the mineralization of organic matter, making inorganic nutrients more readily available (e.g. Dunn and DeBano, 1977; Wells *et al.*, 1979). Fire reduces herbivore populations by direct mortality and indirectly by opening the habitat and making herbivores more vulnerable to predators (Quinn, 1994). The pulse of recruitment that potentially satiates predators (O'Dowd and Gill, 1984) also reduces seedling predation. Other advantages include soil sterilization, which alters microbial populations and reduces pathogens (Fletcher, 1910; Sabiiti and Wein, 1987; Wicklow, 1988).

Costs associated with recruitment in burned sites include delayed reproduction for the many species that accumulate dormant seed banks between fires (e.g. Gadgil and Bossert, 1970). Also, on sites following high-intensity fires, the postfire seedbed may create pH and osmotic conditions unfavourable for the germination of some species (Henig-Sever *et al.*, 1996; Ne'eman *et al.*, 1999). In addition, postfire gaps may be drought-prone, as the increased exposure may lead to elevated evaporation and thus reduced moisture availability at shallower depths, where germination occurs.

Direct effects of fire on germination

Many species accumulate seed banks that are triggered to germinate by fire. These seed banks develop by the accumulation over 1 or more years of dormant or quiescent seeds. Distinguishing between dormancy and quiescence is in part a matter of semantics. For example, some restrict the term dormancy to just those seeds that fail to germinate following imbibition, whereas germination inhibited by seed-coat characteristics (e.g. restricting entry of water or oxygen or release of inhibitors) is considered quiescence (see Murdoch and Ellis, Chapter 8, this volume). Others consider both of these conditions dormancy and distinguish them as 'endogenous' versus 'exogenous' dormancy (e.g. Baskin and Baskin, 1998). We shall follow the latter convention and reserve the term quiescence for seeds held within serotinous cones or fruits.

Heat-induced release of canopy-stored seed banks

Serotiny is the delayed opening of fruits or cones and is often interpreted as an adaptation for timing seed dispersal to favourable seedbed conditions. Some desert species control seed dispersal with serotinous fruits that open following rainfall, whereas, in many fire-prone ecosystems, serotiny cues dispersal to the postfire environment. It is widespread in northern hemisphere coniferous genera, such as *Cupressus* and *Pinus* (Wolf, 1948; Keeley and Zedler, 1998). In the southern hemisphere, serotiny is uncommon in coniferous trees but widespread in shrubby angiosperms, and is particularly well represented in the *Proteaceae* and *Myrtaceae* of Mediterranean-climate South Africa and Western Australia (Lamont *et al.*, 1991).

In all of these taxa, cones or fruits will open and disperse seeds within days of being scorched by fire, resulting in a pulse of seedling recruitment that generates stands of even-aged cohorts. Some species, such as the serotinous *Pinus brutia*, have seeds with endogenous dormancy, which is overcome by cold stratification following release from the cone (Skordilis and Thanos, 1995). In the absence of fire, cones may open due to death of the branch, heating from solar irradiance or other causes, but in communities with closed canopies this generally does not lead to successful recruitment, although on more open sites it may. There are interesting intraspecific patterns of varying degrees of serotiny and consequent seedling recruitment, which generate even-aged or uneven-aged populations, possibly tied to fire-return intervals (reviewed for *Pinus* in Keeley and Zedler, 1998). Retention of seeds is also highly variable across species, ranging from a few months (e.g. *Pinus muricata* cones remain closed through the autumn fire season and disperse seeds in winter) to many years or decades.

The distribution of serotiny is fairly predictable, as illustrated by the genus *Pinus*. Many pines inhabit fire-prone environments, but only a small subset of these species are serotinous, specifically those on sites subject to high-intensity/severity 'stand-replacing' fire regimes (Fig. 13.1).

Heat-shock-stimulated germination of soil-stored seed banks

Many species that disperse seeds at maturity have innate barriers to germination and thus accumulate dormant seed banks, which are triggered to germinate by fire-related cues, such as heat shock (e.g. *Ceanothus crassifolius* in Table 13.1). This is widespread in many fire-prone ecosystems and is common in the *Fabaceae*, *Rhamnaceae*, *Malvaceae*, *Sterculiaceae*, *Cistaceae* and *Convolvulaceae* (e.g. Ballard, 1981; Barro and Poth, 1988; Trabaud and Oustric, 1989; Keeley, 1991, 1995; Kilian and Cowling, 1992; Thanos *et al.*, 1992; Bell *et al.*, 1993; Cocks and Stock, 1997; Keeley and Bond, 1997; Herranz *et al.*, 1998).

Heat-stimulated seeds exhibit exogenous dormancy imposed by a dense palisade tissue beneath the generally smooth and highly cutinized testa. This barrier to
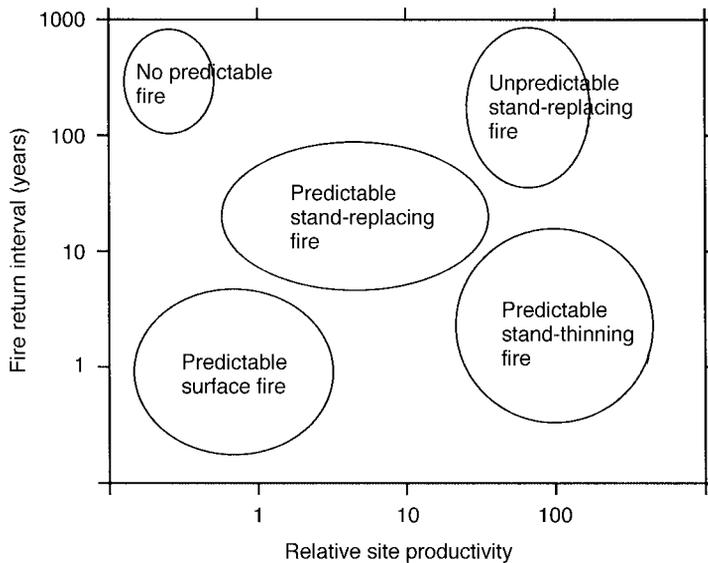
Fig. 13.1. Fire regimes generated by patterns of site productivity and fire recurrence interval (redrawn from Keeley and Zedler, 1998).

