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Germination response of woody species to laboratory-simulated fire severity and airborne nitrogen deposition: a post-fire recovery strategy perspective

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Abstract

Two drivers of global change that affect ecosystem function include wildland fire regimes characterised by frequent, severe fires and increased atmospheric nitrogen (N) deposition. However, their combined effect on the post-fire recovery of Mediterranean forests is still little known. We assessed the interactive effects of two fire severities and N addition on the rate and timing of seed germination of three woody species with different post-fire regeneration strategies in fire-prone forests: *Pinus pinaster*, an obligate-seeder species, and two facultative-seeder species, *Pterospartum tridentatum* (high-resprouting and low-seeding ability) and *Halimium lasianthum* (low-resprouting and high-seeding ability). Seeds were subjected to six combinations of temperature [control (no heat treatment), 60 °C (moderate fire severity) and 120 °C (high fire severity) for 5 min] and N fertilisation (without N and with addition of 4.17 g Nm^{-2} of solid granules of ammonium nitrate, equivalent to three times the current estimate of airborne N deposition in the study area) under laboratory conditions. We found that N fertilisation had a significant, negative effect on the rate of seed germination of the three species under study. Additionally, we detected no differences in *P. pinaster* germination among thermal treatments; while both *P. tridentatum* and *H. lasianthum* had significantly higher germination rates when submitted to high fire-severity conditions. Moreover, the average time of seed germination increased with N fertilisation for *P. pinaster* but increased after the thermal treatments for *H. lasianthum*. These results suggest that increased N availability under intense wildfire regimes may hinder post-fire seed germination, regardless of the species' regeneration strategy, in fire-prone pine forests.

Keywords

Atmospheric nitrogen deposition
Germination
Halimium lasianthum
Pinus pinaster
Pterospartum tridentatum

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Introduction

Recurring disturbances such as wildfires affect the dynamics of many ecosystems worldwide (Turner 2010) and exert a strong evolutionary pressure on plants. As a consequence, numerous species have acquired adaptive traits and mechanisms that confer fitness benefits in repeatedly disturbed environments such as Mediterranean fire-prone ecosystems (Pausas and Keeley 2014). In these ecosystems, the post-fire regeneration of plant species largely depends on their ability to withstand high temperatures during fire (Paula and Pausas 2008) and tolerate repeated burning (e.g. De las Heras et al. 2012), as well as on their strategy for persisting after fire (i.e. essentially, germinating or resprouting; Paula and Pausas 2008; Pausas and Keeley 2014). Indeed, many woody species in these fire-prone environments have heat-tolerant or heat-stimulated germination (e.g. species with physical dormancy; Moreira et al. 2010) that require either a persistent soil/aerial seed bank or the production of heat-resistant seeds (Paula and Pausas 2008; Rivas 2016; Trabaud and Oustric 1989). However, in recent decades, extreme fire events have compromised the natural recovery and the resilience of fire-prone ecosystems across the Mediterranean basin (Doblas-Miranda et al. 2017; San-Miguel-Ayanz et al. 2013 and references therein), with future projections of increased fire extent, frequency, severity and seasonal duration due to climate change and land use transformation (Moreira et al. 2011; Pausas and Paula 2012; Pausas et al. 2008). Under these novel conditions, there might be both a decrease in the resprouting ability of plants and a failure of seeders recruitment, thus altering plant species composition and dominance (e.g. González-De Vega et al. 2016; Moya et al. 2015; Taboada et al. 2017).

To date, many experiments have submitted seeds of Mediterranean woody species to different thermal shock treatments and have confirmed the key role of heat intensity in post-fire germination (see review by Paula and Pausas 2008). Nonetheless, many factors beyond fire temperature influence both the loss of seed dormancy and the rate of post-fire recruitment (e.g. light and daily temperature fluctuations, Baskin and Baskin 2001; smoke, Keeley and Pausas 2018; Moreira and Pausas 2018; Moreira et al. 2010). Indeed, changes in soil nutrient concentrations following fire affect seed germination and seedling recruitment (e.g. Calvo et al. 2008), especially in fire-prone ecosystems (Mayor et al. 2016). In particular, enhanced soil nitrogen (N) availability after fire (Henig-Sever et al. 2000; Marcos et al. 2009; Serrasolses and Vallejo 1999) could help breaking seed dormancy and promoting post-fire germination (Thanos and Rundel 1995). But there is no consistent evidence for a positive effect of the released soil N compounds on seed germination after fire, as this effect might be life form-specific, species-dependent or even inhibitory (Bell et al. 1999; Luna and Moreno 2009; Pérez-Fernández and Rodríguez-Echeverría 2003).

