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Does plant-derived smoke affect seed germination in dominant woody species of the Mediterranean matorral of central Chile?

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Abstract

Studies performed in the fire-prone Mediterranean-type climate shrublands of Australia, California, and South Africa have shown that plant-derived smoke enhances seed germination in many species. Unlike other areas with similar climate, central Chile stands out for the absence of natural fires, suggesting that smoke may not be expected to promote germination. However, anthropogenic fires have been frequent since several millennia, and the role of fire on shaping fire functional traits is not clear at this point. The aim of this study was to evaluate the effects of plant-derived smoke on seed germination of some predominant native woody species from the Mediterranean matorral of central Chile. We exposed seeds of 18 woody species to plant-derived smoke for 30 min and assessed their germination. Five species failed to germinate under either the experimental and control conditions. Smoke significantly stimulated germination in three species, while decreasing it in eight. Species showing smoke-inhibited germination tend to be major dominants in the Chilean matorral vegetation. The three smoke-stimulated species are known colonizers. This suggests that current human-caused fires could drastically change the structure of Chilean matorral. Although our results suggest fire have not played a major role in shaping adaptations for seed germination of woody species in the Chilean matorral, more investigation about ephemeral species is needed. This study provides the first results about smoke-related germination in the Mediterranean-type zone of central Chile, generating the opportunity to investigate the evolutionary context and distribution of smoke-stimulated germination in all the Mediterranean-type ecosystems.

Keywords: Central Chile; Fire; Mediterranean; Seed germination; Smoke

1. Introduction

Recurrent fires are characteristic of Mediterranean-type climate shrublands in Australia, California, Mediterranean Basin, and South Africa (Keeley, 1995). Plant species in these fire-prone ecosystems show a wide variety of reproductive adaptations to fire, such as fire-stimulated flowering of many geophyte species (Le Maitre and Brown, 1992; Rundel, 1996; Lamont et al., 2000), or the presence of serotinous cones and fruits that release and disperse seeds only after fires (Bond and van Wilgen, 1996). Seed germination also shows particular adaptations to one or more of the physical cues provided by fire in these habitats. For instance, seeds of many species are stimulated to germinate by charred wood, nitrogenous substances, ash, or heat-shock (e.g., Keeley, 1987, 1991; Bond and van Wilgen, 1996; Keeley and Fotheringham, 1997; Herranz et al., 1998; Buhk and Hensen, 2006).

Smoke is another of the products generated as a consequence of wildfires, and since the 1990s substantial evidence has accrued for its effects on seed germination. Smoke-stimulated seed germination has been reported for many species in the South African fynbos (de Lange and Boucher, 1990; Brown, 1993; Brown et al., 1993, 1994, 2003; Pierce et al., 1995; Keeley and Bond, 1997). A positive germination response to smoke has also been extensively demonstrated for many species in Australia (Dixon et al., 1995; Roche et al., 1997; Read and Bellairs, 1999; Morris, 2000; Read et al., 2000; Lloyd et al., 2000; Tieu et al., 2001; Williams et al., 2003; Thomas et al., 2003) and Californian chaparral as well (e.g., Keeley and Fotheringham, 1997, 1998a,b). In the Mediterranean Basin,

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however, although a positive response to smoke has been found for some species (Crosti et al., 2006), substantial evidence indicates that smoke-stimulated germination is poorly developed in this area (Buhk and Hensen, 2006; Reyes and Casal, 2006a,b; Rivas et al., 2006). The variation among Mediterranean-type ecosystems on the distribution of fire functional traits has been attributed to differential evolutionary processes (Pausas et al., 2006).

Smoke-stimulated species span different families and genera of gymnosperms, monocotyledons and dicotyledons; also embracing a range of plant forms from geophytes to phanerophytes (van Staden et al., 2000). This range of species from different continents and regions suggest that stimulation of germination by smoke or smoke-derived compounds may be common not only in Mediterranean fire-prone ecosystems. Indeed, plant-derived smoke also enhances germination of species from non-fire-prone habitats (Pierce et al., 1995). Among the chemical compounds of smoke, nitrogen oxides (Keeley and Fotheringham, 1997) and butenolide (van Staden et al., 2006; Flematti et al., 2007) have been proposed as the responsible for seed germination stimulation.

