



Heat shock-stimulated germination in Mediterranean Basin plants in relation to growth form, dormancy type and distributional range

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Abstract Heat shock-stimulated germination is frequently considered a trait restricted to a few plant families with impermeable seed coats in the Mediterranean Basin. We aimed to ascertain this general idea by using 68 eastern Mediterranean plant taxa differing in growth form, dormancy type and geographic distributional range. We conducted a laboratory experiment including heat shocks (60, 80, 100, 120 and 140°C for 5 min) and a control treatment, and monitored germination for each species. Among the studied taxa, 24 (35%) showed a significant positive response for at least one of the treatments. Many Cistaceae and Fabaceae species showed a positive germination response to the heat shocks. However, we also observed heat shock-stimulated germination in the Brassicaceae, Malvaceae, Polygonaceae and Scrophulariaceae, and provided additional evidence for the Asteraceae, Lamiaceae, Liliaceae, Plantaginaceae and Rosaceae in the Mediterranean Basin. Distributional range and dormancy type were significant determinants of germination response to heat shocks whereas growth form and phytogeographic origin had lower and/or non-significant contribution. Species with wide or local distribution were less

tolerant to moderate heat shocks than those with regional distributional ranges. Species with physically dormant seeds showed significantly more stimulated germination after heat shocks than those with permeable seeds. In conclusion, dormancy type is an important determinant of seed response to heat shock, and an association exists between distributional range and germination response to heat shocks. Our findings revealed that heat shock-stimulated germination is observed across a broader taxonomic spectrum in the Mediterranean Basin, including families not possessing physical dormancy.

Keywords fire · geographic distributional range · germination · heat shock · physical dormancy · Mediterranean Basin

Introduction

Fire is a disturbance that has shaped many ecosystems on Earth since the emergence of terrestrial plants (Pausas and Keeley 2009). In fire-prone Mediterranean ecosystems, where natural and human-induced fires frequently occur, dominant vegetation types consist of plant species with regeneration strategies that allow them to persist following frequent fires (Keeley et al. 2012). These species have various strategies to survive after a fire. Buds of some species are protected from fire by the soil (those having underground buds) or a thick bark (for aboveground buds) enabling them to survive and later resprout (i.e. post-fire resprouting). Enhanced

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flowering after fire is observed in many resprouting species, especially in geophytes. Some tree species maintain their cones (or fruits) closed for many years in the tree canopy to protect seeds from fire and release them just after it (i.e. serotiny). Enhanced seed germination after fire is another survival mechanism that involves the stimulation of germination by fire-related cues such as heat shock and smoke (Moreira et al. 2010; Keeley et al. 2011). In Mediterranean ecosystems, seed dormancy plays a significant role in providing a persistent soil seed bank and delaying germination until the occurrence of optimal conditions for germination just after fires (Bell et al. 1993; Moreira and Pausas 2012). Heat shock caused by fire results in the breaking of physical dormancy (PY) in seeds imposed by impermeable seed coats (Thanos and Georghiou 1988). Exposure to heat shock causes morphological changes at a specialized area on the seed coat (i.e. water-gap complex) and small openings that allows water uptake are formed (Gama-Arachchige et al. 2013). This process results in germination and seedling establishment in post-fire environments (Thanos and Georghiou 1988; Tavşanoğlu and Gürkan 2005).

Heat shock-stimulated germination is prominently observed in Mediterranean-type ecosystems of California, the Mediterranean Basin, South Africa and southwestern Australia (Keeley et al. 2012; Baskin and Baskin 2014). Heat shock-stimulated germination is also a phylogenetically conserved trait (Verdú and Pausas 2007) and is therefore restricted to a few families (Keeley 1987; Bell et al. 1993; Moreira et al. 2010). In the Mediterranean Basin, for example, heat shock-stimulated germination is observed mainly in the Fabaceae and Cistaceae (Thanos et al. 1992; Herranz et al. 1998; Reyes and Trabaud 2009; Moreira et al. 2010; Tavşanoğlu 2011; Keeley et al. 2012; Moreira and Pausas 2012); however, evidence for heat shock-stimulated germination is rare beyond these two families (Paula et al. 2009; Moreira et al. 2010). Nonetheless, wide-range distribution of smoke-stimulated germination is noted in the phylogenetic tree of angiosperms (Pausas and Keeley 2009).

In the Mediterranean Basin, many herbaceous and woody species massively establish in the first year after fire but are eliminated from the aboveground plant community through time (Calvo et al. 2002; Kazanis and Arianoutsou 2004; Kavgacı et al. 2010; Tavşanoğlu and Gürkan 2014). The timescale of this elimination process depends significantly on specific life-history

traits of the species (Pausas et al. 2004; Tavşanoğlu and Gürkan 2014). Many species, especially those that have fire-stimulated germination, are known to persist in the soil seed bank between two fires, as revealed by field and laboratory studies on post-fire stimulation of germination (Herranz et al. 1998; Luna et al. 2007; Moreira et al. 2010; Céspedes et al. 2014; Tormo et al. 2014) and studies performed directly on the composition of the soil seed bank (Clemente et al. 2007; Céspedes et al. 2012). Although the relationship between post-fire germination and seedling establishment after fire is well known for some groups, such as the genus *Cistus* (Thanos and Georghiou 1988; Trabaud and Oustric 1989; Tavşanoğlu and Gürkan 2005), information on several other groups known to be established after fire is lacking (but see Tormo et al. 2014 and Céspedes et al. 2014 for community-level evidence). Considering that annual species are an important component of early post-fire communities in the Mediterranean Basin (Kazanis and Arianoutsou 2004; Kavgacı et al. 2010; Tormo et al. 2014), knowledge on fire-stimulated germination in herbaceous species, especially annual species, is scarce (Moreira and Pausas 2018). Thus, further studies are warranted to reveal the processes underlying post-fire establishment patterns in the Mediterranean Basin, particularly in annual species.

Water impermeability of the seed coat (hard-seededness) is the basis for the concept of PY of seeds (Baskin and Baskin 2014). Exposure to fire temperatures (i.e. heat shocks) is well established as an agent for breaking PY of seeds for many taxonomic groups (Baskin 2000). Although fire resistance was recorded in some species in which seeds do not possess PY (e.g. Fichino et al. 2016), in most cases seeds cannot tolerate heat shock temperatures (Keeley 1987; Luna et al. 2007). Although such a dichotomy in the germination (or viability) response to heat shocks is known (Moreira et al. 2010; Baskin and Baskin 2014), the germination response to heat shocks in species with different dormancy types has not yet been compared using empirical data.