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Moreover, post-fire soil N availability in Mediterranean environments is very likely influenced by the elevated rates of atmospheric N deposition in this area due to pollution (García-Gómez et al. 2014; Ochoa-Hueso et al. 2011). These anthropogenic N inputs are currently one of the main threats to Mediterranean ecosystems, leading to the loss of biodiversity and to changes in structure and ecological function (Bobbink et al. 2010; Calvo-Fernández et al. 2018; Jones et al. 2014; Ochoa-Hueso et al. 2013, 2014). Several long-term experiments have demonstrated the interactive effects of wildfires and N addition on soil chemistry and microbiology (e.g. Green et al. 2013; Southon et al. 2012), and on plant species richness and community composition (e.g. Britton and Fisher 2007; Southon et al. 2012). Yet, to our knowledge, no studies have assessed the response of post-fire seed germination and seedling recruitment to increased airborne N deposition in Mediterranean fire-prone environments. Furthermore, how the combination of novel wildfire regimes with even more frequent high-severity fires and enhanced soil N availability might affect the regeneration of Mediterranean ecosystems remains undetermined. It is therefore essential to investigate how the soil temperatures attained during a fire and the rate of N loading jointly influence the post-fire germination of coexisting species typical of Mediterranean fire-prone ecosystems with different regeneration strategies. This information will aid understanding plant competitive interactions at early successional stages after fire and support effective post-fire management.

The aim of this study was to analyse the joint effect of fire severity and increased atmospheric N deposition on the germination response of three typical woody species (one tree and two shrubs), with different post-fire regeneration strategies, from a Mediterranean fire-prone forest ecosystem, i.e. *Pinus pinaster* Ait., an obligate-seeder species (Tapias et al. 2001, 2004), and two facultative-seeder species, *Pterospartum tridentatum* (L.) Willk. (high-resprouting and low-seeding ability; Reyes et al. 2009) and *Halimium lasianthum* subsp. *alyssoides* (Lam.) Greuter (low-resprouting and high-seeding ability; Rivas 2016). To achieve this aim, we experimentally simulated under laboratory conditions (1) the temperatures experienced during a wildfire by submitting the seeds of the three species to three thermal treatments (control, moderate- and high-severity wildfire) for the same exposure time; and (2) the current estimates of airborne N deposition in the study area by the addition of solid granules of ammonium nitrate to the seed germination dishes. Following Keeley (2009) and Key and Benson (2006), we use the term ‘fire severity’ to indicate the magnitude of environmental change caused by fire that is positively correlated with fire intensity (i.e. the energy output from fire) and, thus, with the soil temperatures attained during fire. As such, this approach represents a continuation of a previous study from our research group (Calvo et al. 2016) in which we demonstrated that seed provenance and weight influence both the rate and timing of germination and the early seedling growth of *P. pinaster*. In particular, highly-serotinous *P. pinaster* populations adapted to frequent fires have comparably lighter seeds with lower heat tolerance (lower germination rates, higher germination times and lower seedling lengths) than very low serotinous populations. Although our previous findings will help restoration aimed at forest regrowth in fire-prone pine areas, we still know very little about how post-fire natural tree regeneration will cope with increased N loading, which needs further research.

Based on prior studies, we expect to find: (i) no significant differences in *P. pinaster* germination among the thermal treatments (Calvo et al. 2016; Martínez-Sánchez et al. 1995; Reyes and Casal 2008; Torres et al. 2006), i.e. heat tolerance sensu Paula and Pausas (2008); (ii) enhanced germination of *P. tridentatum* seeds under both low and high fire-severity treatments (Rivas et al. 2006; Valbuena et al. 2002), i.e. heat-stimulated germination sensu Paula and Pausas (2008) and (iii) an increase in the germination of *H. lasianthum* seeds only under the high fire-severity treatment (Herranz et al. 1999; Núñez et al. 2003; Trabaud and Oustric 1989; Valbuena et al. 1992), i.e. heat-stimulated germination. Furthermore, we expect either no effect or a negative effect of high N addition on the post-fire germination of the three woody species studied under the low fire-severity treatment (Bell et al. 1999; Pérez-Fernández and Rodríguez-Echeverría 2003). Additionally, we explore the interactive effects of high fire-severity and N addition on seed germination due to the potential complex effects of high fire-attained temperatures on soil chemistry and enzymatic activities in fire-prone pine ecosystems (Fernández-García et al. 2019a, b).

