

Burning seeds: germinative response to heat treatments in relation to resprouting ability

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Summary

1. In Mediterranean fire-prone ecosystems, plant species persist and regenerate after fire by resprouting, by recruiting new individuals from a seed bank (post-fire seeding), or by both resprouting and post-fire seeding. Since species with resprouting ability are already able to persist in fire-prone ecosystems, we hypothesize that they have been subjected to lower evolutionary pressure to acquire traits allowing or enhancing post-fire recruitment. Consequently, we predict that the germination of non-resprouters is more likely to be increased or at least unaffected by heat than the germination of resprouters.

2. To test this hypothesis we compiled published experiments carried out in Mediterranean Basin species where seeds were exposed to different heat treatments. We compared the probability of heat-tolerant germination (i.e. heated seeds had greater or equal germination than the control), the probability of heat-stimulated germination (i.e. heated seeds had greater germination than the control) and the stimulation magnitude (differences in proportion of germination of the heated seeds in relation to the untreated seeds, for heat-stimulated treatments) between resprouters and non-resprouters.

3. Non-resprouters showed higher probability of heat-tolerance, higher probability of heat-stimulation and higher stimulation magnitude even when phylogenetic relatedness was considered. Differences between life-forms and post-fire seeding ability do not explain this pattern.

4. Non-resprouters appear to have a greater capacity to both (i) persist after fire by means of recruiting (greater heat-tolerance) and (ii) increase their population after fire (greater heat-stimulated germination), than resprouters.

5. *Synthesis.* Our results contribute to understanding the factors that condition the evolution of fire-persistence plant traits and support the hypothesis that resprouting and post-fire recruitment are negatively associated in Mediterranean Basin flora.

Key-words: fire-stimulated germination, heat treatments, Mediterranean Basin, resprouters, seeders

Introduction

Fire is one of the most predictable disturbances faced by plants in Mediterranean ecosystems (Di Castri *et al.* 1981). Plant species have two basic mechanisms for persisting in Mediterranean fire-prone ecosystems (Keeley & Zedler 1978; Pausas *et al.* 2004): by regenerating their above-ground biomass (i.e. resprouting) by plants that survived the fire (persistence at the individual and population-level) and by recruiting new individuals from a fire-resistant seed bank (persistence at the population-level only). Resprouters and seeders are the typical terms used to refer to the species that

regenerate after fire primarily through the first or the second mechanism, respectively (Keeley & Zedler 1978). In fire-prone ecosystems, resprouters and seeders coexist; in addition, many species may have traits that allow them to both resprout and recruit after fire (e.g. Gill 1981; van Wilgen & Forsyth 1992; Enright & Goldblum 1999; Pausas *et al.* 2006). In the Mediterranean Basin, there is a negative correlation between the traits associated with post-fire resprouting and those associated with post-fire seeding such that post-fire seeding traits appeared later in evolution than resprouting traits and were mainly acquired by non-resprouting lineages (Pausas & Verdú 2005). These results suggest that both strategies may be efficient for persistence in Mediterranean fire regimes and that having one of them may reduce the probability of acquiring the other.

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Post-fire recruitment may succeed because the heat of the fire may break seed dormancy or quiescence, and enhance germination (e.g. Thanos *et al.* 1992; Herranz *et al.* 1998; Keeley & Fotheringham 2000). Increased permeability of the seed coat and, to a lesser extent, induction of physiological processes and denaturing of seed coat inhibitors, are implicated in fire-triggered seed germination (Keeley 1991; Thanos *et al.* 1992; Bell *et al.* 1993; van Staden *et al.* 2000). Furthermore, in some species, seeds resist the heat produced by fire, but germination is not fire-stimulated (Trabaud & Casal 1989). Other germination cues related to fire, such as smoke, charcoal and nitrogenous compounds, have also been identified (Keeley & Bond 1997; Keeley & Baer-Keeley 1999; Clarke *et al.* 2000; van Staden *et al.* 2000; Wills & Read 2002; Pérez-Fernández & Rodríguez-Echevarría 2003); nevertheless, to respond to any of these cues, seeds must first survive the high temperatures released during a fire.

Fire-stimulated germination is common in most Mediterranean-climate shrublands although it seems to be taxonomically aggregated, most common in the Cistaceae and Fabaceae, and in some clades of the Rhamnaceae and Malvaceae (Thanos *et al.* 1992; Bell *et al.* 1993; Keeley & Bond 1997; Keeley & Fotheringham 2000). Nevertheless, it has been suggested that this trait is less frequent in the Mediterranean Basin than in other Mediterranean ecosystems (Keeley & Baer-Keeley 1999), and a substantial amount of post-fire recruitment is probably the result of the seeds being tolerant to fire rather than being stimulated by it (Buhk & Heslen 2006; Luna *et al.* 2007).

Both fire-resistant and fire-stimulated germination require the presence of a persistent seed bank or the production of heat-resistant seeds just before fire (Pausas *et al.* 2004). Dormancy, which is strongly correlated with persistence of seed banks (Thompson *et al.* 1998), is a widespread heritable trait among angiosperms (Baskin *et al.* 2000). However, great inter- and intra-variability in seed dormancy and heat-stimulated germination has been found in several species (Keeley 1991; Pérez-García 1997; Herranz *et al.* 1999; Cruz *et al.* 2003a; see Tieu *et al.* 2001 for variability in the germinative response to smoke). Because natural selection acts on the variability of heritable traits, the evolution of heat-stimulated germination could be determined by the intensity of the selective pressure.

Whereas the resistance of seeds to fire only ensures the persistence of the plant population, fire stimulated germination permits a large number of offspring to be produced after fire and increases the population size compared with the pre-fire population (Roy & Sonie 1992; Ladd *et al.* 2005). Rapid post-fire recruitment enhances plant fitness by accessing more resources (Bond & van Wilgen 1996) and thus growing faster, shortening the time to reach maturity after fire and increasing the probability of storing a large amount of seeds before the next fire (Le Maitre & Migdley 1992; Verdú & Traveset 2005). Consequently, post-fire seedling emergence is under strong selective pressure.

We hypothesize that because species with resprouting ability are able to persist in fire-prone ecosystems, they may

have been subjected to lower evolutionary pressure to acquire traits that enable or enhance their recruitment after fire. On the contrary, species with no resprouting ability can only persist in fire-prone environments if they have an efficient post-fire recruitment process. Consequently, we expect a higher germinative response to heat treatments in non-resprouters than in resprouters. That is, we predict that the germination of non-resprouters is more likely to be increased or at least unaffected by heat than the germination of resprouters. To test this hypothesis we performed an exhaustive compilation of published experiments in which seeds from Mediterranean Basin species were exposed to different heat treatments (combinations of temperature and exposure time), and then we compared the germinative response of the resprouters and non-resprouters. The germinative response was characterized as: (i) heat-tolerance, if germination of the heated seeds was greater or equal to that of the control; and (ii) heat-stimulation, if germination of heated seeds was greater than that of the control. The first case is related to the potential persistence of the population regardless of changes in population size, while the second indicates a potential increase in the post-fire population size. So, specifically, we tested whether heat-tolerance and heat-stimulation are higher for non-resprouters than for resprouters.

