

Light and nitrate effects on seed germination of Mediterranean plant species of several functional groups

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Abstract Post-fire conditions are characterized by enhanced light and the availability of nitrogenous compounds in the soil. It is not known, however, to what extent light or nitrogenous compounds control the germination response of species growing in burned areas and, in particular, whether functional groups of plants differ in their response. The germination response to light and nitrate was tested for 53 species representative of the flora of a Mediterranean recently burned area in Central-Eastern Spain. Differences in germination among species, with and without taking into account their phylogeny, were studied by classifying them according to their life-form (chamaephytes, hemicryptophytes), regeneration strategy (non-sprouters, sprouters) and geographical distribution range (Iberian Peninsula endemics, Mediterranean, widely distributed species). The overall germination mean was not affected by any of the two treatments. There were statistically significant interactions between species and the two treatments. That is, not all species were equally affected, and about 30% of the species were significantly affected by light (half of them positively and the other half negatively) and 25% by nitrate (most of them

positively). Species response was related to functional groups. Light response (stimulation vs. non-stimulation) was associated to life-form, regeneration strategy and distribution range. Hemicryptophytes, sprouters and widely distributed species were positively affected by light. No evidence of such an association for nitrate was found. No statistically significant effects of light and nitrate on the mean germination of the various groups (life-form, regeneration strategy, distribution range) were found. Moreover, significant interactions emerged between light and nitrate for all three groups. In summary, the studied set of plants appears to be non-dependent on factors that may change with fire, such as increased light and soil nitrate, for germination. Nonetheless, some species and groups will be affected by such changes. That means that fire will modify the relative balance of germination among species and functional groups. Due to the particular sensitivity of Iberian Peninsula endemics to light, a factor that significantly changes with fire, these species may be at risk under the current fire regime.

Keywords Distribution range · Life-form · Iberian Peninsula endemics · Non-sprouter · Post-fire conditions · Sprouter

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Introduction

Under closed canopy conditions, a low quantity and altered quality of light, reduced water availability, low

nitrogen availability and high predation risk may reduce successful seedling establishment (Fenner 1985). It is therefore not uncommon in periodically disturbed environments that many plant species have evolved mechanisms to ensure seed dormancy until the canopy is removed (Baskin and Baskin 1998). In Mediterranean-type ecosystems, fire is one of the most recurrent disturbances (Naveh 1994). In fire-prone ecosystems, conditions for seedling establishment of many species are particularly favourable just immediately after the passage of fire, as evidenced by the massive recruitment that is commonly observed after fire (Christensen and Muller 1975; Trabaud and Lepart 1980; Arianoutsou and Margaris 1981). Consequently, many Mediterranean plants produce seeds that are released from dormancy after being exposed to some cue directly related to fire, such as heat (Valbuena et al. 1992; Bell et al. 1993; González-Rabanal and Casal 1995; Keeley and Fotheringham 2000), smoke (Brown 1993; Keeley and Fotheringham 1998; van Staden et al. 2004) or ash (Henig-Sever et al. 2000). In other cases, germination may be activated as well by some stimuli related to postfire conditions. After fire has passed through an area, the light conditions of the germination environment will change due to canopy and litter removal. Light-regulated dormancy is probably the most important mechanism by which seeds can detect gaps in vegetation, and light-stimulated germination is to be expected for fire recruiters (Christensen and Muller 1975; Keeley 1987; Pons 1989). On the other hand, Mediterranean soils are usually nutrient-poor, and increases in soil ammonium and nitrate have been usually described shortly after fire (DeBano et al. 1979; Dunn et al. 1979; Kutiel and Shaviv 1989; Marion et al. 1991; Christensen 1994; Serrasolsas and Vallejo 1999). Thus, in fire-areas, nitrogen-induced germination has often been interpreted in terms of its relationship to fire (Thanos and Rundel 1995). The presence of nitrate and ammonium ions in ash have been proposed as germination-stimulatory factors (Henig-Sever et al. 2000). Although there is an abundance of publications on the effects of light and nitrate on seed germination (Hilhorst and Karssen 2000; Pons 2000), the reported responses are usually highly specific, and most studies usually include a few species. Therefore, we still do not have a good framework for understanding the ecological meaning of these factors for seedling establishment in fire-prone Mediterranean areas.

We have studied the germination response to light and nitrate of a group of 53 species representative of the flora growing in a recently burned area. We assumed that light and nitrogen may act as gap-detection mechanisms (Pons 1989) and therefore expected that these factors would activate the germination of species growing in burned areas. In particular, we expected a positive germination response by fire-recruiters when they were exposed to light and nitrate. However, we also anticipated that the links between fire and recruitment would vary according to the plant group—that is, not all species might be equally sensitive to these factors, with their response depending on the traits they possess in relation to their functional characteristics.

In our study, we considered the relationship between light, nitrate and germination in relation to three different plant groups: life-form, regeneration strategy and distribution range. The underlying hypothesis was that the germination of pioneer-type species would be stimulated by high light and/or nitrate availability, whereas that of plants belonging to later succession stages would not be delayed or only delayed slightly. Life-forms typical of the first stages of succession, such as hemicryptophytes (Trabaud 1987), may fall into the first category, whereas chamaephytes (Kazanis and Arianoutsou 1996; Guo 2001), proper of more mature environments, would fall into the second group. In addition, cueing germination to optimal conditions for seedling establishment could be less critical for sprouting species, since the surviving parent can always produce more seeds after a fire event. In this regard, seeds of sprouting species should be less sensitive to changes in germination conditions than non-sprouters (Bell et al. 1995). Thus, non-sprouter species would be stimulated by high nitrogen and light availability, whereas sprouters would not be so. Finally, it has been proposed that the germination niche breadth, a component of the regeneration niche, may be positively related to the distributional range size (Brändle et al. 2003) based on the grounds that species that have broad environmental tolerances and are able to use a wide range of resources will be able to survive in more places and thus over a larger area (Brown 1984). We tested the hypothesis that seeds from geographically widely distributed species would have a wider germination niche and thus would be more responsive to light and nitrate exposure than endemic species.