Materials and methods

Seed material

Seeds were collected at Sierra del Teleno mountain range (NW Spain; 42°15′34″N/06°12′13″W; 850–2100 m a.s.l.; 10% average slope), a landscape dominated by maritime pine (*P. pinaster*) natural forests with a tall (up to 1.5 m height) shrubby understorey with *Erica australis* L., *P. tridentatum* and *H. lasianthum*. The climate is Mediterranean with an average annual rainfall between 650 and 900 mm, mean annual temperature of 10 °C and 2–3 months of summer drought. Soils are Cambisols, very sandy and acidic (pH 4.66 ± 0.25) with low organic matter content (Luis-Calabuig et al. 2002). Wildfires are very frequent, typically caused by dry lightning storms [172 small fires (< 500 ha) in 1974–2007; Santamaría 2015]. From 1978 to 2014, the number of fires that occurred in the area ranged from 1 to 4 (four fire recurrences identified from visual interpretation of 75 Landsat images and validation with official fire reports; Fernández-García et al. 2018). In 1998 (13–14 September, 3670 ha) and 2012 (19–21 August, 11,891 ha) two large high-severity wildfires burned the area (Quintano et al. 2015, 2017) resulting in undermined pine seedling recruitment and altered plant species composition at the initial stages of succession (Taboada et al. 2017): obligate-seeder species dominated in areas burned by a single large fire event, whereas resprouter species dominated after repeated fires. Although *P. pinaster* forests in the study area are highly adapted to intense crown fires with more than 95% of the trees bearing serotinous cones (Tapias et al. 2004), the current fire return intervals (less than 10–15 years) hinder pine reproductive maturity and favour high-flammability shrublands, as in many areas of the western Mediterranean basin (Baeza et al. 2007; Fernandes and Rigolot 2007; González-De Vega et al. 2016).

We purchased *P. pinaster* seeds from the Forest Germplasm Bank of the National Centre of Forest Genetic Resources (Spanish Ministry of Agriculture, Food and Environment). The mature cones from which seeds were obtained had been harvested in November 2015–May 2016 from pre-established stands (1779 ha) within the study area. These established stands are as long-lasting sources from which seeds are collected by the administration for different purposes like research studies, conservation and management activities (see further details in Calvo et al. 2016). We collected *P. tridentatum* and *H. lasianthum* seeds at the study area during summer 2016. After purchase or collection, we kept the seeds in open paper bags, which allowed ventilation, at 10–15 °C in a dry place until they were used.

Thermal shock and nitrogen addition treatments

In November 2016, a total of 1200 seeds (i.e. 48 groups of 25 seeds) from each study species were subjected to six combinations of temperature [control (‘C’), 60 °C for 5 min (‘MS’) and 120 °C for 5 min (‘HS’)] and N addition [without (‘N−’) and with N (‘N+’)] treatments (i.e. eight replicates or groups of 25 seeds per species and treatment combination).

The temperatures and exposure time were selected based on previous studies (Trabaud and Casal 1989) and on the temperatures measured with thermocouples at 1 cm depth during a prescribed burning (Valbuena 1995), to simulate heat exposure reached during a moderate-(MS; 60 °C for 5 min) and a high-severity (HS; 120 °C for 5 min) wildfire. We submitted the seeds to the thermal shocks simultaneously, in pre-heated ceramic capsules using a dry air oven. Just after that, each group of 25 seeds per thermal treatment and species was sown in a Petri dish (8.5 cm diameter, 63.61 cm^2; 144 dishes in total) on four sheets of filter paper saturated with demineralised water to prevent desiccation.

Subsequently, we added 0.034 g of solid granules of ammonium nitrate (i.e. 4.17 $g\ N\ m^{-2}$) to half of the germination dishes (i.e. to a total of 24 dishes per species, and 8 dishes per thermal treatment and species), equivalent to three times the current estimate of airborne N deposition in the study area (European Monitoring and Evaluation Programme 2016) and to the highest predicted N input by 2050 for southern Europe (Galloway et al. 2004). The addition of N to the Petri dishes did not modify pH values remarkably (all values ranged between 6.90 and 7). Solid granules release ammonium and nitrate slowly over the soil surface, and have been used in prior experiments assessing the ecosystem responses to airborne N deposition (e.g. Calvo-Fernández et al. 2018; Taboada et al. 2018).

