TÜBİTAK

Research Article

Turk J Bot
36 (2012) 480-487
© TÜBİTAK
doi:10.3906/bot-1111-12

Germination response of five eastern Mediterranean woody species to smoke solutions derived from various plants

Şükrü Serter ÇATAV, İsmail BEKAR, Büşra Seda ATEŞ, Gökhan ERGAN, Funda OYMAK,
Elif Deniz ÜLKER, Çağatay TAVŞANOĞLU*
Department of Biology, Hacettepe University, 06800 Beytepe, Ankara - TURKEY

Received: 16.11.2011 ● Accepted: 16.04.2012

Abstract: The role of smoke as a fire-related germination cue is well known in many parts of the world, including Mediterranean-type ecosystems; however, it has been neglected in the Mediterranean Basin (MB). We studied the germination response of 5 woody species found in the eastern MB (south-western Turkey) to smoke solutions derived from different plant species. Of the 5 species examined, 2 [*Sarcopoterium spinosum* (L.) Spach and *Satureja thymbra* L.] showed significant increments in germination percentage after smoke treatments compared to the control, while the remaining 3 [*Calicotome villosa* (Poir.) Link, *Cistus salviifolius* L., and *Lavandula stoechas* L.] did not. However, none of the species showed any change in the germination rate. In addition, smoke solutions derived from various plants did not affect the germination response (germination percentage and rate) in all species. The results confirm that the effect of smoke originating from different plant species on germination response is globally similar regardless of the region. Our study helps to fill the gap in the literature on smoke-induced germination in the eastern MB and supports the idea that smoke is important to postfire germination in the MB.

Key words: Aqueous smoke extracts, fire, seed germination, Mediterranean Basin, Turkey

Introduction

Fire plays a key role in shaping the composition and distribution of plant communities (Trabaud, 1994; Bond & Keeley, 2005; Verdú & Pausas, 2007) and is an important evolutionary pressure on plant traits (Keeley et al., 2011). In fire-prone environments, seed germination is triggered by fire-related cues (heat and smoke) in many plants. The positive effect of heat-shock treatments on germination in species with water-impermeable seed coats is well known (Trabaud & Oustric, 1989; Thanos et al., 1992; Doussi & Thanos, 1994; Herranz et al., 1998; Rivas et al., 2006; Paula et al., 2009; Moreira et al., 2010). The stimulatory germinative effect of smoke has also been demonstrated in studies of different world ecosystems, including fire-prone (Brown, 1993; Dixon et al., 1995; Keeley & Fotheringham, 1998; Moreira et al., 2010) and nonfire-prone areas (Drewes et al., 1995; Pierce et al., 1995; Daws et al., 2007). However, the role of smoke in the germination of Mediterranean Basin (MB) plant species has received less attention than other Mediterranean-type ecosystems (Keeley, 1995; Keeley & Baer-Keeley, 1999). Fortunately, many studies conducted regarding the effects of smoke on germination in the western MB in recent years (Pérez-Fernández & Rodríguez-Echevarría, 2003; Crosti et al., 2006; Reyes & Trabaud, 2009; Moreira et al., 2010) showed that smoke-induced germination also

---

* E-mail: ctavsan@hacettepe.edu.tr

plays a significant role in the MB. However, almost all of these studies were conducted in the western MB. With the exception of a few studies (Nun & Mayer, 2005; Tavsanoglu, 2011; Moreira et al., 2012), there is still a lack of information about the role of smoke in germination in the eastern MB.