The distributional range of plant species is another determinant of germination response to various environmental factors (Brändle et al. 2003; Luna and Moreno 2010; Luna et al. 2012). This is expected because species with local distributions could be more adapted to the environmental factors operating at the local scale whereas those having broader distribution might have a more plastic response to various environmental

conditions. Previous studies have failed to show any relationship between locally distributed species and a positive germination response to fire (Riba et al. 2002; Luna and Moreno 2010). Furthermore, Luna et al. (2007) found that species with limited distribution were affected more negatively by heat shock than those having a wider range. Moreover, to the best of our knowledge, the relationship between heat shock-related germination and biogeographical origin of species has not yet been studied. Therefore, the relationship between fire-related germination and distributional range/origin of species should be clarified by testing the above hypothesis by using various datasets.

This study aimed to ascertain the general idea that heat shock-stimulated germination is a trait restricted to a few plant families with impermeable seed coats in the Mediterranean Basin. We also aimed to determine how growth form, dormancy type and distributional range affect the germination response to heat shock in Mediterranean Basin plants. We expected to observe heat shock-stimulated germination in species across various families beyond the well known Cistaceae and Fabaceae because the effect of heat shock on germination has rarely been investigated except these two families. We hypothesized that species with PY seeds, an annual life cycle and wider distributional ranges would show higher germination response to heat shock temperatures because annual or widely distributed species should have broader germination niches, and species with PY seeds are known to respond to heat shocks positively. To test these hypotheses, we performed a laboratory experiment by using 68 plant taxa that differ in their growth form, dormancy type and distributional range. By including various heat shock temperatures in the experiment, we could determine the response of each species to different heat shocks and then analyse the effect of each functional group on the germination response.

Material and methods

Study area and seed collection

In August 2012 ripe fruits were collected from 68 plant taxa belonging to 48 genera and 21 families from natural populations in southwestern Anatolia, Turkey (Tables S1 and S2 in the Electronic Supplementary Material). The study area falls into eastern Mediterranean Basin region and has Mediterranean-type climate

with pronounced drought (between May and September) and wet (between October and April) periods. The annual total precipitation varies between approximately 400 and 1 200 mm depending on the geographic location and altitude. The study area mainly consists of Mediterranean-type vegetation with various types of plant communities, including pine forests, shrublands and scrublands. Dominant fire regime of the sites from where fruits were collected is summer drought-driven crown fire regime, especially in the sites with low altitude; however, in two sites with higher elevation (i.e. Elmalı and Afyon, Table S1 in the Electronic Supplementary Material) surface fire regimes or a mixed fire regime with both surface and crown fires might be dominant.

For each species, fruits were collected from at least 10 individuals (in a few cases, fewer individuals) in the field. Seeds (and, in some cases, indehiscent fruits including a single seed) were separated from fruit tissues by hand or by using sieves with different mesh sizes in the laboratory. Seeds were then stored in paper bags under dark conditions at approximately 20°C with 50% relative humidity for four months until the experiments were conducted.

Taxonomic identification was performed in the herbarium (HUB; Hacettepe University, Ankara, Turkey) by comparing plant specimens collected from the field and herbarium material. The nomenclature follows Davis (1965–1985).

Functional groups

To understand the relationship between various functional groups and heat shock-related germination, we classified the taxa under study into different functional groups such as growth form (annual herb, perennial herb, or woody), seed dormancy type (PY or not; i.e. possessing impermeable vs permeable seeds), geographic distributional range (local, regional, or wide distribution), phytogeographical region (of Mediterranean or non-Mediterranean origin) and taxonomic family (Table S1 in the Electronic Supplementary Material). Functional group data of species were obtained from various resources (Davis 1965–1985; Paula et al. 2009; Baskin and Baskin 2014; Tavşanoğlu and Pausas 2018). For distributional range classes, ‘local’, ‘regional’ and ‘wide’ refer to the species distributed only in Anatolia and, in some cases, also in the Aegean Islands; the species in which distribution range extends to the

Middle East, Southern Europe, or Western Mediterranean regions; and the species distributed beyond the ranges in the 'regional' class toward Central Asia, Southern Asia, or Central Europe, respectively. For dormancy type classes, we first determined the species that are known to possess PY and then the ones with other dormancy types (physiological, morphophysiological, or no dormancy) were classified as the 'not PY' group. If there was no dormancy type information on a species or we could not identify a taxon to the species level, we assigned the dormancy type of that taxon by following the genus or family level dormancy class.

Heat shock treatments

Batches of seeds of each taxon were subjected to temperatures of 60, 80, 100, 120 and 140°C in a temperature-controlled oven for five minutes to simulate temperatures to which seeds are exposed in the soil seed bank during a crown fire under Mediterranean-climate conditions. For each taxon × treatment combination, four batches of 25 seeds were used as replicates. Four replicated non-treated seeds were also included in the experimental design to serve as a control group for heat shock treatments. Ideally, a total of 24 batches, including 600 seeds, were used for each taxon; however, in a few cases in which the total seed number was not sufficient, some heat shock treatments (preferably 60 and 140°C) were excluded from the experiment.

Germination experiments

Immediately after the treatments were applied, seeds were sown into Petri dishes containing agar as the substrate and incubated at $20 \pm 1^\circ\text{C}$ under dark conditions in a temperature-controlled cabinet, which is the suitable germination condition for many Mediterranean plants (Thanos 1993; Luna et al. 2012). The seeds were monitored for germination every two or three days during the first month of the incubation period and then once a week until the end of the experiment. At each germination check, the germinated seeds were counted and removed from the Petri dishes. The criterion for germination was the viable emergence of the radicle. At the end of the experiment (62 days after the incubation was initiated), non-germinated seeds were checked for viability by using the cut test; the ones including with firm, white and healthy embryos were noted as

viable (Baskin and Baskin 2014) whereas ones with rotten embryos as non-viable. During the germination and viability checks, seeds without an embryo (hereafter, 'empty seeds') were also recorded and removed from the Petri dishes.

Data analysis

The chi-squared (χ^2) test was used to assess the independence of categorical variables among functional groups. Because of a small number of species in some categories, we performed the χ^2 tests by using 2,000 iterations and obtained a simulated *P* value for each test. For each heat shock temperature, we separately performed χ^2 tests, as the number of species differed across categories in each heat shock temperature. Because no species was found in the 'woody and wide distribution' category in our dataset, we removed woody species from the analysis while testing the association between growth form and distributional range.