We placed the dishes in a controlled environment cabinet at 20 ± 1 °C with photoperiods of 15-h light/9-h dark using a fluorescent cold light source. We watered the dishes two times per week, and inspected them weekly to determine the rate and time of seed germination. The selected temperature of 20 °C is equivalent to that used in previous germination experiments (Trabaud and Oustric 1989). According to Côme (1970), germination was attained when the radicle could be seen with the naked eye. In agreement with the method proposed by Martínez-Sánchez et al. (1995), the experiment ended after nearly 10 days without germination. After application of the thermal and N fertilisation treatments, we calculated (i) the percentage of seed germination, and (2) the average seed germination time.

We used the following formula by Côme (1970) to calculate the average germination time (*tm*):

$$tm = \frac{N_1T_1 + N_2 \ldots + N_nT_n}{N_1 + N_2 \ldots + N_n}$$

where N_1 is the number of seeds that have germinated during time T_1, N_2 is the number of seeds that have germinated between time T_1 and time T_2 and so on.

Data analysis

Separately for each species, we fit a generalised linear model (GLM) and a linear model (LM) to test the effects of the thermal shock and N fertilisation treatments on the rate and time of seed germination, respectively. The response variable in the GLM was the percentage of seed germination, modelled following a quasi-Poisson error distribution, using the log link function, to account for overdispersion. The response variable in the LM was the average germination time in weeks, modelled assuming a Gaussian error distribution, using the identity link function. The predictor variables in both the GLM and LM were thermal shock treatment [i.e. control (C), 60 °C for 5 min (MS) and 120 °C for 5 min (HS)], N fertilisation treatment (N− and N+) and their interaction. The interaction term was always retained in the models, even when non-significant.

For each species, the GLM structure was:

Response variable (percentage of seed germination) ~ thermal shock × N treatment + error.

Similarly, for each species, the LM structure was:

Response variable (average germination time) ~ thermal shock × N treatment + error.

We obtained predicted values (mean and 95% confidence intervals) of all the response variables in the GLM and LM (i.e. the rate of seed germination and the average germination time) for each species, thermal shock treatment and N fertilisation treatment, using the 'predict()' function.

All data analyses were carried out with R software, version 3.3.1 (R Core Team 2016) using the 'stats', and 'MASS' (Venables and Ripley 2002) packages.

Results

The percentages of seed germination of *P. pinaster* after the thermal shocks (moderate- and high-severity) were similar to those attained in the control treatment (Fig. 1; Table 1). However, the addition of N caused a statistically significant decrease ($\chi^2 = 9.67$, $P = 0.002$) in the rate of seed germination of this species in all thermal treatments. Similarly, there were no significant differences in the average seed germination time of *P. pinaster* among thermal treatments but seed germination time of this species was significantly negatively ($F = 6.27$, $P = 0.022$) affected by N addition, i.e. the average germination time consistently increased after all thermal treatments due to N fertilisation (Fig. 2; Tables 2, 3).

Fig. 1

Model predicted values (mean ± 95% confidence intervals) of the seed germination rate (%) of *P. pinaster*, *P. tridentatum* and *H. lasianthum* after the thermal shock [control (C), 60 °C for 5 min (MS) and 120 °C for 5 min (HS)] and N fertilisation (N−and N+) treatments

