

# Post-fire germination: The effect of smoke on seeds of selected species from the central Mediterranean basin

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## Abstract

In regions with a Mediterranean-type climate wildfires are a frequent occurrence: in such environments fire tolerant/favoured species are frequently encountered. In the Mediterranean basin, many species of fire prone habitats are resprouters while others are known to germinate after fire. Fire causes an enhancement of seed germination in many species from fire prone habitats in the other regions with a Mediterranean-type vegetation such as Western Australia, California and South Africa. Seeds of a number of these species are stimulated to germinate by the smoke generated from burning of plant material in either an aerosol or aqueous form. However, for species from the Mediterranean basin the role of smoke in germination is poorly known, despite the fact that in the field many species seems to be encouraged to germinate after fire. We examined the germination of 10 species native to the Mediterranean basin that were treated with aerosol smoke. Some species were from fire prone habitats while others were not. In relation to the controls, increased germination occurred in three of the species (e.g. *Cistus incanus*), three had more rapid germination but no total increase (e.g. *Rhamnus alaternus*), two showed reduced germination (e.g. *Asphodelus ramosus*) and two exhibited no difference in germination (e.g. *Clematis flammula*). There was additionally no consistent pattern of germination behaviour depending on the habitat from which the species came. Comparison is made between the results of this study and those of other studies on seed germination response to heat and smoke in other areas of Mediterranean-type climate. An understanding of the importance of fire in relation to other disturbances in the vegetation dynamics in the Mediterranean basin needs to be clarified by further detailed studies of the effect of heat and smoke products on seed germination of Mediterranean species. Outcomes of further research, also on a broader range of species, would have important impacts also for conservation, environment management, horticulture and ecosystem restoration.

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## 1. Introduction

Special germination cues (other than the presence of water) are widely spread throughout the world's flora. As plants have only limited ability to select where they grow, having a mechanism which improves chances of successful seedling establishment can be evolutionarily advantageous. Using a ubiquitous predictive cue for suitable establishment conditions is likely to be more efficacious than a very specialised one. For example, for a plant species which utilises animal dispersal to locate a suitable germination site the species may be at risk of local extinction if the animal disperser disappears from the area where the plant grows (e.g. mistletoes). Alternatively the more

general cue of red light is a suitable dormancy breaker in seeds which might be shaded by overstorey plants so when they receive more red than far red light conditions are suitable for germination (Ray et al., 1983).

Other cues for germination are cold followed by warmer temperatures, heat and rainfall sufficient to remove seed coat chemicals that inhibit germination. Another ubiquitous type of germination stimulant is provided by fire. The cue of fire products, such as heat, chemical stimulants and changes in the microsites (Baskin and Baskin, 1998) indicates the clearance of adult plants from a site. The area is then ready for relatively competition-free establishment of seedlings in an environment that may also have slightly higher nutrient levels, particularly on the soil surface, than in an undisturbed system. This type of fire-related cue to germination is found in many species from Mediterranean-type climates (Keeley and Bond, 1997).

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South-Western Australia, the Cape of South Africa, coastal California, mid latitude Chile and the Mediterranean basin are the five mediterraneanoid geographic regions characterised by moderate mean annual temperatures, winter maximum rainfall and a relatively dry, hot summer. Climate is considered to have been a significant selective force in the development of vegetation in mediterraneanoid regions and the similarity/convergence of vegetation structure and plant forms in areas of Mediterranean-type climate has been examined by many authors (Specht, 1979; Cowling and Campbell, 1980; Pignatti and Pignatti, 1985; Pignatti et al., 2002). However, despite the many similarities in vegetation and plant form it has also been considered that the similarities are mainly superficial and that many differences of detail tend to outweigh the general similarities (Barbour and Minnich, 1990).

Many of the dominant species in the drier parts of the Mediterranean-type environments (<600–700 mm/a) are strong resprouters after defoliation by any disturbance, while others have no ability to survive severe damage to the adult, such as occurs in a fire, and rely entirely on seed for regeneration. In South African fire-dependent plant communities, fynbos, fire regime plays an important role in germination (Keeley and Bond, 1997). In many Australian species of the kwongan, fire and appropriate moisture levels are highly favoured as the two most important germination cues, ensuring germination occurs under favourable environmental conditions (Bell, 1999). In Californian chaparral there is a rich flora with different mechanisms for cuing germination to post-fire conditions (Keeley, 1991). In all these regions, where many species have evolved barriers to germination that are normally overcome by fire-related cues (Keeley and Fotheringham, 1997), fire is an important component in the seed bank dynamics with up to 40% of species having enhanced germination following fire. In Chilean matorral, on the other hand, fire-stimulated seed germination as only been shown on few species (Segura et al., 1998) so, at present, there are no evidences of fire being an essential enhancing agent for seeds germination in this region. In the Mediterranean basin, many species of fire prone habitats are resprouters (Naveh, 1975; Piotta et al., 1999), some geophytes sprout and flower (Grove and Rackman, 2001), while only some taxa, e.g. *Cistus*, are known to germinate predominantly after fire (Trabaud and Oustric, 1989; Ojeda, 2001).