For each taxon × treatment × replicate combination, empty seeds were removed from the data and initial seed numbers were corrected before the analyses. Seed dormancy was measured as the proportion of non-germinated viable seeds in the control. Data analyses for germination response to heat shocks at the species level were performed considering the number of germinated and non-germinated seeds. For each taxon, the final germination in each treatment was compared with the control germination by using the analysis of deviance (generalized linear model) assuming a binomial error distribution. In this analysis, we included the germinated versus non-germinated seeds.

Linear mixed models were used to evaluate the relationship between functional groups and the germination response to heat shock. In the analysis, we considered the treatment and functional groups fixed factors and the genus within the family a random factor. The latter allowed us to control the possible effect of taxonomy on the results. In this analysis, we used the magnitude of germination data, which is estimated using the difference between germination percentage in treatment and the corresponding control. Additional linear mixed model analyses were performed for each treatment × functional group combination to elucidate the germination response of functional groups under each heat shock treatment. In linear mixed models, we performed a likelihood ratio test to compare the model including only the random factor (the null model) and those

including both the random factor and fixed factors. When needed, Tukey contrasts was used for multiple comparisons. The magnitude of germination data was arcsine-transformed before all analyses to better approximate the normal distribution.

For functional group analyses, only taxa with a significant result of broken dormancy were considered. That is, if a taxon had zero (or < 10%) germination in control and no germination response in treatments, or unidentified functional characters; then we excluded that taxon from the analysis. Thus, 47 taxa were used for functional group analyses. All statistical analyses, including linear mixed models ('nlme' package; Pinheiro et al. 2017), Tukey contrasts following the linear mixed model ('multcomp' package; Hothorn et al. 2008) and χ^2 tests ('MASS' package; Venables and Ripley 2002) were performed in the R environment (<https://www.R-project.org>).

Results

The level of dormancy varied considerably among the studied taxa (Table 1). Six taxa had < 10% germination in the control treatment whereas approximately one-third of the taxa studied (21) had < 20% germination in the control treatment. Conversely, seeds of fourteen taxa were non-dormant and had more than 80% of germination in the control treatment. Dormancy level was not significantly different between the growth forms (likelihood ratio or L ratio = 3.6, $P > 0.05$; Fig. 1) and distributional range classes (L ratio = 4.1, $P > 0.05$; Fig. 1), but species with PY seeds had higher dormancy levels than those that do not possess PY (L ratio = 11.7, $P = 0.0006$; Fig. 1).

Among the 68 taxa studied, 24 showed a significant positive response under at least one of the heat shock treatments. For low (60 and 80°C), moderate (100°C) and high (120 and 140°C) heat shock temperatures, the germination in 16, 22 and 22 taxa significantly increased compared to that in the control treatment, respectively (Table 1). Conversely, some taxa had a negative germination response to low (4) and moderate (8) heat shocks. Moreover, the germination percentage in 36 taxa significantly decreased after high heat shocks, and a total lethal effect was observed in 22 taxa (Table 1). Of the fourteen taxa possessing seeds with PY, nine (64%) showed significant increments in germination percentage in at least one of the heat shock treatments compared

to that in the control. Moreover, germination in none of the remaining taxa with PY seeds reduced after any heat shock, except in *Cistus parviflorus*, in which all seeds were dead after 140°C heat shock treatment. By contrast, germination in many taxa without PY seeds (i.e. both those possessing seeds with other dormancy types or non-dormant ones) did not enhance after any heat shock treatment. However, ten taxa in which seeds are not PY had significantly enhanced germination after low (4), moderate (8), or even high (3) heat shock temperatures compared to that of the control (Table 1). Among these taxa, *Campanula lyrata* and *Coridothymus capitatus* had improved germination after 140°C heat shock treatment compared to that of the control (Table 1). Seeds of most taxa without PY could tolerate low heat shock temperatures (i.e. 60 and 80°C) except *Bupleurum* sp., *Daucus guttatus*, *Scabiosa reuteriana* and *Polypogon monspeliensis*.

The results of χ^2 tests indicated no association among functional groups used in the study; therefore, they were independent of each other (Table S3 in the Electronic Supplementary Material). Distributional range and dormancy type were significant determinants of the germination response to heat shocks, but the contribution of growth form and phytogeographic origin were lower and non-significant (Table 2). Species with regional distribution had higher germination than those with local and wide distribution in 100, 120 and 140°C heat shock treatments (Fig. 2b). Moreover, these differences between species with regional and wide distribution were statistically significant (Tukey contrasts; $P = 0.049$, $P = 0.009$ and $P = 0.038$ for 100, 120 and 140°C, respectively; Fig. 2b). Dormancy type had significant effect on the magnitude of germination after 80 (L ratio = 10.4, $P = 0.001$), 100 (L ratio = 8.4, $P = 0.005$), 120 (L ratio = 7.7, $P = 0.006$) and 140°C (L ratio = 12.5, $P = 0.0004$) heat shock treatments (Fig. 2c), but no significant difference was detected for 60°C heat shock treatment (L ratio = 0.5, $P > 0.05$; Fig. 2c). Although growth form did not have a significant overall effect on the magnitude of germination (Table 2, Fig. 2a), woody species tolerated the moderate and high heat shock temperatures more than the annual and perennial herbs (Tukey contrasts; $0.10 > P > 0.05$ for 100 and 140°C; Fig. 2a). Notably, among the 23 annual herb species tested in this study, six gave a positive germination response for at least one of the heat shock treatments (Table 1, Table S2 in the Electronic Supplementary Material).