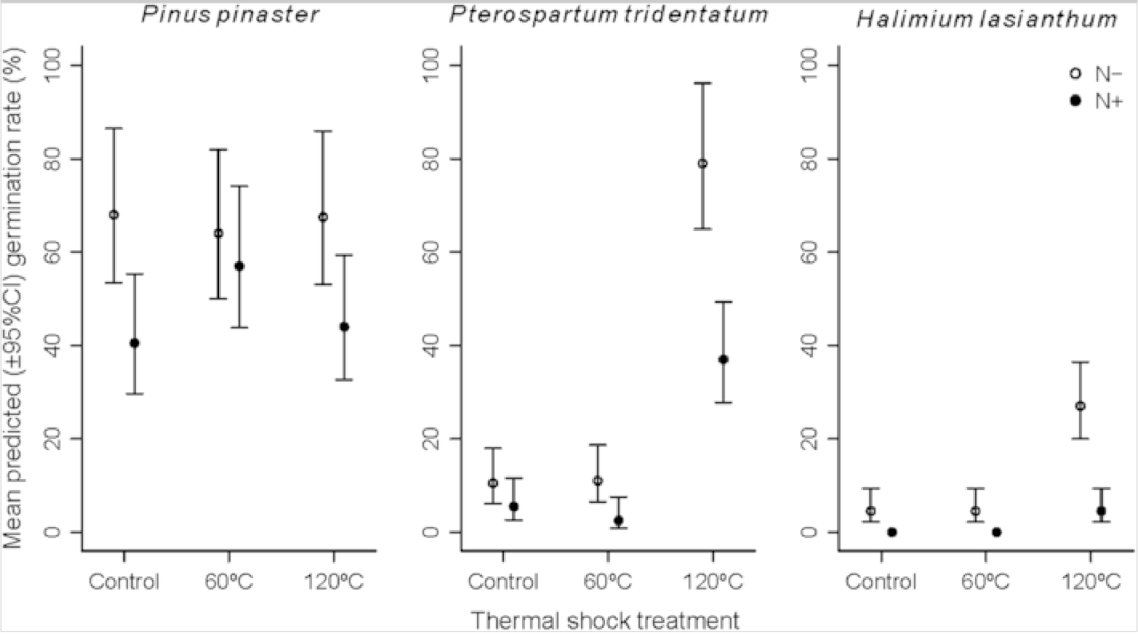

Table 1

Generalised linear model (GLM) results for the effects of the thermal shock treatments [control (C), 60 °C for 5 min (MS) and 120 °C for 5 min (HS)]), N fertilisation treatments (N−and N+) and their interaction on the rate (%) of seed germination of *P. pinaster, P. tridentatum* and *H. lasianthum*

Predictor variable	**Df**	**Deviance**	**Residual deviance**	***P* value**
P. pinaster				
Null			460.00	
Thermal shock treatment	2	5.95	454.05	0.696
N treatment	1	79.31	374.74	**0.002**
Thermal shock treatment:N treatment	2	20.23	354.51	0.291
P. tridentatum				
Null			1535.74	
Thermal shock treatment	2	1058.35	477.39	**< 0.001**
N treatment	1	173.73	303.67	**< 0.001**
Thermal shock treatment:N treatment	2	9.67	294.00	0.468
H. lasianthum				
Null			748.72	
Thermal shock treatment	2	268.84	479.88	**< 0.001**
N treatment	1	223.12	256.76	**< 0.001**
Thermal shock treatment:N treatment	2	19.35	237.42	0.148

Residual deviance is the amount of variation not explained by the models. Residual degrees of freedom = 42. Significant *P* values (< 0.05) are in bold face. *Df* degrees of freedom

Fig. 2

Model predicted values (mean ± 95% confidence intervals) of the average seed germination time (weeks) of *P. pinaster*, *P. tridentatum* and *H. lasianthum* after the thermal shock [control (C), 60 °C for 5 min (MS) and 120 °C for 5 min (HS)] and N fertilisation (N−and N+) treatments