Materials and methods

Seeds of 53 species were collected from an area affected by a wildfire in Serranía Baja de Cuenca (Central-Eastern Spain) (province of Cuenca; 1°20′–1°35′ W, 39°45′–39°54′ N). The area is at 900–1,400 m a.s.l. and has an annual mean temperature of 12–12.5°C and an annual mean rainfall of 500–550 mm. A naturally ignited fire had occurred during the early summer, affecting *Pinus pinaster*, *P. halepensis* and *P. nigra* woodlands, shrublands and woody crops.

From an inventory of the flora in the burned area, we selected a representative group of 53 species that included a wide range of plant families and comprised the two life-forms with higher levels of endemism: chamaephytes and hemicryptophytes. Species were characterized by their geographical distribution range as: (1) IP, which are endemic species with a geographical distribution restricted to the Iberian Peninsula; (2) Med, which are species distributed around the Mediterranean Sea; (3) Wide, which are species distributed across a wider area (Table 1). The species included two modes of regeneration after fire: sprouters (species that are capable of regenerating after fire by sprouting) and non-sprouters (regeneration after fire proceeds only from seeds). While information for all the species' life-form and distribution range is available from the literature (Bolòs and Vigo 1984–2001), the mode of regeneration after fire was based on personal observation in the field, and reliable information for this trait was available only for 43 species. Therefore, analyses including regeneration strategy were carried out with these 43 species, whereas in the rest of analyses the whole set of species was used.

A factorial experiment including two factors, light and nitrate addition, was carried out. These two factors were chosen as representative of some of the characteristic post-fire environmental conditions. The canopy and litter are removed by a fire, thereby allowing light to reach the soil surface; the soil nitrate content also increases (Serrasolsas and Vallejo 1999; Romanya et al. 2001). Therefore, we consider these factors as indirect fire effects. In addition, seed dormancy regulated by light or nitrate can be considered as mechanisms to detect gaps in vegetation and would be an expected characteristic of fire

recruiters. At the beginning of the experiment, seeds were placed on two layers of moistened [1.2 ml of distilled water (no nitrate) or 20 mM potassium nitrate (+ nitrate) solution; AOSA 1981; ISTA 1993] filter paper (Whatman no. 1) in plastic petri dishes (diameter 5.5 cm) and incubated in a chamber at 17.5°C. Half of the dishes were incubated under light conditions (continuous white light at $110.2 \pm 4.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ provided by Philips TL-D/54 fluorescent tubes), and the other half were incubated in the dark (wrapped in aluminum foil) in the same chamber. Four replicates, of 25 seeds each, were used per treatment and species. Germination was recorded only once, at the end of the incubation period, after 6 weeks of incubation. Radicle emergence was the criterion used for scoring a seed as germinated. The tetrazolium test was used to check seed viability in seeds that did not germinate, and germination percentages were corrected accordingly.

Prior to carrying out the statistical analyses, germination percentages were arcsine transformed, but for ease of interpretation, the data are presented here untransformed. The significance of differences in germination between species and levels of light and nitrate treatments was tested by a three-way analysis of variance (ANOVA; species, light and nitrate treatments). Differences in germination means among treatments were analysed by two-way ANOVA for each species separately. A posteriori Tukey tests were performed to determine differences between treatment means. Species with germination percentages $\geq 20\%$ were classified according to their response to light and nitrate treatments as: (1) stimulated species, which were those that experienced a germination increase with the treatment; (2) non-stimulated species, which included species that were non-sensitive to the treatment as well as species inhibited by it (Table 2). The germination response (stimulated, non-stimulated) was compared across treatments and functional groups (life-form, regeneration strategy and distribution range) by means of χ^2 analysis.

Differences in germination percentages between the light and nitrate treatments and functional groups (life-form, regeneration strategy and geographical distribution groups) were examined through a split-plot nested ANOVA with two levels (level 1: functional groups; level 2: species within each functional group).

Table 1 List of plant species, families, life-forms, regenerative strategies and geographical distribution range