water entry inhibits seeds from imbibing water and has led to the term 'hard-seeded'. Fire disrupts the water-impermeable tissues, allowing imbibition, which typically leads to germination. While it is generally thought that heat directly disrupts the palisade tissues, in certain cases it appears to be tied to fire-triggered desiccation of the seed-coat (Brits *et al.*, 1993). In some hard-seeded species the barrier to germination may not be lack of imbibition but embryo anoxia, due to seed-coat restriction of oxygen (Brits *et al.*, 1995). While the breaking of the barrier to water or oxygen entry may suffice to germinate many species, for others the exogenous dormancy is coupled with endogenous dormancy and thus germination occurs only when heat shock is coupled with other environmental cues, such as light (Keeley, 1987; Bell, 1994) or cold stratification (Keeley, 1991).

Hard-seeded species with postfire seedling recruitment appear to differ substantially in the intensity and duration of heat shock most stimulatory to germination. Some exhibit optimal germination after brief bursts of high temperatures (e.g. 5 min at 105°C), whereas others have

higher germination after a long duration at lower temperature (e.g. 1 h at 70°C). The same applies to lethal temperature regimes, e.g. large-seeded species survive a short duration at high temperature but are killed by a long duration at lower temperature, whereas very small seeds exhibit the opposite pattern (Keeley *et al.*, 1985). Soil moisture during heating also diminishes heat tolerance (Westermeier, 1978; Parker, 1987). Such differences in stimulation/tolerance regimes may explain some of the variance in microhabitat segregation of postfire floras (e.g. Davis *et al.*, 1989). In addition, variations in heating may affect subsequent seedling growth (Hanley and Fenner, 1998).

Since many species are stimulated by a long duration at 70–80°C, they are not strictly tied to postfire environments – such conditions may be encountered by seeds exposed to direct sun-rays on open sites. Thus, heat-shock-stimulated germination does not limit recruitment to burned sites; rather, such species can establish in gaps created by other types of disturbance as well. Also, since unburned landscapes often comprise a heterogeneous collection of suitable and unsuitable recruitment

sites, it is not surprising that most heat-stimulated species have polymorphic seed pools (Keeley, 1991, 1995). Thus, while the bulk of the seed bank may be deeply dormant, a portion may germinate readily and establish in the absence of fire, for reasons elaborated upon by Westoby (1981).

Heat-stimulated species are common in all Mediterranean-climate shrublands, where they are regularly exposed to intense stand-replacing fires (Keeley, 1991, 1995; Bell *et al.*, 1993; Arianoutsou and Thanos, 1996). Outside these ecosystems, heat-stimulated germination and postfire recruitment are not common but are present in species from a diversity of families and vegetation types. For example, it is known from temperate forests and heathlands, in species of *Anacardiaceae* (Marks, 1979; Washitani, 1988), *Convolvulaceae* (McCormac and Windus, 1993), *Ericaceae* (Jaynes, 1968), *Fabaceae* (Cushwa *et al.*, 1968; Martin *et al.*, 1975; Grigore and Tramer, 1996), *Geraniaceae* (Abrams and Dickmann, 1984), *Hypericaceae* (Mallik and Gimingham, 1985), *Restionaceae* (Musil and de Witt, 1991) and *Malvaceae* (Baskin and Baskin, 1997). In grasslands, it is apparently present in both temperate (McCormac and Windus, 1993) and tropical legumes (Sabiiti and Wein, 1987).

Smoke- and charred-wood-stimulated germination of soil-stored seed banks

It has only recently become evident that, in some fire-prone environments, the majority of species that recruit after fires lack heat-stimulated germination, but that chemical products of biomass combustion trigger germination (Table 13.1). This response is present in hundreds of species from the Mediterranean-climate ecosystems of California, South Africa and Western Australia (Jefferey *et al.*, 1988; Keeley, 1991, 1995; Brown, 1993a; Dixon *et al.*, 1995; Roche *et al.*, 1997; Keeley and Fotheringham, 1998b). Preliminary surveys in the other two Mediterranean-climate regions – central Chile and the Mediterranean basin – have thus far failed

to find clear-cut examples of charred-wood- or smoke-stimulated germination (Keeley and Keeley, 1999; J.E. Keeley, C.J. Fotheringham and W.J. Bond, unpublished data). This may be linked with natural lightning fires being less predictable in these two regions. While knowledge of charred-wood- or smoke-stimulated germination is relatively recent, the phenomenon was apparently recognized centuries ago by early Americans (Indians) in the western USA, who routinely sowed tobacco seeds in postfire ash beds (Harrington, 1932). At least one of these species, *Nicotiana attenuata*, is known to be smoke-stimulated (Baldwin *et al.*, 1994).

Charred-wood- or smoke-stimulated germination is found in a wide diversity of families, although it is largely lacking in the families noted for heat-stimulated germination. In Mediterranean-climate regions of California, it is common in members of the *Hydrophyllaceae*, *Papaveraceae*, *Polemoniaceae* and *Scrophulariaceae* – families with centres of radiation in western North America. It is also known from families with more cosmopolitan distributions – *Asteraceae*, *Boraginaceae*, *Brassicaceae*, *Caryophyllaceae*, *Lamiaceae*, *Loasaceae*, *Onagraceae* and *Solanaceae*. In the southern hemisphere, it is known from some of the same families, e.g. *Asteraceae* and *Scrophulariaceae*, but is most common in other families – the *Dilleniaceae*, *Epacridaceae*, *Ericaceae*, *Goodeniaceae*, *Haemodoraceae*, *Myrtaceae*, *Poaceae*, *Proteaceae*, *Restionaceae*, *Rutaceae* and *Thymelaceae* (Brown, 1993a; Baxter *et al.*, 1994; Dixon *et al.*, 1995; van Staden *et al.*, 1995; Enright *et al.*, 1997; Keeley and Bond, 1997; Roche *et al.*, 1997). Smoke-stimulated germination has also been demonstrated for species from both tropical and temperate grasslands (Baxter *et al.*, 1994; Read and Bellairs, 1999).