In many of the studies testing the germination response of species to smoke, researchers have used plant material from a mixture of plant species (Dixon et al., 1995; Pérez-Fernández & Rodríguez-Echevarría, 2003; Thomas et al., 2010) or from a single species abundant in the study region (Reyes & Trabaud, 2009; Moreira et al., 2010) to prepare aqueous smoke solutions or airborne smoke. A few studies showed that smoke derived from different plants did not generally affect the germination response in plant species (Baxter et al., 1995; Jäger et al., 1996). However, these studies were only performed in South Africa, and there have been no reports on this issue from any other part of the world. It has recently been discovered that a group of compounds (butenolides or karrikins) found in burning plant material is responsible for the main stimulatory effect of smoke on germination (Flematti et al., 2004; Van Staden et al., 2004; Chiwocha et al., 2009; Light et al., 2009); however, it has been suggested that some other compounds found in smoke may be responsible for the inhibition of germination in some species (Daws et al., 2007). Therefore, there is still a need for research to determine whether smoke originating from different plant species or plant materials produces different germination responses in certain species.

The aims of our study were to obtain evidence for smoke-induced germination in the eastern MB and to confirm that smoke solutions derived from various plant species have no different effects on germination response. We hypothesised that at least some of the eastern MB species growing in fire-prone habitats should have smoke-triggered germination and that smoke solutions obtained from the burning of different plant species should not result in any change in the germination response of the species studied. To test these hypotheses, seeds of 5 eastern Mediterranean plant species [*Calicotome villosa* (Poir.) Link, *Cistus salviifolius* L., *Lavandula stoechas* L., *Sarcopoterium spinosum* (L.) Spach, and *Satureja thymbra* L.] were subjected to different smoke solutions prepared from 3 species that differ in growth form (tree, shrub, and perennial herb). Germination percentages and rates of the species were determined under different smoke treatments, and the differences were compared to a control and among treatments.

Materials and methods

Study species and study area

We selected 5 woody shrub species growing in burned areas of the Marmaris region of south-western Turkey, eastern MB (36°54′N, 28°08′E), to test their germination responses to smoke solutions. The study area was characterised by a typical Mediterranean climate with dry summers and wet winters. The dominant vegetation cover is *Pinus brutia* Ten. woodlands; however, frequent fires have created a vegetation mosaic that includes patches of shrub-dominated maquis and regenerating pine stands. There was proof of postfire seedling emergence for each of the selected species throughout their range in the MB (Tavşanoğlu & Gürkan, 2005; Paula et al., 2009). The main ecological characteristics of the study species are given in Table 1.

Seed collection, storage, and size

Ripe fruits were collected from a minimum of 10 individuals for each species in August 2010 (*Cistus salviifolius* seeds were collected in June 2009). Seeds were removed from fruits by hand and stored in paper envelopes under room conditions until the experiment was conducted. For each species, 4 replicates of 100 seeds (2 replicates in *Calicotome villosa* and *Satureja thymbra* due to the limited number of seeds) were weighed using a digital balance to obtain mean seed mass (Table 1).

Preparing the smoke solutions

To prepare different smoke solutions, we selected 3 species differing in growth form that are abundant in the study region: *Pinus brutia* (tree), *Quercus infectoria* Olivier subsp. *boissieri* (Reut.) O.Schwarz (tall shrub), and *Chrysopogon gryllus* (L.) Trin. subsp. *gryllus* (perennial herb). Dry leaves (*Quercus infectoria*) or needles (*Pinus brutia*) of the woody species and leaves and stem of the herbaceous species

Table 1. List of the study species and their main ecological characteristics. Seed size is given in mg (mean ± SE).

Species	Family	GF	RM	SC	Seed size	Range
Sarcopoterium spinosum	*Rosaceae*	Ss	R+ S+	WP	1.47 ± 0.05	EMB
Satureja thymbra	*Lamiaceae*	Ss	R- S+	WP	0.48 ± 0.01	EMB
Lavandula stoechas	*Lamiaceae*	Ss	R- S+	WP	0.68 ± 0.01	MB
Calicotome villosa	*Fabaceae*	Ts	R+ S+	WI	6.32 ± 0.12	MB
Cistus salviifolius	*Cistaceae*	Ss	R- S+	WI	0.97 ± 0.01	MB

Abbreviations: GF = growth form (Ts = tall shrub, Ss = short shrub), RM = regenerative mode (R = resprouting, S = seeding; + and – indicate the presence or absence of the relevant RM, respectively), SC = seed coat type (WI = water-impermeable, WP = water-permeable). Range refers to the distribution of the species (MB = throughout Mediterranean Basin, EMB = restricted to eastern Mediterranean Basin).

