Ann Sci For (1997) 54, 553-562

Original article

Effects of high temperatures and ash on seed germination of two Iberian pines (*Pinus nigra* ssp *salzmannii, P sylvestris* var *iberica*)

A Escudero*, S Barrero, JM Pita

Dpto Biología Vegetal, EUIT Agrícola, Universidad Politécnica de Madrid, 28040 Madrid, Spain

(Received 1 June 1996; accepted 19 December 1996)

Summary — The effect of high temperatures and ash on seed germination of two Iberian pines (*Pinus nigra* ssp *salzmannii* and *P sylvestris* var *iberica*) has been studied. These two pines are widely distributed in the oromediterranean and supramediterranean bioclimatological belts of the eastern half of the Iberian Peninsula. Our results are clearly very similar for both pines. Seed cover protects embryos up to 70 °C (germination percentage above 90%), which is a very low temperature for a wildfire, catastrophically failing when this temperature is surpassed. Addition of ash solutions did not modify this trend. As has been previously reported, both pines have photophillous seeds, which indicates that they can regenerate rapidly after disturbance, except wildfires, as our results illustrate. These results confirm the field observations after very large fires in extensive and homogeneous pine forests (> 10 000 Ha), in the sense that recruitments of both pines are extremely rare after disturbance. At a community level, our results seem to indicate that pine formations must be naturally confined to the oromediterranean belt or at permanent stands in spurs, crests or steep rocky slopes where density is very low and wildfires do not become catastrophic. The existense of formations in the supramediterranean belt must be man-induced (landscape changes) and driven, not necessarily planted, and can be rapidly substituted by oak formations after intense wildfires.

ash / heat treatment / *Pinus nigra* / *Pinus sylvestris* / seed germination / wildfires

Résumé — Effet des températures élevées et des cendres sur la germination de deux espèces de pins ibériques (*Pinus nigra* ssp *salzmannii* et *Pinus sylvestris* var *iberica*). L'effet des températures élevés et des cendres sur la germination des graines a été étudié chez *Pinus nigra* ssp *salzmannii* et *Pinus sylvestris* var *iberica,* pins qui ont une vaste distribution dans les aires oroméditerranéenne et supraméditerranéenne de la moitié est de la péninsule Ibérique. Les résultats obtenus sont voisins pour les deux espèces de pins : le pourcentage de germination, à des températures inférieures à 70 °C, est

* Correspondence and reprints
Tel: (34) 1 54 45 58 00; fax: (34) 1 549 300 2

proche au 90 % ; l'augmentation de la températures fait descendre brusquement ce taux de germination et l'addition des cendres ne modifie pas ces résultats. D'autres travaux ont mis en évidence la photosensibilité positive des graines chez les deux espèces de pins ; cette caractéristique permet la rapide régénération de ces formations de pins après perturbations de ces écosystèmes, sauf dans le cas des incendies forestiers. Ces résultats pourraient expliquer les difficultés de régénération après des incendies très importants (>10 000 ha) sur forêts très homogènes. Au niveau des communautés, ces résultats pourraient aussi expliquer l'apparition des formations de ces pins dans l'aire oroméditerranéenne ou sur des zones rocheuses très localisées, où la densité des formations est très faible et où les incendies forestiers ne sont pas catastrophiques. Par ailleurs l'existence des formations de l'aire supraméditerranéenne est probablement directement ou indirectement liée à l'intervention humaine. D'autre part, elles peuvent rapidement être remplacées, après incendies, par des formations de chênes.

cendres / germination / incendie forestier / *Pinus nigra* / *Pinus sylvestris* / température

INTRODUCTION

Pinus nigra ssp *salzmannii* and several local varieties of *P sylvestris* are widely distributed on the Iberian peninsula, mainly in the eastern part (Ceballos and Ruiz de la Torre, 1971; Amaral Franco, 1986). The pine-forests dominated by these trees form climax communities in the oromediterranean belt and permanent formations are found in spurs or crests on thin rocky soils at lower altitudes (Rivas-Martínez, 1987). In the more moist supramediterranean belt, these two pines are mainly interspersed with oaks (*Quercus pyrenaica, Q faginea, Q humilis*) and even beeches (*Fagus sylvatica*) in secondary forests that can cover large areas (Elena-Roselló and Sánchez-Palomares, 1991; Catalán, 1991; Pausas and Fons, 1992). The economic importance of these pine forests is also noteworthy (Ceballos and Ruiz de la Torre, 1971).