Species	Plant family	Life-form ^a	Regenerative strategy ^b	Distribution range ^c
<i>Arenaria erinacea</i> Boiss.	Caryophyllaceae	Ch		IP
<i>Telephium imperati</i> L.	Caryophyllaceae	Hc	NS	Med
<i>Fumana ericoides</i> (Cav.) Gand.	Cistaceae	Ch	NS	Wide
<i>F. procumbens</i> (Dunal) Gren. & Godron.	Cistaceae	Ch	NS	Wide
<i>Halimium viscosum</i> (Willk.) P. Silva	Cistaceae	Ch	NS	Med
<i>Helianthemum apenninum</i> (L.) Miller	Cistaceae	Ch	NS	Wide
<i>H. hirtum</i> (L.) Miller	Cistaceae	Ch	NS	Med
<i>H. rotundifolium</i> Dunal	Cistaceae	Ch	NS	Med
<i>Tuberaria lignosa</i> (Sweet)Samp.	Cistaceae	Ch	NS	Med
<i>Achillea ageratum</i> L.	Compositae	Hc	S	Med
<i>Catananche caerulea</i> L.	Compositae	Hc	S	Med
<i>Centaurea pinae</i> Pau	Compositae	Hc	NS	IP
<i>Chondrilla juncea</i> L.	Compositae	Hc	NS	Wide
<i>Helichrysum serotinum</i> Boiss.	Compositae	Ch	NS	Med
<i>H. stoechas</i> (L.) Moench.	Compositae	Ch	NS	Wide
<i>Inula montana</i> L.	Compositae	Hc	S	Med
<i>Jasonia tuberosa</i> (L.) DC	Compositae	Hc	S	IP
<i>Leucanthemopsis pallida</i> (Miller) Heywood	Compositae	Hc	NS	IP
<i>Leuzea conifera</i> (L.) DC	Compositae	Hc	S	Med
<i>Santolina chamaecyparissus</i> L.	Compositae	Ch	NS	Med
<i>Scolymus hispanicus</i> L.	Compositae	Hc		Wide
<i>Staehelina dubia</i> L.	Compositae	Ch	NS	Med
<i>Alyssum serpyllifolium</i> Desf.	Cruciferae	Ch		Med
<i>Scabiosa turoloensis</i> Pau ex Willk	Dipsacaceae	Hc	S	IP
<i>Erica cinerea</i> L.	Ericaceae	Ch	NS	Wide
<i>Acinos meridionalis</i> (Nyman) P. W. Ball	Labiatae	Ch		Med
<i>Lavandula latifolia</i> Medicus	Labiatae	Ch	NS	Med
<i>L. pedunculata</i> (Miller) Cav.	Labiatae	Ch	NS	IP
<i>Marrubium supinum</i> L.	Labiatae	Ch		Med
<i>Nepeta nepetella</i> L.	Labiatae	Ch		Med
<i>Phlomis lychnitis</i> L.	Labiatae	Ch	S	Med
<i>Prunella laciniata</i> (L.)L.	Labiatae	Hc	S	Wide
<i>Salvia lavandulifolia</i> Vahl.	Labiatae	Ch	S	IP
<i>S. verbenaca</i> L.	Labiatae	Hc	S	Wide
<i>Sideritis hirsuta</i> L.	Labiatae	Ch	S	Med
<i>S. tragoriganum</i> Lag.	Labiatae	Ch		IP
<i>Teucrium capitatum</i> L.	Labiatae	Ch	NS	Med
<i>T. expansum</i> Pau	Labiatae	Ch	NS	IP
<i>T. gnaphalodes</i> L'Hér	Labiatae	Ch	S	IP
<i>Thymus leptophyllus</i> Pau	Labiatae	Ch	NS	IP
<i>T. mastichina</i> L.	Labiatae	Ch	NS	IP
<i>T. vulgaris</i> L.	Labiatae	Ch	NS	Med
<i>Psoralea bituminosa</i> L.	Leguminosae	Hc	NS	Med

Table 1 continued

Species	Plant family	Life-form ^a	Regenerative strategy ^b	Distribution range ^c
<i>Linum narbonense</i> L.	Linaceae	Ch	S	Wide
<i>Plantago sempervirens</i> Crantz.	Plantaginaceae	Ch	NS	Med
<i>Reseda lutea</i> L.	Resedaceae	Hc		Wide
<i>R. luteola</i> L.	Resedaceae	Hc		Wide
<i>Galium fruticosescens</i> Cav.	Rubiaceae	Hc	S	IP
<i>Anarrhinum bellidifolium</i> (L.)Willd.	Scrophulariaceae	Hc	S	Wide
<i>Antirrhinum litigiosum</i> Pau	Scrophulariaceae	Hc		IP
<i>Verbascum rotundifolium</i> Ten.	Scrophulariaceae	Hc	NS	Med
<i>Daucus carota</i> L.	Umbelliferae	Hc	S	Wide
<i>Thapsia villosa</i> L.	Umbelliferae	Hc	S	Med

^a Ch, Chamaephyte; Hc, hemicryptophyte

^b S, Sprouter; NS, non-sprouter

^c IP, Endemic species with a geographical distribution restricted to the Iberian Peninsula; Med, species distributed around the Mediterranean Sea; Wide, species distributed across a wider area

In addition, phylogenetic relatedness among taxa was taken into account to avoid pseudoreplication derived from common ancestry (Harvey and Pagel 1991). The phylogenetic analyses were run in PDAP software (Garland et al. 1993), which creates a computer simulation of a null distribution that incorporates the phylogenetic relationships among species. Significance tests were obtained by contrasting the observed F values against simulated distributions after 1000 phylogenetic permutations run in the PDRANDOM module of the PDAP programme (Lapointe and Garland 2001) and consecutive nested ANOVA analyses. When the F values of the real data were smaller than at least 95% of the randomized values, there was evidence of a phylogenetic effect. When the F values of the real data were higher than the 95 percentile, significant differences were confirmed independently of phylogenetic relatedness. The large-scale structure of the tree for the 53 species studied here was based on phylogenetic interrelationships of angiosperm orders compiled from recent cladistic analyses by Davies et al. (2004) (see Luna et al. 2007, for the structure of the tree).

Results

The mean overall percentage germination was 26.9 ± 1.14 . There was a great variability among

species, with 20% having germination percentages below 10%, and other species failing to germinate entirely (*Erica cinerea*, *Halimium viscosum*, *Salvia lavandulifolia* and *Thapsia villosa*) (Table 2). When all species were analysed together, that is, the germination percentages of all 53 species, no statistically significant differences for any of the treatments, light or nitrate, emerged (light: $F_{1,52} = 0.02$, $P = 0.88$; nitrate: $F_{1,51} = 0.01$, $P = 0.98$). However, their effects varied according to species for both light and nitrate treatments (light \times species: $F_{52,52} = 10.55$ $P < 0.001$; nitrate \times species: $F_{51,51} = 2.01$ $P < 0.001$), suggesting that even though the overall mean was not affected by the treatments, individual species did have specific responses. In fact, when exposed to light, about a third of the species were significantly affected and, of these, about half were stimulated by light, whereas the other half was inhibited by it (Table 2). In comparison, nitrate produced a significant effect in a lower number of species (around 25%), but in most cases the effect was positive. Negative effects were found in only four species (*Achillea ageratum*, *Anarrhinum bellidifolium*, *Prunella laciniata* and *Salvia verbenaca*), and these were stimulated by light. A significant interaction effect between light and nitrate was found for 20% of the species (Table 2).