(*Chrysopogon gryllus*) were collected from the field and separated into small pieces in the laboratory. For each species, 4 replicates of 5 g were separately heated in an oven for 30 min at 190-195 °C, a temperature range and period that produces active components in smoke for germination (Jäger et al., 1996) that were observed on the soil surface where seeds are sown (Trabaud, 1979). After the treatment was applied, 50 mL of distilled water was added to the plant material, and the mixture was left for 10 min. The mixture was filtrated into a bottle to obtain smoke in liquid form (Jäger et al., 1996; Moreira et al., 2010). This method allows for the capture of compounds found in smoke in the water; it represents the contact of smoke with soil, which contains some moisture, under natural conditions during a fire (Jäger et al., 1996). The procedure was repeated for each species to obtain 3 different smoke solutions for use in the experiment. The pH values of smoke solutions derived from *Pinus brutia*, *Quercus infectoria*, and *Chrysopogon gryllus* were 4.45, 5.37, and 5.22, respectively; the pH of the distilled water was 5.81.

The experiment

Seeds of each species were incubated in the different aqueous smoke solutions for 24 h. Another group of seeds from each species were incubated in distilled water for 24 h and served as the control for the smoke treatments. After the treatments were applied, seeds were sown in Petri dishes containing agar as a substrate. Each dish contained 25 seeds, and there were 4 replicate dishes for each treatment and control (100 seeds for each in total). The dishes were then placed in a germination cabinet and incubated at 20.0 ±1 °C in darkness. The seeds were checked for germination under a stereomicroscope every 2 or 3 days during the first 2 weeks and then weekly until the end of the experiment. Germinated seeds were counted and removed from the Petri dishes at every check. Radicle emergence was the criterion for recording germination. Seeds without an embryo (empty seeds) and those with significant signs of rottenness (rotten seeds) were also removed and recorded. The experiment was finalised on the 35th day of the incubation period (30 March to 4 May 2011).

Data analysis

Empty seeds were removed from the data before analysis, whereas rotten ones were included as the nongerminated proportion of the initial seed number for each replicate of each treatment. The data sets were analysed by one-way analysis of variance (ANOVA) to determine the effect of treatments (different smoke solutions) on seed germination for each species. Data normality and homoscedasticity were tested using the Shapiro-Wilk test and Bartlett's test before each analysis, respectively. The time to reach 50% germination (t_{50}) was determined with CurveExpert Basic software (Hyams, 2010) for each treatment × species combination. The germination curve of each replicate was fit to a logistic curve, and t_{50} was calculated as the point on the curve intersecting the line for 50% germination (Kettenring et al., 2006). Data on t_{50} were log-transformed before analysis by one-way ANOVA to obtain the normal distribution. Post-hoc comparisons were conducted with Tukey's honestly significant difference test at $\alpha = 0.05$.

Results

Among the studied species, *Sarcopoterium spinosum* and *Satureja thymbra* showed significant increments in germination percentage after at least one smoke treatment compared to the control (Table 2, Figure 1). No significant increase or decrease was found in the other species, apart from an obvious but nonsignificant increase in *Lavandula stoechas* after smoke treatments. All of the species had low germination percentages (<12.5%) in the control with the exception of *L. stoechas*, which reached 81.0% germination (Table 2).

In addition, smoke solutions derived from various plants did not change the results of the germination percentage and rate in all of the studied species (Table 2). The exception was the significant difference between germination rates after Q and Ch treatments in *L. stoechas*. For all treatments, most of the germinations occurred between the first and the second weeks of the incubation period (during the first week in *L. stoechas*), producing a sigmoid germination (%) time curve (Figure 1). Consequently, none of the smoke treatments significantly increased or decreased the germination rate (t_{50}) compared to the control in the studied species (Table 2).