Wildfire has been demonstrated as being a major factor in determining structural and functional features of Mediterranean communities (Naveh, 1974). Most Mediterranean conifers, excluding *P canariensis* and several *Juniperus* taxa, are obligatory seed regenerators after disturbance. When a wildfire occurs, cones open and trees find an opportunity for their natural regeneration (Walter, 1973). Seeds are normally stimulated by light via the phytochrome system as in *P sylvestris* (Toole, 1973) and *P nigra* (Orlandini and Malcoste, 1972). *P halepensis* and *P pinaster,* two common Iberian pines, have been characterized as typical pyrophytes, which regenerate well after fire (Acherar et al, 1984; Trabaud and Oustric, 1989a; Castro et al, 1990). However, several authors have recently noted that both pines are not real pyrophytes (Martínez-Sánchez et al, 1995), as they are not positively stimulated by high temperatures as many Mediterranean shrubs, such as *Cistaceae* and *Leguminosae* (Vuillemin and Bulard, 1981; Troumbis and Trabaud, 1986; Trabaud and Oustric, 1989b; Corral et al, 1990; Tárrega et al, 1992; González-Rabanal and Casal, 1995; Trabaud, 1995). Although *P nigra* and *P sylvestris* are considered typical opportunist conifers with high resilience after wildfires and other disturbances (Barbero et al, 1990), they present severe problems in recruitment after intense wildfires (Trabaud and Campant, 1991). Almost no regeneration was observed 1 year after a large fire in a *Pinus nigra* forest (15 000 ha) in southern Cuenca, eastern Spain and in Catalonia (> 25 000 ha) (Retana, pers comm).

With these premises in mind several questions arise. First, what is the seed behaviour of *P nigra* ssp *salzmannii* and *P sylvestris* after a wildfire? Second, what is the effect of ash, a typical element in the post-fire environment? Third, what are the implications at the community level?

In this paper seeds were subjected to different 'fire intensity' treatments at varying temperatures and lengths of time to simulate responses to different fire regimes (Gill and Groves, 1981) or microtopographic heterogeneity (Trabaud and Oustric, 1989a). Similarly, different concentrations of an ash solution were used to test the effect of ash on germination. The obtained results were used to discuss the implications of wildfire at the community level.

MATERIAL AND METHODS

Pinus nigra Arnold ssp *salzmannii* (Dunal) Franco and *P sylvestris* L var *iberica* Svob seeds, collected in 1995 in the southern Sistema Ibérico (Cuenca), were obtained from the Institute for Nature Conservation (ICONA), Ministry of Agriculture. Seeds were stored at 6 °C in darkness in open containers.

Germination tests were performed with 25 seeds per petri dish on filter paper regularly moistened with distilled water. Four replicates were used per treatment. The dishes were then placed in controlled environment cabinets at an alternating temperature of 15 °C/25 °C with a 16 h light/8 h dark photoperiod (Osram fluorescent tubes L20 W/105, 30–45 $Em^{-2}s^{-1}$). The criterion of germination was visible radicle protusion. Germination was checked daily and the germinated seeds were removed.

