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ScienceDirect
Environmental and Experimental Botany 60 (2007) 324–333
Environmental and Experimental Botany
www.elsevier.com/locate/envexpbot

Heat-shock and seed germination of a group of Mediterranean plant species growing in a burned area: An approach based on plant functional types

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Received 12 January 2006; received in revised form 2 August 2006; accepted 28 December 2006

Abstract

Many plants from Mediterranean-type ecosystems show enhanced germination when exposed to heat and other fire-related cues. Whether Mediterranean-type plants are fire recruiters and need fire to germinate is subject of discussion. In the present work, we tested the above hypothesis by subjecting seeds from 57 species representative of a recently burned plant community to various heat pulses. Differences in germination among species, taking into account their phylogeny, were studied by dividing them according to their life-form (chamaephytes, hemicryptophytes), regeneration strategy (non-sprouters, sprouters) and geographical distribution range (Iberian Peninsula endemics, Mediterranean, widely distributed species). Seeds were exposed to 80, 100 and 120 °C during 10 min, and then, incubated at 17.5 °C for 6 weeks in darkness. Maximum germination was reached at 80 °C and control treatments and minimum germination was at 120 °C. Most species were tolerant to heat-shocks, only a few of them were stimulated by heat, and around 20% suffered a reduction in germination with heat. The germination response to heat-shock differed according to regenerative strategy and distribution range, but not to life-form. These results were supported independently of phylogeny. As expected, sprouters and Iberian endemics were more sensitive to heat-shock than non-sprouters and widely distributed species, respectively. As a conclusion, the studied plant group appears to exhibit resistance to heat but not dependence on it for germination. Therefore, recruitment could be high after low intensity fires, but might be significantly reduced for most species after more intense fires.

Keywords: Chamaephyte; Distribution range; Fire; Hemicryptophyte; Iberian Peninsula endemics; Non-sprouter; Sprouter

1. Introduction

Forest fires are common these days in the Mediterranean region (Moreno et al., 1998). There is evidence that, at least since the onset of the Holocene, fires were an important component in the wilderness of the Mediterranean region (Carrión, 2002), but humans substantially contributed to alter the fire regime through grazing and agricultural practices (Carrión et al., 2003). Few areas, if any at all, have escaped from intensive use of the land by humans. Thus, many species may have thrived in environments devoid of fire, or where this may have played a marginal role.

As intensive use of the land has relinquished and forest fires have become more frequent and extensive, a question of interest is to know how extant communities subject today to burning may respond to fire. In fire-prone ecosystems, conditions for seedling establishment are particularly favourable just after the passage of a fire. Indeed, in Mediterranean-type ecosystems recruitment is frequently massive after fire (Christensen and Muller, 1975; Trabaud and Lepart, 1980; Arianoutsou and Margaris, 1981) and the temporal window for seedling establishment after fire is usually short (Quintana et al., 2004). Consequently, many Mediterranean plants produce seeds that are released from dormancy only after being exposed to fire-related factors, such as heat (Trabaud, 1987; Bell et al., 1993; Bond and van Wilgen, 1996; Keeley and Fotheringham, 2000). Enhanced germination in heated seeds has been showed for many Mediterraenan species, mostly shrubs and trees (Thanos et al., 1992; Bell, 1999; Herranz et al., 1999; Valbuena et al., 2002). Nevertheless, information about other life-form types is limited. This is the case of

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✠ Deceased, 16th December, 2006.

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doi:10.1016/j.envexpbot.2006.12.014

low-stature, perennial species, such as hemicryptophytes (perennial herbs) and chamaephytes (subshrubs). This group of species account for a large number of species in any given Mediterranean community (Verlaque et al., 2001), abound in the earlier and mid-successional stages (Kazanis and Arianoutsou, 1996; Gondard et al., 2001; Guo, 2001; Bonet, 2004), and comprise an important fraction of the endemic Mediterranean flora (Cowling et al., 1996; Melendo et al., 2003). However, little is known about their germination ecology, particularly in response to fire. As germination response is frequently related to growth form (Keeley and Bond, 1997), this gap of knowledge precludes having a comprehensive framework about the germination response to fire of Mediterranean ecosystems. In this sense, classifying plants into groups, sharing a common trait easily identifiable (Gitay and Noble, 1997) might be a useful way of dealing with the response of the great diversity of plants to changed disturbance regimes or shifts in other stressors (Woodward and Cramer, 1996; Lavorel and Cramer, 1999; Rusch et al., 2003).