Table 2. Mean germination percentage (G) and the mean time to reach 50% germination (t_{50}, in days) of the studied species in controls and different treatments.

Species		Smoke treatments				Statistics	
		Cont	P	Q	Ch	F	P
Sarcopoterium spinosum	G	11.0 **a** (2.5)	32.0 **b** (2.3)	26.0 **b** (2.6)	25.0 **b** (3.0)	11.40	**0.0008**
	t_{50}	18.2 (2.2)	11.4 (1.6)	11.5 (2.2)	12.1 (0.8)	3.00	0.0726
Satureja thymbra	G	12.4 **a** (3.6)	34.4 **b** (3.9)	24.3 **ab** (4.1)	-	7.77	**0.0102**
	t_{50}	15.0 (3.2)	13.0 (1.4)	11.6 (1.1)	-	0.67	0.5378
Lavandula stoechas	G	81.0 (4.3)	93.1 (1.7)	90.6 (1.6)	89.3 (3.7)	1.76	0.2076
	t_{50}	3.1 **ab** (0.3)	2.9 **ab** (0.5)	2.1 **a** (0.1)	3.9 **b** (0.5)	3.94	**0.0360**
Calicotome villosa	G	8.3 (1.0)	6.7 (2.7)	16.1 (7.3)	-	1.19	0.3475
	t_{50}	4.7 (1.3)	6.0 (3.1)	4.2 (0.4)	-	0.01	0.9930
Cistus salviifolius	G	3.0 (1.0)	1.0 (1.0)	1.0 (1.0)	1.1 (1.1)	0.90	0.4706
	t_{50}	-	-	-	-		

Abbreviations: Cont = control; P, Q, and Ch correspond to the treatments of smoke solutions produced from *Pinus brutia*, *Quercus infectoria*, and *Chrysopogon gryllus*, respectively. F-values show the results of one-way ANOVA, and probability values (P) indicating a significant difference among groups at α = 0.05 are given in bold. The SE of the mean is given in parenthesis. T_{50} data were log-transformed before analysis to obtain normality. Different letters next to the values indicate a significant difference for the 2 relevant groups at α = 0.05. Ch treatment was not performed in *Satureja thymbra* and *Calicotome villosa* due to the limited number of seeds; no t_{50} result was obtained for *Cistus salviifolius* for any treatment due to very low germination percentages.