Experiment 1: effect of temperature

Based on similar studies (Keeley, 1987; Keeley and Keeley, 1987; Trabaud and Oustric, 1989; Martínez-Sánchez et al, 1995) it was decided to test the following heat treatments, covering a wide range of conditions encountered by seeds during fires: control, 50 °C/3 min, 50 °C/8 min, 70 °C/3 min, 70 °C/5 min, 90 °C/5 min, 100 °C/2 min and 130 °C/2.5 min. Germination percentage, previously subjected to angular transformation, was analyzed by a one-way ANOVA. Pairwise comparisons among treatments were performed with the Scheffé test.

Experiment 2: effect of temperature and ash

Two factors were considered in the experimental design: temperature and ash. The temperature was considered at three levels: control, 90 °C/5 min and 130 °C/2.5 min. The ash was also considered at three levels: control and two ash solution: 10 g/L and 20 g/L. Ash (completely burnt material) was obtained from *P sylvestris* and *P nigra* branches and leaves and the ash solution used to moisten petri dishes was prepared following Keeley and Keeley (1987). Four replicates of 25 seeds were prepared for each factor/level combination (3 × 3). A two-factor ANOVA was subsequently performed.

RESULTS

Temperature treatments up to 70 °C did not seem to affect the germination of *P nigra* or *P sylvestris* (figs 1 and 2, and table I). Germination reached high values (> 90%) in all cases, and there were no differences with the control. However, when temperatures surpassed 70 °C, germination decreased significantly ($P < 0.001$). Heat treatments above 100 °C resulted in almost null germination (< 10%), which seems to indicate that such temperatures cause the seeds to die. The germination behaviour of *P nigra* and *P sylvestris* was very similar. The values for T_{50} (days to reach 50% of germination) showed no significant delays in germination among treatments with high germination responses (tables I and II).

In the second experiment ash did not significantly modify the germination percentage of seeds in these two pines (table II) and no interactions between temperature and ash were found (table III).

DISCUSSION

Pine species in Mediterranean climates and fire-prone environments have been interpreted as 'obligate seeders' (following Kee-

Table I. Effect of heat treatments on the germination of *Pinus nigra* and *P sylvestris* seeds, 36 days after sowing. Treatments (mean values ± standard deviation) with the same letter are not significantly different ($P < 0.05$). T_{50} indicate days to reach 50% germination.

	Pinus nigra		Pinus sylvestris	
	Germination (%)	T_{50}	*Germination (%)*	T_{50}
Control	95 ± 5.0 b	6.5	91 ± 6.8 c	8.0
50 °C/3 min	98 ± 2.3 b	8.0	92 ± 5.7 c	8.5
50 °C/8 min	95 ± 5.0 b	7.5	97 ± 5.0 c	8.5
70 °C/3 min	96 ± 4.6 b	8.5	94 ± 4.0 c	8.5
70 °C/5 min	91 ± 6.8 b	7.5	95 ± 2.0 c	9.0
90 °C/5 min	12 ± 3.8 a	—	17 ± 5.7 b	—
100 °C/2 min	23 ± 9.2 a	—	4 ± 0.0 a	—
130 °C/2.5 min	8 ± 3.8 a	—	1 ± 2.0 a	—

Table II. Effect of heat and ash treatments on the germination of *Pinus nigra* and *P sylvestris* seeds, 36 days after sowing. Treatments (mean values ± standard deviation) with the same letter are not significantly different ($P < 0.05$). T_{50} indicate days to reach 50% germination.

	Pinus nigra		Pinus sylvestris	
	Germination (%)	T_{50}	*Germination (%)*	T_{50}
Control	95 ± 5.0	6.5	91 ± 6.8	8.0
10 g/L	94 ± 5.2	7.5	92 ± 6.5	8.0
20 g/L	95 ± 7.6	7.0	91 ± 10.5	8.5
90 C/5 min:10 g/L	22 ± 3.8	—	16 ± 9.5	—
90 C/5min:20 g/L	11 ± 5.0	—	10 ± 5.2	—
130 C/2.5 min:10 g/L	9 ± 5.0	—	0 ± 0.0	—
130 C/2.5 min:20 g/L	4 ± 0.0	—	0 ± 0.0	—

Table III. Two-way ANOVA of the effect of heat and ash treatments on the germination of *Pinus nigra* and *P sylvestris* seeds.