One ubiquitous factor in these mediterraneanoid areas is the importance of fire in the vegetation dynamics of the regions (di Castri, 1981). There has been considerable debate over the degree to which other environmental factors responsible for the death of above ground plant parts such as grazing, landslides and drought have contributed to the evolution of the flora which now has a number of fire resistant traits (Naveh, 1994; Pignatti and Pignatti, 1999; Ojeda, 2001; Grove and Rackman, 2001; Ladd et al., 2004). However it is still considered that there is “a striking evolutionary adaptation” of this system to fire (Naveh, 1999).

Smoke is a by-product of fire and it is used to break the dormancy of seeds of many species from some of the

mediterraneanoid regions and has been studied in detail over the last 10 years. A butenolide compound has been recently isolated from the cocktail of smoke chemicals and shown to be as effective as smoke, in general, in enabling germination of seeds which would normally have no or very low germination without smoke treatment (Flematti et al., 2004; van Staden et al., 2004). While fire is ubiquitous in Mediterranean-type climates smoke enhanced germination is most frequent in the Cape of South Africa (de Lange and Boucher, 1990; Brown et al., 1993, 1994) and Southern Australian species (Dixon et al., 1995; Roche et al., 1997a,b; Enright et al., 1997; Read and Bellairs, 1999), less so in Californian species (Keeley and Fotheringham, 1997, 1998); in Chilean species, to our knowledge, the effect of smoke on germination has never been accurately investigated. For Mediterranean basin species the role of smoke in seed germination has only recently started to be examined (Pérez-Fernández and Rodríguez-Echeverría, 2003) and is still not fully understood, although smoke is a specific feature that more than others could be rigorously related to fire.

In South Africa and Western Australia, smoke is currently used in restoration projects with native species from nursery production to direct application on site for significant improvement in recruitment from the soil seed bank (Roche et al., 1997b; Brown and van Staden, 1998; Crosti et al., 2003)

## 2. Aim

To examine the effect of aerosol smoke on the germination of a selected range of species typical of the Mediterranean basin plant communities. The null hypothesis was that smoke had no effect on germination of seed of the selected species.

## 3. Materials and methods

### 3.1. Seeds

#### 3.1.1. Seed collection

The species selected were representative of maquis which is frequently burnt and other vegetation which rarely experiences fire. Seeds of most of the species were purchased from accredited commercial collectors while others were self hand-harvested.

#### 3.1.2. Seed viability

The presence of white, healthy and intact embryo was determined through the cut test method. Viability was evaluated from three replicates of 30 seeds each and only species with seed viability higher than 15% were used in the experiment. Although initially 25 selected species were examined, only 10 had the acceptable viability and minimum germination values applicable for the experiment. Minimum germination was set at >5%.

#### 3.1.3. Seed treatment

The ex situ experiment was undertaken at the Kings Park and Botanic Gardens, Perth, Western Australia (*ex altera parte*

*terrae*') where a specific and standard protocol was established (Tieu et al., 1999) and where horticultural expertise, applied conservation advice and facilities were provided. Twenty-five seeds were sown in pasteurised seed sowing mix (four replicates) and watered before being exposed to smoke. The smoke was generated in a large metal drum by slow and controlled combustion of a mixture of fresh and dried plant material. The cooled aerosol smoke was blown over the seed trays for 1 h within an enclosed area.

Seed trays were moved to a glasshouse where germinants were monitored and removed after emergence each week for 12 weeks. Germination of smoked seeds was compared to unsmoked controls.

### 3.2. Statistical analysis

Data were tested for parametric assumptions with the Anderson–Darling normality test and Levene's test for variance homogeneity; output showed that there was no or just mild violation of data distribution. Consequently the two sample *t*-test, for unpaired comparison was used and differences were considered significant if  $P < 0.05$ . Figures are expressed as percentage germination from mean values of the replicates with  $\pm 1$  S.E. Germination results were not adjusted to account for non-viable seeds.