When species with germination percentages above 20% were classified according to their germination response to light or nitrate (stimulated germination

Table 2 Effect of light (L) and nitrate (N) treatments on seed germination of the two-way analysis of variance (ANOVA) of 53 species from a burned area in Cuenca, Spain

	Means of treatments				F-values and significance			Response ^a	
	L–N–	L–N+	L+N–	L+N+	Light	Nitrate	L × N	L	N
<i>A. ageratum</i>	0.0 ± 0.0	2.6 ± 2.6	98.5 ± 0.0	65.7 ± 11.4	207.81**)	5.91*	11.90**	+	–
<i>A. meridionalis</i>	47.8 ± 2.7	70.0 ± 3.0	53.1 ± 9.2	62.0 ± 7.9	0.03 n.s.	5.65*	0.94 n.s.	0	+
<i>A. serpyllifolium</i>	72.0 ± 5.4	87.0 ± 5.3	45.9 ± 5.1	88.0 ± 5.4	3.72 n.s.	27.33***	4.75*	0	+
<i>A. bellidifolium</i>	0.0 ± 0.0	0.0 ± 0.0	77.5 ± 7.0	27.6 ± 16.0	34.42***	6.84*	6.84*	+	–
<i>A. litigiosum</i>	0.0 ± 0.0	0.0 ± 0.0	17.2 ± 11.4	0.0 ± 0.0	2.69 n.s.	2.69 n.s.	2.69 n.s.		
<i>A. erinacea</i>	19.8 ± 7.4	22.1 ± 5.0	4.5 ± 2.6	28.6 ± 8.2	0.84 n.s.	6.12*	2.70 n.s.	0	+
<i>C. caerulea</i>	10.5 ± 7.6	10.5 ± 7.6	4.7 ± 2.7	2.4 ± 2.4	0.89 n.s.	0.11 n.s.	0.11 n.s.		
<i>C. pinae</i>	48.9 ± 17.9	73.1 ± 8.4	78.8 ± 8.5	31.2 ± 11.2	0.12 n.s.	0.58 n.s.	7.22*	0	0
<i>C. juncea</i>	94.2 ± 1.4	64.2 ± 21.5	87.9 ± 4.0	94.5 ± 2.0	1.33 n.s.	1.09 n.s.	3.34 n.s.	0	0
<i>D. carota</i>	62.0 ± 4.4	46.1 ± 3.8	33.7 ± 14.4	49.0 ± 8.5	2.13 n.s.	0.01 n.s.	2.99 n.s.	0	0
<i>E. cinerea</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0					
<i>F. ericoides</i>	2.1 ± 1.2	2.1 ± 1.2	5.3 ± 2.6	4.2 ± 2.4	0.91 n.s.	0.11 n.s.	0.11 n.s.		
<i>F. procumbens</i>	13.7 ± 4.5	11.9 ± 5.6	0.0 ± 0.0	6.9 ± 4.8	7.72*	0.46 n.s.	2.15 n.s.		
<i>G. frutescens</i>	11.7 ± 5.2	41.7 ± 8.1	4.9 ± 2.0	2.5 ± 1.4	23.70***	3.75 n.s.	9.13*	–	0
<i>H. viscosum</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0					
<i>H. apenninum</i>	19.6 ± 1.1	24.0 ± 8.8	18.2 ± 4.1	22.7 ± 2.5	0.02 n.s.	0.49 n.s.	0.06 n.s.	0	0
<i>H. hirtum</i>	19.7 ± 3.1	21.2 ± 3.7	28.3 ± 7.0	23.0 ± 3.0	1.01 n.s.	0.07 n.s.	0.34 n.s.	0	0
<i>H. rotundifolium</i>	23.7 ± 6.1	19.5 ± 7.0	23.8 ± 4.1	17.4 ± 5.2	0.01 n.s.	1.02 n.s.	0.04 n.s.	0	0
<i>H. serotinum</i>	15.2 ± 7.5	32.5 ± 9.7	26.5 ± 9.6	53.9 ± 6.5	4.00 n.s.	7.43*	0.18 n.s.	0	+
<i>H. stoechas</i>	7.7 ± 3.3	18.1 ± 5.3	38.7 ± 8.0	21.3 ± 1.7	11.32**	0.00 n.s.	6.70*	+	0
<i>I. montana</i>	0.0 ± 0.0	0.0 ± 0.0	21.0 ± 8.2	9.0 ± 6.2	10.22**	1.05 n.s.	1.05 n.s.	+	0
<i>J. tuberosa</i>	0.0 ± 0.0	1.6 ± 1.6	1.6 ± 1.6	0.0 ± 0.0	0.00				
<i>L. latifolia</i>	0.0 ± 0.0	16.5 ± 15.1	0.0 ± 0.0	0.0 ± 0.0	1.68 n.s.	1.68 n.s.	1.68 n.s.		
<i>L. pedunculata</i>	1.1 ± 1.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.00 n.s.	1.00 n.s.	1.0 n.s.		
<i>L. pallida</i>	43.9 ± 12.9	79.1 ± 5.0	56.6 ± 14.9	63.7 ± 6.4	0.03 n.s.	3.82 n.s.	1.88 n.s.	0	0
<i>L. confiera</i>	88.6 ± 2.9		55.3 ± 10.4		10.55*			–	
<i>L. narbonense</i>	47.8 ± 3.3	48.4 ± 9.9	5.9 ± 4.5	3.3 ± 3.3	50.92***	0.14 n.s.	0.21 n.s.	–	0
<i>M. supinum</i>	27.9 ± 2.1	32.0 ± 6.3	28.8 ± 6.2	28.7 ± 7.0	0.07 n.s.	0.09 n.s.	0.11 n.s.	0	0
<i>N. nepetella</i>	0.0 ± 0.0	21.7 ± 5.0	10.5 ± 10.5	6.9 ± 4.0	0.26 n.s.	5.14*	4.60 n.s.	0	+
<i>P. lychnitis</i>	97.3 ± 1.0	98.1 ± 0.5	94.3 ± 1.6	94.2 ± 2.0	7.21*	0.15 n.s.	0.14 n.s.	–	0
<i>P. sempervirens</i>	99.5 ± 0.5	89.7 ± 3.5	55.2 ± 21.6	41.7 ± 11.8	15.47**	1.26 n.s.	0.29 n.s.	–	0
<i>P. laciniata</i>	2.1 ± 2.1	0.0 ± 0.0	84.5 ± 6.2	4.2 ± 2.4	78.63***	61.48***	46.43***	+	–
<i>P. bituminosa</i>	15.4 ± 2.2	10.4 ± 2.9	12.6 ± 3.9	6.9 ± 4.0	1.50 n.s.	3.05 n.s.	0.18 n.s.		
<i>R. lutea</i>	5.9 ± 5.9	25.3 ± 6.1	0.0 ± 0.0	10.8 ± 5.2	4.32 n.s.	13.00**	0.24 n.s.	0	+
<i>R. luteola</i>	0.0 ± 0.0	0.0 ± 0.0	46.9 ± 5.4	72.8 ± 5.0	500.22***	11.81**	11.81**	+	+
<i>S. lavandulifolia</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0					
<i>S. verbenaca</i>	0.0 ± 0.0	0.0 ± 0.0	39.8 ± 9.8	8.6 ± 5.0	30.33***	8.16*	8.16*	+	–
<i>S. chamaecyparissus</i>	37.8 ± 2.9	83.9 ± 6.1	68.4 ± 4.1	81.5 ± 6.1	4.15 n.s.	25.20***	6.44*	0	+
<i>S. turolensis</i>	89.4 ± 2.4	75.3 ± 4.9	35.7 ± 14.5	15.9 ± 15.9	22.13**	2.76 n.s.	0.23 n.s.	–	0
<i>S. hispanicus</i>	8.8 ± 3.7	2.9 ± 2.9	4.4 ± 2.8	15.1 ± 7.9	0.48 n.s.	0.01 n.s.	3.02 n.s.		
<i>S. hirsuta</i>	43.1 ± 3.8	74.1 ± 2.9	23.7 ± 5.7	42.1 ± 16.7	6.20*	3.47 n.s.	0.56 n.s.	–	0
<i>S. tragoriganum</i>	69.4 ± 4.2	71.5 ± 2.5	44.9 ± 8.9	69.9 ± 6.0	4.60 n.s.	5.15*	3.74 n.s.	0	+