	Pinus nigra			Pinus sylvestris		
	df	*SS*	P	*df*	*SS*	P
Temperature	2	31666	0	2	38661	0
Ash	2	115	0.36	2	48	0.61
Temp x ash	4	161	0.57	4	55	0.88
Residual	33	1810		33	1616	

df, degrees of freedom; SS, sum of squares; *P*, significance level.

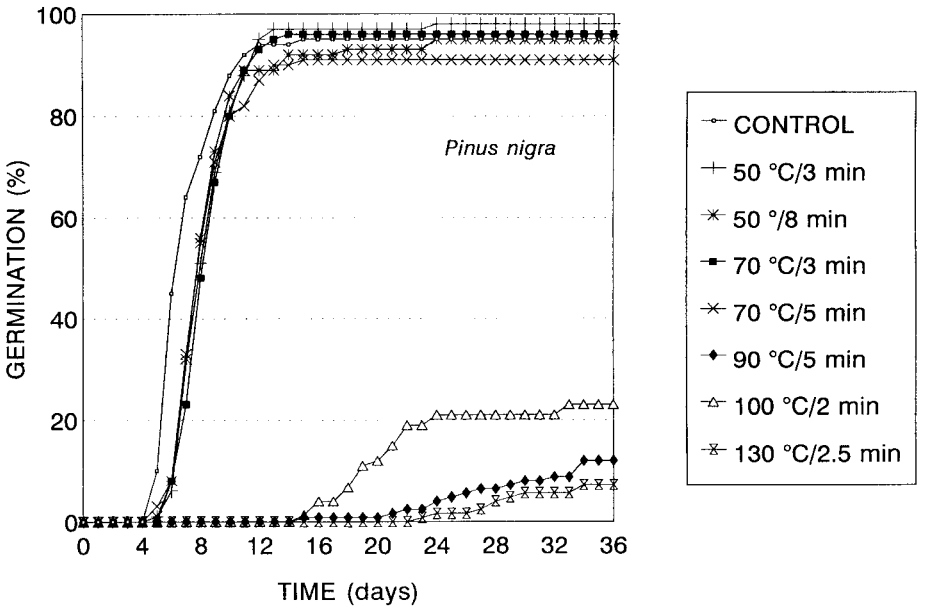

Fig 1. Curves of germination percentage for *Pinus nigra* treatments (heat experiment 1).

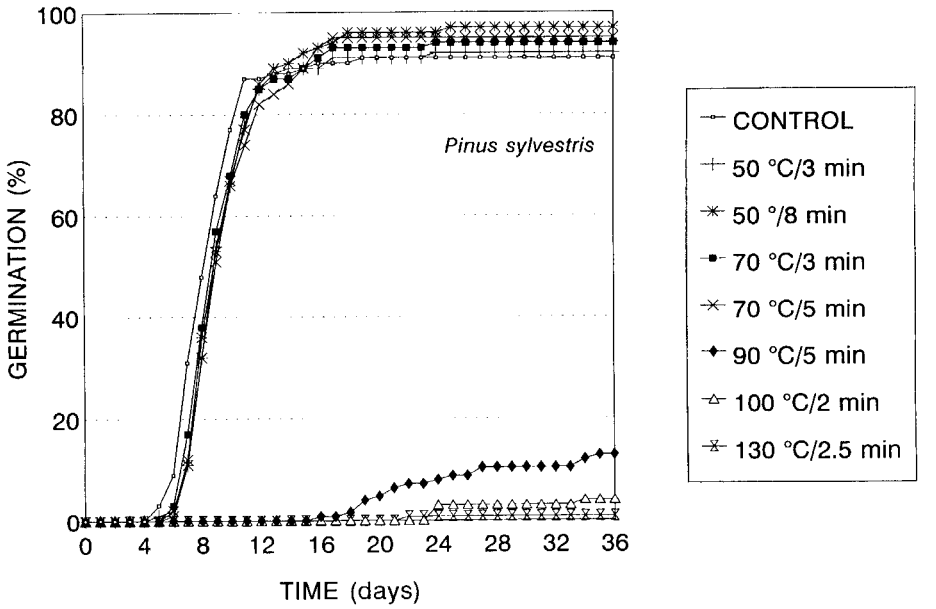

Fig 2. Curves of germination percentage for *Pinus sylvestris* treatments (heat experiment 1).