Methods

DATA SET

We compiled a data set on heat experiments, that is, experimental germination tests under different temperatures and exposure times, performed on species of the Mediterranean Basin. We considered only dry-heat exposure experiments (cases using scarification with boiling water were not included) and only those in which the temperatures applied were ≥ 50 °C. For each study and species, we compiled the percent germination of the control and the percent germination of each heat treatment (combination of temperature and exposure time). Cases in which both the control and the treatment showed 0% germination were excluded. For experimental designs in which seeds of the same species and population were subjected to different storage conditions (e.g. with and without stratification) and/or incubation regime (e.g. in dark and in light conditions), we included only the germination test in which the untreated seeds showed the highest germination. This is a conservative criterion for avoiding pseudo-replication in the data set. Experiments performed on seeds from serotinous species were discarded because seeds inside cones are protected from the heat of a fire (Habrouk *et al.* 1999). In the Mediterranean Basin, serotiny is only found in some conifers (Pausas 1999), and the amount of serotinous cones varies greatly among populations (Goubitz *et al.* 2004; Tapias *et al.* 2004); furthermore, the selective pressure of fire on serotinous species may act on different traits from seed traits (e.g. cone traits). To ensure consistency, all coniferous species were excluded from the data set; our analysis was thus restricted to angiosperms.

For the compilation, species names were standardized following the European Science Foundation – European Documentation System (ESFEDS) which is largely based on *Flora Europaea* (Tutin *et al.* 1964–80). The ESFEDS database was checked in the Global Plant Checklist of the International Organization for Plant Information (IOPI 1996–2005). Other criteria were followed in cases where

some important taxonomical updates had been carried out (e.g. Talavera *et al.* 1999 for Genistaceae) or when some species were missing in the ESFEDS database (e.g. Greuter *et al.* 1984–89 for Cistaceae). For family names, the Angiosperm Phylogenetic Group standards were used (Bremer *et al.* 2003).

We found 53 references reporting appropriate data on heat experiments for 164 species or subspecies included in 28 families and 85 genera (Appendix S1 in Supplementary material). This yielded a total of 1684 entries. Most of these studies (78%) report the statistical test between the control and the treatment.

For each species in the data set, we compiled its post-fire response based on bibliographic references and personal field observations. Because the germinative response to fire cues is related to the life-form (Keeley & Bond 1997; Clarke *et al.* 2000; van Staden *et al.* 2000), we also compiled this trait, mostly from local floras. The life-forms considered were: woody plants, perennial herbs (including hemicryptophytes, geophytes and some plants slightly lignified at the base) and annuals. We considered that a species had the ability to resprout (R+) if there was field evidence of resprouting after 100% scorching (Gill 1981; Pausas *et al.* 2004); otherwise, it was considered a non-resprouter (R-). Species with field evidence of post-fire seedling emergence from a soil seed bank or from seeds produced just before fire were considered seeders (S+); otherwise they were considered non-seeders (S-). Note that species recruiting after fire from outside populations (arriving by dispersal) were not regarded as S+ as their seeds are not subjected to fire. Therefore, four post-fire strategies are possible: R+S-, R+S+, R-S+ and R-S- (Pausas *et al.* 2004). Life-form was assigned to all species, but resprouting and post-fire seeding was obtained for 120 and 105 species, respectively; thus, when testing the resprouting or seeding factor, the total cases used were lower (1399 and 1451, respectively). In general, most species were woody plants (61%), with similar frequency among R+ and R-, whereas most of the perennial herbs were R+. S+ species were more abundant than S- and their frequency was higher among R- than among R+ (80% and 41%, respectively).

ANALYSIS

Heat experiments involve very different combinations of temperature and exposure time. To estimate the accumulated heat dose received by the seeds in each treatment, we multiplied the temperature (in degrees Celsius) by the natural logarithm of the exposure time plus one (in minutes). This heat index (H) is analogous to the concentration-time product used in toxicology (e.g. Wang *et al.* 2004 and references therein). In the compiled data, essayed temperatures ranged from 50 to 300 °C, exposure times ranged from 1 min to 24 h and the heat index (H) ranged from 34.7 to 727.3 units (Fig. 1).

For each treatment, the germinative response was first classified as greater, equal or lower than the control (i.e. stimulated, unaffected or inhibited by heat, respectively) on the basis of the significance of the statistical test provided in each study. A set of cases (22%) did not include any statistical test. These cases include both resprouting and non-resprouting species (51% and 49%, respectively). In order to avoid any loss of information, we classified the germinative response of statistically non-tested cases by comparing them with the tested experiments. For the statistically tested experiments, we plotted the frequency distribution (and the smoothed density distribution) of the difference in percent germination between control and treatment for the cases with greater, equal and lower germination than the control. The intersections between the three smoothed density distributions were -13 and 14. We then used these thresholds to classify the statistically non-tested treatments as stimulated

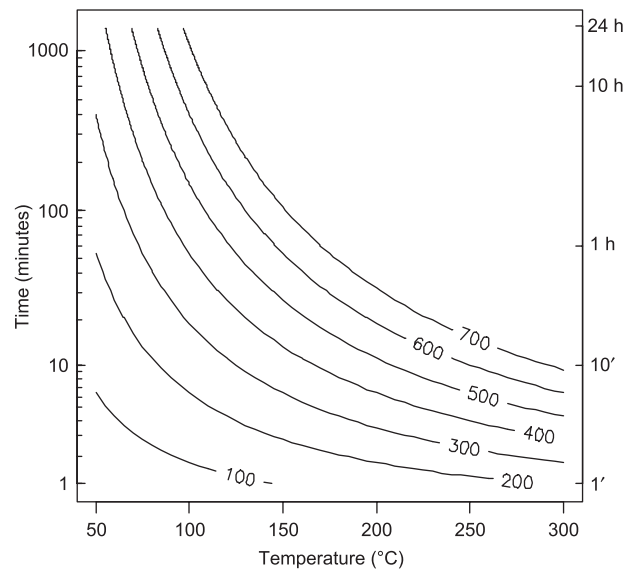


Fig. 1. Relationship between temperature and exposure time for different heat index (H) values (contour lines).

(differences in percent germination between control and heated seeds higher than 14%), inhibited (differences lower than -13%), or unaffected (in between) germination. If we apply these thresholds to the statistically tested treatments we observe that the percentage of misclassified cases is 10%. This classification error was mainly (6.9%) due to the failure to detect a significant difference when it was different (type II error or false negative); therefore, the classification is conservative. Furthermore the frequency of treatments that stimulate, do not affect or inhibit germination was not significantly different between the tested and non-tested treatments, both when considering all species ($\chi^2 = 0.54$, d.f. = 2, $P = 0.762$) or each resprouting ability separately (R+: $\chi^2 = 4.99$, d.f. = 2, $P = 0.083$; R-: $\chi^2 = 0.67$, d.f. = 2, $P = 0.715$). The close-to-significant χ^2 -test for R+ is due to a slight over-representation of inhibited germination cases in the statistically non-tested data set, and thus caution should be taken only if the results comparing heat-tolerance between resprouting abilities (see below) were not strongly significant. It is notable that the whole data set includes more treatments (29%), more species (8%) and more treatments per species (19%) than the tested subset, and a wider overall range of heat index (34.7–727.3 for the whole data set vs. 34.7–456.7 for the tested treatments).