Table 2 continued

	Means of treatments				F-values and significance			Response ^a	
	L–N–	L–N+	L+N–	L+N+	Light	Nitrate	L × N	L	N
<i>S. dubia</i>	100 ± 0.0	100 ± 0.0	50.0 ± 28.9	0.0 ± 0.0	27.00***	3.00 n.s.	3.0 n.s.	–	0
<i>T. imperati</i>	0.0 ± 0.0	2.2 ± 1.3	1.1 ± 1.1	1.1 ± 1.1	0.00 n.s.	1.20 n.s.	1.20 n.s.		
<i>T. capitatum</i>	0.0 ± 0.0	0.0 ± 0.0	3.7 ± 3.7	0.0 ± 0.0	1.00 n.s.	1.00 n.s.	1.0 n.s.		
<i>T. expansum</i>	37.5 ± 21.7	0.0 ± 0.0	18.8 ± 18.8	0.0 ± 0.0	0.43 n.s.	3.86 n.s.	0.43 n.s.	0	0
<i>T. gnaphalodes</i>	0.0 ± 0.0	0.0 ± 0.0	10.3 ± 6.0	2.8 ± 2.8	4.00 n.s.	0.89 n.s.	0.89 n.s.		
<i>T. villosa</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0					
<i>T. leptophyllus</i>	0.0 ± 0.0	0.0 ± 0.0	5.1 ± 5.1	0.0 ± 0.0	1.00 n.s.	1.00 n.s.	1.0 n.s.		
<i>T. mastichina</i>	65.8 ± 1.7	52.8 ± 4.0	62.3 ± 6.3	64.8 ± 7.0	0.74 n.s.	0.92 n.s.	2.18 n.s.	0	0
<i>T. vulgaris</i>	0.0 ± 0.0	0.0 ± 0.0	18.9 ± 18.9	18.9 ± 18.9	2.00 n.s.	0.00 n.s.	0.0 n.s.		
<i>T. lignosa</i>	3.1 ± 2.0	2.1 ± 1.2	1.0 ± 1.0	1.0 ± 1.0	1.09 n.s.	0.03 n.s.	0.03 n.s.		
<i>V. rotundifolium</i>	0.0 ± 0.0	5.3 ± 5.3	5.3 ± 5.3	72.8 ± 9.6	26.20***	26.20***	15.51**	+	+

Significance: n.s. non-significant, * 0.05 ≥ P > 0.01, ** 0.01 ≥ P > 0.001, *** 0.001 ≥ P > 0.0001

^a Those species with germination percentages above 20% were classified in relation to their germination response to light (L) and nitrate (N) treatments as: +, species with germination stimulated by the treatment; 0, species with non-stimulated germination, non-sensitive to the treatment; –, species with germination reduced by the treatment

vs. non-stimulated germination) and then tested for the null hypothesis that their germination was not stimulated by light or nitrate, respectively, we found a differential response among functional groups. The number of light-stimulated species differed significantly from those non-stimulated (which included species not significantly affected and those negatively affected) for all functional groups tested. Hence, a higher proportion of hemicryptophytes was stimulated by light in comparison with chamaephytes (Fig. 1a) ($\chi^2 = 7.99, P < 0.01$). Similarly, a higher proportion of sprouters was stimulated by light when compared to non-sprouters (Fig. 1a) ($\chi^2 = 3.91, P < 0.05$). Likewise, in contrast to endemic species, widely distributed species were stimulated by light (Fig. 1a) ($\chi^2 = 6.56, P < 0.05$). Conversely, the null hypothesis of non-stimulation by nitrate was accepted for all three functional groups (Fig. 1b). While this was not statistically significant, it is worth noting that fewer hemicryptophytes than chamaephytes were stimulated by nitrate, and fewer sprouters than non-sprouters (Fig. 1b).