## 4. Results

Between the initial 25 tested species, only 10 had the minimum viability and germination values required for the experiment. Consequently, only these 10 species were considered to assess differences in germination. Within the assessed species, response to smoke was independent of taxon, geographical range, successional status and habitat. All except one (*Asphodelus ramosus* – a geophyte abundant in Mediterranean areas disturbed by grazing) were phanerophytes. Seed weights of the species varied widely and the seed bank type was almost equally divided between transient and persistent (Table 1).

Table 1  
Biological and ecological characteristics of the study species

| Species                 | PF             | R | E | $P < 0.05$ | LF | CT | 1000 Seed weight (g) | Seed bank type | Established strategy | Successional status | Phytosociological class |
|-------------------------|----------------|---|---|------------|----|----|----------------------|----------------|----------------------|---------------------|-------------------------|
| <i>A. glutinosa</i>     | Betulaceae     | + | □ | ○          | P  | EA | <10                  | T              | CS                   | Late                | Q-F                     |
| <i>A. ramosus</i>       | Liliaceae s.l. | – |   | ○          | G  | SM | <100                 | T              | SR                   | Early               | T-B                     |
| <i>C. incanus</i>       | Cistaceae      | + | □ | ○          | N  | SM | <1                   | P              | CS                   | Mid                 | C-L                     |
| <i>C. flammula</i>      | Ranunculaceae  | = |   |            | P  | EM | <10                  | P              | CS                   | Mid                 | Q                       |
| <i>C. vitalba</i>       | Ranunculaceae  | + | □ | ○          | P  | EA | <10                  | P              | CS                   | Mid                 | Q                       |
| <i>E. arborea</i>       | Ericaceae      | = | □ |            | P  | SM | <1                   | T              | CS                   | Mid                 | Q                       |
| <i>F. ornus</i>         | Oleaceae       | – |   | ○          | P  | EA | <100                 | T              | CS                   | Mid                 | Q-F                     |
| <i>J. o. macrocarpa</i> | Cupressaceae   | = | □ |            | P  | EM | <100                 | P              | CS                   | Early               | Q                       |
| <i>L. stoechas</i>      | Labiatae       | = |   |            | P  | SM | <1                   | P              | CS                   | Mid                 | C-L                     |
| <i>R. alaternus</i>     | Rhamnaceae     | + | □ |            | N  | EM | <100                 | P              | CS                   | Late                | Q                       |

R: germination response to smoke; E: earlier germination; LF: life form; Ch: chorological type; PF: plant family, + increased germination, – reduced germination, = no difference in final values of germination, □ at least two weeks, ○ difference statistically significant, P: phanerophytes; N: nanophanerophytes; G: geophytes; EA: eurasiatic, EM: euromediterranean; SM: stenomediterranean; T: transient; P: persistent; C: competitor; S: stress tolerant; R: ruderal; Q-F: *Quercus-Fageteta*; T-B: *Thero-Brachypoidietea*; C-L: *Cisto-Lavanduletea*; Q: *Querceteta ilicis*. Data were taken from literature, personal communications and authors' observations.

Final germination rates of most of the species were below 25%, and germination of un-treated seeds varied from a minimum of 7%, 8% and 10%, respectively, for *Clematis vitalba*, *Clematis flammula* and *Alnus glutinosa* to a maximum of 13%, 14% and 20%, respectively, for *Erica arborea*, *Cistus incanus*, *Juniperus oxycedrus macrocarpa* and *Fraxinus ornus*. *Lavandula stoechas*, *Rhamnus alaternus* and *A. ramosus* had final germination rates below 75%, with germination of un-treated seeds, respectively, of 48%, 52% and 73%.

Seed treated with smoke versus control showed that:

- the germination of *C. vitalba* and *C. incanus* (which are both species frequent in fire prone habitat), and of *A. glutinosa* (which instead occurs in swampy habitat) increased with smoke, in particular the latter showed seedling emergence 7 weeks in advance. Germination of these species increased, respectively, to 170%, 50% and 60%;
- earlier emergence of seedlings, but without statistical differences in final germination values, occurred in *E. arborea* (15% versus 13%), *J.o. macrocarpa* (10% versus 14%) and *R. alaternus* (65% versus 52%) (all these are species distinctive in the Mediterranean vegetation);
- at our tested smoke concentrations levels, the germination of *A. ramosus* and *F. ornus* (a tree which belongs to the Mediterranean woodland plant community) was reduced, respectively, by 56% and 55%.
- *L. stoechas* and *C. flammula* (species typically found in the Mediterranean thermophilous vegetation) exhibited no difference in germination rates.