The probability of heat-tolerance (i.e. of having greater or equal germination than the control) and heat-stimulation (i.e. of having greater germination than the control) was analysed using a GLM model with a binomial error distribution and logit link function, and tested by an analysis of deviance (McCullagh & Nelder 1989). To analyse the extent to which germination was different between resprouting abilities, we used resprouting as a factor and the heat index (H) as a covariable. Since all life-forms and post-fire seeding abilities were not equally represented in the data set between R+ and R- (see above), we also compared the probability of tolerance and stimulation between life-forms and between post-fire seeding abilities (S). We expect a decreasing probability of heat-tolerance with H and a unimodal model of heat-stimulated germination probability in relation to H (i.e. low germination at low and high intensities); thus, we tested a monotonic response of heat-tolerance to H and a quadratic response of heat-stimulation to H (i.e. $H + H^2$). In all

analyses, species was also included in the model, nested in either post-fire regeneration abilities or life-form.

For treatments that produced stimulation, we evaluated to what extent the heat treatment increased germination in a different manner between R+ and R-, by testing the differences in the proportion of seeds germinating between the heated and the control treatments (hereafter, stimulation magnitude) against H and resprouting using the analysis of variance. As for the stimulation probability, we assumed a unimodal model in relation to H and included species as a factor nested in resprouting.

Because both resprouting and post-fire seeding are phylogenetically structured in the Mediterranean Basin (Herrera 1992; Pausas & Verdú 2005; Verdú & Pausas 2007), our differences in germination response between resprouting abilities could be driven by species relatedness. To evaluate this, we performed a test of the effect of resprouting ability on the probability of heat-tolerance and heat-stimulation, and on the stimulation magnitude, considering the phylogenetic relatedness among the species in our data set. We first assembled a phylogenetic tree with branch lengths for our species with the help of the Phylomatic software implemented in PHYLOCOM 3.41 (Webb *et al.* 2007) and using the angiosperm megatree version R20050610.new. Then, we classified all the studied heat treatments in the following H classes: very low ($H < 100$), low ($100 < H < 200$), medium ($200 < H < 300$), high ($300 < H < 400$) and very high ($H > 400$). To conduct the phylogenetic analyses we recalculated the three dependent variables as follows: for each species and each H class we counted the cases with successful heat-tolerance and heat-stimulation, and computed the average magnitude. Finally, for each H class we tested the effect of resprouting ability on each of the dependent variables using a generalized estimating equation and including the phylogenetic relatedness among species (obtained from the phylogenetic tree) as a correlation matrix in the model (see Paradis & Claude 2002). As in the non-phylogenetic analyses, we assumed a binomial error distribution and logit link function for heat-tolerance and heat-stimulation, and a normal error distribution for magnitude. The advantages of using generalized estimating equation rather than other comparative methods is that it permits the use of qualitative variables (such as resprouting ability), the presence of polytomies in the phylogenetic tree, and the use of binomial error distributions (for germination probabilities). This analysis was performed using the APE software (Paradis *et al.* 2004).

Results

HEAT-TOLERANCE: GERMINATION GREATER THAN OR EQUAL TO THE CONTROL

The probability of seed heat-tolerance was very high (close to 1) at low H values, decreasing with H either progressively or suddenly depending on the life-form and the post-fire regeneration strategy (Fig. 2). The probability of heat-tolerance was higher for R- species than for R+ ones (Fig. 2a). Both the H and its interaction with resprouting ability were significant (Table 1), suggesting that the probability of heat-tolerance decreases with H, and the decreasing pattern was quicker for R+ than for R- species (Fig. 2a). Considering the phylogeny, there were no differences between R+ and R- for the very low and low H classes ($P = 0.484$ and $P = 0.207$, respectively), but differences were significant and marginally significant for the moderate and high H class ($P = 0.039$ and $P = 0.053$,

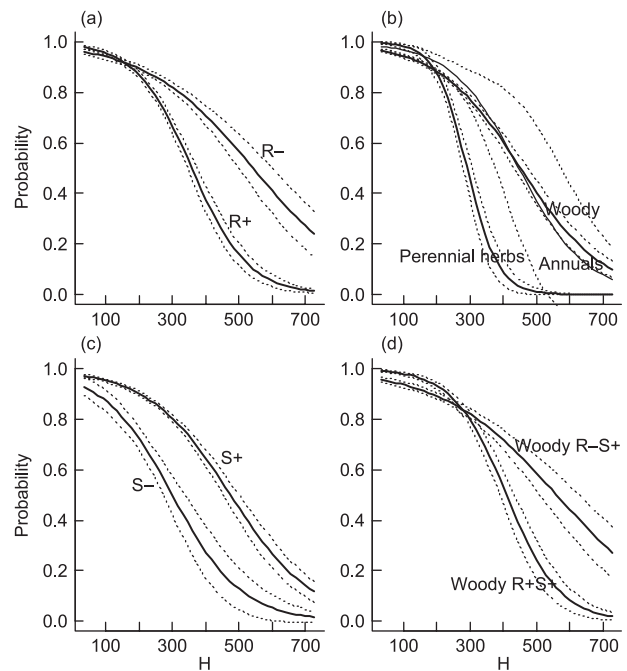


Fig. 2. Tolerance probability in relation to heat treatments for the different resprouting abilities (a, d), life-forms (b) and post-fire seeding abilities (c). In figure d, only woody S+ species were considered. Fits include significant ($P < 0.05$) effects only (see Tables 1 and 2 for further statistical details). Dotted lines refer to SEs of the fitted line.

respectively). Nevertheless, differences between resprouting abilities for the very high H class were non-significant ($P = 0.109$) and thus attributable to the phylogenetic arrangement of the species at the higher end of the H gradient.

Differences between life-forms were also significant, with perennial herbs showing the lowest probability of heat-tolerance (Table 1, Fig. 2b). The interaction between life-form and H was also highly significant (Table 1): woody plants and annuals showed some degree of tolerance even at high H, whereas for perennial herbs tolerance decreased rapidly (Fig. 2b). S+ showed a higher heat-tolerance probability than S-, although the pattern of tolerance probability with H was quite similar for both S+ and S- (no significant interaction; Table 1, Fig. 2c). Considering all these results, the previous differences detected between resprouting abilities could be due to the fact that, in our data set, S- and perennial herbs were more frequent in R+ species than in R- (see Methods) and both had a low heat-tolerance probability (Table 1, Fig. 2b and c). However, when this comparison was restricted to woody S+ species (i.e. comparison between R+S+ and R-S+), we still detected differences between R+ and R-, although for high H values only (significant resprouting ability-H interaction; Table 2, Fig. 2d).