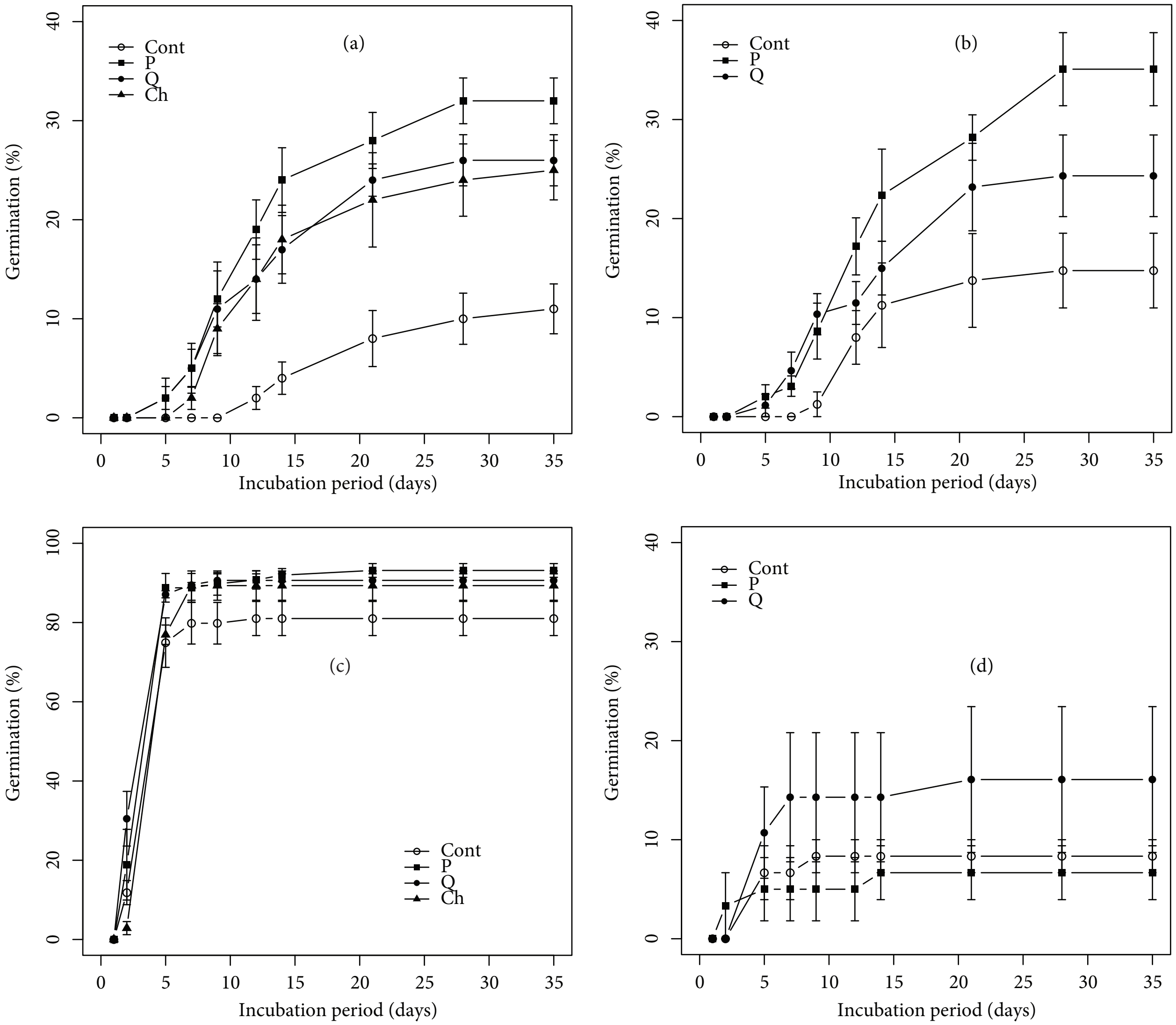

Figure 1. Mean germination percentages (±SE) of *Sarcopoterium spinosum* (**a**), *Satureja thymbra* (**b**), *Lavandula stoechas* (**c**), and *Calicotome villosa* (**d**) under different treatments and the control during the incubation period. Cont = control; P, Q, and Ch correspond to treatments of smoke solutions produced from *Pinus brutia*, *Quercus infectoria*, and *Chrysopogon gryllus*, respectively. *Cistus salviifolius* is not shown here due to low germination (<3%).

Discussion

Our results show that the germinations of 2 eastern Mediterranean species (*Sarcopoterium spinosum* and *Satureja thymbra*) are stimulated by smoke. This is the third report for the evidence of smoke-induced germination in the eastern MB; the first was related to a parasitic weed distributed over a broad range in Eurasia (Nun & Mayer, 2005), and the second was on a species distributed throughout the MB (Moreira et al., 2012). However, our study presents the first evidence of smoke-stimulated germination among species endemic to the eastern MB. This supports the idea that fire-induced germination is important throughout the MB (Moreira et al., 2010) by providing evidence that smoke-stimulated germination extends from the western MB to the eastern part of the MB.