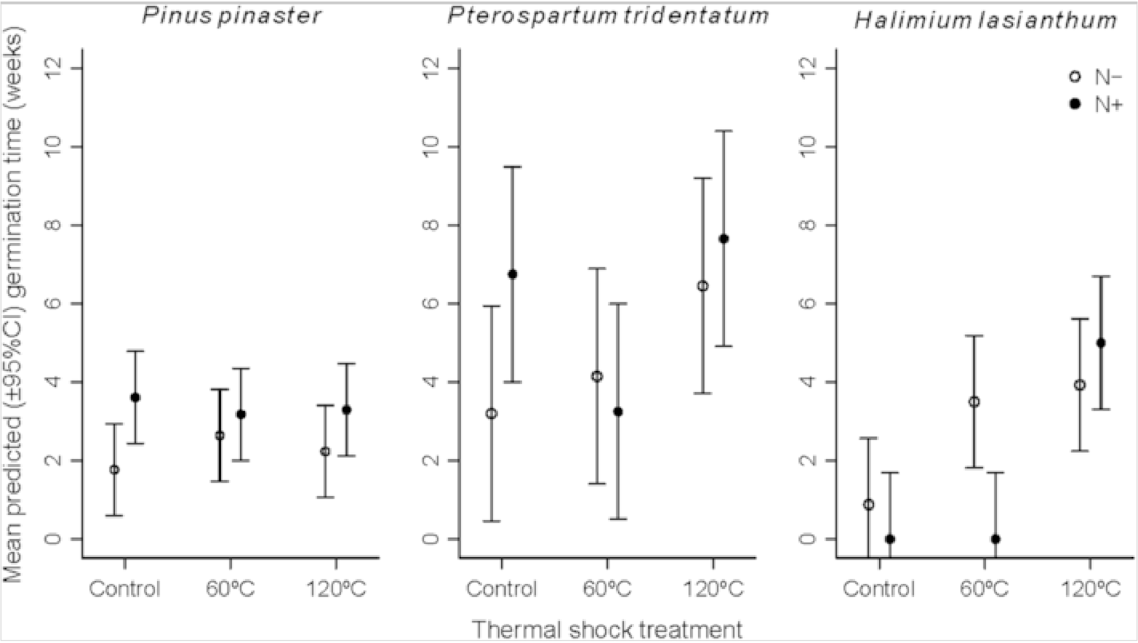

Table 2

Mean and standard deviation (SD) germination time (weeks) for *P. pinaster, P. tridentatum* and *H. lasianthum*

	P. pinaster		***P. tridentatum***		***H. lasianthum***	
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
CN−	1.8	0.6	3.2	1.7	0.9	1.2
CN+	3.6	1.5	6.8	4.5	0.0	0.0
MSN−	2.6	0.5	4.2	2.7	3.5	3.5
MSN+	3.2	1.0	3.3	2.2	0.0	0.0
HSN−	2.2	0.5	6.5	1.0	3.9	0.7
HSN+	3.3	1.8	7.7	2.2	5.0	1.2

Thermal shock and N fertilisation treatment combinations: CN− = control without N addition; CN+= control plus N addition; MSN−= moderate fire severity without N addition; MSN+ = moderate fire severity plus N addition; HSN− = high fire severity without N addition and HSN+ = high fire severity plus N addition

The rate of seed germination of *P. tridentatum* was significantly lower ($\chi^2 = 166.21$, $P < 0.001$) in the control and moderate-severity treatments than in the high-severity one (Fig. 1; Table 1). There was also a statistically significant decrease ($\chi^2 = 27.28$, $P < 0.001$) in the percentage of seed germination of this species after the addition of N in all thermal treatments. However, we found no differences in the average seed germination time of *P. tridentatum* neither among thermal treatments nor between N treatments (Fig. 2; Tables 2, 3).

In general, we obtained very low values of seed germination for *H. lasianthum*. Nevertheless, the percentage of seed germination of this species was significantly higher ($\chi^2 = 53.04$, $P < 0.001$) in the high-severity treatment than in the control and moderate-severity ones (Fig. 1; Table 1). Moreover, no seed germination was detected after the addition of N in the control and moderate-severity treatments; whereas the added N caused a significant decrease ($\chi^2 = 44.02$, $P < 0.001$) in the rate of seed germination in the high-severity treatment. We also found a significant interaction ($F = 4.08$, $P = 0.035$) between thermal treatment and N treatment for the average seed germination time of this species (Fig. 2; Table 3). Compared to the control, the average germination time increased in the moderate- and high-severity treatments without N addition; but only in the high-severity treatment when N was added (Fig. 2; Tables 2, 3).

Table 3

Linear model (LM) results for the effects of the thermal shock treatments [control (C), 60 °C for 5 min (MS) and 120 °C for 5 min (HS)], N fertilisation treatments (N−and N+) and their interaction on the average time (weeks) of seed germination of *P. pinaster*, *P. tridentatum* and *H. lasianthum*

Predictor variable	**Df**	**Sum of squares**	***F* value**	***P* value**
P. pinaster				
Thermal shock treatment	2	0.205	0.08	0.922
N treatment	1	7.866	6.27	**0.022**
Thermal shock treatment:N treatment	2	1.738	0.69	0.513
Residuals	18	22.597		
P. tridentatum				
Thermal shock treatment	2	45.986	3.37	0.057
N treatment	1	9.920	1.45	0.244
Thermal shock treatment:N treatment	2	19.779	1.45	0.261
Residuals	18	122.843		
H. lasianthum				
Thermal shock treatment	2	67.46	13.07	**< 0.001**
N treatment	1	7.27	2.82	0.111
Thermal shock treatment:N treatment	2	21.06	4.08	**0.035**
Residuals	18	46.47		

Significant *P* values (< 0.05) are in bold face

Df degrees of freedom

Discussion

Under laboratory conditions, the germinative response to the thermal treatments of the three woody species tested was only partially as expected in relation to their post-fire regeneration strategies. Firstly, the rate and average time of seed germination of *P. pinaster*, an obligate-seeder species, showed no significant differences when submitted to the two heat shocks simulating a moderate-(60 °C for 5 min) and a high-severity (120 °C for 5 min) wildfire and the control treatment, in agreement with our predictions and with earlier studies (e.g. Martínez-Sánchez et al. 1995; Reyes and Casal 2008; Torres et al. 2006).