ley and Zedler, 1978). After severe wildfires, genets are almost always killed and reproduction, which is normally very effective (Trabaud et al, 1985; Barbero et al, 1987; Mansanet, 1987; Papió, 1987; Thanos et al, 1989; Martínez-Sánchez et al, 1995; Thanos et al, 1996), depends entirely on seeds. Traditionally, Mediterranean pines have been considered as 'active pyrophytes' (Kuhnholtz-Lordat, 1958; Trabaud, 1970; Le Houerou, 1974), but Trabaud (1987) introduced the more realistic term 'adapted to fire' to describe their behaviour. Martínez-Sánchez et al (1995) indicate that the seed germination of *P pinaster* and *P halepensis* from xeric southern Spain, is not favoured by an increase in temperature, although the seed cover can protect the embryo at a wide range of temperatures (germination only decreased above 200 °C). Thus, these plants can be interpreted as efficient colonizers in burnt areas, although some difficulties have been reported in the reestablishment of *P pinaster* after intense fires (Castro et al, 1990).

Our results suggest an even more restricted behaviour for *P nigra* and *P sylvestris* after wildfires. The seed cover only confers a smooth protection to heat shocks. Thus, temperatures above 70 °C become lethal and germination is not affected by ash. Reyes and Casal (1995) found that the critical point must be located between 90 °C /1 min and 90 °C /5 min for *P sylvestris* seeds. A similar effect of ash on seed germination has been reported for *P halepensis* (Neéman et al, 1993). Ash from totally consumed wood, ie, very intense wildfires, has shown no positive effect on seed germination (Trabaud and Casal, 1989; Neéman et al, 1993; González-Rabanal and Casal, 1995), whereas charred wood can facilitate germination, probably via nitrates (Keeley, 1987; Thanos and Rundel, 1995) or even via ammonium (Christensen, 1973; Christensen and Muller, 1975).

Both pines have been considered generalist conifers with a high capacity for spatial selection (Barbero and Quézel, 1989; Barbero et al, 1990). This implies that seeds achieve a rapid recovery after fire or other disturbances (Barbero et al, 1990). As previously demonstrated, pine seed germination is stimulated by light via the phytochrome system (Thanos and Skordilis, 1987). This is also true for *P nigra* and *P sylvestris* (Orlandini and Malcoste, 1972; Toole, 1973; Orlandini and Bulard, 1975). This clearly indicates the photophilous nature of these two pines, which allows for the germination of their seeds mainly in open and well-illuminated areas. However, according to Trabaud and Campant (1991), Trabaud (1995) and our field observations, recruitment after wildfire is not efficient for these pines. They present good biological and ecological selection to colonization after disturbance but not after intense fires, mainly crown fires.

On the Iberian Peninsula, pine forests dominated by *P nigra* are mainly found in the southern half, and those dominated by *P sylvestris* in central and northern Spain. These forests are considered 'climax' communities of the highest mountains on the oromediterranean belt (Rivas-Martínez, 1987; Peinado and Rivas-Martínez, 1987), whereas they form permanent communities on rocky sites (such as spurs, crests and steep slopes) (Regato and Escudero, 1990). In such situations, tree population density results in a patchy distribution of scattered, low cover forests, surrounded by a general matrix of creeping scrubs, caespitose grasses and bare rock outcrops. Although wildfires in these forests vary according to the fuel load and the weather, they are normally surface fires that rarely turn into catastrophic crown fires. Only on the lower boundary of the oromediterranean belt is the canopy almost continuous and can the fuel load reach critical values leading to severe fires as reported for supramediterranean forests. Thus, under the fire regime of high moun-

tains, oromediterranean pines are highly competitive. Many trees can survive, as fire scars in very old scot pines indicate (Di and Ende, 1990), and the postfire environment leads to successful pine recruitment by seeds, with almost no competiton from other trees.