Main results are summarized in Table 1 and Fig. 1.

## 5. Discussion

The response to smoke of the tested species was independent of life form, geographic range, habitat and seed weight. While some species that occur in the fire prone Mediterranean vegetation such as *C. incanus* and *C. vitalba* showed an increase

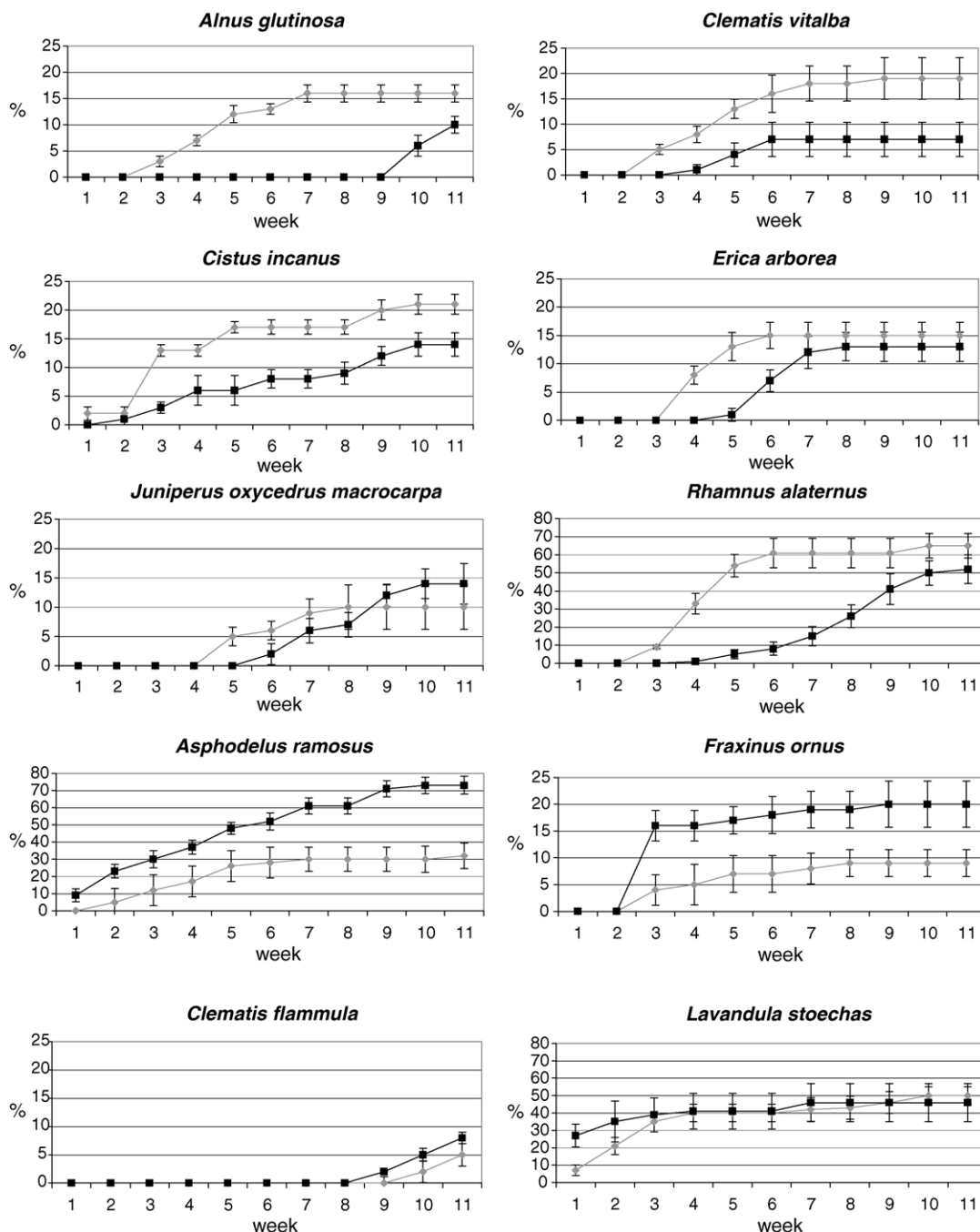


Fig. 1. Time courses of germination from 1–11 weeks. Figures represent mean percentages ( $\pm 1$  S.E.) of sown seeds  $n = 25$ . Germination results were not adjusted to account for non-viable seeds. ■ = control; ● = smoked; two different scale on the y-axis.

in germination with smoke treatment others from the same type of vegetation were unaffected.