In the Mediterranean-type zone of central Chile, thousands of human-caused fires occur each year over the summer season, and the sclerophyllous vegetation (called the matorral) is the most damaged plant association (CONAF, 2003). Unlike other Mediterranean zones of the world, lightning-ignited fires are very rare in central Chile under current environmental conditions (Mooney, 1977; Armesto et al., 1995). The sedimentary records of charcoal and fossil pollen suggest that this has been true for millennia (Aravena et al., 2003). Due to the rarity of natural fires, it has been hypothesized that fire has not play an important role on plant species evolution in the Chilean matorral (Armesto and Gutierrez, 1978; Avila et al., 1981; Muñoz and Fuentes, 1989). However, anthropogenic fires have occurred since the first indigenous settlements (ca. 14,000 BP), with higher occurrences during pre-cultural periods (*agroalfarero* period, 2300 BP), and increasing exponentially their frequency since Spaniard colonization (1536–1542) to the present (Aravena et al., 2003). As a consequence, the importance of fire on shaping adaptive traits in native plant species of the Mediterranean-type zone of central Chile is not clear at this point.

There is not a great deal of literature on post-fire germination in the Mediterranean-type zone of central Chile, and the scarce researches conducted so far has been focused only on dominant woody species (Muñoz and Fuentes, 1989; Segura et al., 1998). For instance, the study of Muñoz and Fuentes (1989) experimentally assessed the effect of heat and fire-treated soils (ash-soils) on seed germination of several dominant species of the matorral. They found that ash-soil treatment failed to promote seed germination among the studied species, and only two out of seven species tested (*Muehlembeckia hastulata* and *Trevoa trinervia*), significantly increased their germination by heat (100 °C, 5 min). Segura et al. (1998) demonstrated a lack of viable seeds under shrubs burned by high-intensity fires. However, low-severity fires generally allowed native woody species to emerge, and species such as *M. hastulata* and *T. trinervia* increased their seed germination after low-intensity fires (Segura et al., 1998). This suggests that, after low severity fires, where the soil temperature is not lethal for seeds (<50 °C, Gómez-González et al., unpublished data), other fire-related cues, such as smoke, could trigger post-fire seed germination in the matorral. However, the effect of smoke on seed germination has not been evaluated in this ecosystem.

Our aim here was to experimentally explore the effects of plant-derived smoke on seed germination among predominant native woody species from the Mediterranean matorral of central Chile. This study provides the first information about germination responses to smoke in this Mediterranean-type zone of the world, generating an opportunity for investigating the evolutionary context and distribution of smoke-stimulated germination in all the Mediterranean-type ecosystems.

2. Materials and methods

2.1. Seed preparation

Bulk collections of mature seeds of 18 woody species (mostly trees and shrubs) (Table 1) were made in populations located in the Cordillera de Los Andes immediately east of the city of Santiago, and in the Coastal Range immediately to the west of Santiago. All seeds were collected over the period summer to autumn of 1998 and stored in paper bags at ambient temperature in the laboratory for 3 months. The plant species selected for this study included the main dominants of the typical lowland sclerophyllous matorral (e.g., *Lithrea caustica*, *Cryptocarya alba*, *Quillaja saponaria*) and montane sclerophyllous woodland (e.g., *Kageneckia angustifolia*, *K. oblonga*). Many of these species, in addition to being physiognomic dominants, are widely distributed in central Chile, and thus can be considered typical of the Mediterranean sclerophyllous vegetation of the region (Arroyo et al., 1995). Moreover, 50% of the species tested are endemic to Chile (Table 1).

Two sets (control and smoke treatment) of four replicates (50 seeds each) were prepared for each species, discarding any aborted and insect-damaged seeds. Seeds were placed on filter paper in petri dishes without any previous stratification or scarification because we were interested in detecting the effect of smoke *per se* on germination.

2.2. Smoke treatment

The smoke treatment was applied to dry seeds in open petri dishes in a sealed $1.7\ \mathrm{m} \times 1.7\ \mathrm{m} \times 0.3\ \mathrm{m}$ polyethylene chamber connected to a smoke source generated in a 50 l metal drum through combustion of plant material. The metal drum was connected to the sealed chamber by a 5-cm diameter, 1.6-m length metal tube, fitted with a serpentine water cooling system designed to cool the smoke such as to maintain the smoke-treated and control seeds at a similar temperature. The combusted material comprised a 50:50 mixture of dry litter and green foliage of *L. caustica* and *Q. saponaria*. These species

