Original article

Light quality and not quantity segregates germination of grazing *increasers* from *decreasers* in Mediterranean grasslands

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ABSTRACT

Grassland plant species have traditionally been classified into two groups, *increasers* and *decreasers*, based on changes in their relative abundance in the presence or absence of grazing. However, the ecophysiological mechanisms underlying these opposing strategies remain unclear. Seeds of ten Mediterranean species of known grazing status were germinated in different light environments to test the hypothesis that grazing selects light-dependent germination amongst grazing *increasers*. Two light quantity levels (Photosynthetical Active Radiation, PAR) and five light quality levels (red:far-red ratio, R:FR) were used to quantify percentages of germination of viable seeds and number of days elapsed to reach 50% of germination (T50), measured using five replicates of each light treatment and species combination. There were no differences in response to light quantity between the two grazing status groups; germination was inhibited in both groups at higher light intensities. However, *increasers* had lower germination percentages at low R:FR ratios, while *decreasers* were not affected by light quality. Germination speed (T50) was affected differently by light quality in each grazing status. There was an increase in germination speed at the lowest R:FR ratio only in *increaser* seeds, whereas *decreaser* germination speed was not affected by the treatment. PAR affected T50, regardless of grazing status; germination was faster at lower light intensities. *Increaser* seeds germinated faster than *decreasers*. These results reveal that the differential control of germination by light quality is a key factor in determining the species composition of grassland plant communities affected by herbivores in semi-arid Mediterranean grasslands.

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1. Introduction

Grazing is a complex disturbance that has both direct and indirect effects on plant communities (Crawley, 1997; Danell and Bergström, 2002; Hodson and Illius, 1996). Trampling and damage by defoliation are two of the principal direct effects (Bokdam, 2001; Kohler et al., 2004), and plant persistence is achieved by several physiological and phenological mechanisms that confer either avoidance or damage tolerance (Briske, 1986; Herms and Mattson, 1992; McIntyre et al., 1999). Avoidance mechanisms include accumulation of secondary metabolites and morphological and phenological adjustments that allow plants to escape from herbivores. Tolerance mechanisms include compensatory growth and enhanced fecundity. However, grazing can also induce indirect effects, which have been far less explored. Herbivore damage to vegetation causes shifts in competitive relationships (Grime, 1979; Huntly, 1991) because it reduces the competitive pressure of dominant species and thus facilitates the establishment and survival of other species. Herbivores also affect seed availability via flower and fruit consumption and seed dispersal by endozoochory and exozoochory (Malo and Suarez, 1995; Pakeman et al., 1998; Tackenberg et al., 2006). Local extinction and colonization rates in grasslands are affected by herbivore activity, which largely explains the composition and diversity of grassland plant communities (Olff and Ritchie, 1998).

Local extinction of species involves changes in the plant environment, and affects resource availability and acquisition rates (Bokdam, 2001). Plant tissue loss and other grazing-induced disturbances such as trampling lead to changes in vegetation cover, creating gaps and new opportunities for colonization due to changes in the light environment experienced by seeds, amongst other causes (Fenner and Thompson, 2005).

Germination dynamics play an important role in the colonization of these gaps, especially in annual grasslands (Peco, 1989).

Germination is mediated by multiple physical factors such as light, temperature regime, water availability and the presence of organic and inorganic chemicals (Baskin and Baskin, 1998; Pearson et al., 2002). Quantity and quality of light are two important features that can regulate seed germination in many plant species (Casal and Sanchez, 1998). The influence of light on plant performance has traditionally been linked to the ecology of seedlings and adults, in particular their shade tolerance (Valladares and Niinemets, 2008). However, other studies reveal a lack of correlation between the light requirements for germination and the light requirements of juveniles and adults (see Figueroa and Lusk, 2001, and references therein).

Light quantity mediates the high irradiance response (HIR), which prevents germination at high irradiance in many plant species (Pons, 2000). This mechanism is important in dry ecosystems because it can prevent germination of seeds lying on the soil surface, as they are more prone to drought conditions during the summer (Fenner and Thompson, 2005). Light quality is detected by phytochromes, which are particularly sensitive to the red (660 nm) and far red (730 nm) regions of the spectrum. In many seeds, the red:far-red ratio (R:FR) determines either the induction or the inhibition of germination (Casal and Sanchez, 1998). As with light quantity, plant canopies modify light quality, since plant tissue differentially absorbs more photons in the red region than in the far red one. Seeds from certain species avoid germination at low R:FR ratios, thus minimizing the risks of germination under highly competitive conditions (Fenner and Thompson, 2005). It has been shown that some seeds are able to detect and respond to very subtle changes in the R:FR ratio (Batlla et al., 2000).

The influence of grazing on plant communities has been widely studied on the basis of changes in species frequencies (Peco et al., 2006). Changes due to the species response to grazing have been reflected in a classification of plants into two categories or statuses: increasers (species that increase their relative abundances with grazing) and decreasers (species that reduce their relative abundance with grazing). This classification has inconsistencies due to different species responses under different environmental conditions (Vesk and Westoby, 2001). Some attempts to identify groups of functional traits associated with correlation-based plant species responses to grazing have also been explored (Bullock et al., 2001; McIntyre et al., 1999; Peco et al., 2005; Vesk and Westoby, 2001). However, specific plant trait responses to grazing within each grazing category, and the underlying community processes in which they are involved, remain unclear. Field and lab experiments have been done to test the defoliation tolerance of grazing increasers vs decreasers (Del-Val and Crawley, 2004, 2005), but the germination responses to light quality and quantity of these two grazing response groups have not been analysed previously.