The enhanced germination of *A. glutinosa* that grows in swampy areas is inconsistent with its habitat preference. However, there are other examples of taxa that are not from fire prone areas which have smoke responsive seeds, such as celery (Thomas and van Staden, 1995), *Lactuca sativa* (Gardner et al., 2001) and species from Tasmanian alpine vegetation (Marsden-Smedley et al., 1997). The active chemical compound isolated from smoke (Flematti et al., 2004; van Staden et al., 2004) may act in a similar manner to other chemicals or stimuli which

release seed dormancy (K.W. Dixon, unpublished; Gardner et al., 2001) and thus may not only be active in species from fire prone areas.

Two species showed adverse effects of smoke on germination and again this is not uncommon even in species which can have enhanced germination at low smoke concentration but are inhibited above a particular concentration (Enright et al., 1997; Pérez-Fernández and Rodríguez-Echeverría, 2003). *A. ramosus* is a species of disturbed ground around the Mediterranean basin; fire may be uncommon in such environments due to low fuel loads. Similarly, the habitat of *F. ornus* is not subject to

frequent fires and the species is likely dependent on gaps in the vegetation canopy for establishment rather than on disturbance such as fire.

Time to embryo emergence for smoke treated seed was reduced in the species which had enhanced germination and also in three species which ultimately showed no enhanced germination. Of these latter species *E. arborea* has been studied extensively in relation to germination and resprouting after fire. The earlier emergence after smoke treatment correlates with similar behaviour of heat treated seeds. Heat treatment of *E. arborea* seeds at 100 and 120 °C for 2 min reduced time of germination in seeds germinated in the light while in the closely related *E. australis* there was no difference from controls (Valbuena and Vera, 2002).

This pattern of a correlation between heat and smoke is being found increasingly as studies on more species with fractious seed germination are completed. *Cistus* is the epitome of the Mediterranean pyrogenic recruiter. While *Cistus* seedlings recruit after any disturbance (Delgado et al., 2001) or after consumption by red deer (Malo and Suarez, 1996) and just the opening of the vegetation canopy would be enough to encourage recruitment (Thanos and Georghiou, 1988), until recently only heat had been shown to dramatically increase seed germination over unheated controls. Although Pérez-Fernández and Rodríguez-Echeverría (2003) showed that smoke effects germination of seed in *C. ladanifer*, *C. monspeliensis*, *C. crispus* and *C. salvifolius* collected in southwestern Spain. For *C. incanus* in this present study germination of smoked seeds was 50% greater than the control. *C. incanus* from central Italy had from 40% to 60% increase in germination over controls for temperatures of 120 and 180 °C for between 1.5 and 2 min; similarly, heat enhanced germination in *C. monspeliensis* up to 40% above control (Mazzoleni, 1989) in *C. albidus* (Roy and Sonie, 1992) and *C. psilosepalus* (González-Rabanal and Casal, 1995). For *C. incanus* heat and smoke may be additive in their action. In some of the species described above the comparisons have to be made between different laboratories and seeds collected from populations of a species from widely separated parts of the total range around the Mediterranean basin. It has been shown that there may be variation in the response of seeds from different parts of the species' range in *Anigozanthus manglesii* from Western Australia (Tieu et al., 2001a) and the same may be the case for widespread Mediterranean species.

In a number of Australian species the effects of smoke and heat on seed germination have been shown to be additive (Keith, 1997; Gilmour et al., 2000; Thomas et al., 2003), synergistic (Kenny, 2000), unitive (Thomas et al., 2003) or variable depending on population location (Tieu et al., 2001a). While in *Cistus* species heat seems more efficacious in promoting germination, in many Australian species smoke promotes germination more than heat does (e.g. *Grevillea* species, Morris, 2000; Kenny, 2000). However in a number of species the interaction of particular levels of smoke and heat produces the best germination response (e.g. *Actinotus leucocephalus* – Tieu et al., 2001b; *Gahnia sieberiana* and *Kunzea ambigua* – Thomas et al., 2003). As with *E. arborea*