Although the results of previously conducted studies on the stimulation of germination in *Sarcopoterium spinosum* have been contradictory, there is evidence that light quality (Roy & Arianoutsou-Faraggitaki, 1985) and heat shock (Keeley & Baer-Keeley, 1999) improve germination and that charred wood does not (Keeley & Baer-Keeley, 1999). The recruitment of *S. spinosum* seedlings after fire is high (Seligman & Henkin, 2000; Paula et al., 2009), and this demonstrates the presence of a soil seed bank (Osem et al., 2007). In light of these earlier studies and the ability of smoke to partially replace the light requirement for germination in several light-sensitive species (Merritt et al., 2006), the first results on smoke-stimulated germination obtained by our study contribute to the explanation of postfire establishment behaviour in *S. spinosum*. These results suggest an increase in the role of fire in the postfire germination of this species, in addition to the role of increasing light quality due to foliage removal (Roy & Arianoutsou-Faraggitaki, 1985). To date, our results provide the first record of fire-promoted germination in *Satureja thymbra*, a common fire-follower seeder species in the eastern MB (Kazanis & Arianoutsou, 2004; Tavşanoğlu & Gürkan, 2009). This finding also supports the frequent appearance of smoke-stimulated germination in western MB species belonging to the family *Lamiaceae* (Moreira et al., 2010).

Smoke treatments failed to improve germination percentages compared to the control in *Cistus salviifolius*, *Calicotome villosa*, and *Lavandula stoechas*. The lack of response to smoke solutions is likely to occur in the former 2 species due to the physical dormancy imposed by their hard seed coats (Thanos & Georghiou, 1988; Thanos et al., 1992; Doussi & Thanos, 1994). However, since there is evidence for smoke- and charred wood-stimulated seed germination in *L. stoechas* (Keeley & Baer-Keeley, 1999; Moreira et al., 2010; Moreira et al., 2012), we expected to find a significant increase in the germination percentage of this species after smoke treatments. Our results contradicted this prediction, and the same result was obtained by Crosti et al. (2006). We believe that the reason why Crosti et al. (2006) and the current study did not find any significant difference in germination between any treatment and the control in *L. stoechas* was the loss of seed dormancy (81% germination in the control in our study) after 7.5 months of seed storage when we conducted the experiment. It seems that seed dormancy in *L. stoechas* starts to break down just a few months after ripening, and a longer storage period may lead to loss of dormancy. It is also possible that the species response to smoke can change over time due to dormancy cycling (Baker et al., 2005). More studies are needed to create a better understanding of dormancy loss in this species.

Some species give better germination responses to the compounds known to stimulate germination in plants (butenolides or karrikins) than the smoke water itself, and in some cases there is an inhibitory effect of smoke on germination (Crosti et al., 2006; Merritt et al., 2006; Light et al., 2010). This suggests that as a chemical soup, smoke may include some chemicals that inhibit germination as well as those that promote germination (Daws et al., 2007). Obviously, identifying the cumulative effect of the mixture of smoke chemicals is more important for understanding the natural role of smoke in fire-prone environments than identifying the effect of specific chemicals. In this context, our study confirms that smoke solutions derived from various plant species have no different effect on germination response, at least in the eastern MB species that we considered. Our results are in accordance with those of Baxter et al. (1995) and Jäger et al. (1996), and along with these studies, our findings support the argument that the effect of smoke originating from different plant species on germination response is globally similar regardless of region.

In conclusion, our study is a step towards filling the gap in the literature on smoke-induced germination in the eastern MB and supports the idea that smoke is an important fire-related germination cue for the MB. More research is still needed to establish the role of fire-related cues (especially smoke) in the eastern Mediterranean species and to better understand the dynamics of postfire recovery in this region.

References

Baker KS, Steadman KJ, Plummer JA, Merritt DJ & Dixon KW (2005). The changing window of conditions that promotes germination of two fire ephemerals, *Actinotus leucocephalus* (Apiaceae) and *Tersonia cyathifolia* (Gyrostemonaceae). *Annals of Botany* 96: 1225-1236.

Baxter BJM, Granger JE & Van Staden J (1995). Plant-derived smoke and seed germination: is all smoke good smoke? That is the burning question. *South African Journal of Botany* 61: 275-277.

Bond WJ & Keeley JE (2005). Fire as global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20: 387-394.

Brown NAC (1993). Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytologist* 123: 575-583.