On the other hand, there are extensive forests with milder macroclimatic conditions located on most of the Iberian mountains of the eastern half in the supramediterranean belt. These forests have been suffering catastrophic fires (> 10 000 ha) for the last two decades (Vázquez and Moreno, 1993). This is most likely to be due to landscape homogenization resulting from a decrease in man-induced disturbances, as reported for most of the northern Mediterranean forest ecosystems (Barbero et al, 1990). After wildfires almost all seeds, both in the canopy and the soil, are killed. Dissemination of anemochorous seeds from surviving edge pines, is strongly limited after very large fires as they rarely surpass 100 m, as in the case of *P halepensis* and *P brutia* (Trabaud et al, 1985; Barbero et al, 1987; Richardson, 1988; Thanos et al, 1989; Thanos et al, 1996). Subsequently, resprouters, such as different *Quercus* species, which are usually interspersed in the subcanopy, or seeders, such as *Betula*, achieve early control of the newly opened space (Ceballos and Ruiz de la Torre, 1971) and pines can become locally extinct. From a community perspective, this implies great landscape and economical changes. In only a few years, very productive pine forests are transformed into sclerophyllous (*Q ilex* and *Q rotundifolia*) and deciduous oak forests (*Q humilis, Q faginea* and *Q pyrenaica*) as pointed out by Retana (pers comm) after some large fires in Catalonia (Spain). This seems to agree with the idea that these supramediterranean extensive pine forests are, in many cases, man-induced and the mature or climax communities are normally oak forests, except in sunny and rocky areas where pines can take refuge (Peinado and Rivas-Martínez, 1987). From an economical point of view, *P nigra* ssp *salzmannii* and *P sylvestris* are the species most widely used in Iberian forestry. The landscape changes induced by wildfire as a consequence of forest homogenization and fuel loading are significant, as extensive territories depend almost exclusively on the exploitation of these forests.

ACKNOWLEDGEMENTS

We thank Lori J De Hond for her linguistic assistance. This work was financied by a CAM project No 06M/003/96.

REFERENCES

Acherar M, Lepart J, Debussche M (1984) La colonisation des friches par le pin d'Alep (*Pinus halepensis* Mill) en Languedoc méditerranéen. *Acta Oecologica, Oecol Plant* 19, 179–189

Amaral Franco J (1986). Pinaceae. In: *Flora Iberica I: Plantas vasculares de la Península Ibérica e Islas Baleares (Lycopodiaceae–Papaveraceae)* (S Castroviejo et al, ed), CSIC Madrid

Barbero M, Quézel P (1989) Structures, architectures forestières à sclérophylles et prévention des incendies. *Bull Ecol* 2, 7–14

Barbero M, Bonin G, Loisel R, Miglioretti F, Quézel P (1987) Incidence of exogenous factors on the regeneration of *Pinus halepensis* after fires. *Ecol Medit* 12, 40–51

Barbero M, Bonin G, Loisel R, Quézel P (1990) Changes and disturbances of forest ecosystems caused by human activities in the western part of the mediterranean basin. *Vegetatio* 87, 151-173

Castro JF, Bento J, Rego F (1990) Regeneration of *Pinus pinaster* forests after wildfire. In: *Fire in Ecosystem Dynamics* (JG Goldammer, MJ Jenkins, ed), SPB Academic Publishing, The Hague, 71-75

Catalán G (1991) *Regiones de Procedencia de* Pinus sylvestris *L*, Pinus nigra *Arn ssp salzmannii (Dunal) Franco*. MAPA, Madrid