Table 1 Mean (\pm SE) germination percentage of taxa under study in heat shock treatments and in the control

Taxa	Heat shock treatments					
	Control	60°C, 5 min	80°C, 5 min	100°C, 5 min	120°C, 5 min	140°C, 5 min
Apiaceae						
<i>Bupleurum</i> sp.	75.2 \pm 2.8	42.9 \pm 7.5****	47.6 \pm 5.1****	55.5 \pm 8.5****	53.6 \pm 4.6****	66.2 \pm 5.9 ^{ns}
<i>Daucus guttatus</i>	84.5 \pm 3.5	69.5 \pm 3.2*	78.6 \pm 2.5 ^{ns}	81.0 \pm 6.0 ^{ns}	40.2 \pm 2.8****	0****
Asteraceae						
<i>Carthamus</i> sp.	58.0 \pm 2.2	—	44.9 \pm 3.8 ^{ns}	26.3 \pm 5.5****	0****	—
<i>Centaurea Cariensis</i> subsp. <i>microlepis</i>	66.2 \pm 5.9	70.3 \pm 6.2 ^{ns}	76.6 \pm 9.1 ^{ns}	51.8 \pm 7.8*	38.3 \pm 16.0****	0****
<i>Crepis sancta</i>	45.8 \pm 9.3	33.3 \pm 4.7 ^{ns}	43.7 \pm 5.6 ^{ns}	42.1 \pm 1.8 ^{ns}	37.3 \pm 6.9 ^{ns}	20.2 \pm 8.8**
<i>Inula anatolica</i>	77.0 \pm 3.6	82.7 \pm 4.9 ^{ns}	78.1 \pm 3.0 ^{ns}	66.2 \pm 2.4 ^{ns}	55.2 \pm 7.4**	29.3 \pm 18.9****
<i>Pallenis spinosa</i>	94.1 \pm 3.5	97.4 \pm 0.9 ^{ns}	96.0 \pm 1.8 ^{ns}	95.0 \pm 3.1 ^{ns}	94.2 \pm 1.9 ^{ns}	12.5 \pm 12.5****
<i>Tragopogon</i> sp.	38.5 \pm 11.2	—	—	41.6 \pm 3.0 ^{ns}	16.5 \pm 10.4 ^{ns}	—
<i>Xeranthemum annuum</i>	84.0 \pm 3.1	82.7 \pm 2.4 ^{ns}	88.3 \pm 3.0 ^{ns}	92.3 \pm 1.2 ^{ns}	0****	0****
Asteraceae 1	34.8 \pm 14.2	40.1 \pm 9.4 ^{ns}	60.4 \pm 15.7**	64.5 \pm 16.6**	44.5 \pm 18.5**	—
Asteraceae 2	10.5 \pm 2.8	18.4 \pm 1.3 ^{ns}	17.7 \pm 2.0 ^{ns}	15.9 \pm 1.7 ^{ns}	16.2 \pm 3.4 ^{ns}	0**
Boraginaceae						
<i>Heliotropium hirsutissimum</i>	11.3 \pm 1.1	15.4 \pm 2.5 ^{ns}	8.2 \pm 1.7 ^{ns}	3.0 \pm 1.9*	0****	0****
Brassicaceae						
<i>Alyssum caricum</i>	79.7 \pm 2.4	79.8 \pm 3.2 ^{ns}	84.9 \pm 2.2 ^{ns}	100.0 \pm 0.0****	59.6 \pm 17.4**	2.3 \pm 2.3****
<i>Alyssum corsicum</i>	7.8 \pm 5.6	17.0 \pm 3.3 ^{ns}	18.4 \pm 2.6 ^{ns}	5.8 \pm 2.1 ^{ns}	10.8 \pm 2.4 ^{ns}	0 ^{ns}
<i>Iberis carica</i>	45.0 \pm 5.0	36.3 \pm 5.9 ^{ns}	42.0 \pm 3.7 ^{ns}	75.4 \pm 5.1****	0****	0****
Campanulaceae						
<i>Campanula lyrata</i> subsp. <i>lyrata</i>	59.8 \pm 4.4	51.4 \pm 8.8 ^{ns}	56.1 \pm 1.4 ^{ns}	55.8 \pm 3.8 ^{ns}	78.5 \pm 6.8****	73.8 \pm 4.7**
Caryophyllaceae						
<i>Dianthus</i> sp.	99.0 \pm 1.0	96.1 \pm 1.6 ^{ns}	98.0 \pm 1.1 ^{ns}	100.0 \pm 0.0 ^{ns}	100.0 \pm 0.0 ^{ns}	0****
<i>Silene behen</i>	0	—	0 ^{ns}	0 ^{ns}	0 ^{ns}	—
<i>Silene tunicoides</i>	70.1 \pm 4.1	58.8 \pm 3.4 ^{ns}	73.1 \pm 5.4 ^{ns}	81.5 \pm 9.8 ^{ns}	1.3 \pm 1.3****	0****
Cistaceae						
<i>Cistus creticus</i>	4.7 \pm 1.9	13.0 \pm 3.0 ^{ns}	27.2 \pm 12.9****	50.0 \pm 8.4****	65.6 \pm 4.5****	45.7 \pm 15.9****
<i>Cistus laurifolius</i>	1.9 \pm 1.9	8.6 \pm 3.4 ^{ns}	30.1 \pm 9.0****	17.3 \pm 3.7**	0.9 \pm 0.9 ^{ns}	0 ^{ns}
<i>Cistus parviflorus</i>	4.5 \pm 1.8	3.5 \pm 2.0 ^{ns}	31.9 \pm 18.8****	84.1 \pm 3.0****	45.1 \pm 20.9****	0*
<i>Cistus salvifolius</i>	11.7 \pm 4.3	12.2 \pm 3.0 ^{ns}	20.4 \pm 5.5 ^{ns}	61.4 \pm 3.3****	65.9 \pm 3.0****	68.5 \pm 2.6****
Dipsacaceae						
<i>Scabiosa reuteriana</i>	40.5 \pm 15.7	11.6 \pm 2.2****	6.6 \pm 2.2****	21.2 \pm 2.2**	22.8 \pm 4.7**	0****
Fabaceae						

Table 1 (continued)