HEAT-STIMULATION: GERMINATION GREATER THAN THE CONTROL

The probability of heat-stimulated germination was different between resprouting abilities (Table 3). R- showed a higher

Table 1. Analysis of deviance for the probability of heat-tolerant germination in relation to resprouting ability, life-form, seeding ability and heat index

Source of variation	d.f.	Deviance	Residual d.f.	Residual deviance	<i>P</i>
Null			1398	1183.26	
Resprouting (R)	1	8.80	1397	1174.46	**
Heat index (H)	1	147.79	1396	1026.67	****
R × H	1	12.38	1395	1014.29	***
Species in R	118	321.77	1277	692.52	****
Explained deviance (%)		41.47			
Null			1683	1435.43	
Life-form (LF)	2	8.18	1681	1427.24	*
Heat index (H)	1	165.09	1680	1262.15	****
LF × H	2	13.51	1678	1248.64	**
Species in LF	167	438.84	1511	809.79	****
Explained deviance (%)		43.59			
Null			1450	1178.32	
Seeding (S)	1	21.66	1449	1156.66	****
Heat index (H)	1	132.22	1448	1024.44	****
S × H	1	0.36	1447	1024.09	0.55
Species in S	104	283.22	1343	740.87	****
Explained deviance (%)		37.13			

All species are included in the analysis. (Levels of significance: **P* < 0.05; ***P* < 0.01; ****P* < 0.001; *****P* < 0.0001; *P* values are shown when *P* ≥ 0.05).

Table 2. Analysis of deviance for the probability of heat-tolerant germination in relation to resprouting ability and heat index considering only woody S+ species

Source of variation	d.f.	Deviance	Residual d.f.	Residual deviance	<i>P</i>
Null			1055	787.92	
Resprouting (R)	1	0.66	1054	787.26	0.42
Heat index (H)	1	90.29	1053	696.97	****
R × H	1	11.82	1052	685.15	***
Species in R	52	143.41	1000	541.75	****
Explained deviance (%)		31.24			

(Levels of significance: **P* < 0.05; ***P* < 0.01; ****P* < 0.001; *****P* < 0.0001; *P* values are shown when *P* ≥ 0.05).

stimulation probability than R+ (Fig. 3a). Moreover, the relationship between stimulation probability and H differed between them (Table 3): for low H values, the stimulation probability increased with H at a similar rate in R+ and R−, reaching their respective maximum values of probability for slightly different H values; stimulation was negatively affected by H sooner in R+ than in R−, in such a way that for very high H values, no R+ species was stimulated whereas some *Cistus* species (R−) were still stimulated (Fig. 3a). This pattern was mostly maintained when phylogeny was considered: differences in heat-stimulated probability between R+ and R− were detected for very low, low and moderate H classes (*P* = 0.0024, *P* < 0.0001, *P* = 0.0027, respectively), but they disappeared for high H (*P* = 0.334), indicating that such differences in high H values are attributable to phylogeny and not to resprouting ability. In fact, this was expected as the phylogenetic affiliations of the data in the high H class differed between R+ (Anacardiaceae and Rosaceae) and R− (Cistaceae and Fabaceae). This comparison was not conducted for very high H, because only R− species were stimulated, all of them pertaining to the genus *Cistus*.

The heat-stimulation probability was higher for woody plants than for herbs, and slightly higher for annuals than for perennial herbs (Table 3, Fig. 3b). The pattern followed by the stimulation probability with H was the same for all life-forms (non-significant life-form–H interaction; Table 3, Fig. 3b). As expected, S+ species showed a higher stimulation probability than S− ones, although the maximum stimulation probability was always < 0.4; the stimulation probability for S− was < 0.1 (Fig. 3c). The interaction between seeding ability and H was not significant (Table 3, Fig. 3c). To discount whether the differences between resprouting abilities in the probability of heat-stimulated germination were due to the heterogeneous distribution of life-forms and seeding abilities between R+ and R−, we repeated the comparison but considered only woody S+ species. For this data subset, differences between R+ and R− were detected and the interaction between resprouting ability and H remained highly significant (Table 4, Fig. 3d).

The magnitude of the stimulation differed between resprouting abilities (Table 5), being higher for R− (R−: 39.7 ± 19.9 and R+: 31.8 ± 18.3, expressed as mean ± SD). The magnitude

Source of variation	d.f.	Deviance	Residual d.f.	Residual deviance	P
Null			1398	1608.12	
Resprouting (R)	1	45.66	1397	1562.47	****
Heat index (H + H ²)	2	41.09	1395	1521.38	****
R × (H + H ²)	2	11.90	1393	1509.48	**
Species in R	118	357.28	1275	1152.2	****
Explained deviance (%)		28.35			
Null			1683	1891.74	
Life-form (LF)	2	48.28	1681	1843.46	****
Heat index (H + H ²)	2	45.49	1679	1797.97	****
LF × (H + H ²)	4	3.86	1675	1794.12	0.43
Species in LF	166	441.88	1509	1352.24	****
Explained deviance (%)		28.52			
Null			1450	1736.96	
Seeding (S)	1	42.09	1449	1694.87	****
Heat index (H + H ²)	2	53.70	1447	1641.17	****
S × (H + H ²)	2	2.47	1445	1638.70	0.29
Species in S	104	293.86	1341	1344.83	****
Explained deviance (%)		22.58			

All species are considered. Note that the heat index was fitted as a quadratic response. Levels of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; P values are shown when $P \geq 0.05$.

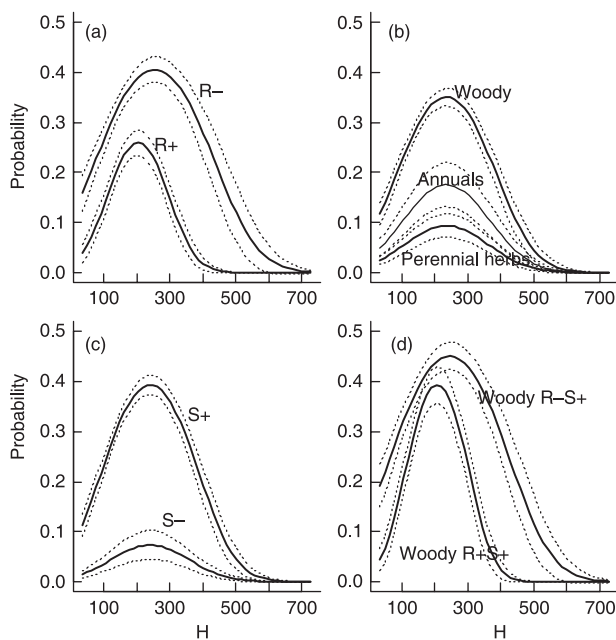


Fig. 3. Stimulation probability in relation to heat treatments for the different resprouting abilities (a, d), life-forms (b) and seeding abilities (c). In figure d, only woody S+ species were considered. Fits include significant ($P < 0.05$) effects only (see Tables 3 and 4 for further statistical details). Dotted lines refer to SEs of the fitted line.

of stimulation was independent of H and the differences between resprouting abilities were unaffected by H (non-significant resprouting ability-H interaction; Table 5). In the phylogenetic analyses, differences in the magnitude of heat-stimulation between resprouting abilities (higher in R-) were

Table 3. Analysis of deviance for the probability of heat-stimulated germination in relation to resprouting ability, life-form, post-fire seeding ability and heat index

significant for the very low, low and moderate H classes ($P = 0.0006$, $P < 0.0001$, $P < 0.0001$, respectively), but non-significant for high H ($P = 0.294$), because stimulation was phylogenetically aggregated for these H values (see before). Differences between R+ and R- in the magnitude of stimulation for the very high H class were not tested because none of the R+ species was stimulated.