When germination percentages were analysed and tested for treatment effects, we found that no significant effects were found for any of the two treatments (light, nitrate) and any of the three groups (life-form, regeneration strategy or distribution range) (Figs. 2–4; Tables 3–5). However, some

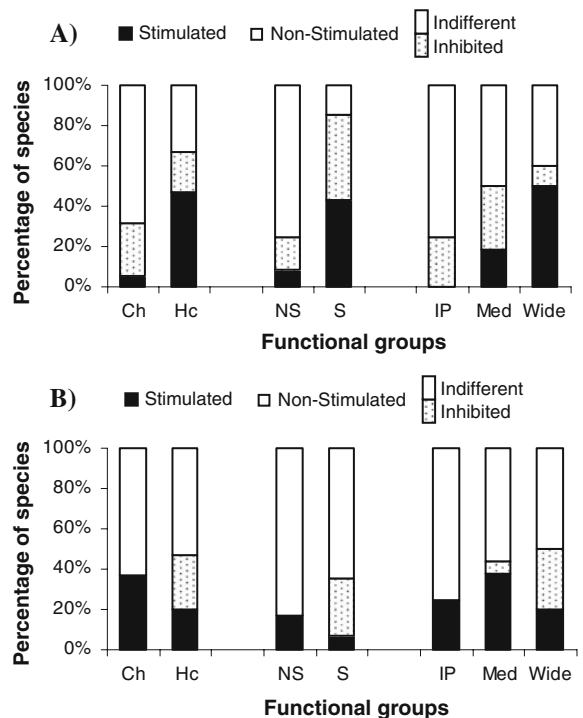


Fig. 1 Percentage of species classified by functional groups stimulated or not (see Table 2) by light (a) and nitrate (b). Functional groups: life form (*Ch* chamaephyte, *Hc* hemicryptophyte), regeneration strategy (*NS* non-sprouter, *S* sprouter), distribution range (*IP* Iberian Peninsula endemics, *Med* Mediterranean, *Wide* widely distributed species)

significant interactions did appear. Life-form and treatments (light and nitrate) (Table 3) interacted so that the germination of hemicryptophytes was stimulated by light whereas that of chamaephytes was reduced (Fig. 2a); similarly, the germination of hemicryptophytes decreased with nitrate, in contrast to that of chamaephytes (Fig. 2b). The differential response of chamaephytes and hemicryptophytes to both treatments is revealed by the significant interaction among life-form, light and nitrate treatments (Table 3). No other significant interaction for light and regeneration strategy was found (Fig. 3a) except in the case of nitrate (Table 4), whereby non-sprouters virtually did not respond to nitrate but the germination of sprouters decreased with this

treatment (Fig. 3b). Finally, there was a significant interaction between light and geographic distribution range (Table 5), whereby Iberian Peninsula endemics were negatively affected by light, Mediterranean species were indifferent, and widely-distributed species were stimulated (Fig. 4a). No significant interactions were found for nitrate and geographic distribution range (Fig. 4b).

The results obtained after accounting for phylogeny were rather similar to those that did not consider it (Tables 3–5). Once the phylogenetic relationships were taken into account, there was no evidence of a phylogenetic effect in the interactions mentioned above, with the exception that the real F value was higher than the simulated after 1000 randomizations.

Table 3 Results of the split-plot, nested, non-phylogenetic ANOVA for the effects of light and nitrate treatment on the germination of 53 Mediterranean plant species classified by life-form

Source of variation	df	Non-phylogenetic ANOVA			Phylogenetic ANOVA
		MS	F	P	F
Life-form	1	0.414	0.187	n.s.	4.250
Species within life-form	51	2.213	25.499	<0.0001	1.431*
Light	1	0.202	0.073	n.s.	14.709
Nitrate	1	0.169	0.258	n.s.	48.419
Light \times nitrate	1	0.365	0.362	n.s.	1072.026
Life-form \times light	1	2.777	32.002	<0.0001	3.949*
Life-form \times nitrate	1	0.656	7.561	<0.01	3.933*
Light \times nitrate \times life-form	1	1.007	11.604	<0.001	3.480*
Error	789	0.087			

* Significant differences

The 95 percentile of F values for the phylogenetic analyses are also included ($n = 1000$). When the F value of the non-phylogenetic analyses is higher than the 95 percentile of the phylogenetic analyses, the significant difference observed is independent of phylogenetic relatedness

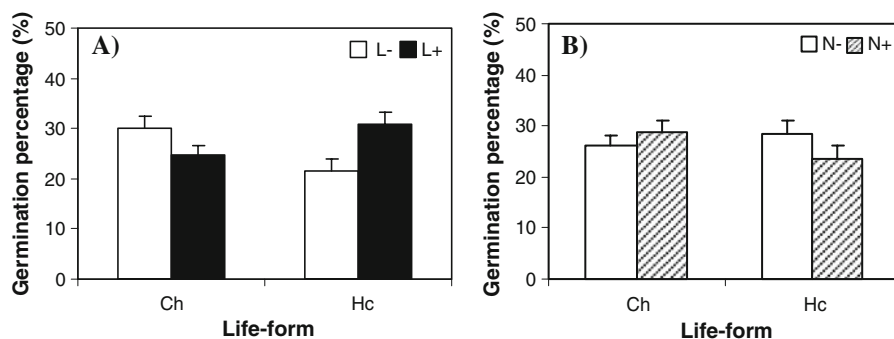


Fig. 2 Germination percentages in response to light (a) and nitrate (b) treatments for the two life-forms: chamaephytes (Ch , $n = 31$) and hemicryptophytes (Hc , $n = 22$). N Nitrogen, L Light, + present, – absent. Error bars Standard error of means