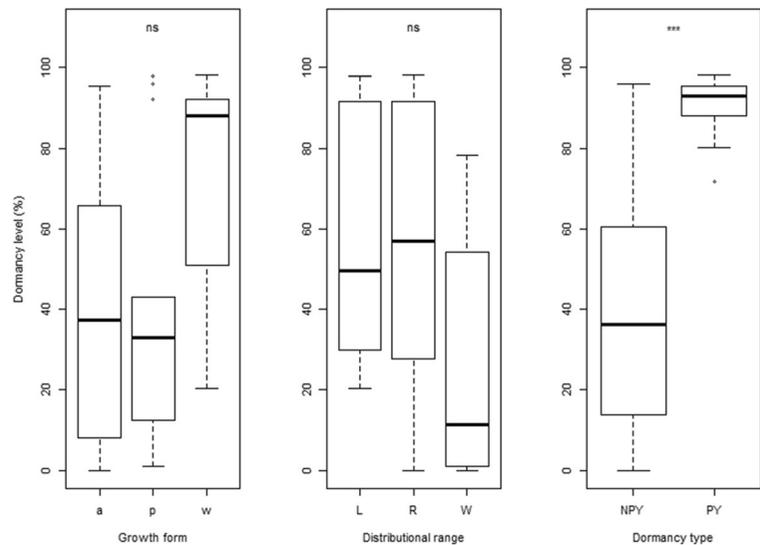
Taxa	Heat shock treatments					
	Control	60°C, 5 min	80°C, 5 min	100°C, 5 min	120°C, 5 min	140°C, 5 min
<i>Anagris foetida</i>	21.1 ± 5.3	15.8 ± 3.7 ^{ns}	14.1 ± 5.3 ^{ns}	14.0 ± 5.3 ^{ns}	25.0 ± 6.8 ^{ns}	31.9 ± 1.2 ^{ns}
<i>Calicotome villosa</i>	12.1 ± 7.2	—	—	35.5 ± 8.7 ^{ns}	0 ^{ns}	—
<i>Trifolium angustifolium</i> var. <i>angustifolium</i>	28.4 ± 3.3	30.4 ± 3.3 ^{ns}	30.8 ± 3.6 ^{ns}	28.6 ± 8.2 ^{ns}	33.6 ± 5.9 ^{ns}	18.5 ± 9.6 ^{ns}
<i>Trifolium arvense</i>	3.6 ± 2.3	—	—	2.3 ± 1.3 ^{ns}	—	—
<i>Trifolium campestre</i>	6.2 ± 3.2	3.6 ± 1.2 ^{ns}	10.4 ± 5.1 ^{ns}	17.8 ± 4.7*	44.7 ± 6.2 ^{****}	1.0 ± 1.0 ^{ns}
<i>Trifolium mesogitanum</i>	4.6 ± 2.6	5.3 ± 2.2 ^{ns}	6.1 ± 2.6 ^{ns}	3.1 ± 2.0 ^{ns}	19.3 ± 5.8**	29.1 ± 13.0 ^{****}
<i>Trifolium</i> sp. 1	19.8 ± 2.2	15.8 ± 4.0 ^{ns}	20.2 ± 4.4 ^{ns}	12.4 ± 3.5 ^{ns}	26.4 ± 6.3 ^{ns}	72.6 ± 11.4 ^{****}
<i>Trifolium</i> sp. 2	10.2 ± 2.5	5.0 ± 1.0 ^{ns}	10.2 ± 3.6 ^{ns}	12.9 ± 2.5 ^{ns}	12.0 ± 5.9 ^{ns}	22.1 ± 3.7*
Hypericaceae						
<i>Hypericum empetrifolium</i>	66.0 ± 10.6	66.2 ± 5.9 ^{ns}	68.6 ± 3.3 ^{ns}	66.8 ± 7.2 ^{ns}	75.6 ± 3.3 ^{ns}	42.8 ± 15.3**
<i>Hypericum</i> sp.	54.2 ± 9.8	69.9 ± 3.8*	48.5 ± 4.3 ^{ns}	66.1 ± 7.0 ^{ns}	57.0 ± 5.0 ^{ns}	50.3 ± 6.2 ^{ns}
Lamiaceae						
<i>Coridothymus capitatus</i>	14.2 ± 5.3	22.1 ± 4.2 ^{ns}	36.2 ± 6.6**	27.3 ± 6.2*	38.2 ± 9.7 ^{****}	39.0 ± 10.1 ^{****}
<i>Lavandula stoechas</i> subsp. <i>stoechas</i>	58.7 ± 4.9	—	72.9 ± 6.3*	73.5 ± 2.7*	80.6 ± 3.5**	—
<i>Origanum onites</i>	49.0 ± 4.4	44.7 ± 3.8 ^{ns}	40.4 ± 6.3 ^{ns}	50.6 ± 9.3 ^{ns}	54.4 ± 4.4 ^{ns}	42.0 ± 12.8 ^{ns}
<i>Phlomis bourgaei</i>	8.5 ± 3.0	10.8 ± 3.6 ^{ns}	3.6 ± 3.6 ^{ns}	0*	0*	0*
<i>Phlomis grandiflora</i>	56.0 ± 7.5	54.6 ± 2.3 ^{ns}	54.6 ± 4.9 ^{ns}	72.5 ± 7.4*	15.2 ± 15.2 ^{****}	0 ^{****}
<i>Prunella vulgaris</i>	99.0 ± 1.0	95.0 ± 1.9 ^{ns}	99.0 ± 1.0 ^{ns}	95.0 ± 2.5 ^{ns}	58.9 ± 23.1 ^{****}	1.0 ± 1.0 ^{****}
<i>Satureja thymbra</i>	4.6 ± 2.7	3.1 ± 2.2 ^{ns}	3.8 ± 1.5 ^{ns}	4.6 ± 1.7 ^{ns}	8.3 ± 2.8 ^{ns}	0 ^{ns}
<i>Stachys</i> sp.	17.1 ± 1.8	13.6 ± 9.6 ^{ns}	15.4 ± 6.6 ^{ns}	4.4 ± 2.6**	0 ^{****}	0 ^{****}
<i>Teucrium chamaedrys</i>	4.1 ± 3.0	1.0 ± 1.0 ^{ns}	3.0 ± 1.9 ^{ns}	10.0 ± 3.1 ^{ns}	0 ^{ns}	0 ^{ns}
<i>Teucrium divaricatum</i> subsp. <i>divaricatum</i>	1.0 ± 1.0	0 ^{ns}	0 ^{ns}	2.1 ± 1.2 ^{ns}	0 ^{ns}	0 ^{ns}
<i>Teucrium lamiifolium</i> subsp. <i>lamiifolium</i>	56.8 ± 6.6	76.3 ± 9.5**	68.9 ± 12.2 ^{ns}	60.9 ± 6.3 ^{ns}	20.8 ± 9.6 ^{****}	0 ^{****}
<i>Teucrium polium</i>	1.0 ± 1.0	0 ^{ns}	0 ^{ns}	0 ^{ns}	0 ^{ns}	0 ^{ns}
<i>Vitex agnus-castus</i>	2.0 ± 1.1	1.8 ± 1.0 ^{ns}	0.9 ± 0.9 ^{ns}	0 ^{ns}	0 ^{ns}	0 ^{ns}
Liliaceae						
<i>Allium paniculatum</i> subsp. <i>paniculatum</i>	92.5 ± 7.5	80.6 ± 11.4 ^{ns}	86.0 ± 5.5 ^{ns}	90.0 ± 10.0 ^{ns}	100.0 ± 0.0**	0 ^{****}
Malvaceae						
<i>Alcea apterocarpa</i>	2.0 ± 1.2	1.9 ± 1.1 ^{ns}	25.4 ± 21.4 ^{****}	73.8 ± 6.4 ^{****}	85.5 ± 5.3 ^{****}	25.5 ± 14.8 ^{****}
<i>Lavatera punctata</i>	1.2 ± 1.2	—	2.6 ± 2.6 ^{ns}	6.4 ± 1.2 ^{ns}	1.3 ± 1.3 ^{ns}	—
Plantaginaceae						
<i>Plantago lagopus</i>	62.7 ± 5.1	60.0 ± 2.9 ^{ns}	75.0 ± 0.9 ^{ns}	94.3 ± 2.4 ^{****}	100.0 ± 0.0 ^{****}	1.0 ± 1.0 ^{****}
Poaceae						