Discussion

As predicted, the germinative response of seeds after heat exposure was greater in non-resprouters (R-) than in resprouters (R+), because R- seeds show higher heat-tolerance and heat-stimulation (the latter expressed as both probability and magnitude). These results were maintained even when phylogenetic relatedness was included in the analyses. Similar results were found in the Fynbos for smoke-stimulated germination, being more frequent in R- species (van Staden *et al.* 2000). In the Mediterranean Basin, R+S- and R-S+ are more frequent than could be expected by chance, even when phylogenetic relatedness is considered (Pausas & Verdú 2005). Therefore, differences between R+ and R- in the germinative response to heat could be due to differences between S+ and S-. Nevertheless, when the probability of heat-tolerance or heat-stimulation was compared in terms of S+ species only, the differences between resprouting abilities remained significant. Recently, a study carried out with a subset of the data included in our analysis found that the percent germination after heat-shock did not differ between R+ and R- (Luna *et al.* 2007), although germination after high temperatures (100 and 120 °C for 10 min) was higher for R-. The wider spatial and taxonomic range of our data set and the great amount of combinations of temperature and exposure time tested in our

Table 4. Analysis of deviance for the probability of heat-stimulated germination in relation to resprouting ability and heat index, considering woody S+ species only

Source of variation	d.f.	Deviance	Residual d.f.	Residual deviance	<i>P</i>
Null			1055	1337.28	
Resprouting (R)	1	16.14	1054	1321.14	****
Heat index ($H + H^2$)	2	46.11	1052	1275.13	****
$R \times (H + H^2)$	2	12.70	1050	1262.43	**
Species in R	52	173.92	998	1088.51	****
Explained deviance (%)		18.60			

Note that the heat index was fitted as a quadratic response. Levels of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; *P* values are shown when $P \geq 0.05$.

Table 5. Analysis of variance for the difference in percent germination (for treatments that produced stimulation) in relation to resprouting ability and heat index

Source of variation	d.f.	SS	Residual d.f.	Residual SS	<i>F</i>	<i>P</i>
Null			365	142 012		
Resprouting (R)	1	4850	364	137 162	15.86	****
Heat index ($H + H^2$)	2	543	362	136 619	0.89	0.41
$R \times (H + H^2)$	1	551	361	136 068	1.80	0.18
Species in R	55	42 470	306	93 598	2.53	****

Note that the heat index was tested as a quadratic response. Levels of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; *P* values are shown when $P \geq 0.05$.

study increase the power of the analyses and thus highlight the differences between resprouting abilities.

As a result of post-fire germination, R- species have a higher potential than R+ species to persist and even to increase their population size after fire. Moreno & Oechel (1991a) found a Californian example in which the post-fire emergence of an obligate seeder (R-S+; *Ceanothus greggii*) was higher than for a facultative seeder (R+S+; *Adenostoma fasciculatum*), especially after high-intensity fires. The authors proposed differences in the germinative response and in the seed burial depth in the soil as possible explanations for this finding. Our results support the first hypothesis, although the latter cannot be discarded. Similar results have also been found in serotinous species from Western Australia (Enright & Lamont 1989). Nevertheless, effective post-fire recruitment also depends on the amount of seed availability and seedling survival. Regarding seed availability, obligate resprouters (R+S-) typically produce fewer seeds than obligate seeders (R-S+), although the differences between R+ and R- in seed production do not always occur in S+ species (Pausas *et al.* 2004). In the Mediterranean Basin, species with both resprouting and seeding ability are less frequent than species that persist by means of only one of the recovery mechanisms (Pausas & Verdú 2005); therefore, differences in seed production between R+ and R- are expected, with the latter being higher (Pausas *et al.* 2004). Moreover, congeneric comparisons of three co-occurring R+ and R- pairs have suggested that viable seed density in the soil is higher for R- species (Kelly & Parker 1990; see Enright & Lamont 1989 for similar results in serotinous species). On the other hand, seedling establishment is the most critical phase in the life-history of Mediterranean

species, mostly limited by seasonal dryness (Mejias *et al.* 2002). Seedling survival under seasonal water stress is frequently higher for R- than for R+ species (Keeley & Zedler 1978; Zammit & Westoby 1987; Davis *et al.* 1998; Enright & Goldblum, 1999). In fact, at least at leaf level, R- species show higher potential for structural resistance to drought and higher water-use efficiency than R+ (Paula & Pausas 2006). In conclusion, differences in seed availability, post-fire germination and seedling survival indicate that effective recruitment is higher in R- than in R+.

The magnitude of the stimulation was independent of the heat index. Hence seed populations are quite homogeneous in relation to their heat-sensitivity, showing both refractory and non-refractory seeds (*sensu* Keeley 1991), but virtually no seeds with intermediate heat resistance. Thus, a pulse of germination is produced only when refractory seeds are exposed to a certain heat threshold, and the amount of germinated seeds depends on the proportion of refractory seeds, which is higher for R- species. Moreover, this heat threshold is different between resprouting abilities, since the probability of heat-stimulation was significantly affected by H. Indeed, at high H values, the probability of heat-stimulation decreases quicker in R+ than in R-, and the maximum probability of heat-stimulated germination is reached at slightly higher H values for R-.

The relationship found between heat-stimulated germination and life-form is consistent with the results obtained from other fire-prone ecosystems (Keeley & Bond 1997; Clarke *et al.* 2000; Keeley & Fotheringham 2000). Differences between life-form have also been found for other fire cues, such as smoke or charred wood (Keeley & Bond 1997; van

Staden *et al.* 2000). We found the highest probability of heat-tolerant and heat-stimulated germination in woody plants and the lowest in perennial herbs, whereas the annuals showed an intermediate position. A predominance of species with refractory seeds has been found in the Californian chaparral and in the South African Fynbos (Keeley & Bond 1997). In these ecosystems, annuals are frequently stimulated by heat and, in many cases, also by charred wood or smoke, which are germination cues more specifically linked to fire (Keeley 1991; Keeley & Bond 1997; Keeley & Fotheringham 2000). In the Mediterranean Basin, annuals are not necessarily linked to burned sites and tend to colonize sites recently affected by any types of disturbance (Bonet & Pausas 2004; Buhk & Hensen 2006). Furthermore, the generation time of annuals is much shorter than the fire intervals in the Mediterranean Basin, and thus fire may represent a low selective pressure for these species. Consequently, the relatively low fire-enhanced germination that we found may be expected. Nevertheless, annuals are poorly represented in the data set (they represent only 10% of the species and 6% of the treatments) and, thus, future experiments with annuals may throw further light in this regard.