Table 1
Information about species studied; endemic status in Chile (E: endemic), life form (tree, shrub or woody vine), resprout ability (+: presence of resprout ability; −: absence of resprout ability; ?: no information), post-fire seedling emergence (+: presence of seedling observed after fire; −: absence of seedlings observed after fire; ?: no information) and the net effect plant-derived smoke on seed germination (+: significantly increased seed germination; −: significantly decreased germination; 0: non-significant effect; n.g.: no germination detected in either treatment)

Species	Family	Endemic status	Life form	Resprout ability[a]	Post-fire seedlings[b]	Smoke effect	*P*
Acacia caven (Mol.) Mol.	Mimosaceae		Tree	+	+	+	0.0001
Baccharis vernalis F.H. Hellwig	Asteraceae	E	Shrub	?	?	+	<0.0001
Baccharis linearis (Ruiz et Pav.) Pers.	Asteraceae		Shrub	+	+	0	
Colletia hystrix Clos	Rhamnaceae		Shrub	?	?	n.g.	
Colliguaja odorifera Mol.	Euphorbiaceae	E	Shrub	+	+	n.g.	
Cryptocarya alba (Mol.) Looser	Lauraceae	E	Tree	+	+	−	
Eccremocarpus scaber Ruiz et Pav.	Bignoniaceae		Woody vine	?	?	−	0.0003
Escallonia pulverulenta (Ruiz et Pav.) Pers.	Escalloniaceae		Shrub	?	?	0	
Haplopappus schumannii (O.K.) Br.et Clark	Asteraceae	E	Shrub	?	?	−	<0.0001
Kageneckia angustifolia D. Don	Rosaceae	E	Tree	?	?	−	0.0002
Kageneckia oblonga Ruiz et Pav.	Rosaceae	E	Tree	+	?	−	<0.0001
Litera caustica (Mol.) H. et A.	Anacardiaceae	E	Tree	+	+	−	0.001
Maytenus boaria Mol.	Celastraceae		Tree	?	?	−	<0.0001
Quillaja saponaria Mol.	Rosaceae	E	Tree	+	+	−	<0.0001
Schinus polygamus (Cav.) Cabr.	Anacardiaceae	E	Tree	?	−	n.g.	
Solanum ligustrinum Lodd.	Solanaceae		Shrub	?	?	n.g.	
Trevoa quinquenervia (Gill. et Hook.) Johnst.	Rhamnaceae	E	Shrub	+	?	+	<0.0001
Trevoa trinervia Miers	Rhamnaceae		Shrub	+	+	n.g.	

[a] Resprout ability according to Montenegro and Ginocchio (1995) and Araya and Ávila (1981).
[b] Information extracted from Muñoz and Fuentes (1989), Segura et al. (1998), and Gómez-González and Cavieres (unpublished data). *P* values are from ANOVA evaluating the effect of plant-derived smoke on seed germination.

were chosen because they are dominant elements in typical sclerophyllous matorral. After a 3–4-min period during which the chamber was filled, seeds were exposed to smoke for a period of 30 min. A wide variety of exposure times have been used in the literature, spanning from 5 to 90 min (Dixon et al., 1995; Keeley and Fotheringham, 1997). We selected 30 min following the original methodology of de Lange and Boucher (1990) and in order to make our results comparable with the majority of published papers that have shown positive effects of plant-derived smoke on seed germination (e.g., Brown et al., 1993, 1994; Brown and van Staden, 1997; Gilmour et al., 2000).

2.3. Germination trials

Germination was conducted in a walk-in germination room under 20 °C/10 °C (day/night), cold white light (250 μmol m^{-2} s^{-1}), and a 12 h/12 h (light/dark) photoperiod regime. This thermoperiod simulate the temperature conditions during the fall season, when seedlings emergence begins for all these species. Control and smoke-treated seeds were initially irrigated with 5 ml of distilled water containing a commercial fungicide. The closed dishes were placed in ziplocked polyethylene bags to avoid desiccation and contamination of the controls through the escape of any volatile smoke derivates. Germination was monitored on day 5 after exposure to smoke, and thereafter at 7–8-day intervals over a period of 61 days. Dishes were watered with distilled water as necessary. A seed was considered to have germinated with the emergence of both the cotyledon and radicle. The final percent of germination was analyzed with one-way ANOVA on arcsine transformed data.

3. Results

Overall, there were four different types of behavior exhibited by seeds under smoke treatments: smoke-depressed germination, smoke-stimulated germination, smoke indifferent germination and no germination.