Fig. 3 Germination percentage in response to light (a) and nitrate (b) treatments for the two regeneration strategies: non-sprouters ($n = 24$) and sprouters ($n = 19$). Error bars Standard error of means

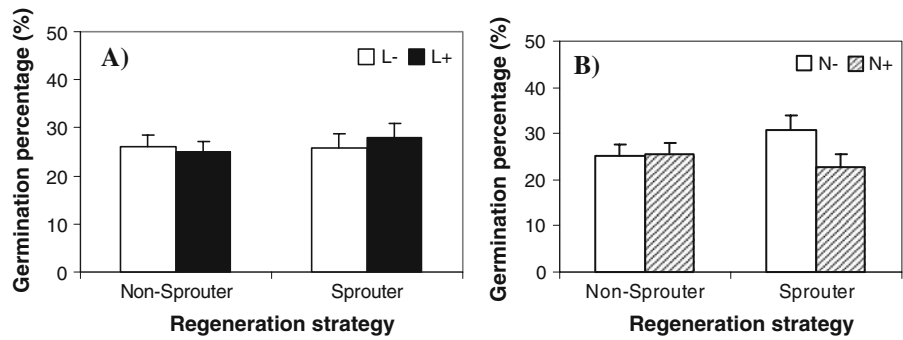


Table 4 Results of the split-plot, nested, non-phylogenetic ANOVA for the effects of light and nitrate treatment on the germination of 43 Mediterranean plant species classified by regeneration strategy

Source of variation	df	Non-phylogenetic ANOVA			Phylogenetic ANOVA
		MS	F	P	F
Regeneration strategy	1	0.024	0.010	n.s.	4.039
Species within regeneration strategy	41	2.322	24.487	<0.0001	1.472
Light	1	0.020	0.072	n.s.	42.969*
Nitrate	1	0.888	1.032	n.s.	60.241
Light × nitrate	1	0.602	2.423	n.s.	641.308
Regeneration strategy × light	1	0.273	2.882	n.s.	4.361
Regeneration strategy × nitrate	1	0.860	9.069	<0.01	3.902*
Light × nitrate × regeneration strategy	1	0.248	2.620	n.s.	3.540
Error	639	0.095			

* Significant differences

The 95 percentile of F values for the phylogenetic analyses are also included ($n = 1000$). When the F value of the non-phylogenetic analyses is higher than the 95 percentile of the phylogenetic analyses, the significant difference observed is independent of phylogenetic relatedness

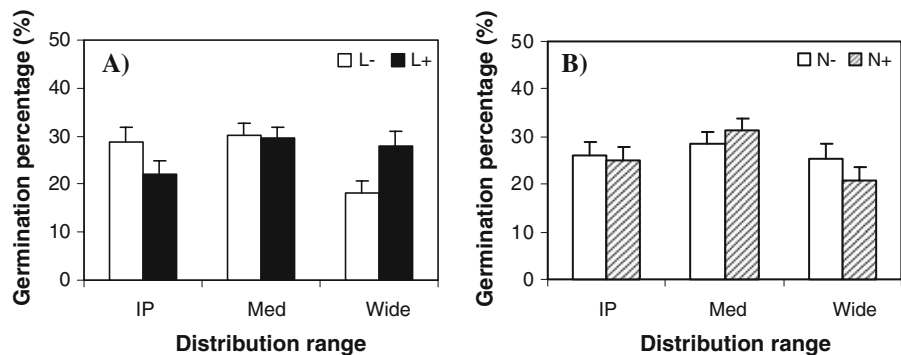
Table 5 Results of the split-plot, nested, non-phylogenetic ANOVA for the effects of light and nitrate treatment on the germination of 53 Mediterranean plant species divided by distribution range

Source of variation	df	Non-phylogenetic ANOVA			Phylogenetic ANOVA
		MS	F	P	F
Distribution range	2	0.697	0.311	n.s.	3.255
Species within distribution range	50	2.237	25.036	<0.0001	1.432*
Light	1	0.063	0.079	n.s.	1.905
Nitrate	1	0.127	1.986	n.s.	3.866
Light × nitrate	1	0.313	36.754	<0.05	68.400
Distribution range × light	2	0.800	8.957	<0.01	3.280*
Distribution range × nitrate	2	0.064	0.718	n.s.	3.093
Light × nitrate × distribution	2	0.009	0.095	n.s.	3.337
Error	786	0.089			

* Significant differences

The 95 percentile of F values for the phylogenetic analyses are also included ($n = 1000$). When the F value of the non-phylogenetic analyses is higher than the 95 percentile of the phylogenetic analyses, the significant difference observed is independent of phylogenetic relatedness

Fig. 4 Germination percentage in response to light (a) and nitrate (b) treatments for the three distribution range groups: Iberian Peninsula endemics (IP, $n = 14$), Mediterranean (Med, $n = 25$), widely distributed species (Wide, $n = 14$). Error bars Standard error of means



This implies that significant interactions in the cross-species analyses are supported independently of phylogenetic relatedness.

Discussion

About half of the species did not show a significant response to either nitrate addition or exposure to light. This overall lack of dependency on light and/or nitrate for germinating suggests that indirect effects of fire, such as those of eliminating the canopy and litter, plus the increment in nitrate in the soil that follows fire may have not played an important role in determining the germination response. Further, these species did not need to be exposed to the direct effects of fire, such as heat-shock, to germinate (Luna et al. 2007). Therefore, fire seems not to have played a decisive role in selecting the germination traits. Our results indicate that half of the species may be able to establish in mature environments without the need of light and nitrate stimulation. In addition, a great diversification in the germination responses was found, which supports again the lack of specific post-fire germination requirements. Nevertheless, despite this diversification of responses, our study does reveal that functional groups are important for characterizing germination responses to light and nitrate.