Chiwocha SDS, Dixon KW, Flematti GR, Ghisalberti EL, Merritt DJ, Nelson DC, Riseborough JAM, Smith SM & Stevens JC (2009). Karrikins: a new family of plant growth regulators in smoke. *Plant Science* 177: 252-256.

Crosti R, Ladd PG, Dixon KW & Piotto B (2006). Post-fire germination: the effect of smoke on seeds of selected species from the central Mediterranean basin. *Forest Ecology and Management* 221: 306-312.

Daws MI, Davies J, Pritchard HW, Brown NAC & Van Staden J (2007). Butenolide from plant-derived smoke enhances germination and seedling growth of arable weed species. *Plant Growth Regulation* 51: 73-82.

Dixon KW, Roche S & Pate JS (1995). The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. *Oecologia* 101: 185-192.

Doussi MA & Thanos CA (1994). Post fire regeneration of hardseed plants: ecophysiology of seed germination. In: Viegas DX (ed.) *Proceedings of the 2nd International Conference on Forest Fire Research*, 21-24 November, Portugal, pp. 1035-1044.

Drewes FE, Smith MT & Van Staden J (1995). The effect of plant-derived smoke extract on the germination of light-sensitive lettuce seed. *Plant Growth Regulation* 16: 205-209.

Flematti GR, Ghisalberti EL, Dixon KW & Trengove RD (2004). A compound from smoke that promotes seed germination. *Science* 305: 977.

Herranz JM, Ferrandis P & Martínez-Sánchez JJ (1998). Influence of heat on seed germination of seven Mediterranean Leguminosae species. *Plant Ecology* 136: 95-103.

Hyams DG (2010). CurveExpert Basic software, release 1.4. Website http://www.curveexpert.net/ [accessed 20 June 2011].

Jäger AK, Light ME & Van Staden J (1996). Effects of source of plant material and temperature on the production of smoke extracts that promote germination of light-sensitive lettuce seeds. *Environmental and Experimental Botany* 36: 421-429.

Kazanis D & Arianoutsou M (2004). Long term post-fire vegetation dynamics in *Pinus halepensis* forests of Central Greece: a functional group approach. *Plant Ecology* 171: 101-121.

Keeley JE (1995). Seed-germination patterns in fire-prone Mediterranean-climate regions. In: Arroyo MTK, Zedler PH & Fox MD (eds.) *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia*, pp. 239-273. New York: Springer-Verlag.

Keeley JE & Baer-Keeley M (1999). Role of charred wood, heat-shock, and light in germination of postfire phrygana species from the eastern Mediterranean Basin. *Israel Journal of Plant Sciences* 47: 11-16.

Keeley JE & Fotheringham CJ (1998). Smoke-induced seed germination in California chaparral. *Ecology* 79: 2320-2336.

Keeley JE, Pausas JG, Rundel PW, Bond WJ & Bradstock RA (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16: 406-411.

Kettenring KM, Gardner GM & Galatowitsch SM (2006). Effect of light on seed germination of eight wetland *Carex* species. *Annals of Botany* 98: 869-874.

Light ME, Daws MI & Van Staden J (2009). Smoke-derived butenolide: towards understanding its biological effects. *South African Journal of Botany* 75: 1-7.

Light ME, Burger BV, Staerk D, Kohout L & Van Staden J (2010). Butenolides from plant-derived smoke: natural plant-growth regulators with antagonistic actions on seed germination. *Journal of Natural Products* 73: 267-269.

Merritt DJ, Kristiansen M, Flematti GR, Turner SR, Ghisalberti EL, Trengove RD & Dixon KW (2006). Effects of a butenolide present in smoke on light-mediated germination of Australian *Asteraceae*. *Seed Science Research* 16: 29-35.

Moreira B, Tormo J, Estrelles E & Pausas JG (2010). Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. *Annals of Botany* 105: 627-635.

Moreira B, Tavsanoglu Ç & Pausas JG (2012). Local versus regional intraspecific variability in regeneration traits. *Oecologia* 168: 671-677.