In the smoke-depressed behavior, plant-derived smoke significantly depressed seed germination in 8 out of the 18 tested species (Table 1). A wide range of responses was detected among species in this group. On the one hand, in the common sclerophyllous tree *C. alba*, seed germination was completely inhibited by smoke, in comparison with 100% germination obtained in control treatment (Fig. 1). Seed germination of *L. caustica* and *Maytenus boaria*, two additional common tree species in the matorral of central Chile, showed limited germination on controls, and yet significantly less under the smoke treatment (Table 1). In *Eccremocarpus scaber* and *Haplopappus schumannii*, smoke strongly depressed germination over moderate amounts (Fig. 1). In the three rosaceous trees, *K. oblonga*, *K. angustifolia*, and *Q. saponaria*, smoke-depressed germination by 15–80% compared to the high germination percentages (84–100%) observed in the controls (Fig. 1).

Among the smoke-stimulated germination behavior, exposure to smoke significantly enhanced germination of seeds in three species (*Acacia caven*, *Baccharis vernalis* and *Trevoa quinquenervia*), and again responses were variable (Fig. 1). Especially notable is the case of *T. quinquenervia* where more than 80% germination was obtained with smoke in comparison with 21% in the controls (Fig. 1). Although the hard seeds of the *A. caven* showed little germination (2%) in the controls, 18% germination occurred in the smoke treatments (Fig. 1).

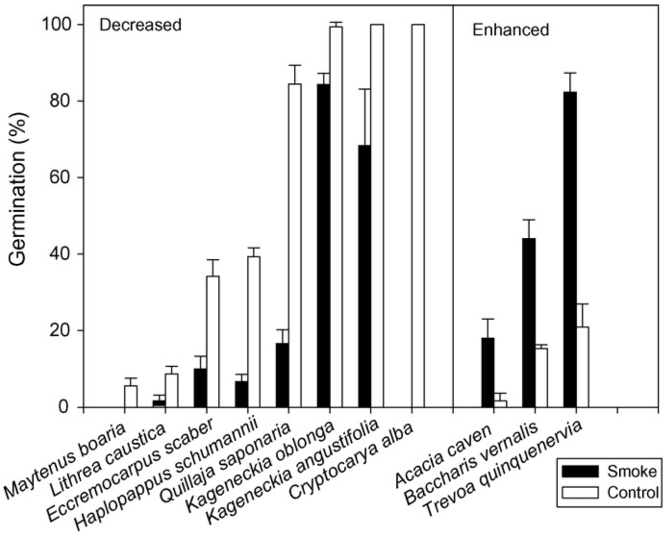

Fig. 1. Seed germination with plant-derived smoke among dominant woody species from the matorral of the Mediterranean-type zone of central Chile. Error bars indicate 2 S.E.

Regarding smoke indifferent germination, exposure to smoke had no significant effect on the germination of *Escallonia pulverulenta* and *B. linearis*. In both of these species, 100% germination occurred in the control and smoke-treated seed. In both species all seeds had germinated both in the controls and smoke treatments between days 5 and 12.

Finally, germination failed entirely or was negligible under the control and smoke treatments in five species (*Schinus polygamus*, *Solanum ligustrinum*, *T. trinervia*, *Colletia hystrix*, and *Colliguaja odorifera*; Table 1).

4. Discussion

Overall, our results suggest that smoke-stimulated germination is poorly represented among the predominant woody species in the central Chilean matorral; only 3 out of the 18 tested species (17%) showed greater germination under smoke treatment. This contrast with what has been reported in the majority of studies that has evaluated the effects of smoke on seed germination at the community level in fire-prone Mediterranean-type climate ecosystems. For instance, Brown et al. (1993, 1994) reported smoke-stimulated germination in 81% of 32 and 65% of 40 species natives to the South African fynbos. Dixon et al. (1995) found smoke-stimulated germination in 47% of 94 Australian heathland species, while Roche et al. (1997) reported ca. 60% of smoke-stimulated germination in 180 species surveyed from Western Australia. Keeley and Fotheringham (1998a) reported smoke-stimulated germination in 65% out of 34 species studied from the chaparral in California.

An interesting contrast with other Mediterranean-type climate ecosystems is the high frequency of species with smoke-depressed germination in our experiment (8 out of the 13 species that germinated in control treatments). To our knowledge, no previous studies in fire-prone ecosystems have reported smoke-depressed germination, although smoke exposure duration longer than 10 min can have negative effects in some species of the Californian chaparral (Keeley and Fotheringham, 1998b). Clarke et al. (2000) reported that smoke suppressed germination of six species from woodlands and forest from New South Wales, Australia. Given that smoke treatment did not affect embryo viability in those species, these authors suggested that smoke-induced dormancy in forb species in grassy communities is a cue for a delayed germination in competitive post-fire environments (Clarke et al., 2000).