Perennial herbs showed the lowest probability of heat-stimulation and heat-tolerance. A possible explanation is that perennial herbs are normally resprouters (only 9% were R–), and their fire-germinative response is thus low (see comparison between R+ and R–). The mean frequency of heat-stimulation for perennial herbs is also lower than for woody plants when only R+ are considered ($4 \pm 14\%$ for perennial herbs and $19 \pm 24\%$ for woody plants, expressed as mean \pm SD). This low germinative response of perennial herbs to heat has been found in other fire-prone ecosystems (Keeley & Bond 1997; Clarke *et al.* 2000), and both the longevity of the seed bank and grazing pressure have been adduced to explain it (Clarke *et al.* 2000).

As in the Californian chaparral and the Fynbos (Keeley & Bond 1997), heat-stimulated germination in the Mediterranean Basin is quite common: of the 164 taxa included in our data set, 41% were heat-stimulated in at least one treatment and 28% in at least 25% of the treatments. Nevertheless, fire-stimulated germination appears to be phylogenetically aggregated in the Mediterranean Basin: stimulation was detected in 39% of the families, and 60% of the treatments that produced stimulated germination corresponded to a single family, the Cistaceae. Moreover, the few species stimulated at high H values were also Cistaceae. These results explain the high phylogenetic and phenotypic clustering found in communities under high fire frequency (Verdú & Pausas 2007; Pausas & Verdú, in press). We are aware that our data set is biased, and that the species for which heat-stimulated germination is expected were over-represented (e.g. 39% of the treatments were carried out with Cistaceae). Nevertheless, the broad taxonomic and phylogenetic spectrum included in this data set suggests that any possible bias in selection of the species studied may also represent the taxonomic aggregation of the heat-stimulated germination trait. This aggregation has been explained by the relationship between germination

patterns and seed anatomy, with the latter being highly conserved at high taxonomic levels (see Keeley & Bond 1997 and references therein).

Our results highlight the importance of heat intensity for understanding post-fire germination; because it also affects resprouting ability (Moreno & Oechel 1991b; Lloret & López-Soria 1993; Cruz *et al.* 2003b), it is a major factor in the post-fire recovery of Mediterranean Basin ecosystems. In fact, germination ability of seeds in response to heat is missing in most global trait databases (e.g. Cornelissen *et al.* 2003) and could be a valuable trait to improve the quality and the predictive value of such compilations. Nevertheless, other fire-related factors may also stimulate seed germination (e.g. smoke, charred wood). These other germination cues have not yet been studied extensively and, at present, they seem to be relatively unimportant in the Mediterranean Basin (Keeley & Baer-Keeley 1999; Pérez-Fernández & Rodríguez-Echeverría 2003; Rivas *et al.* 2006; Crosti *et al.* 2006). However, given that the differences between R+ and R– observed in this paper are similar to those observed in smoke-stimulated germination for South Africa flora (van Staden *et al.* 2000), we expect R– species to be stimulated more by any fire-related germination cue. Further research is undoubtedly needed to understand fully the role of these mechanisms on post-fire regeneration.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 List of species considered, life-form, fire response and data sources.

This material is available as a part of the online article from:
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Appendix S1

List of species considered in this study with their life form (LF), resprouting ability (R), post-fire seeding (S) and data source of heat treatments (Sources; complete reference at the bottom of the table). AH= annual herb; PH; perennial herb; W = woody plant; NA= no reliable data.

Species	Family	LF	R	S	Sources
<i>Acinos alpinus</i> (L.) Moench ssp. <i>meridionalis</i> (Nyman) P.W. Ball	Lamiaceae	W	NA	NA	21
<i>Adenocarpus lainzii</i> (Castrov.) Castrov.	Fabaceae	W	+	+	37
<i>Agrostis curtisii</i> Kerguélen	Poaceae	PH	+	+	14, 15
<i>Agrostis delicatula</i> Pourret ex Lapeyr.	Poaceae	PH	+	NA	15
<i>Alyssum serpyllifolium</i> Desf.	Brassicaceae	AH	-	NA	21
<i>Allium</i> sp.	Liliaceae	PH	+	-	20
<i>Anarrhinum bellidifolium</i> (L.) Willd.	Scrophulariaceae	PH	NA	NA	21
<i>Anthyllis lagascana</i> Benedí	Fabaceae	W	NA	NA	31
<i>Antirrhinum litigiosum</i> Pau	Scrophulariaceae	PH	NA	NA	21
<i>Arbutus unedo</i> L.	Ericaceae	W	+	-	22
<i>Arenaria aggregata</i> (L.) Loisel. ssp. <i>erinacea</i> (Boiss.) Font Quer	Caryophyllaceae	W	NA	NA	21
<i>Argyrolobium zanonii</i> (Turra) P.W.Ball	Fabaceae	W	NA	+	17
<i>Asterolinon linum-stellatum</i> (L.) Duby	Primulaceae	AH	-	+	7
<i>Avenula marginata</i> (Lowe) J. Holub	Poaceae	PH	+	NA	14, 15
<i>Betula pendula</i> Roth	Betulaceae	W	+	-	32, 33
<i>Brachypodium retusum</i> (Pers.) Beauv.	Poaceae	PH	+	-	7
<i>Briza maxima</i> L.	Poaceae	AH	-	-	38
<i>Briza media</i> L.	Poaceae	PH	-	-	38
<i>Calicotome intermedia</i> C. Presl	Fabaceae	W	+	+	7
<i>Calluna vulgaris</i> (L.) Hull	Ericaceae	W	NA	+	12, 15, 52
<i>Catananche caerulea</i> L.	Asteraceae	PH	NA	NA	21
<i>Centaurea alba</i> L. ssp. <i>alba</i>	Asteraceae	PH	NA	NA	36
<i>Centaurea aspera</i> L. ssp. <i>aspera</i>	Asteraceae	PH	NA	NA	36
<i>Centaurea boissieri</i> DC. ssp. <i>duffourii</i> Dostál	Asteraceae	PH	NA	NA	36
<i>Centaurea boissieri</i> DC. ssp. <i>pinæ</i> (Pau) Dostál	Asteraceae	PH	-	NA	21
<i>Centaurea calcitrapa</i> L.	Asteraceae	PH	NA	NA	36
<i>Centaurea cyanus</i> L.	Asteraceae	AH	-	NA	36
<i>Centaurea leucophaea</i> Jordan ssp. <i>leucophaea</i>	Asteraceae	PH	NA	NA	36
<i>Centaurea linifolia</i> L. ssp. <i>linifolia</i>	Asteraceae	PH	+	-	36
<i>Centaurea maculosa</i> Lam. ssp. <i>albida</i> (Lecoq & Lamotte) Dostál	Asteraceae	PH	NA	NA	36
<i>Centaurea maculosa</i> Lam. ssp. <i>maculosa</i>	Asteraceae	PH	+	+	36
<i>Centaurea melitensis</i> L.	Asteraceae	AH	-	-	36
<i>Centaurea ornata</i> Willd. ssp. <i>ornata</i>	Asteraceae	PH	NA	NA	21
<i>Centaurea ornata</i> Willd. ssp. <i>saxicola</i> (Lag.) Dostál	Asteraceae	PH	NA	NA	36
<i>Centaurea pau</i> Loscos	Asteraceae	PH	NA	NA	36
<i>Centaurea pectinata</i> L. ssp. <i>pectinata</i>	Asteraceae	PH	+	+	36
<i>Centaurea rouyi</i> Coincy	Asteraceae	PH	NA	NA	36
<i>Centaurea scabiosa</i> L. ssp. <i>scabiosa</i>	Asteraceae	PH	+	NA	36
<i>Centaurea seridis</i> L.	Asteraceae	PH	NA	NA	36
<i>Centaurea solstitialis</i> L. ssp. <i>solstitialis</i>	Asteraceae	AH	-	+	36
<i>Centaurea spinabadia</i> Bubani ex Timb.-Lagr. ssp. <i>hanryi</i> (Jordan) Dostál	Asteraceae	PH	NA	NA	36
<i>Centaurea uniflora</i> L. ssp. <i>emigrantis</i> (Bub.) Pau et F.Q.	Asteraceae	PH	NA	NA	36
<i>Centaurea vinyalsii</i> Sennen	Asteraceae	PH	NA	NA	36
<i>Ceratonía siliqua</i> L.	Fabaceae	W	+	-	2, 27
<i>Cistus albidus</i> L.	Cistaceae	W	-	+	7, 9, 40, 44, 45, 53
<i>Cistus clusii</i> Dunal	Cistaceae	W	-	+	7, 8, 18, 23, 44
<i>Cistus creticus</i> L.	Cistaceae	W	-	+	20, 28, 43, 48