In particular, our laboratory results are consistent with previous findings indicating that seed germination of *P. pinaster* is not heat-stimulated (Álvarez et al. 2005, 2007; Escudero et al. 1999; Martínez-Sánchez et al. 1995; Reyes and Casal 2001) and that seeds tolerate temperatures lower than 130 °C and short exposure times (Fernandes and Rigolot 2007, references therein). Our studied population exhibits high levels of serotiny (i.e. high percentage of trees bearing serotinous cones) evolved under frequent crown fires (Tapias et al. 2004) and low seed weights (Calvo et al. 2016) resulting in comparatively greater seed sensitiveness to high temperatures and lower seed resistance to fire than heavier seeds (Álvarez et al. 2007; Escudero et al. 2000; Reyes and Casal 2001). Yet, it has been amply proven that serotinous cones: (i) ensure seed viability during a high-severity fire (Alexander and Cruz 2012; Reyes and Casal 2002); (ii) promote seed resistance (Moya et al. 2013; Salvatore et al. 2010); (iii) guarantee seed mechanical and thermal protection (Fernandes and Rigolot 2007; Moya et al. 2008) and (iv) produce the massive discharge of seeds several days after a wildfire (De las Heras et al. 2012), delaying germination until optimal temperatures are achieved at the surface level (Hernández-Serrano et al. 2013; Saracino et al. 1997). This advantageous fire-adaptive strategy of the studied population with seeds retained predominantly inside serotinous cones, therefore, ensures high levels of post-fire seed germination and sufficient seedling recruitment to obtain adequate natural tree regeneration after a single fire event (Calvo et al. 2008; see also Fernández et al. 2008; Gil et al. 2009; Rodríguez-García et al. 2010).

Secondly, the rates of germination of *P. tridentatum* and *H. lasianthum* were enhanced only when seeds were exposed to the high fire-severity treatment (i.e. heated seeds had greater germination than untreated ones). Meanwhile we found no differences in the average time of seed germination of *P. tridentatum* between the two heat shocks and the control treatment, but significantly greater germination time for *H. lasianthum* after exposure to both the moderate- and high-severity thermal shocks. Contrary to our expectations and other findings (Rivas et al. 2006; Valbuena et al. 2002; Vasques et al. 2012), *P. tridentatum*, a facultative-seeder species with high-resprouting ability, had heat-stimulated germination rates just after submission of the seeds to the highest temperatures (120 °C for 5 min) under laboratory conditions, but equal average germination times. This may indicate that the light thermal shock (60 °C for 5 min) applied to simulate a moderate-severity fire was insufficient to promote significantly greater percentages and faster times of seed germination of this species consistent with Valbuena and Vera (2002).

In the case of *H. lasianthum*, a facultative-seeder species with low-resprouting ability, the greater rates of seed germination in response to the high fire-severity treatment agreed with previous results on the species (Herranz et al. 1999; Núñez et al. 2003; Trabaud and Oustric 1989; Valbuena et al. 1992). Whereas the slower germination times of the heated seeds compared to the untreated ones possibly revealed a delay in the start of germination after the thermal treatments (Rivas 2016). All in all, our laboratory-based findings only partially agree with prior laboratory heat experiments from the Mediterranean basin demonstrating that, in general, non-resprouter species exhibit higher probabilities of fire-stimulated germination and greater capacity to increase their populations after fire than resprouter species (Paula and Pausas 2008).