Ceballos L, Ruiz de la Torre J (1971) *Árboles y Arbustos de la España Peninsular*. ETSI Montes, Madrid

Corral R, Pita JM, Pérez–García F (1990) Some aspects of seed germination in four species of *Cistus* L. *Seed Sci Technol* 18, 321–325

Christensen NL (1973) Fire and the nitrogen cycle in Californian chaparral. *Science* 181, 66–68

Christensen NL, Muller CH (1975) Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. *Ecol Monogr* 45, 29–55

Di X, Ende J (1990) The forest conflagration of May 1987 in Northeastern China. In: *Fire in Ecosystem Dynamics* (JG Goldammer, MJ Jenkins, eds), SPB Academic Publishing, The Hague, 169-174

Elena-Roselló R., Sánchez-Palomares (1991) *Los Pinares Españoles de* Pinus nigra *Arn: Síntesis Ecológica*. MAPA, Madrid

Gill AM, Groves RH (1981) Fire regimes in heathlands and their plant ecologic effects. In: *Ecosystems of the World. Vol 9B: Heathland and Related Shrublands* (RL Specht, ed), Elsevier, Amsterdam, 61–84

González-Rabanal F, Casal M (1995) Effect of high temperatures and ash on germination of ten species from gorse shrubland. *Vegetatio* 116, 123–131

Keeley JE (1987) Role of fire in seed germination of woody taxa in California chaparral. *Ecology* 68, 434–443

Keeley JE, Keeley SC (1987) Role of fire in the germination of chaparral herbs and suffrutescents. *Madroño* 34, 240–249

Keeley JE, Zedler PH (1978) Reproduction of chaparral shrubsafter fire: a comparison of sprouting and seeding strategies. *Amer Midl Natur* 99, 142– 161

Kuhnholtz-Lordat G (1958) L'écrant vert. *Memoires du Muséum national d'histoire naturelle,* Série B 9, Paris

Le Houérou HN (1974) Fire and vegetation in the Mediterranean Basin. *Tall Timbers Fire Ecology Conference* 13, 237–277

Mansanet CM (1987) Incendios forestales en Alicante. *Estudio de la Evolución de la Vegetación Quemada*. Caja de Ahorros Provincial, Alicante

Martínez-Sánchez JJ, Marín A, Herranz JM, Ferrandis P, De las Heras J (1995) Effects of high temperatures on germination of *Pinus halepensis* Mill. and *P pinaster* Aiton ssp. *pinaster* seeds in southeast Spain. *Vegetatio* 116, 69–72

Naveh Z (1974) Effects of fire in the Mediterranean region. In: *Fire and Ecosystems* (TT Kozlowski, CE Ahlgren, eds), Academic Press, New York, 401–434

Neéman G, Meir I, Neéman R (1993) The effect of ash on the germination and early growth of shoots and roots of *Pinus*, *Cistus* and annuals. *Seed Sci Technol* 21, 339–349

Orlandini M, Bulard C (1975) Principales caractéristiques de la germination des graines photosensibles de pins ; comparaison avec d' autres matériels. *Travaux scientifiques du parc national de la Vanoise* 6, 95–114

Orlandini M, Malcoste R (1972) Étude du phytochrome des graines de *Pinus nigra* Arn par spectrophotometric bichromatique in vivo. *Planta* 105, 310–316

Papió C (1987) Regeneració del pi blanc despres d'un incendi. *Quaderns Ecologia Aplicada*. 10, 83–91

Pausas JG, Fons, J (1992) Estructura i el creixement d'algunes pinedes en diferents condicions topográfiques. *Fol Bot Misc* 8, 199–213

Peinado M, Rivas-Martínez S (1987) *La Vegetación de España*. Publicaciones Universidad de Alcalá de Henares, Madrid.