It is especially noteworthy that the smoke-depressed species in our experiment, such as *Q. saponaria*, *L. caustica*, *M. boaria* and *C. alba*, are some of the major sclerophyllous dominants in the matorral of central Chile (Rundel, 1981). Segura et al. (1998) reported that seedlings emergence of these species is very infrequent or absent after low-severity fires, despite they were present in pre-fire vegetation. This agrees with our finding of a negative effect of plant-derived smoke on the seed germination of these dominant elements of the Chilean matorral.

In our experiment, *T. trinervia* did not show seed germination in both, control and smoke treatment. This species has been found recruiting after fires in the matorral (Muñoz and Fuentes, 1989; Segura et al., 1998) and is particularly abundant in areas where fire frequency is high (Gomez-González, S., personal observation). Furthermore, Muñoz and Fuentes (1989) showed that heat-shock promoted germination in *T. trinervia*. This suggests that heat or the combination of heat and smoke, but not smoke alone, could be involved in post-fire recruitment of this colonizing species.

Like *T. trinervia*, the three smoke-stimulated species found in this study (*A. caven*, *T. quinquenervia* and *B. vernalis*) tend to be colonizing species. For example, *A. caven* becomes very common on human-disturbed mid-elevation sites (Rundel, 1981). In a recent study of the soil seedbank of a typical matorral, Gómez-González and Cavieres (unpublished data) found that seedlings of *A. caven* emerged from soil seedbank only after low-intensity fires (soil temperature <50 °C), and that there were no emergence of this species when fire was intense (soil temperature > 100 °C) or when soils were unburned. Thus, we could expect that smoke favors the seedling emergence of *A. caven* in patches where fire severity is low, whereas heat-shock may favor the emergence of *T. trinervia* in severely burnt patches.

Plant-derived smoke can both stimulate and inhibit germination depending on exposure time (van Staden et al., 2000). For example, in the Californian chaparral, Keeley and Fotheringham (1997) found that several species with enhanced seed germination after 5-min exposure has reduced germination for exposures of 8 min or more. Under this scenario, 30 min of exposure to smoke seems to be a long time relative to that reported for the Californian Chaparral. However, most of the studies reporting a stimulating effect of smoke on seed germination have used exposures of 30 min (de Lange and Boucher, 1990; Brown et al., 1993, 1994; Brown and van Staden, 1997; Gilmour et al., 2000) or more (Roche et al., 1997; Read et al., 2000; Tieu et al., 2001) to smoke. Therefore, our result is completely comparable to those reported in the above-mentioned studies, although we are aware that further studies addressing this topic are needed.

Heat-stimulated germination is other fire-related germination cue in fire-prone Mediterranean-type ecosystems (Keeley, 1995). In central Chile, only the study of Muñoz and Fuentes (1989) has experimentally assessed the effect of heat on seed germination of several dominant species of the matorral. They found that only two (*M. hastulata* and *T. trinervia*) out of seven species tested significantly increased their germination after 5 min at 100 °C. Despite not being significantly different, some level of promotion was also observed in *C. odorifera* (Muñoz and Fuentes, 1989). Ash-soils also failed to promote seed germination of these seven species. In the case of *Q. saponaria*, Muñoz and Fuentes (1989) reported that the seeds did not germinate after being buried in fire-treated soil (ash-soils), while ca. 50% of the seeds buried in untreated soil germinated. Additionally, these authors showed that after controlled fires in the field there was no seedling emergence of any species. Similarly, Segura et al. (1998) demonstrated a lack of viable seeds under shrubs burned by high-intensity fires. Hence, fire stimulated germination (cued by heat, ash-soils or smoke) is not well developed among most of the species natives to the Chilean matorral that have been evaluated up to date (Muñoz and Fuentes, 1989; Segura et al., 1998; the present study), which are dominant species in this system.