Table 1 (continued)

Taxa	Heat shock treatments					
	Control	60°C, 5 min	80°C, 5 min	100°C, 5 min	120°C, 5 min	140°C, 5 min
<i>Briza maxina</i>	89.8 ± 3.8	85.0 ± 6.1 ^{ns}	88.9 ± 2.0 ^{ns}	85.9 ± 3.2 ^{ns}	78.7 ± 5.0 ^{ns}	—
<i>Bromus sterilis</i>	100.0 ± 0.0	100.0 ± 0.0 ^{ns}	36.0 ± 18.2*			
<i>Chrysopogon gryllus</i> subsp. <i>gryllus</i>	67.7 ± 22.0	97.3 ± 1.7***	66.0 ± 17.4 ^{ns}	26.2 ± 6.9***	16.5 ± 6.5***	0****
<i>Cynosurus echinatus</i>	100.0 ± 0.0	100.0 ± 0.0 ^{ns}	44.5 ± 25.1*			
<i>Cynosurus effusus</i>	100.0 ± 0.0	100.0 ± 0.0 ^{ns}	77.4 ± 21.6 ^{ns}			
<i>Phleum exaratum</i> subsp. <i>exaratum</i>	78.7 ± 4.5	79.7 ± 3.8 ^{ns}	87.8 ± 3.4 ^{ns}	84.8 ± 3.2 ^{ns}	82.2 ± 3.6 ^{ns}	59.3 ± 18.5**
<i>Poa</i> sp.	93.3 ± 3.8	92.9 ± 1.4 ^{ns}	91.4 ± 1.2 ^{ns}	95.9 ± 1.7 ^{ns}	91.5 ± 3.8 ^{ns}	92.9 ± 2.5 ^{ns}
<i>Polygonon monspeltensis</i>	21.8 ± 3.3	11.8 ± 7.4**	8.3 ± 1.6*	7.6 ± 2.8*	8.0 ± 5.4 ^{ns}	4.9 ± 2.0**
Polygonaceae						
<i>Rumex crispus</i>	98.2 ± 1.9	96.0 ± 2.8 ^{ns}	98.0 ± 2.0 ^{ns}	96.9 ± 1.0 ^{ns}	0****	0****
<i>Rumex scutatus</i>	87.6 ± 1.7	100.0 ± 0.0**	99.0 ± 1.0*	88.0 ± 5.9 ^{ns}	64.2 ± 11.4***	0****
Primulaceae						
<i>Anagallis arvensis</i> is var. <i>caerulea</i>	2.0 ± 2.0	0 ^{ns}	1.0 ± 1.0 ^{ns}	0 ^{ns}	1.0 ± 1.0 ^{ns}	0 ^{ns}
Rhamnaceae						
<i>Paliurus spina-christi</i>	7.8 ± 4.1	6.0 ± 3.5 ^{ns}	13.9 ± 4.1 ^{ns}	9.7 ± 2.4 ^{ns}	0 ^{ns}	0 ^{ns}
Rosaceae						
<i>Sarcopoterium spinosum</i>	8.8 ± 0.9	8.1 ± 3.0 ^{ns}	10.4 ± 3.5 ^{ns}	19.6 ± 4.1*	0****	0****
Rubiaceae						
<i>Crucianella latifolia</i>	99.0 ± 1.0	100.0 ± 0.0 ^{ns}	99.0 ± 1.0 ^{ns}	49.1 ± 28.3****	0****	0****
<i>Galium</i> sp.	70.4 ± 6.1	64.8 ± 2.6 ^{ns}	63.4 ± 4.9 ^{ns}	59.9 ± 1.5 ^{ns}	34.6 ± 16.6****	0****
Scrophulariaceae						
<i>Misopates orontium</i>	43.2 ± 4.0	40.6 ± 3.4 ^{ns}	38.1 ± 2.0 ^{ns}	65.5 ± 8.9**	81.9 ± 3.8****	11.6 ± 2.8****
<i>Scrophularia</i> sp.	65.0 ± 1.7	59.0 ± 5.4 ^{ns}	68.0 ± 5.8 ^{ns}	67.8 ± 2.8 ^{ns}	61.8 ± 1.0 ^{ns}	16.9 ± 8.7****

Statistical significance of the difference between each treatment and the corresponding control (analysis of deviance, GLM) is given for each treatment and each taxon (ns – $P > 0.05$, * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$, **** – $P < 0.0001$); ‘-’ indicates the treatment was not applied because of lack of sufficient number of seeds. Full nomenclature and functional properties of taxa are given in Table S1 in the Electronic Supplementary Material

Fig. 1 Dormancy level (percentage of non-germinated viable seeds in control) in categories of growth form (a – annual herb, p – perennial herb, w – woody), distributional range (L – local, R – regional, W – wide) and dormancy type (NPY – non-physical dormancy, PY – physical dormancy). The results of statistical tests (linear mixed models) are shown at the top of each subplot; ns – non-significant ($P > 0.05$), *** – significant at $P < 0.001$.



Phytogeographic origin had no significant effect on the magnitude of germination in any of the heat shock treatments ($P > 0.05$; Fig. S1 in the Electronic Supplementary Material). However, taxonomic family was a determinant of species' response to heat shock and differed in the degree of resistance of seeds to high heat shock doses (Fig. S2 in the Electronic Supplementary Material). Seeds of most of the species belonging to Fabaceae and Cistaceae, which are mostly PY, were resistant to all heat shock treatments whereas significant decreases in the magnitude of germination were observed at high heat shock doses in the Lamiaceae, Poaceae and Asteraceae, all of which are not PY (Fig. S2 in the Electronic Supplementary Material). Furthermore, a significant increase in the magnitude of germination was found for 100°C heat shock treatment in Cistaceae ($P < 0.05$; Fig. S2 in the Electronic Supplementary Material) and slight but non-significant germination increases were noted for the 120 and 140°C heat shock treatments in the Fabaceae (Fig. S2 in the Electronic Supplementary Material).