heat reduced the time to germination of the Tasmanian endemic *Epacris tasmanica* (also Ericaceae) but the combination of heat and smoke even further reduced time to germination. In contrast to *E. arborea* germination success in *E. tasmanica* was also increased by heat and it was even better with both heat and smoke. In the Cape Floristic Region on 40 *Erica* spp. tested, germination enhancement following smoke treatment was shown by 26, suggesting that under natural conditions smoke from fynbos fires provides an important cue for triggering seed germination in this family (Brown et al., 1993). Apart from this present study there has been no work published on the reaction of Mediterranean basin *Erica* species to smoke. However the effect of heat has been examined in some species; while *E. arborea* and *E. australis* do not seem to show increased final germination with heat (Valbuena and Vera, 2002) other ericaceous species have enhanced germination after heat treatment (e.g. *Daboecia cantabrica* – Valbuena and Vera, 2002 and *E. umbellata* and *E. ciliaris* – González-Rabanal and Casal, 1995). There is clearly much variation in germination response between species in the fire prone vegetation of the Mediterranean basin which would repay combined studies of heat and smoke.

In the Mediterranean basin various shrubs, some grasses and therophytes are listed as having enhanced post fire recruitment (Naveh, 1975). However it is not entirely clear for most species that some specific factor associated with fire (and not a general feature of disturbance) enhances recruitment. Many Fabaceae species have enhanced germination in the Mediterranean basin after heat (Anorbe-Urmeneta et al., 1990) and this is also the situation with leguminous species in other areas of Mediterranean-type climate such as South Africa, California and Southern Australia (Keeley and Bond, 1997). However in many cases the enhancement of germination is actually less than for mechanical scarification (Herranz et al., 1998). This supports the view of Izhaki et al. (2000) that “legumes are opportunistic species, exploiting the post-fire open areas rather than being fire followers”. Keeley and Bond (1997) pointed out that in some cases there are phylogenetic patterns in germination behaviour, such as in the legumes where heat will commonly enhance germination. However in all cases the species may be placed on a continuum of response – each species has different proportions of seeds that are “hard-seeded”. For example seed of the Fabaceae species *Scorpiurus muricatus* and *Dorycnium pentaphyllum* are virtually unaffected by dry heat up to 150 °C while *Cytisus striatus* (Herranz et al., 1998) and *Genistella tridentata* (Valbuena and Vera, 2002) have germination over double that of control seeds from 90 to 100 °C. In almost all cases scarified seeds had higher germination than dry heat treated seeds. While there are phylogenetic patterns there are also biogeographical patterns. Keeley and Bond (1997) further noted that in California and South Africa germination of annuals is commonly triggered by chemicals from smoke or charred wood. However, in Southern Australia woody plants from a wide range of families (e.g. many species in the Proteaceae and Myrtaceae) and perennial herbs (Stylidiaceae) are the more commonly smoke responsive species (Roche et al., 1997a).

The pattern for Mediterranean basin species in relation to specifically fire stimulated germination is still not clear. Many species show no germination enhancement from heat (Riba et al., 2002). Due to the lack of charred wood induced germination in post-fire species, Keeley and Baer-Keekey (1999) suggested that heat stimulated germination in the Fabaceae and Cistaceae family could be an homologous, rather than convergent, adaptation in Mediterranean climate ecosystem. Furthermore many studies showed reduced germination on seeds treated with ash compared to control (Ne'eman et al., 1993; González-Rabanal and Casal, 1995; Izhaki et al., 2000).

While this present study has demonstrated that some species have increased or have a more rapid germination in response to smoke chemicals, others from the same sort of vegetation do not and the overwhelming evidence so far from other studies is that heat is very commonly linked with enhanced seed germination. However, the heat response is often variable and may be a surrogate for the more general cue of disturbance. With the long history of grazing and agricultural activity in the Mediterranean basin perhaps species have become more reliant on general disturbance cues rather than specifically fire related ones to initiate plant establishment in an environment with lowered competition.

Further research to unravel the influence of smoke products and/or heat on seed germination will help clarify whether general or more specific disturbances (such as fire) are of primary importance in vegetation dynamics in the Mediterranean basin. This will assist with decisions about how best to rehabilitate many types of vegetation in the region opening up opportunities to utilise in restored sites species with low germination, or that are impractical to cultivate in nursery (such as the assessed *R. alaternus*), so to return, with closer approximation, to the original species assemblage present prior to disturbance.

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