Although these evidences suggest that fire is not playing a major role in shaping adaptations for seed germination in the Chilean matorral, this must be viewed with care. Our study was concentrated on woody species, whereas other surveys have considered several life forms simultaneously. Some evidence now exists for differences in the frequency of smoke-stimulated germination among life forms (Keeley and Bond, 1997; Brown et al., 2003), with smoke-stimulated germination being particularly well represented among annuals, absent in geophytes and moderately represented among perennial herbs and woody species. In central Chile, the history of anthropogenic fires is relatively recent (several millennia, according to Aravena et al., 2003). However, this time may be enough to select fire functional traits in ephemeral annual species. Indeed, some native forbs like *Oxalis micrantha* (Oxalidaceae), *Dichondra sericea* (Convolvulaceae), and *Loasa triloba* (Loasaceae) have been observed emerging after high-intensity fires in the coastal matorral of central Chile (Gomez-González et al., unpublished data). Thus, the role of anthropogenic fires in shaping fire adaptive traits on native species to the matorral must be assessed.

Another aspect that cannot be evaluated satisfactorily on the basis of the present information is potential phylogenetic effects. Our sample is biased taxonomically by the inclusion of three species of Rosaceae, two species of Rhamnaceae (the same genus), and three species of Asteraceae distributed in two genera. While responses among rosaceous trees were in the same direction, a uniform trend was not evident in the Asteraceae, where three different responses were detected. In South Africa, by comparison, 9 out of 10 species of Asteraceae showed smoke-stimulated germination, suggesting perhaps a more phylogenetically related response in fire-prone fynbos (Brown, 1993). Information about seed germination responses to smoke in large samples of species across the five Mediterranean-type climate areas is needed to evaluate the phylogenetic constraints of this fire-related cue.

Finally, the fact that smoke may kill seeds or significantly depresses seed germination in several woody dominants in the matorral of central Chile could have important connotations for vegetation composition in a highly human impacted landscape such as central Chile. An average of 26,000 ha of woodlands are subjected to anthropogenic-derived fire annually in the Mediterranean-type climate zone of central Chile (CONAF, 2003), which probably last much longer than the 30 min of smoke exposure used in our experiment. Such anthropogenic fires, added to absence or small persistent soil seedbank (Jiménez and Armesto, 1992; Figueroa and Jaksic, 2004) can be expected to have dramatic effects on recruitment from seeds in smoke-depressed species, leading to potential local shifts in species abundance. In fact, several studies have shown significant vegetation changes after wildfires in the Chilean matorral (e.g., Armesto and Gutierrez, 1978; Avila et al., 1981).

Further work is needed to determine the germination responses of different life forms and the effects of different exposure times to plant-derived smoke in the matorral of central Chile. This information will be helpful to assist land-managers for an effective rehabilitation of native vegetation after the recurrent human-caused fires.

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References

Aravena, J.C., Le Quesne, C., Jimenez, H., Lara, A., Armesto, J.J., 2003. Fire history in central Chile: tree-ring evidence and modern records. In: Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.W. (Eds.), Fire and Climatic Change in Temperate Ecosystems of the Western Americas. Springer, New York, pp. 343–356.

Araya, S., Ávila, G., 1981. Rebrote de arbustos afectados por fuego en el matorral chileno. Anales del Museo de Historia Natural de Valparaíso 14, 107–113.

Armesto, J.J., Gutierrez, J.R., 1978. Efecto del fuego en la estructura de la vegetación de Chile central. Anales del Museo de Historia Natural de Valparaíso (Chile) 11, 43–48.

Armesto, J.J., Vidiella, P.E., Jiménez, H.E., 1995. Evaluating causes and mechanisms of succession in the Mediterranean regions of Chile and California. In: Arroyo, M.T.K., Zedler, P.H., Fox, M. (Eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia. Springer-Verlag, New York, pp. 418–433.

Arroyo, M.T.K., Cavieres, L.A., Marticorena, C., Muñoz-Schik, M., 1995. Convergence in the Mediterranean floras in central Chile and California: insights from comparative biogeography. In: Arroyo, M.T.K., Zedler, P.H., Fox, M. (Eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia. Springer-Verlag, New York, pp. 43–88.

Avila, G., Aljaro, M.E., Silva, B., 1981. Observaciones en el estrato herbáceo del matorral después del fuego. Anales del Museo de Historia Natural de Valparaíso 14, 99–105.

Bond, W.J., van Wilgen, B.W., 1996. Fire and Plants. Chapman and Hall, New York.

Brown, N.A.C., 1993. Promotion of germination of fynbos seeds by plant-derived smoke. New Phytol. 123, 575–583.

Brown, N.A.C., Kotze, G., Botha, P.A., 1993. The promotion of seed germination of Cape *Erica* species by plant-derived smoke. Seed Sci. Technol. 21, 573–580.