Regato P, Escudero A (1990) Caracterización fitoecológica de las comunidades de *Pinus nigra* ssp. *salzmannii* en los afloramientos rocosos del Sistema Ibérico Meridional. *Bot Complutensis* 15, 149–161

Reyes O, Casal M (1995) Germination behaviour of three species of the genus *Pinus* in relation to high temperatures suffered during fores fires. *Ann Sci For* 52, 385–392

Richardson DM (1988) Age structure and regeneration after fire in a self– sown *Pinus halepensis* forest on the Cape Peninsula, South Africa. *SA J Bot* 54, 140–144.

Rivas-Martínez S (1987) *Memoria del Mapa de Series de Vegetación de España*. MAPA, Madrid

Tárrega R, Calvo L, Trabaud L (1992) Effect of high temperatures on seed germination of two woody leguminosae. *Vegetatio* 102, 139–147

Thanos CA, Rundel PW (1995.) Fire-followers in chaparral: nitrogenous compounds trigger seed germination. *J Ecol* 83, 207–216

Thanos CA, Daskalakou EN, Nikolaidou S (1996) Early post-fire regeneration of a *Pinus halepensis* forest on Mount Párnis, Greece. *J Veg Sci* 7, 273–280

Thanos C, Marcou S, Christodoulakis D, Yannitsaros A (1989) Early post-fire regeneration in *Pinus brutia* forest ecoystems of Samos island (Greece). *Acta Oecologica, Oecol Plant* 10, 79-94

Thanos CA, Skordilis A (1987) The effects of light, temperature and osmotic stress on the germination of *Pinus halepensis* and *P brutia* seeds. *Seed Sci Technol* 15, 163–174

Toole VK (1973) Effects of light, temperature and their interactions on the germination of seeds. *Seed Sci Technol* 1, 339–396

Trabaud L (1970) Quelques valeurs et observations sur la phytodynamique des surfaces incendiées dans le Bas-Languedoc. *Naturalia Monspeliensia, Serie Bot* 21, 231–242

Trabaud L (1987) Dynamics after fire of sclerophyllous plant communities in the Mediterranean basin. *Ecol Medit* 13, 25–37

Trabaud L (1995) Modalités de germination des cistes et des pins méditerranéens et colonisation des sites perturbés. *Rev Ecol (Terre Vie)* 50, 3–14

Trabaud L, Campant C (1991) Difficulté de recolonisation naturelle du pin de Salzmann *Pinus nigra* Arn. ssp. *salzmannii* (Dunal) Franco après incendie. *Biol Conserv* 58, 329–343

Trabaud L, Casal M (1989) Réponses des semences de *Rosmarinus officinalis* à différents traitements simulant une action de feu. *Acta Oecologica Oecol Applic* 10, 355–363

Trabaud L, Michels C, Grosman J (1985) Recovery of burnt *Pinus halepensis* Mill. Forest. II. Pine reconstitution after wildfire. *For Ecol Manag* 13,167–179

Trabaud L, Oustric J (1989a) Influence du feu sur la germination des semences de quatre espéces ligneuses méditerranéennes à reproduction sexuée obligatoire. *Seed Sci Technol* 17, 589–599

Trabaud L, Oustric J (1989b) Heat requirements for seed germination of three *Cistus* species in the garrique of Southern France. *Flora* 183, 321–325

Troumbis A, Trabaud L (1986) Comparison of reproductive biological attributes of two *Cistus* species. *Acta Oecologica Oecol Plant* 7, 235–250

Vázquez A, Moreno JM (1993) Sensitivy of fire occurrence to meteorological variables in Mediterranean and Atlantic areas of Spain. *Landscape and Urban Planning* 24, 129–142

Vuillemin J, Bulard C (1981) Écophysiologie de la germination de *Cistus albidus* L. et *Cistus monspeliensis* L. *Naturalia Monspeliensia Serie Bot* 46,1–11

Walter H (1973) *Vegetation of the Earth in Relation to Climate and Ecophysiological Conditions*. Springer Verlag, New York