The objective of this study was to evaluate the response of seeds from 57 low-stature, perennial plant species, representative of a post-fire plant community to various heat pulses. The main hypothesis to be tested is that if seedling establishment is linked to fire ("fire-recruiters") most species would show enhanced germination after exposition to heat. Moreover, species were classified into various functional groups, which may respond differently to heat pulses. Three criteria were considered: life-form (chamaephytes versus hemicryptophytes), regeneration strategy (non-sprouters versus sprouters) and geographical distribution range (Iberian Peninsula endemics, Mediterranean and widely distributed species). We expected that hemicryptophytes, which reach a maximum of plant cover in the first or second year after fire (Keeley et al., 2005) would have a more fire-dependent recruitment, and consequently germination would be massively stimulated by heat, compared to chamaephytes. Similarly, we expected that non-resprouter species would also be more dependent on heat for germination than resprouters, which may respond vegetatively to fire. Finally, it has been proposed that the germination niche breadth, a component of the regeneration niche, may be related to the distributional range size (Brändle et al., 2003). We tested the hypothesis that seeds from endemics species, having a more restricted germination niche, would be sensitive to heat compared to more widely distributed species.

2. Material and methods

Seeds were collected from an area affected by a large fire (province of Cuenca; 1°20′–1°35′W and 39°45′–39°54′N). Altitude ranges between 900 and 1400 m above sea level, the climate is typically Mediterranean, with an annual mean temperature of 11.5–12.5 °C and an annual total rainfall of 400–600 mm. A naturally ignited large fire took place during summer (July), affecting *Pinus pinaster*, *Pinus halepensis* and *Pinus nigra* woodlands, shrublands and woody crops.

From an inventory of species registered in the flora of burned and surrounding unburned areas, a representative group of 57 species with viable seeds were selected. These species included a wide range of plant families and comprised the two life-forms with higher levels of endemicity: chamaephytes and hemicryptophytes. Species were characterized regarding to their geographical distribution ranges as IP: endemic species with a geographical distribution restricted to the Iberian Peninsula; Med: species distributed around the Mediterranean Sea, and Wide: species distributed across a wider area (Table 1). The species included two modes of regeneration after fire: sprouters (species that are capable of regenerating after fire by sprouting) and non-sprouters (regeneration after fire proceeds only from seeds). The mode of regeneration after fire was based on personal observations in the field, after the wildfire. Reliable information was available only for 47 species, and these are the only ones that were used.

Seed samples were collected from ripe fruits during summer and fall. Seeds were cleaned by removing fruit tissues that would normally be lost in dispersal. In many cases the "seed" that was sown included the entire fruit, such as in achenes. Seeds were separated from fruits and stored in paper bags in the dark at room temperature.

Prior to incubation, seeds were heated at 80, 100 and 120 °C in an oven during 10 min. These treatments tried to simulate some range of temperature-time curves that have been found in experimental fires over shrublands (Trabaud, 1979; Moreno et al., 2004; B. Céspedes, pers. com.). Indeed, Trabaud (1979) showed that the duration of the heat wave during the course of fire in Mediterranean shrublands is no longer than 10 min. Seeds were then incubated at 17.5 °C for 6 weeks in plastic Petri dishes (5.5 cm in diameter) over two caps of filter paper (Whatman no. 1) moistened with 1.2 ml of distilled water at the beginning of the experiment. Four replicates of 25 seeds each were used per treatment. All Petri dishes were sealed with parafilm to prevent them from desiccating. Petri dishes were laid at random on a temperature and humidity controlled chamber (Model G-21, Ibercex). Experiments were carried out in the dark by wrapping aluminum foil around the Petri dishes. Germination was recorded only once, at the end of the incubation period, after 6 weeks of treatment. A periodic checking of germination was not carried out because green safelight, commonly utilized for checking germination in dark experiments, was demonstrated to alter the germination of some species (Doussi and Thanos, 1997; Luna et al., 2004). Radicule emergence was the criterion used for scoring a seed as germinated.

Germination data were corrected with seed-viability analyses that were carried out in the ungerminated seeds by means of the tetrazolium test (Cottrell, 1947). Germination percentages were arcsine transformed previously to statistical analyses, but for ease of interpretation, data will be presented without transformation. Differences in germination means among heat-shocks treatments were analyzed by one-way ANOVA separately for each species. A posteriori Tukey tests were performed to detect any significant differences in the comparison between levels of the treatment over germination percentages. Species with germination percentages above 20% were classified in relation to their responses to heat-shock treatment into three categories: (I) species stimulated by heat-shock (those species that statistically significantly increased their germination under any of the