Discussion

The results showed that one-third of the species under study could germinate better at least one of the heat shock treatments and various heat treatments managed to break dormancy in species with PY seeds. However, seeds of nearly all species could survive after low and moderate heat shocks. Reduced germination was only observed at high heat shock temperatures in many

species. Moreover, we found significant differences in the stimulation of germination in species with different dormancy types and distributional ranges. However, such a difference was not noted among growth forms.

A possible drawback of our study is that our germination results are based on one incubation temperature (20°C) under dark conditions. Although this germination condition is suitable for several plants in the Mediterranean Basin (Thanos 1993; Luna et al. 2012), the incubation temperature and photoperiod conditions might alter the dormancy status of species, especially those with water-permeable seeds (e.g. Batlla and Benech-Arnold 2015; Tavşanoğlu et al. 2017). However, this problem might have only been noted in a few species in which heat shock treatments did not break high-level seed dormancy. Fortunately, since we removed these species from the functional group datasets before analyses, the overall results would not be different if we had used various temperature or light regimes in our experiment.

Heat shock-stimulated germination has been known to be restricted to a few families in the Mediterranean Basin (Keeley et al. 2012) because it is well known especially in the Cistaceae and Fabaceae (Thanos et al. 1992; Herranz et al. 1998; Reyes and Trabaud 2009; Moreira et al. 2010); however, little evidence has also been obtained for other species belonging to other families. To date, seeds of a few species of the Ericaceae (Moreira et al. 2010) and Lamiaceae (Keeley and Baer-Keeley 1999; Moreira et al. 2010) and one species

Table 2 Summary of linear mixed models for magnitude of germination data for the treatment, growth form, distributional range and phylogeographical region, as well as dormancy-type grouping factors included in the study

Models	<i>d.f.</i>	<i>AIC</i>	<i>LogLik</i>	<i>LR</i>	<i>P</i>
Growth form					
Null	4	313.0	-152.5		
Treat	8	249.4	-116.7	71.6	< 0.0001
GF	10	248.9	-114.4	4.5	0.105
Treat*GF	18	248.9	-106.4	16.0	0.042
Distributional Range					
Null	4	313.0	-152.5		
Treat	8	249.4	-116.7	71.6	< 0.0001
DR	10	242.5	-111.3	10.9	0.004
Treat*DR	18	235.7	-99.8	22.8	0.004
Phylogeographical region					
Null	4	313.0	-152.5		
Treat	8	249.4	-116.7	71.6	< 0.0001
PR	9	251.2	-116.6	0.2	0.644
Treat*PR	13	256.9	-115.4	2.3	0.680
Dormancy type					
Null	4	313.0	-152.5		
Treat	8	249.4	-116.7	71.6	< 0.0001
Dorm	9	239.8	-110.9	11.6	0.0007
Treat*Dorm	13	219.9	-96.9	28.0	< 0.0001

Model analyses tested for difference between the null model including only the random factor (genus within the family) and models including both the random and fixed factors. The analysis was performed on arcsine-transformed data. 'Treat' is the treatment, *GF* is the growth form, *DR* is the distributional range, *PR* is the phylogeographical region, 'Dorm' is the dormancy type, *d.f.* is the degree of freedom, *AIC* is the Akaike Information Criterion, *LogLik* is log-likelihood, *LR* is likelihood ratio test estimate. *P* values in bold indicate statistically significant ($P < 0.05$) results

each of the Drosophyllaceae (Cross et al. 2017), Anacardiaceae (Ne'eman et al. 1999), Poaceae (Reyes and Trabaud 2009), Rosaceae (Paula et al. 2009), Rubiaceae (Keeley and Baer-Keeley 1999), Plantaginaceae (Keeley and Baer-Keeley 1999) and Asteraceae (Luna et al. 2007) were found to have enhanced germination after moderate to high heat shocks in the Mediterranean Basin. Because of the limited evidence obtained except for the Cistaceae and Fabaceae in this region, it is suggested that heat shock-stimulated germination is not a clear adaptation to fires in the Mediterranean Basin (Bradshaw et al. 2011;

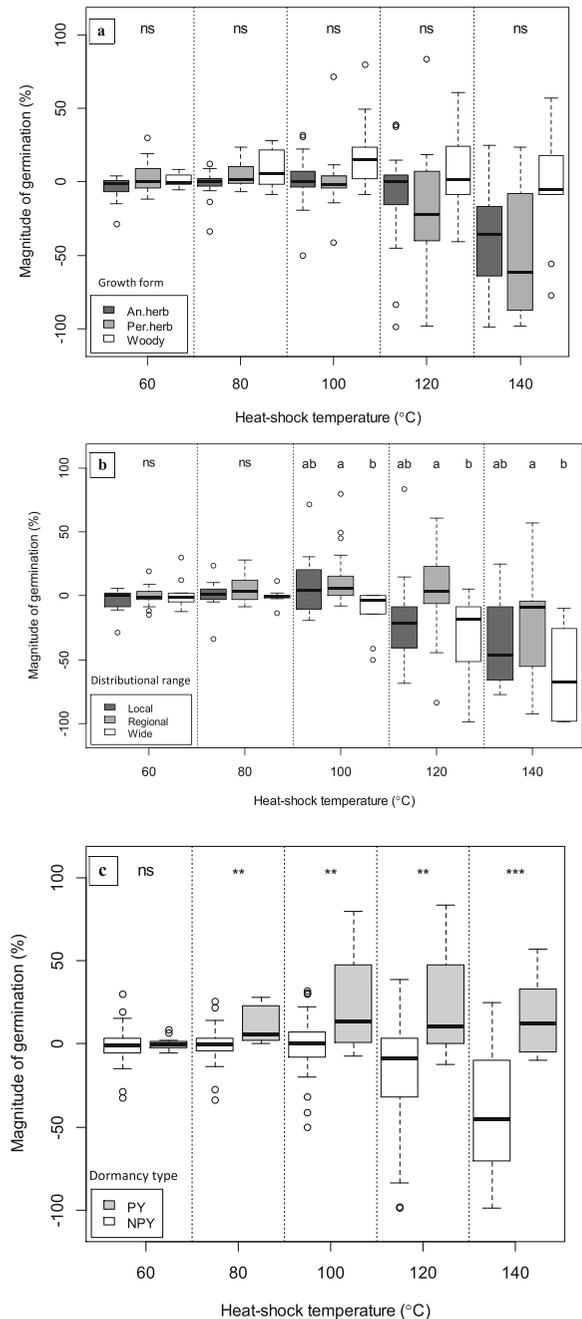


Fig. 2 Magnitude of germination (%) in heat shock treatments for growth forms (a), distributional range groups (b) and seed dormancy types (c). In the distributional range graph, different letters indicate statistically significant differences between groups (linear mixed model followed by Tukey contrasts, $P < 0.05$). In dormancy type graph, statistically significant differences (linear mixed model) are marked with ** ($P < 0.01$) and *** ($P < 0.001$). Non-significant differences are indicated by 'ns' ($P > 0.05$).