Nun NB & Mayer AM (2005). Smoke chemicals and coumarin promote the germination of the parasitic weed *Orobanche aegyptiaca*. *Israel Journal of Plant Sciences* 53: 97-101.

Osem Y, Konsens I, Perevolotsky A & Kigel J (2007). Soil seed bank and seedling emergence of *Sarcopoterium spinosum* as affected by grazing in a patchy semiarid shrubland. *Israel Journal of Plant Sciences* 55: 35-43.

Paula S, Arianoutsou M, Kazanis D, Tavsanoglu C, Lloret F, Buhk C, Ojeda F, Luna B, Moreno JM, Rodrigo A, Espelta JM, Palacio S, Fernández-Santos B, Fernandes PM & Pausas JG (2009). Fire-related traits for plant species of the Mediterranean Basin. *Ecology* 90: 1420.

Pérez-Fernández MA & Rodríguez-Echevarría S (2003). Effect of smoke, charred wood, and nitrogenous compounds on seed germination of ten species from woodland in central-western Spain. *Journal of Chemical Ecology* 29: 237-251.

Pierce SM, Esler K & Cowling RM (1995). Smoke-induced germination of succulents from fire-prone and fire-free habitats in South Africa. *Oecologia* 102: 520-522.

Reyes O & Trabaud L (2009). Germination behaviour of 14 Mediterranean species in relation to fire factors: smoke and heat. *Plant Ecology* 202: 113-121.

Rivas M, Reyes O & Casal M (2006). Influence of heat and smoke treatments on the germination of six leguminous shrubby species. *International Journal of Wildland Fire* 15: 73-80.

Roy J & Arianoutsou-Faraggitaki M (1985). Light quality as the environmental trigger for the germination of the fire-promoted species *Sarcopoterium spinosum* L. *Flora* 177: 345-349.

Seligman N & Henkin Z (2000). Regeneration of a dominant Mediterranean dwarf-shrub after fire. *Journal of Vegetation Science* 11: 893-902.

Tavsanoglu C (2011). Fire-related cues (heat shock and smoke) and seed germination in a *Cistus creticus* population in Southwestern Turkey. *Ekoloji* 20: 99-104.

Tavşanoğlu Ç & Gürkan B (2005). Post-fire dynamics of *Cistus* spp. in a *Pinus brutia* forest. *Turkish Journal of Botany* 29: 337-343.

Tavşanoğlu Ç & Gürkan B (2009). Post-fire regeneration of a *Pinus brutia* (Pinaceae) forest in Marmaris National Park, Turkey. *International Journal of Botany* 5: 107-111.

Thanos CA & Georghiou K (1988). Ecophysiology of fire-stimulated seed germination in *Cistus incanus* subsp. *creticus* (L.) Heywood and *C. salviifolius* L. *Plant Cell and Environment* 11: 841-849.

Thanos CA, Georghiou K, Kadis C & Pantazi C (1992). Cistaceae: a plant family with hard seeds. *Israel Journal of Botany* 41: 251-263.

Thomas PB, Morris EC, Auld TD & Haigh AM (2010). The interaction of temperature, water availability and fire cues regulates seed germination in a fire-prone landscape. *Oecologia* 162: 293-302.

Trabaud L (1979). Etude du comportement du feu dans la Garrigue de Chêne kermes à partir des températures et des vitesses de propagation. *Annals of Forest Science* 36: 13-38.

Trabaud L (1994). Postfire plant community dynamics in the Mediterranean Basin. In: Moreno JM & Oechel WC (eds.) *The Role of Fire in Mediterranean-Type Ecosystems*, pp. 1-15. New York: Springer-Verlag.

Trabaud L & Oustric J (1989). Heat requirement for seed germination of three *Cistus* species in the garrigues of southern France. *Flora* 183: 321-325.

Van Staden J, Jäger AK, Light ME & Burger BV (2004). Isolation of the major germination cue from plant-derived smoke. *South African Journal of Botany* 70: 654-659.

Verdú M & Pausas JG (2007). Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology* 95: 1316-1323.