Charred wood and smoke are equally effective in triggering germination of a wide range of species (Brown, 1993b; Keeley and Fotheringham, 1998b). The combustion products that trigger germination are transferred to seeds as vapour or liquid and this may occur directly from

smoke or be secondarily transferred from soil particles (Fig. 13.2). Heating of wood products is sufficient to release active agents (Keeley and Pizzorno, 1986) and the same applies to heating of (organic matter in) soil (Keeley and Nitzberg, 1984). Thus, the conclusion that 'chemical constituents from smoke do not appear to provide a stimulus separate from the effects of heat' (Enright *et al.*, 1997), which was based upon heat treatments of soil, should be re-evaluated.

Two factors make it critical that experimental determination of smoke-stimulated germination include a dosage–response curve: species differ both in level of smoke products stimulatory to germination and in the level that is lethal to seeds (e.g. Table 13.1). This is well illustrated by two California chaparral species with deeply dormant seed banks. Only 1 min of direct exposure to smoke will induce 100% germination of the annual *Emmenanthe penduliflora*, but fails to stimulate the perennial *Romneya coulteri*. On the other

hand, if seeds are sown in soil exposed to smoke for 30 s, both species germinate completely. However, germination of *Emmenanthe* is inhibited by soils exposed to a longer duration (30 min exposure is lethal), whereas *Romneya* germinates well in soils exposed to 30 min of smoke treatment (Keeley and Fotheringham, 1998b).

Considering the postfire increase in soil nitrate levels (Christensen, 1973), it is worth considering the role of this ion. Pons (1989b) showed that nitrate-triggered germination is a potential cue for germination on open sites for weedy species, particularly light-inhibited weeds (Hilhorst and Karssen, 1989). Thanos and Rundel (1995) suggested that nitrate was the 'trigger' that cued species to respond to postfire conditions in California chaparral. However, the nitrate ion alone has been shown to be insufficient in triggering germination (Table 13.1), whereas nitrogen dioxide (at levels found in biomass smoke) is highly effective for some species (Fig. 13.3).
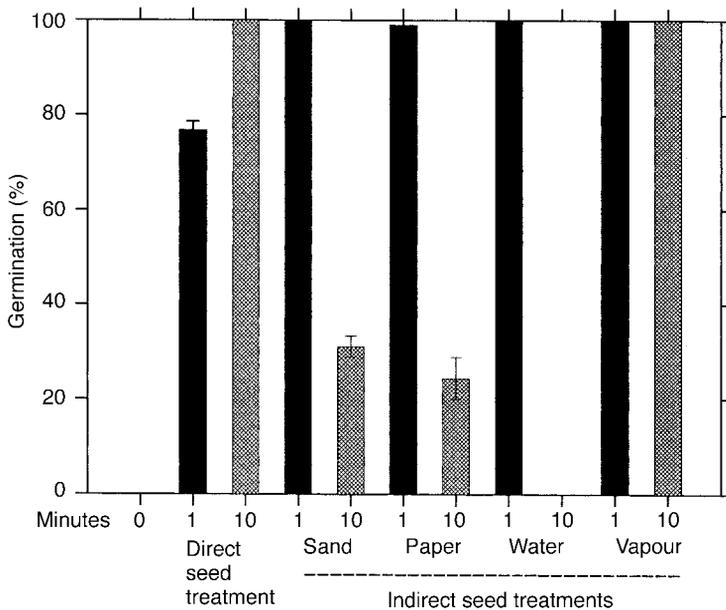
Seed-coats of smoke-stimulated species

Fig. 13.2. Germination of *Emmenanthe penduliflora* for control (0) and smoke treatments of 1- or 10-min exposures for direct treatment (smoke-treated seeds incubated on non-treated filter-paper) and indirect treatments (untreated seeds incubated on smoke-treated sand or filter-paper or untreated seeds incubated with smoke water or exposed to gases emitted by smoke-treated filter-paper) (redrawn from Keeley and Fotheringham, 1997).

Table 13.1. California chaparral species illustrating the range of variation in germination response (mean percentage germination + SE, n = 3 replicates of 30 seeds) (data from Keeley and Fotheringham, 1998b, and unpublished).

Species	Family	Control	70°C 1 h	105°C 5 min	115°C 5 min	CW[a]	Smoke (min) 5	Smoke (min) 15	Scar	Scar + GA[b]	GA[b]	Nitrate[c] (mol m^{-3}) 1	Nitrate[c] (mol m^{-3}) 10	Nitrate[c] (mol m^{-3}) 100
Ceanothus crassifolius	*Rhamnaceae*	0	50	87	47	0	0	0	98	99	0	0	0	0
Emmenanthe penduliflora	*Hydrophyllaceae*	0	0	0	0	80	100	15	100	100	0	0	2	1
Phacelia grandiflora	*Hydrophyllaceae*	1	0	0	0	44	59	66	99	95	0	0	4	0
Romneya coulteri	*Papaveraceae*	0	0	0	0	46	74	99	19	100	0	0	0	0
Silene multinervia	*Caryophyllaceae*	8	7	4	8	84	98	92	98	95	29	15	47	9
Dicentra chrysantha	*Papaveraceae*	0	0	0	0	0	0	0	0	0	0	0	0	0