Jaganathan 2015; Troia and Laguna 2015). On the other hand, PY breaking mechanisms in some Mediterranean

lineages are related to temperatures in the soil only reached under fire-related conditions, which leads to the conclusion that heat shock-stimulated germination has an adaptive value in an evolutionary sense in the Mediterranean Basin (Keeley et al. 2011; Keeley et al. 2012; Moreira and Pausas 2012). Insufficient taxonomic coverage of studies regarding the effect of heat shocks on germination seems to be one of the reasons for the underestimation of the role of fire in the life histories of Mediterranean plants. Most of the studies were performed only on Cistaceae and Fabaceae species (e.g. Thanos and Georghiou 1988; Trabaud and Oustric 1989; Thanos et al. 1992; Herranz et al. 1998, 1999; Hanley et al. 2001; Tavsanoğlu 2011; Moreira and Pausas 2012; Moreira et al. 2012; Yeşilyurt et al. 2017) and studies evaluating many species belonging to various plant families are rare (Keeley and Baer-Keeley 1999; Luna et al. 2007; Reyes and Trabaud 2009; Moreira et al. 2010). In our study, we found novel evidence for the presence of heat shock-stimulated germination in Mediterranean Basin species belonging to the Brassicaceae (2 species), Malvaceae (1 species), Polygonaceae (1 species) and Scrophulariaceae (1 species). Moreover, we provided additional evidence on the stimulation of germination after heat shock temperatures in the Lamiaceae (3 species), Asteraceae (1 species), Liliaceae (1 species), Plantaginaceae (1 species) and Rosaceae (1 species) in the Mediterranean Basin. Interestingly, heat shock-stimulated germination has been linked with the presence of PY in seeds (Baskin and Baskin 2014), but these families are not listed among the families possessing PY except the Malvaceae (Baskin et al. 2000). Therefore, heat shock-stimulated germination does not seem to be restricted only to families possessing PY seeds in the Mediterranean Basin. However, Mediterranean species with PY seeds have significantly higher germination percentages after heat shocks compared to those that have seeds without PY, and water-permeable seeds are more likely to be sensitive to more intense heat shock treatments. We also observed the same trends at the family level. Among the five most common families in our dataset, three (Poaceae, Asteraceae and Lamiaceae) consisting of species that have seeds without PY showed a decrease in germination as the heat shock temperature increased. By contrast, seeds of species belonging to families with PY (i.e. Fabaceae and Cistaceae) resisted even high heat shock temperatures and

showed increment in germination. Heat shock-stimulated germination is also widespread in Mediterranean-type ecosystems of California, South Africa and Australia (Keeley et al. 2012), and has been observed in species with PY seeds, in particular, in the Fabaceae, Rhamnaceae and Malvaceae families (Bell et al. 1993; Keeley and Bond 1997). To our knowledge, heat shock-stimulated germination in a few species that do not have PY was only documented by Tieu et al. (2001) in other Mediterranean-type ecosystems, but there are observations of heat shock-stimulated germination in species having physiologically dormant seeds in other fire-prone ecosystems such as southeastern Australia (Keith 1997; Mackenzie et al. 2016). Our findings reveal that heat shock-stimulated germination is observed at a wider scale on the phylogenetic tree than previously thought in the Mediterranean Basin and might expand our limited understanding on heat shock-stimulated germination in Mediterranean-type ecosystems. Further analyses on water uptake capacity and seed coat structure of seeds showing heat shock-stimulated germination are needed for a better understanding of the mechanisms of heat shock-stimulated germination in species with a water-permeable seed coat.

Our results on the relationship between the distributional range of species and germination response to heat shocks indicate that widely distributed and local species are less tolerant to moderate heat shocks than species with regional distributional ranges. This finding contradicts the results of Riba et al. (2002), who found no difference between rare and widespread Mediterranean *Centaurea* species regarding the germination response to heat shocks. In their study, which included several Mediterranean species, Luna and Moreno (2010) obtained results supporting this conclusion and suggested that a distinction between life form might help to understand the germination patterns regarding the distributional range. Conversely, our results partly corroborate the findings of a study that included many Mediterranean species (Luna et al. 2007) and found relatively lower germination percentages in heat shock treatments in locally distributed species than in those with wider distribution. Small range size of a species is often attributed to its narrow niche (Slatyer et al. 2013), and germination niche breadth was

found to be correlated to range size in widely distributed species (Brändle et al. 2003). However, studies have also suggested no relationship between these two (Thompson and Ceriani 2003). Narrow endemic species invest less energy in reproductive organs (e.g. producing fewer flowers and seeds) compared to their widespread congeners (Lavergne et al. 2004), and they are less tolerant to environmental stress (Lavergne et al. 2003). On the other hand, widespread species are frequently found in post-fire habitats in the Mediterranean Basin as opportunistic species (Kavgacı et al. 2010) in which seeds come from outside burned areas and are not needed to be fire-adapted to survive. Therefore, weaker germination responses of Mediterranean species with local and wide distribution to heat shocks may have different drivers. The reasons behind this observation need to be explored by performing more experimental studies on the relationship between germination in local (or endemic) Mediterranean species and various fire cues (i.e. heat shock and smoke).

In conclusion, our study suggests that heat shock-stimulated germination is not strictly restricted to a few families with impermeable seed coat in the Mediterranean Basin and can be observed across a broader taxonomic spectrum, including families that do not possess PY. Moreover, our results showed that the type of seed dormancy is an important determinant of germination stimulation by heat shock. Geographic distribution range also has an effect on the germination response of Mediterranean species; species with regional distribution have higher germination percentages after heat shock than those with local or wide distribution. Conversely, growth form was not a determinant of germination stimulation by heat shock.

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