As predicted, the rate of seed germination of the three species studied was reduced by the addition of N in the unheated treatment as well as after application of the two heat shocks simulating a moderate- and a high-severity wildfire under laboratory conditions. Correspondingly, we found either no effect (in case of *P. tridentatum*) or a negative effect of N addition on the average time of seed germination (i.e. greater average germination times) after all thermal treatments (in case of *P. pinaster*) or just after the high-severity one (in case of *H. lasianthum*). Under the current context of increased airborne N deposition (García-Gómez et al. 2014), these results might indicate that the combination of high temperatures during fire and improved N availability may hinder the post-fire germinative response of a number of woody species typical from Mediterranean fire-prone ecosystems like the ones tested in our study. This may, in turn, have an unprecedented effect on plant competitive interactions and community composition following fire (see Taboada et al. 2017; Vourlitis and Pasquini 2009). Nonetheless, as our results were obtained under the controlled conditions from a laboratory experiment, they should be supported by further field-based research on the key environmental drivers of post-fire seed germination of woody species in fire-prone ecosystems under elevated N availability.

Generally, the regrowth of Mediterranean pine forests after a wildfire is attained by direct regeneration of the preceding plant community, owing to the activation of resprouter species and to fire-stimulated seed germination (Calvo et al. 2012; De las Heras et al. 2012; Pausas et al. 2008). Fast-growing resprouter species are well adapted to frequent fire (Calvo et al. 2012; Pausas and Vallejo 1999); meanwhile obligate-seeder species are benefited by high-severity fires (Pausas and Keeley 2014) and high water limitation (Moya et al. 2015). As discussed above, non-resprouter species are thus highly tolerant to heat exposure and have higher potential than resprouter species to persist and even to increase their populations (i.e. owing to heat-stimulated germination) after extremely intense wildfires (Paula and Pausas 2008). Therefore, unless fires occur at a return interval shorter than the minimum required time for obligate-seeder species to reach reproductive maturity (e.g. less than 10–15 years in case of *P. pinaster*; Fernandes and Rigolot 2007; Tapias et al. 2001), they usually achieve high rates of seed germination and seedling emergence following fire (e.g.. Hernández-Serrano et al. 2013).

In the studied maritime pine forests adapted to dry environments and low nutrient availability (Marcos et al. 2018), the increase in soil fertility immediately after fire (Calvo et al. 2008) together with the improved post-burn environmental conditions (i.e. high availability of space and low seed predation risk; Hernández-Serrano et al. 2013) most likely result in greater competition for light, water and nutrients between gradually-recruited seedlings and fast-growing resprouter species (Calvo et al. 2013; Taboada et al. 2017). Such fire-induced changes in plant competitive interactions may overcome the potential effects of enhanced airborne N availability on post-fire seed germination, as the newly emerged seedlings and the new shoots produced by resprouter species may rapidly cause the depletion of nutrients in the upper soil layer. Meanwhile obligate-seeder species usually allocate nutrient resources to growth and rapid reproductive maturity (Bell 2001; Rodríguez-García and Bravo 2013), resprouter species devote them to below-ground storage structures to ensure survival after the next fire (Knox and Clarke 2005, and references therein). This might therefore imply that facultative-seeder species with high-resprouting abilities like *P. tridentatum* would be benefited at fertile sites with elevated N loading, making them better competitors than obligate seeders after frequent fires at short return intervals (Clarke et al. 2005; Knox and Clarke 2005; Reyes et al. 2009).

Moreover, the magnitude and direction of the effects of high N inputs on the post-fire germination of Mediterranean plant species may vary along moisture gradients (Bell et al. 1999; see also Li et al. 2011) or depend on the species' light tolerance (Bell et al. 1999; Luna and Moreno 2009). However, the underlying mechanisms determining the role of elevated N availability on seed germination after fire are still unclear. For instance, as suggested by recent studies, enhanced airborne N loading could influence seed production and early seedling growth differently, either depending on the availability of soil phosphorous (P) (Zhang et al. 2013) related to fire severity (Fernández-García et al. 2019a, b), or even mediated by an indirect effect of improved N loads on the maternal environment (Li et al. 2011).

Finally, prior research has determined increased N availability could have less of an effect on post-fire seed germination in Mediterranean fire-prone environments than other fire-related germination cues such as smoke and charred wood (Pérez-Fernández and Rodríguez-Echeverría 2003, references therein). What is more, under real-world scenarios, post-fire abiotic conditions [e.g. absence of vegetation cover, increased soil temperature fluctuations; Jaganathan (2015)] could also interact with greater N loads caused by atmospheric pollution. Thus, further work is needed to disentangle the complex relations among the myriad of factors potentially affecting the post-fire germinative response of coexisting Mediterranean woody species at fire-prone ecosystems under the current context of elevated airborne N inputs.

Publisher's Note

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