<i>Cistus creticus</i> L. ssp. <i>corsicus</i> (Loisel.) Greuter & Burdet	Cistaceae	W	-	+	44
<i>Cistus crispus</i> L.	Cistaceae	W	-	+	18, 44
<i>Cistus ladanifer</i> L.	Cistaceae	W	-	+	9, 11, 30, 49
<i>Cistus laurifolius</i> L.	Cistaceae	W	-	+	9, 19, 25, 49
<i>Cistus libanotis</i> L.	Cistaceae	W	-	+	18
<i>Cistus monspeliensis</i> L.	Cistaceae	W	-	+	23, 28, 40, 44, 45, 53
<i>Cistus palhinhae</i> Ingram	Cistaceae	W	-	+	44
<i>Cistus parviflorus</i> Lam.	Cistaceae	W	-	+	44
<i>Cistus populifolius</i> L. ssp. <i>populifolius</i>	Cistaceae	W	-	+	18
<i>Cistus psilosepalus</i> Sweet	Cistaceae	W	-	+	15, 44
<i>Cistus salviifolius</i> L.	Cistaceae	W	NA	+	7, 9, 23, 41, 43, 44, 45, 48
<i>Clematis vitalba</i> L.	Ranunculaceae	W	+	-	41
<i>Convolvulus lanuginosus</i> Desr.	Convolvulaceae	W	NA	+	7
<i>Crucianella angustifolia</i> L.	Rubiaceae	AH	-	+	20
<i>Cytisus multiflorus</i> (L'Hér.) Sweet	Fabaceae	W	+	+	1, 34
<i>Cytisus oromediterraneus</i> Rivas Mart. & al.	Fabaceae	W	+	+	1
<i>Cytisus scoparius</i> (L.) Link ssp. <i>reverchonii</i> (Degen & Hervier) Rivas Goday	Fabaceae	W	+	+	17
<i>Cytisus scoparius</i> (L.) Link ssp. <i>scoparius</i>	Fabaceae	W	+	+	37, 42
<i>Cytisus striatus</i> (Hill) Rothm.	Fabaceae	W	+	+	17, 34, 37
<i>Chamaerops humilis</i> L.	Arecaceae	W	+	-	41
<i>Chondrilla juncea</i> L.	Asteraceae	PH	NA	NA	21
<i>Daboecia cantabrica</i> (Hudson) C. Koch	Ericaceae	W	+	+	15, 51
<i>Danthonia decumbens</i> (L.) DC.	Poaceae	PH	+	+	38
<i>Daucus carota</i> L.	Apiaceae	PH	NA	+	21
<i>Dipcadi serotinum</i> (L.) Medicus	Liliaceae	PH	+	-	7
<i>Dorycnium pentaphyllum</i> Scop.	Fabaceae	W	+	+	17
<i>Elaeoselinum tenuifolium</i> (Lang.) Lange	Apiaceae	PH	+	NA	7
<i>Erica arborea</i> L.	Ericaceae	W	+	NA	13, 22, 51
<i>Erica australis</i> L.	Ericaceae	W	+	+	10, 13, 51, 52
<i>Erica ciliaris</i> L.	Ericaceae	W	+	+	12, 15
<i>Erica erigena</i> R. Ross	Ericaceae	W	NA	NA	12
<i>Erica scoparia</i> L.	Ericaceae	W	+	NA	13
<i>Erica tetralix</i> L.	Ericaceae	W	+	+	13
<i>Erica umbellata</i> L.	Ericaceae	W	-	+	13, 15
<i>Erica vagans</i> L.	Ericaceae	W	+	+	13, 26
<i>Fumana ericoides</i> (Cav.) Gand.	Cistaceae	W	NA	+	7, 21
<i>Fumana laevipes</i> (L.) Spach	Cistaceae	W	-	+	7
<i>Fumana procumbens</i> (Dunal) Gren. & Godr.	Cistaceae	W	-	+	21
<i>Fumana thymifolia</i> (L.) Spach ex Webb	Cistaceae	W	-	+	7
<i>Galium frutescens</i> Cav.	Rubiaceae	PH	+	NA	21
<i>Genista berberidea</i> Lange	Fabaceae	W	+	+	37
<i>Genista florida</i> L.	Fabaceae	W	+	+	25, 42
<i>Genista triacanthos</i> Brot.	Fabaceae	W	-	+	37
<i>Gladiolus illyricus</i> Koch	Iridaceae	PH	+	-	7
<i>Halimium atriplicifolium</i> (Lam.) Spach.	Cistaceae	W	-	+	7, 18
<i>Halimium halimifolium</i> (L.) Willk ssp. <i>halimifolium</i>	Cistaceae	W	-	+	18, 44
<i>Halimium halimifolium</i> (L.) Willk ssp. <i>multiflorum</i> (Dunal) Maire	Cistaceae	W	-	+	18
<i>Halimium lasianthum</i> (Lam.) Spach ssp. <i>alyssoides</i> Greuter	Cistaceae	W	-	+	15, 25
<i>Halimium ocymoides</i> (Lam.) Willk.	Cistaceae	W	-	+	18, 44
<i>Halimium umbellatum</i> (L.) Spach	Cistaceae	W	-	+	25, 52
<i>Halimium viscosum</i> (Wilk.) P. Silva	Cistaceae	W	-	+	18, 21
<i>Helianthemum apenninum</i> (L.) Mill.	Cistaceae	W	NA	+	21
<i>Helianthemum cinereum</i> (Cav.) Pers ssp. <i>rotundifolium</i> (Dunal) Greuter & Burdet	Cistaceae	W	-	+	21