[a]CW = 10% aqueous leachate from charred wood.
[b]GA = gibberellic acid (GA$_3$) highest germination with 1, 5 or 10 mmol m^{-3}.
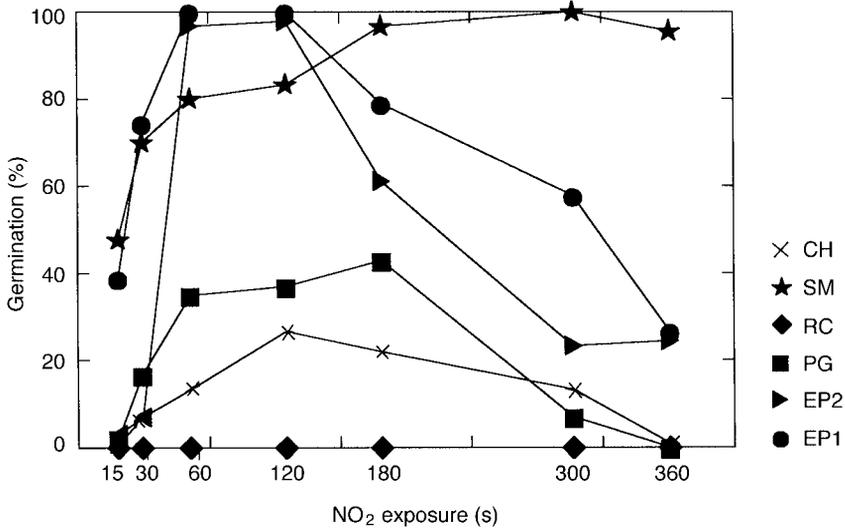[c]KNO$_3$ in distilled water, pH ~6.

Fig. 13.3. Germination response to nitrogen dioxide (7.7×10^3 mg m^{-3}) at different durations of exposure applied to dry seeds for smoke-stimulated California chaparral species: *Caulanthus heterophyllus* (CH), *Silene multinervia* (SM), *Romneya coulteri* (RC), *Phacelia grandiflora* (PG) and two populations of *Emmenanthe penduliflora* (EP1 and EP2) (redrawn from Keeley and Fotheringham, 1998b).

are structurally quite different from those of heat-stimulated species. Outer seed-coats are highly sculptured and, in all cases so far examined, they lack a dense palisade layer. Commonly, the outer coat comprises loosely packed tissues with a subdermal semi-permeable cuticle. Most of the species so far tested fully imbibe water during dormancy, indicating endogenous dormancy (Keeley and Fotheringham, 1998b).

Mechanism of smoke- and charred-wood-stimulated germination

It is unknown what chain of reactions triggers germination of smoke-stimulated species and there is every likelihood that the mechanism is not the same in all species. One of the best-studied species is *E. penduliflora* and it provides a useful model system for investigating smoke-induced germination because of the following:

1. Historically, it was the species first identified to have charred-wood-stimulated germination (Wicklow, 1977) and its ger-

mination behaviour has been well characterized (Jones and Schlesinger, 1980; Keeley and Nitzberg, 1984; Keeley *et al.*, 1985; Keeley, 1987, 1991; Keeley and Fotheringham, 1997, 1998a, b).
2. This species has deeply dormant seed pools, often with zero germination under 'control' conditions, and this is consistent across most chaparral populations, unlike some other smoke-stimulated species, where a sizeable fraction of the seed bank germinates in the absence of fire-related cues.
3. Germination is light-neutral and most populations are cold-stratification-dependent.

Emmenanthe germinates in response to either charred wood, smoke or aqueous extracts or vapours from either of these combustion products (Fig. 13.2). Under the proper concentrations, these fractions generate 100% germination of otherwise completely dormant seed pools. Chemicals eliminated as germination cues include nitrate ion, nitrous oxide, carbon dioxide, ethylene and methane (Keeley and Fotheringham, 1997, 1998a). Some

compounds, e.g. carbon monoxide, sulphuric acid and hydrogen peroxide, are capable of stimulating substantial germination, but the strongest and most consistent response is to nitrogen oxides (Fig. 13.3). Several characteristics suggest that this may be the active component of smoke-stimulated germination. Nitrogen dioxide is capable of stimulating complete germination at the levels present in biomass smoke and, like smoke, it can stimulate germination by direct exposure or indirectly by binding to soil particles and being transferred in water or vapours (Keeley and Fotheringham, 1997).

Dormant *Emmenanthe* seeds readily imbibe water. However, while the seed-coat layers are permeable to water and solutes, there is a semi-permeable subdermal cuticle, which allows water to pass but blocks larger-molecular-weight solutes, e.g. eosin and other dyes (Keeley and Fotheringham, 1997, 1998a, b). Smoke or low levels (7.7×10^3 mg m^{-3}) of nitrogen dioxide change the characteristics of this membrane and allow diffusion of solutes that would otherwise be blocked. It is unknown whether or not this change in membrane diffusivity has any role in the germination of this species, but one characteristic suggests it might: seeds germinate completely following seed-coat (including the subdermal cuticle) scarification (Table 13.1). However, scarification-induced germination is widespread in many species, and may not reflect on the smoke-induced germination mechanism. It has been posited (K. Bradford, 1997, personal communication) that scarification-induced germination is a 'wound response', widely selected for because of the inevitable microbial infection to be expected once the integrity of the seed-coat is broken. Further evidence that the basis for scarification- and smoke-induced germination may differ is the fact that in *Emmenanthe* a gibberellic acid inhibitor prevents germination of scarified seeds but not of smoke-treated seeds (Keeley and Fotheringham, 1998a).

In characterizing the germination response of *Emmenanthe*, it has been shown that germination is strongly dependent upon oxidizing agents or a combination of acidity and certain anions, such as nitrate or sulphate (however, these ions alone are ineffective). Many characteristics of *Emmenanthe* germination fit Cohn's model of dormancy-breaking behaviour of weak acids, which increase membrane permeability in the disassociated form (Cohn *et al.*, 1983, 1987; Cohn and Castle, 1984; Cohn and Hughes, 1986; Cohn, 1989, 1996). However, alternatives have been proposed (e.g. Hendricks and Taylorson, 1972; Keeley and Fotheringham, 1998a; Raven and Yin, 1998).