Brown, N.A.C., Jamieson, H., Botha, P.A., 1994. Stimulation of seed-germination in south-African species of Restionaceae by plant-derived smoke. Plant Growth Regul. 15, 93–100.

Brown, N.A.C., van Staden, J., 1997. Smoke as a germination cue: a review. Plant Growth Regul. 22, 115–124.

Brown, N.A.C., van Staden, J., Dwas, M.I., Johnson, T., 2003. Patterns in the seed germination response to smoke in plants from the Cape floristic region, South Africa. South Afr. J. Bot. 69, 514–525.

Buhk, C., Hensen, I., 2006. ''Fire seeders'' during early post-fire succession and their quantitative importance in south-eastern Spain. J. Arid Environ. 66, 193–209.

Clarke, P.J., Davison, E.A., Fullon, L., 2000. Germination and dormancy of grassy woodland and forest species: effects of smoke, heat, darkness and cold. Aust. J. Bot. 48, 687–700.

CONAF, 2003. Estadística de Incendios Forestales. Corporación Nacional Forestal de Chile (CONAF), Ministerio de Agricultura http://www.CONAF.cl.

Crosti, R., Ladd, P.G., Dixon, K.W., Piotto, B., 2006. Post-fire germination: the effect of smoke on seeds of selected species from central Mediterranean basin. Forest Ecol. Manage. 221, 306–312.

de Lange, J.H., Boucher, C., 1990. Autoecological studies on *Audonia capitata* (Bruniaceae). I. Plant-derived smoke as a germination cue. South Afr. J. Bot. 56, 188–202.

Dixon, K.W., Roche, S., Pate, J.S., 1995. The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. Oecologia 101, 185–192.

Figueroa, J.A., Jaksic, F.M., 2004. Latencia y banco de semillas en plantas de la región mediterránea de Chile central. Revista Chilena de Historia Natural 77, 201–215.

Flematti, G.R., Goddard-Borger, E.D., Merritt, D.J., Ghisalberti, E.L., Dixon, K.W., Trengove, R.D., 2007. Preparation of 2*H*-furo[2,3-c]pyran-2-one derivatives and evaluation of their germination-promoting activity. J. Agric. Food Chem. 55, 2189–2194.

Gilmour, C.A., Crowden, R.K., Koutoulis, K., 2000. Heat shock, smoke and darkness: partner cues in promoting seed germination in *Epacris tasmanica* (Epacridaceae). Aust. J. Bot. 48, 603–609.

Herranz, J.M., Ferrandis, P., Martínez-Sánchez, J.J., 1998. Influence of heat on seed germination of seven Mediterranean Leguminosae species. Plant Ecol. 136, 95–103.

Jiménez, H.E., Armesto, J.J., 1992. Importance of the soil seed bank of disturbed sites in Chilean matorral in early secondary succession. J. Veg. Sci. 3, 579–586.

Keeley, J.E., 1987. Role of fire in seed germination of woody taxa in California Chaparral. Ecology 68, 434–443.

Keeley, J.E., 1991. Seed germination and life history syndromes in the California chaparral. Bot. Rev. 57, 81–116.

Keeley, J.E., 1995. Seed germination patterns in fire-prone Mediterranean-climate regions. In: Arroyo, M.T.K., Zedler, P.H., Fox, M. (Eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia. Springer-Verlag, New York, pp. 239–273.

Keeley, J.E., Bond, W.J., 1997. Convergent seed germination in South African fynbos and Californian chaparral. Plant Ecol. 133, 153–167.

Keeley, J.E., Fotheringham, C.J., 1997. Trace gas emissions and smoke-induced seed germination. Science 276, 1248–1250.

Keeley, J.E., Fotheringham, C.J., 1998a. Smoke-induced seed germination in California chaparral. Ecology 79, 2320–2336.

Keeley, J.E., Fotheringham, C.J., 1998b. Mechanism of smoke-induced seed germination in a post-fire chaparral annual. J. Ecol. 86, 27–36.

Lamont, B.B., Swanborough, P.W., Ward, D., 2000. Plant size and season of burn affect flowering and fruiting of the grasstree *Xanthorrhoea preissii*. Aust. Ecol. 25, 268–272.

Le Maitre, D.C., Brown, P.J., 1992. Life cycles and fire-stimulated flowering in geophytes. In: van Wilgen, B.W., Richardson, D.M., Kruger, F.J., van Hensbergen, H.J. (Eds.), Fire in South African Mountain Fynbos. Springer-Verlag, Berlin, pp. 145–160.