<i>Helianthemum croceum</i> (Desf.) Pers.	Cistaceae	W	-	NA	44
<i>Helianthemum hirtum</i> (L.) Mill.	Cistaceae	W	-	+	21
<i>Helianthemum pilosum</i> (L.) Pers.	Cistaceae	W	NA	NA	44
<i>Helichrysum italicum</i> (Roth) G. Don fil. ssp. <i>serotinum</i> (Boiss.) P. Fourn.	Asteraceae	W	NA	NA	21
<i>Helichrysum stoechas</i> (L.) Moench	Asteraceae	W	NA	NA	21
<i>Hippocrepis ciliata</i> Willd.	Fabaceae	AH	-	NA	7
<i>Hippocrepis multisiliquosa</i> L.	Fabaceae	AH	-	NA	16
<i>Holcus lanatus</i> L.	Poaceae	PH	-	+	38
<i>Inula montana</i> L.	Asteraceae	PH	+	NA	21
<i>Lavandula latifolia</i> Medicus	Lamiaceae	W	-	+	21
<i>Lavandula stoechas</i> L.	Lamiaceae	W	NA	+	20, 21
<i>Leucanthemopsis pallida</i> (Miller) Heywood	Asteraceae	PH	-	NA	21
<i>Leuzea conifera</i> (L.) DC.	Asteraceae	PH	NA	NA	21
<i>Linum narbonense</i> L.	Linaceae	PH	+	NA	21
<i>Marrubium supinum</i> L.	Lamiaceae	PH	NA	NA	21
<i>Medicago arborea</i> L.	Fabaceae	W	+	NA	28
<i>Misopates orontium</i> (L.) Rafin	Scrophulariaceae	AH	-	+	20
<i>Nepeta nepetella</i> L.	Lamiaceae	W	NA	NA	21
<i>Ononis ornithopodioides</i> L.	Fabaceae	AH	-	+	7
<i>Paronychia capitata</i> (L.) Lam.	Caryophyllaceae	W	NA	NA	21
<i>Periploca laevigata</i> Aiton ssp. <i>angustifolia</i> (Labill.) Markgraf	Apocynaceae	W	+	-	7
<i>Phillyrea latifolia</i> L.	Oleaceae	W	+	-	41
<i>Phlomis fruticosa</i> L.	Lamiaceae	W	+	+	28
<i>Phlomis lychnitis</i> L.	Lamiaceae	W	+	NA	21
<i>Pistacia lentiscus</i> L.	Anacardiaceae	W	+	-	41
<i>Plantago sempervirens</i> Crantz	Plantaginaceae	W	NA	NA	21
<i>Prunella laciniata</i> (L.) L.	Lamiaceae	PH	+	-	21
<i>Pseudarrhenatherum longifolium</i> (Thore) Rouy	Poaceae	PH	+	+	14, 38
<i>Psoralea bituminosa</i> L.	Fabaceae	PH	NA	+	17, 21
<i>Pterospartum tridentatum</i> (L.) Willk.	Fabaceae	W	+	+	37, 51, 52
<i>Quercus ilex</i> L. ssp. <i>rotundifolia</i> (Lam.) T. Morais	Fagaceae	W	+	-	35
<i>Quercus pyrenaica</i> Willd.	Fagaceae	W	+	-	33, 35, 50
<i>Quercus robur</i> L.	Fagaceae	W	+	-	33, 35
<i>Reseda lutea</i> L.	Resedaceae	PH	+	-	21
<i>Reseda luteola</i> L.	Resedaceae	PH	NA	NA	21
<i>Rhus coriaria</i> L.	Anacardiaceae	W	+	+	24
<i>Rosmarinus officinalis</i> L.	Lamiaceae	W	-	+	41, 46
<i>Salvia pratensis</i> L.	Lamiaceae	PH	+	NA	21
<i>Salvia verbenaca</i> L.	Lamiaceae	PH	+	NA	21
<i>Santolina chamaecyparissus</i> L.	Asteraceae	W	NA	NA	21
<i>Sarcopoterium spinosum</i> L.	Rosaceae	W	+	+	28, 39
<i>Scabiosa turolensis</i> Pau ex Willk.	Dipsacaceae	PH	+	NA	21
<i>Scolymus hispanicus</i> L.	Asteraceae	PH	NA	NA	21
<i>Scorpiurus muricatus</i> L.	Fabaceae	AH	-	+	17
<i>Sideritis hirsuta</i> L.	Lamiaceae	W	+	+	21
<i>Sideritis tragoriganum</i> Lag.	Lamiaceae	W	NA	NA	21
<i>Silene mellifera</i> Boiss. & Reuter	Caryophyllaceae	PH	+	NA	21
<i>Stachelina dubia</i> L.	Asteraceae	W	+	NA	21
<i>Stipa tenacissima</i> L.	Poaceae	PH	+	-	7
<i>Telephium imperati</i> L.	Caryophyllaceae	PH	-	NA	21
<i>Teucrium carthaginense</i> Lange	Lamiaceae	W	+	NA	7
<i>Teucrium expansum</i> Pau	Lamiaceae	W	NA	NA	21
<i>Teucrium polium</i> L. ssp. <i>capitatum</i> (L.) Arcangeli	Lamiaceae	W	NA	NA	21
<i>Teucrium pseudo-chamaepitys</i> L.	Lamiaceae	PH	NA	+	7
<i>Thapsia villosa</i> L.	Apiaceae	PH	+	NA	21
<i>Thymus leptophyllus</i> Lange	Lamiaceae	W	NA	NA	21
<i>Thymus mastichina</i> L.	Lamiaceae	W	NA	NA	21

<i>Thymus vulgaris</i> L.	Lamiaceae	W	NA	+	6, 21
<i>Trifolium campestre</i> Schreb.	Fabaceae	AH	-	+	47
<i>Trifolium glomeratum</i> L.	Fabaceae	AH	-	+	47
<i>Tuberaria guttata</i> (L.) Fourr.	Cistaceae	AH	-	+	15
<i>Tuberaria lignosa</i> (Sweet) Samp.	Cistaceae	W	-	+	21, 44
<i>Ulex europaeus</i> L.	Fabaceae	W	+	+	29
<i>Ulex parviflorus</i> Pourr.	Fabaceae	W	-	+	3, 4, 5

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