It is likely that the mechanism of smoke-stimulated germination is different between species, which should be expected, considering its wide phylogenetic distribution. Some smoke-stimulated chaparral species share many of the same germination responses with *Emmenanthe*, including response to nitrogen dioxide, but not all (Fig. 13.3). Two other smoke-stimulated species are worth noting, because they illustrate some of the variation in a single community. The response of *Romneya coulteri* to smoke is not unlike that of *Emmenanthe*, but *Romneya* fails to respond to nitrogen dioxide (although it is stimulated by nitrite ions), to seed-coat scarification or to treatment by strong acids and oxidizing agents (Keeley and Fotheringham, 1998b). *Dicentra chrysantha* fails to germinate under all conditions (Table 13.1), unless seeds are first pretreated by a long period (*c.* 1 year) of soil burial. Following burial, seeds are still dormant but are now highly sensitized and will germinate in response to smoke (Keeley and Fotheringham, 1998b). Ageing has been shown to increase the response to smoke in a great many Australian species (Roche *et al.*, 1997). However, in the case of *Dicentra*, ageing *per se* is insufficient, since shelf-stored seeds fail to respond to smoke, suggesting that interactions with the soil environment are necessary. It is apparent that smoke-stimulated seeds have different barriers to germination, which require a particular order of environmental cues. It is conceivable that such differences in response may affect postfire community structure, both spatially and temporally.

Further variation is evident in the response of *Nicotiana attenuata,* an annual widespread in scrub and woodlands throughout arid parts of western North America. As with chaparral species so far studied, *Nicotiana* seeds freely imbibe water in the dormant state and thus have endogenous dormancy (Baldwin *et al.*, 1994). It has been proposed that germination in this species is not tied to nitrogenous compounds, because germination is triggered by treatment with pyrolysis products of α-cellulose (Baldwin *et al.*, 1994). Whether or not nitrogen is involved remains to be determined, since these experiments were all conducted with ~10 mol m^{-3} KNO$_3$ in the incubation medium of controls and treatments. Previous studies on other smoke-stimulated species have shown that, while nitrate in water fails to stimulate germination (e.g. Table 13.1), under acidic conditions, either from buffers or added pyrolysis products, nitrate is stimulatory to germination (Keeley and Fotheringham, 1998a), suggesting that the combination of protons and the nitrate anion were involved in the germination response. *Nicotiana* requires further work before a role for nitrogenous compounds can be ruled out.

Induced or enforced dormancy in soil-stored seed banks

As discussed above, many species have innate seed dormancy, which is overcome by fire-related cues, such as heat and charred wood. However, some species in fire-prone environments do not exhibit innate dormancy at the time of dispersal and will germinate readily under laboratory conditions, but develop dormancy under field conditions. For example, California chaparral annuals – *Cryptantha* spp., *Nicotiana* spp., *Papaver californica* and others – collected from recent burn sites have non-dormant seeds, which germinate readily upon wetting (Keeley, 1987, 1991; Keeley and Fotheringham, 1998b). In the field, however, populations of these species are abundant only immediately

after fire, arising from dormant seed banks. Their persistence is closely tied to the post-fire environment and they decline in subsequent years, some disappearing entirely by the third postfire year (J.E. Keeley, unpublished data). This is circumstantial evidence that dormancy is induced or enforced by environmental factors developing after fire; Harper (1977) distinguishes induced dormancy as an acquired inability to germinate and enforced dormancy as imposed by an environmental constraint, such as lack of light or the presence of an inhibitor. One of the earliest cases studied was that of chemical inhibition (allelopathy) of herbaceous species by chemicals leached from the shrub canopy, putatively selected to inhibit competitors (Muller *et al.*, 1964; McPherson and Muller, 1969; cf. Keeley and Keeley, 1989). Alternatively, inhibition of germination may represent induced dormancy and result from an evolved sensitivity to compounds indicative of unfavourable shrub-dominated environments (Koller, 1972; Angevine and Chabot, 1979; Keeley, 1991); such compounds are perhaps best described as 'infochemicals' (Smith and van Staden, 1995). Preston and Baldwin (1999) have recently provided field evidence consistent with the idea of negative effectors enforcing dormancy on *N. attenuata,* and they appear to be associated with specific shrub species (Baldwin and Morse, 1994).

Studies of chemical inhibition (allelopathy) have proposed that postfire germination is triggered by high-temperature destruction of inhibitory compounds in the soil environment (Muller *et al.*, 1964; McPherson and Muller, 1969). This, of course, implies enforced dormancy, although it is possible that the chemical environment in unburned soils induced dormancy by converting the seeds to a state where germination required heat or smoke.

In California chaparral, there is evidence that species most closely tied to postfire environments – i.e. strict 'fire-following species' – have innate dormancy, and germination is not chemically inhibited by the prefire soil environment, whereas the more 'opportunistic' species,

arising under a variety of disturbances, have dormancy that is induced by chemicals in the soil environment. Evidence of this is in the 'allelopathy' experiments reported by Christensen and Muller (1975). They found that several postfire endemics (e.g. *Allophyllum glutinosum, Emmenanthe penduliflora* and *Lotus scoparius*) were insensitive to shrub leachates, even when primed to germinate by scarification (Table 13.1). In contrast, several of the opportunistic species (e.g. *Centaurea melitensis, Cryptantha intermedia* and *Lactuca serriola*) were highly sensitive to shrub leachates (Table 13.2).