Lloyd, M.V., Dixon, K.W., Sivasithamparam, K., 2000. Comparative effects of different smoke treatments on germination of Australian native plants. Aust. Ecol. 25, 610–615.

Montenegro, G., Ginocchio, R., 1995. Ecomorphological characters as a resource for illustrating growth-form convergence in matorral, chaparral and mallee. In: Arroyo, M.T.K., Zedler, P.H., Fox, M.D. (Eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia. Springer-Verlag, New York, pp. 160–176.

Mooney, H.A. (Ed.), 1977. Convergent evolution of Chile and California Mediterranean Climate Ecosystem. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

Morris, E.C., 2000. Germination response in seven east Australian *Grevillea* species (Proteaceae) to smoke, heat exposure and scarification. Aust. J. Bot. 48, 179–189.

Muñoz, M.R., Fuentes, E.R., 1989. Does fire induce shrub germination in the Chilean matorral? Oikos 56, 177–181.

Pausas, J.G., Keeley, J.E., Verdú, M., 2006. Inferring differential evolutionary processes of plant persistence traits in Northern Hemisphere Mediterranean fire-prone ecosystems. J. Ecol. 94, 31–39.

Pierce, S.M., Esler, K., Cowling, R.M., 1995. Smoke-induced germination of succulents (Mesembryanthemaceae) from fire-prone and fire-free habitats in South Africa. Oecologia 102, 520–522.

Read, T.R., Bellairs, S.M., 1999. Smoke affects the germination of native grasses of New South Wales. Aust. J. Bot. 47, 563–576.

Read, T.R., Bellairs, S.M., Mulligan, D.R., Lamb, D., 2000. Smoke and heat effects on soil seed bank germination for the re-establishment of a native forest community in New South Wales. Aust. Ecol. 25, 48–57.

Reyes, O., Casal, M., 2006a. Can smoke affect the germination of *Pinus sylvestris*, *P. nigra*, *P. uncinata* and *P. pinaster*? Forest Ecol. Manage. 234S, S184.

Reyes, O., Casal, M., 2006b. Seed germination of *Quercus rubor*, *Q. pirenaica* and *Q. ilex* and the effects of smoke, heat, ash and charcoal. Ann. Forest Sci. 63, 205–212.

Rivas, M., Reyes, O., Casal, M., 2006. Influence of heat and smoke treatments on the germination of six leguminous shrubby species. Int. J. Wildland Fire 15, 73–80.

Roche, S., Dixon, K.W., Pate, J.S., 1997. Seed ageing and smoke: partner cues in the amelioration of seed dormancy in selected Australian native species. Aust. J. Bot. 45, 783–815.

Rundel, P.W., 1981. The matorral zone of central Chile. In: di Castri, F.,Goodall, D.W., Spech, R.L. (Eds.), Mediterranean Type Shrublands. Elsevier Scientific Publishing Company, Amsterdam, pp. 175–201.

Rundel, P.W., 1996. Monocotyledoneous geophytes in the Californian flora. Madroño 43, 355–368.

Segura, A.M., Holmgren, M., Anabalón, J.J., Fuentes, E.R., 1998. The significance of fire intensity in creating local patchiness in the Chilean matorral. Plant Ecol. 139, 259–264.

Thomas, P.B., Morris, E.C., Auld, T.D., 2003. Interactive effects of heat shock and smoke on germination of nine species forming soil seed banks within the Sydney region. Aust. Ecol. 28, 674–683.

Tieu, A., Dixon, K.W., Meney, K.A., Sivasithamparam, K., 2001. The interaction of heat and smoke in the release of seed dormancy in seven species from Southwestern Western Australia. Ann. Bot. 88, 259–265.

van Staden, J., Brown, N.A.C., Jäger, A.K., Johnson, T.A., 2000. Smoke as a germination cue. Plant Species Biol. 15, 167–178.

van Staden, J., Sparg, S.G., Kulkarni, M.G., Light, M.E., 2006. Post-germination effects of the smoke-derived compound 3-methyl-2*H*-furo[2,3-*c*]pyran-2-one, and its potential as a preconditioning agent. Field Crops Res. 98, 98–105.

Williams, P.R., Congdon, R.A., Grice, A.C., Clarke, P.J., 2003. Fire-related cues break dormancy of six legumes of tropical eucalypt savannas in north-eastern Australia. Aust. Ecol. 28, 507–514.