Light

Light was an important factor controlling the germination of functional groups (life-form, regeneration strategy and distribution range groups). A higher proportion of hemicryptophytes was stimulated by light. Further, the germination of hemicryptophytes

increased under light conditions, while that of chamaephytes germination tended to be reduced. These findings may be related to the role of these groups in succession, with chamaephytes being more common in later successional stages than hemicryptophytes. Herbaceous growth is promoted in the aftermath of a fire (Arianoutsou 1998; Keeley et al. 2005). As succession progresses, the canopy closes and litter develops, and herbaceous vegetation will be restricted to small openings. Our results support the idea that herbaceous hemicryptophytes have germination characteristics that are more adapted to the colonization of open sites, which is contrary to the situation for woody chamaephytes, whose germination appears to be associated with closed-canopy vegetation. Bell et al. (1999) also reported perennial shrubs to be inhibited by light in Western Australia, while Clarke et al. (2000) found germination responses to light similar across growth forms.

In relation to regeneration strategy, germination under optimal conditions for seedling establishment could be considered less critical for sprouting species than for non-sprouters, since the surviving parent can produce more seeds after a fire. On the other hand, it can be reasoned that seeds of non-sprouter species may have well-developed dormancy, which would be broken by direct fire-related cues, thus allowing re-establishment. In this respect, Bell et al. (1995) found non-sprouter (i.e. obligate seeding) species to be generally more responsive to conditions of light than sprouters. Nonetheless, contrary to our expectations, we found a higher number of sprouters than non-sprouters were stimulated by light, even if the mean number of germinates was similar.

Non-sprouters may have more specific germination requirements which, either alone or through

interaction with light or other factors may stimulate the germination of these species. In fact, the non-sprouters seeds from our study appeared to be more resistant to heat-shock than those of sprouter species (Luna et al. 2007). In other studies, non-sprouters were also probably more heat- or smoke- stimulated than sprouters (van Staden et al. 2000; Paula and Pausas 2008). Our results support the idea that light may not be a particularly strong controlling factor for the germination of non-sprouter species that it is an important factor for sprouters.

Light stimulated the germination of widely distributed species, while it was inhibited the germination of endemics. Among various potential causes for rarity, one explanation could be that rare species have more narrow germination niches than widespread ones. The niche breadths of species have been argued to be positively correlated with their range sizes on the basis that species that have broad environmental tolerances and are able to use a wide range of resources will be able to survive in more places and thus over a large area (Brown 1984). Thus, while widespread species presumably tolerate wider differences in germination conditions, endemic species must germinate under more restricted conditions to ensure seedling establishment. Thus, rare species may be specialized for a particular habitat or niche but lack the flexibility and adaptability to expand into other habitats. In our study, in agreement with Brown's (1984) proposal, endemics showed narrower regenerative niches than widely distributed species. Therefore, fires, by eliminating the canopy and litter and increasing light conditions, would promote the germination of widespread species at the expense of endemics.

Nitrate

Nitrate appeared not to affect the germination of the plants studied; rather, it stimulated germination in only a fifth of the species and, therefore, the germination response did not seem to be determined by the post-fire conditions, as has been found in other investigations (Cruz et al. 2003; Buhk and Hensen 2006). Nitrate levels increase shortly after a fire (Marion et al. 1991; Christensen 1994; Serrasolsas and Vallejo 1999; Romanya et al. 2001), and it has been proposed as the active component of charred wood-stimulated germination (Thanos and Rundel

1995) and as a germination stimulatory factor in ash extracts (Henig-Sever et al. 2000).

Most of the species sensitive to nitrate were stimulated by it, and in the cases of only four species was germination decreased, which can be explained based on the observation that the concentration of KNO_3 is critical, with supra-optimal nitrate concentrations being able to inhibit germination (Baskin and Baskin 1998). For several species, an interaction effect was found between the light and nitrate treatments. In some cases, when germination was light stimulated, the addition of nitrates inhibited it. Nitrates can change the light response of seeds noticeably, influencing the maximum photon dose for promotion or inhibition of germination. Positive responses to nitrate are linked to phytochrome (Grubisic and Konjevic 1990), whereby nitrate may enhance the number of Pfr-receptors (Hilhorst and Karssen 1990) or may act as a Pfr cofactor (Grubisic and Konjevic 1990).

Although at the level of species we did not find a significant association between any of the three groups and nitrate, at the level of germination means we found some significant interactions which in fact were parallel to the findings at the level of species, even if the association tests were non-significant. Hemicryptophytes relative to chamaephytes, and sprouters relative to non-sprouters appeared to be negatively affected by nitrate addition, which was related to a positive interaction with light. Although publications reporting a positive interaction between light and nitrate are frequent in literature (Hilhorst and Karssen 2000), some examples of negative interactions between both factors have also appeared. Keeley and Baer-Keeley (1999) observed that the germination of *Lavandula stoechas* increased when exposed to charred wood in the dark but not in the light. A very similar pattern was observed for several summer deciduous elements in California chaparral (Keeley 1987) or for serotinous eucalypts from Western Australia (Bell et al. 1999). Although no clear explanations have emerged, it has been proposed that the concentration of nitrate is critical for the germination response. In addition, the negative effect of nitrogenous compounds on seed germination has been also related to the ability to colonize soils with low nitrogen concentration (Pérez-Fernández and Rodríguez-Echevarría 2003).

In conclusion, we found that our study set of plants, as an example of Mediterranean flora that may grow in burned areas, appears to be non-dependent on changes induced by fire, such as increased light and soil nitrate, for germinating and, eventually, establishing after the blaze. Nonetheless, these factors may alter the overall balance of the germinating plants, as some species were sensitive to these factors. Light appeared to be more important than nitrate in changing the germination of these groups of plants, and functional groups provided some clues as to which type of species may be more or less affected. In this regard, if a fire occurs, and seeds survive, it can be expected that hemicryptophytes, sprouters and widely distributed species will thrive as a result of their response to light. However, part of the positive effect may be offset by the negative response of these groups, in particular, the first two, to nitrate. The particular sensitivity of Iberian Peninsula endemics to light, specific to burned environments, threatens the persistence of these species under the current fire regime.

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