Other examples of induced or enforced dormancy include the highly opportunistic coastal sage-scrub vegetation in California. These subligneous shrubs readily recruit in a variety of disturbances (DeSimone and Zedler, 1999). Dominants, such as *Artemisia californica, Salvia mellifera* and *Mimulus aurantiacus*, have seeds that exhibit a marked interaction between light and charred wood. Seeds have a positive photoblastic response – germinating readily in the light – but are dormant in the dark, thus cueing germination to gaps but blocking germination of buried seeds. However, following fire, this dark-induced dormancy is broken by chemicals leached from charred wood (Keeley, 1991). As with the opportunistic *N. attenuata* (Preston and Baldwin, 1999), these subshrubs appear to be responding to both positive and negative effectors.

Ecological distribution of fire-dependent regeneration

Fire-dependent seed release from serotinous cones/fruits or smoke/heat-triggered germination is largely concentrated in

Table 13.2. Effect of leaf leachate from the dominant chaparral shrub, *Adenostoma fasciculatum*, on germination of herbaceous species, including: (i) 'opportunistic' species (common in many types of disturbance); and (ii) 'postfire endemics' (closely associated with fire; *Convolvulus cyclostegius* and *Lotus scoparius* are heat-stimulated and the rest are smoke-stimulated). Seedcoats of these postfire endemics were scarified to overcome innate dormancy. (Based on data from Christensen and Muller, 1975.)

| | Percentage germination (mean ± SD) | |
Species	Controls	Leachate
Opportunistic species		
Bromus rigidus (*Poaceae*)	94 ± 6	97 ± 4
Centaurea melitensis (*Asteraceae*)	93 ± 5	0 ± 0
Cryptantha intermedia (*Boraginaceae*)	93 ± 7	3 ± 6
Erigeron divergens (*Asteraceae*)	94 ± 1	0 ± 0
Lactuca serriola (*Asteraceae*)	94 ± 1	37 ± 11
Postfire endemics		
Allophyllum glutinosum (*Polemoniaceae*)	90 ± 0	83 ± 0
Convolvulus cyclostegius (*Convolvulaceae*)	92 ± 2	90 ± 6
Emmenanthe penduliflora (*Hydrophyllaceae*)	80 ± 14	73 ± 7
Eucrypta chrysanthemifolia (*Hydrophyllaceae*)	95 ± 2	91 ± 9
Lotus scoparius (*Fabaceae*)	96 ± 2	95 ± 4
Phacelia grandiflora (*Hydrophyllaceae*)	6 ± 5	4 ± 3

ecosystems prone to stand-replacing fire regimes (Fig. 13.1). Characteristics in common with such systems include predictable but infrequent ignitions and moderate site productivity, sufficient to accumulate woody fuels but insufficient for arborescent growth forms capable of 'outgrowing' fire effects (e.g. high canopy, self-pruning, thick bark, etc.). These are mostly Mediterranean-climate shrublands, where the winter/spring rainfall occurs under mild temperatures, conducive to moderate biomass production, but the severe summer drought limits the stature of the vegetation, maintaining a dense flammable vegetation capable of fire spread through the canopy and over large areas. Other vegetation types conducive to stand-replacing fire regimes, such as densely stocked *Pinus contorta* forests at mid-elevations in the Rocky Mountains and high-latitude small-stature *Pinus banksiana* forests, are also dominated by postfire recruitment from serotinous cones. These forests, however, generally lack an understorey vegetation with dormant seed banks that cue seed recruitment to postfire conditions. Most grasslands are subject to frequent stand-replacing fires, but, with a few exceptions, these species are not known to establish dormant seed banks dependent upon fire for recruitment.

Risks associated with fire-dependent recruitment

In woody plants, vegetative regeneration from underground stems or roots is often associated with postfire regeneration, and this provides a measure of protection in the event of seed recruitment failure following fire. However, with the exception of certain gymnosperms, there is little evidence that such resprouting has evolved in response to fire, as it is almost ubiquitous in woody dicotyledonous plants (Keeley, 1981; Keeley and Zedler, 1998). In this light, it is particularly interesting that, in the most fire-prone habitats (i.e. shrublands of California, South Africa and Western Australia), shrub species in a number of genera have evolutionarily lost the ability to resprout and thus are dependent upon seedling recruitment. These obligate-seeding species are vulnerable to localized extirpation if fire regimes fall outside their range of tolerance, in terms of time to maturity, adult longevity and seed-bank persistence (Parker and Kelly, 1989). They
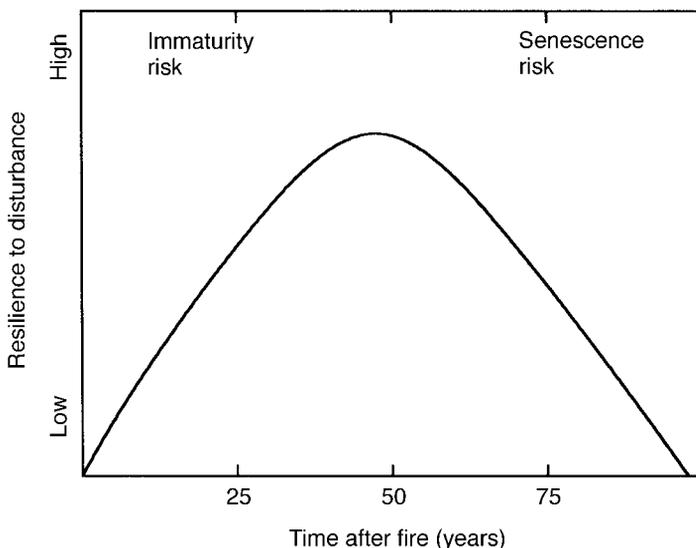

Fig. 13.4. Risks associated with fire-dependent obligate seed regeneration.

face an 'immaturity risk' (Fig. 13.4) if fires are too frequent, i.e. occur before sufficient seed banks have established. On the other hand, if the fire return interval exceeds the lifespan of the shrubs and their seed bank, the population faces a 'senescence risk'. At present, humans contribute sufficiently to the fire regime in most shrubland regions (e.g. Keeley *et al.*, 1999b) for the senescence risk to be minimal (cf. Bond, 1980); however, such is not the case for the immaturity risk. There are a number of well-documented cases where human intervention in fire regimes has increased fire frequency sufficiently to threaten fire-dependent species (van Wilgen and Kruger, 1981; Zedler *et al.*, 1983; Haidinger and Keeley, 1993; Keeley *et al.*, 1999a).

Another risk is the potential loss of inclusive fitness due to delayed reproduction (e.g. Schaffer, 1974). Various arguments have been proposed to account for the selective factors involved in the evolution of dormancy (Cohen, 1968). Ellner's (1986) hypothesized parent–offspring conflict in seed germination would be interesting to examine in these fire-type species. Germination of heat-shock-stimulated seeds is controlled by maternal seed-coat tissues, but smoke-stimulated species appear to have endogenous (embryonic) control of germination. We posit that due to the time-varying nature of fire-prone ecosystems, rapid germination is avoided, because the chances for successful recruitment are nil in competition with the dominant vegetation.

Life-history syndromes

Fire-dependent recruitment appears to be tied to other life-history characteristics, including tolerance to drought stress and shading (Keeley, 1998). Dormant soil-stored seed banks triggered to germinate by smoke/charred wood (and heat shock) are not randomly distributed across growth forms, but rather are common in annuals and shrubby perennials, uncommon in trees and rare in herbaceous perennials (Keeley, 1991, 1995; Keeley and Bond, 1997). In California chaparral, species with

dormant seed banks have markedly smaller seeds than those lacking dormancy (Keeley, 1991), a phenomenon observed in other vegetation types as well (Rees, 1996). Species with fire-dependent recruitment are predominantly passive seed dispersers – seeds are dispersed in time rather than in space because, when fires occur, they generate gaps of extraordinary size. Indeed, animal-dispersed seeds in most Mediterranean-climate shrublands lack seed dormancy and animals play a crucial role in targeting seeds to localized safe sites present during the fire-free interval (Keeley, 1991, 1992b, 1995).

Phylogenetic distribution of fire-dependent regeneration

Serotiny versus soil-borne seed banks

Distribution of canopy- versus soil-stored seeds differs globally. In the northern hemisphere, serotiny is largely restricted to conifer trees – primarily *Pinus* and *Cupressus* – and soil-stored seed banks are widespread in angiosperm shrubs. Hypotheses for why gymnosperms have evolved to adopt serotiny rather than soil seed banks include: (i) lack of genetic potential for the evolution of seed-coat/embryo characteristics that enforce dormancy and cue germination to heat or smoke; (ii) selection for serotiny is linked to other cone characteristics that reduce predation; and (iii) serotinous conifer habitats have moderate productivity and long intervals between fires, resulting in forest-floor fuel loads that essentially sterilize soil-stored seeds when a fire occurs (Thomas and Wein, 1994; Ne'eman, 1997; Keeley and Zedler, 1998). Concomitantly, lack of serotiny in northern-hemisphere angiosperms may be tied to fuel structure in these lower-stature shrubs, which leads to fire intensities sufficient to decimate above-ground seed banks.

In the southern hemisphere, particularly in the South African and Western Australian Mediterranean-climate shrublands, serotiny is widespread in angiosperm

shrubs (Lamont *et al.*, 1991). This is in sharp contrast to the lack of serotiny in California chaparral and we hypothesize that the infertile soils typical of these southern-hemisphere sites reduce production and consequently reduce fire intensity (van Wilgen and van Hensbergen, 1992), thus making canopy seed storage less likely to succumb to fire than would be the case in California chaparral. Also, the nutrient-poor soils of these regions place a premium on nutrient-rich seeds and thus another selective advantage of canopy over soil storage may be predator avoidance (Keeley, 1992a).

Heat- and smoke-stimulated germination

No detailed phylogenetic studies of fire-stimulated germination are available.

However, some generalizations are reasonable. Based on the taxonomic distribution of smoke- versus heat-stimulated germination, it is clear that there is a strong phylogenetic component to these germination responses. For example, countless numbers of species with heat-stimulated germination are known worldwide for the *Fabaceae* and yet no example has been reported for smoke-stimulated germination in this family. It appears that this generalization applies equally well to other families with heat-stimulated germination, such as the *Rhamnaceae* and *Malvaceae*. These families are also tied together in terms of their seed-coat structure – a relatively conservative trait (Atwater, 1980).

Smoke-stimulated germination in distantly related families in the northern and southern hemispheres is reasonably interpreted as convergent evolution, although
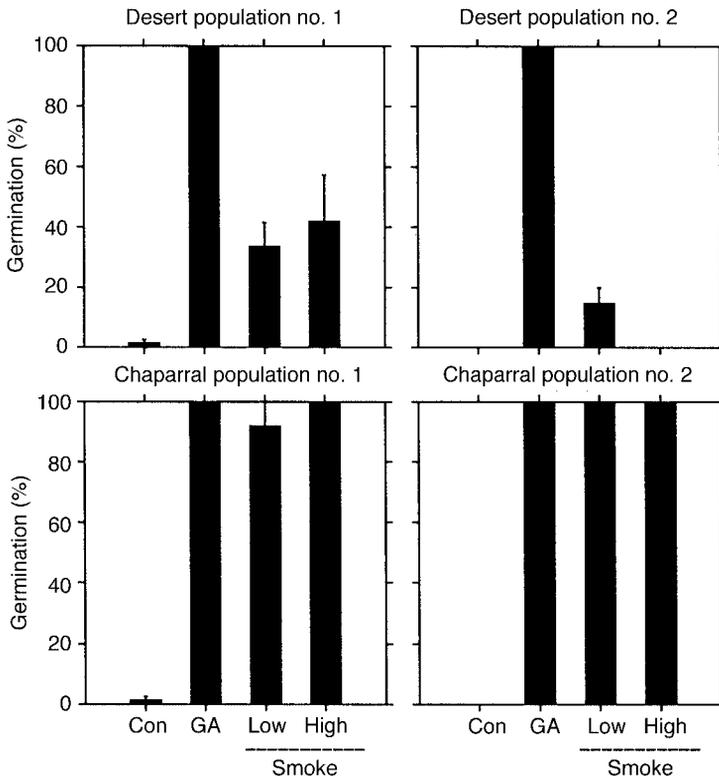

Fig. 13.5. Germination response for *Emmenanthe* populations from desert and chaparral; Con, control; GA, gibberellic acid (GA$_3$); low smoke, half sheet of a 10 min smoked filter-paper, high smoke, whole smoked filter-paper (redrawn from Fotheringham, 1999). GA$_3$ germination demonstrates high viability in all populations. (Where columns are absent, germination was zero.)

within family lineages it may have arisen one or more times.

Recent studies have focused on widespread species distributed in both fire-prone chaparral and non-fire-prone desert habitats (Fotheringham, 1999). Of particular interest is the observation that desert populations of smoke-stimulated chaparral species have a low level of smoke-triggered germination (Fig. 13.5). Smoke-stimulated germination has also been demonstrated in arid karoo species of South Africa, where fires are rare, and it has been suggested that this observation calls into question the adaptive role of smoke-stimulated germination in fire-prone habitats (Pierce *et al.*, 1995). There are alternative explanations. In some chaparral species, it is apparent that nitrogen oxides in smoke are the chemical cue for germination. Biotic production of nitrogen oxides are additional sources and may even be more important triggers in recent burns or even in non-fire-prone environments. In deserts, such cues would be associated with resource islands in and around shrubs. Consistent with this notion is the fact that there is significant microhabitat segregation – smoke (or nitrogen oxide)-stimulated germination is commonly found in species growing in association with shrubs (Fotheringham, 1999).

Indirect effects of fire on seed regeneration

Light

European heathland species accumulate substantial seed banks, which contribute to postfire recruitment, and yet there is little evidence that they are directly stimulated by heat or fire-related chemicals (Hobbs *et al.*, 1984; Mallik *et al.*, 1984; Mallik and Gimingham, 1985). Two of the more common heath species, *Calluna vulgaris* and *Erica tetralix*, have seeds that are light-stimulated and it is proposed that burning, as well as other disturbances, open the site sufficiently for light to trigger germination (Pons, 1989a).

Alternating temperatures

Some species accumulate seed banks with innate dormancy that is broken by the more extreme diurnal fluctuation in soil temperatures on sites opened up by fire (Brits, 1986; Pierce and Moll, 1994). These are typically short-lived seed banks, which also recruit on other open sites and are not strictly tied to fire.

Colonization

In many conifer forests, trees and shrubs are highly dependent upon disturbances such as fire to produce gaps suitable for seedling recruitment. Natural lightning-ignited fires are frequent in these forests and, because of the high site productivity, woody fuels lead to a mixed-intensity stand-thinning fire regime (Fig. 13.1). While much of the forest remains intact, gaps of the order of 10^2–10^4 m^2 are common. Species such as *Pinus ponderosa* often require these gaps for successful seedling recruitment, but, because they do not maintain dormant seed banks, they also require a seed source within dispersal distance. Mature trees typically survive these fires, because site productivity is sufficient to promote rapid growth, which maintains the canopy of many trees above the flame length, self-pruning of dead branches limits fire spread into the canopy and thick bark protects stems at flame level (Keeley and Zedler, 1998).

Other species, such as *Epilobium angustifolium* (Solbreck and Andersson, 1987) or *Betula* spp. (Hobbs *et al.*, 1984), have long-distance wind-dispersed seeds capable of colonizing distant burned sites. Such species typically have no dormancy and establish rapidly upon encountering suitable growing conditions (Romme *et al.*, 1995). Success of these colonizing species is controlled by burn severity, which affects gap size and competition, and by fire size, which affects proximity of seed sources (Turner *et al.*, 1997). These species commonly recruit on burned sites but they are capable of capitalizing on other disturbances as well.

Fire-induced flowering

A wide variety of species exhibit varying degrees of flowering restriction to postfire sites. The most extreme case is that of the South African lily *Cyrtanthus ventricosus,* which has only ever been observed to flower after fire. Generally, it flowers within a week following fire, regardless of the season (Le Maitre and Brown, 1992), and flowering is triggered by smoke (Keeley, 1993). Other geophytes in several fire-prone habitats show a marked flowering response in the first growing season after fire, tied to increased light or nutrients or alternating soil temperatures. The demography of such species has not been studied in much detail, but seedling recruitment appears to be restricted to subsequent postfire years. The typical pattern is resprouting from buried vegetative structures that survive fire and flowering and dispersing seeds in the first postfire year, followed by massive seedling recruitment in the second year. This pattern is evident in many geophytes and also perennial grasses in grasslands and savannahs, as well as subshrubs in coastal scrub vegetation.

Bamboo fire cycle

It is a widespread characteristic in long-lived woody bamboos to delay flowering and seed production for many decades and then to synchronize flowering and fruiting at the landscape scale, followed by massive mortality of bamboo clones. There are numerous reports in the literature of a linkage between bamboo mortality, wildfires and seedling recruitment, e.g. 'fierce forest fires followed the death of the bamboo to be accompanied almost immediately thereafter by copious natural regeneration' (Kadambi, 1949). It has been hypothesized that delayed reproduction, mast flowering and semelparity are a character syndrome selected to promote catastrophic wildfires, which open forest canopies and maintain the early successional stages necessary for seedling success and long-term persistence of clones (Keeley and Bond, 1999). In essence, mast mortality has been selected as a niche construction mechanism (e.g. Odling-Smee *et al.*, 1996) that increases the likelihood of wildfires and promotes successful recruitment.

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