We conducted an experiment with seeds of ten Mediterranean species of known grazing status to test the following hypotheses: 1 increaser seeds inhibit their germination at low R:FR values because the R:FR ratio is presumably increased by grazing; 2 decreaser seeds are not affected by different R:FR values for their germination; and, 3, high irradiance decreases germination in plants of both grazing status due to a prevalence of the HIR in the Mediterranean ecosystems studied.

2. Material and methods

Seeds of ten grassland plant species were collected in the Cerro de San Pedro area (40°43′N 3°43′W, Madrid, Spain) in late spring 2004, and stored in paper bags at room temperature until the start of the experiment in May 2007. All selected species were known to have different grazing increaser or decreaser status (sensu Peco et al., 2006) and were abundant in the study area. Five species were

considered as decreasers: Holcus setiglumis Boiss. & Reut. (Poaceae), Agrostis castellana Boiss. & Reut. (Poaceae), Silene scabriflora Brot. (Caryophylaceae), Dactylis glomerata L. (Poaceae) and Festuca ampla Hack (Poaceae). The other five species were increasers: Crassula tillaea Lest.-Garl. (Crassulaceae), Spergularia purpurea (Pers.) D. Don (Caryophylaceae), Plantago coronopus L. (Plantaginaceae), Anthemis arvensis L. (Compositae) and Hypochoeris glabra L. (Compositae). Since seed mass is related to light dependence for germination (Jensen and Gutekunst, 2003; Milberg et al., 2000), we selected species that covered approximately the same rank of seed mass in both grazing status. Decreaser seed dry weight ranged from 0.064 mg to 0.910 mg, while increasers ranged from 0.011 mg to 0.778 mg (Peco et al., 2009, and personal communication).

To analyse the results of the experiment in the field condition context, R:FR ratio and PAR measurements were taken at ground level in the main microhabitats of the study area in two consecutive years. Field measurements were taken on Cerro de San Pedro in October 2005 and November 2006 (autumn), December 2005 and February 2006 (winter), and in March 2006 and June 2007 (spring), between 11:30 and 15:30 h. Ten random measurements were obtained for each microhabitat on each date: gaps (bare soil > 600 cm^2), annual grazed pasture, perennial ungrazed pasture and pasture under shrub (ten under Cytisus scoparius (L.) Link and ten under Lavandula stoechas subsp. pedunculata (Miller) Rozeira) All R:FR ratios were measured using SKR 100/116 equipment with optic fibre probe (Skye Instruments Ltd., Powys, UK) at 1 cm above ground level. All PAR measurements were recorded with a Quantum Photo/Radiometer HD 9021 connected to an HD 9021 RAD/PAR probe (Delta OHM, Caselle di Selvazzano, Italy), at 5 cm above ground level due to physical probe limitations.

To test for the influence of R:FR ratio on germination percentages, an experiment was designed with five R:FR levels (1.00, 0.86, 0.74, 0.59 and 0.24) but similar R + FR irradiances, and hence similar temperature regimes at ground level. Each level was determined using commercial polyester and polycarbonate filters (Rosco Supergel and E-Color Series, Rosco Laboratories Inc., Stanford, USA). These levels were chosen according to the R:FR ratio range observed in the main site environments where the selected species were frequent (Fig. 1).

The experiment was conducted in Ibercex V-450-D chambers (ASL, S.A., Madrid, Spain) with fluorescent (OSRAM L 18 W/20) and incandescent (generic 15 W) lamps as light sources. PAR in the chambers was 125.85 ± 15.92 SE μmol/m^2/s. The five above-mentioned R:FR levels had 30% of the PAR available in the chamber. To check for the effect of PAR variations on germination, we defined an additional treatment with 100% PAR and a high (1.1) R:FR ratio, comparable with the first R:FR treatment at 30% PAR.

Five replicates for each treatment level of 25 seeds per species were placed in 5 cm diameter Petri dishes, over 1.11 g of vermiculite and filter paper. Each dish was moistened with 7.5 ml of a heavily diluted (66.7 mg/l) solution of multipurpose Caddy fungicide (Bayer AG, Leverkusen, Germany), and wrapped in plastic film to maintain the moisture. Ten Petri dishes, each containing one of the ten species, were placed on aluminium trays beneath the filters.

Seeds were kept in a regime of 12 h (25 °C)–12 h (10 °C) light/ dark time and temperature. There were no differences in temperature between the different light treatments.

During the 40 day experiment, germination was recorded twice a week under a green safety light (Niedzwiedzsiegien and Lewak, 1989) of 2.1 μmol/m^2/s and 0.14 R:FR ratio. Moisture was controlled by visual inspection of each dish in each counting session, and lost water was replaced with distilled water until the filter paper became saturated. In order to refine our estimates of viable seeds, at the end of the experiment, the filters were removed and 800 ppm of gibberellic acid was applied to the remaining seeds, which were
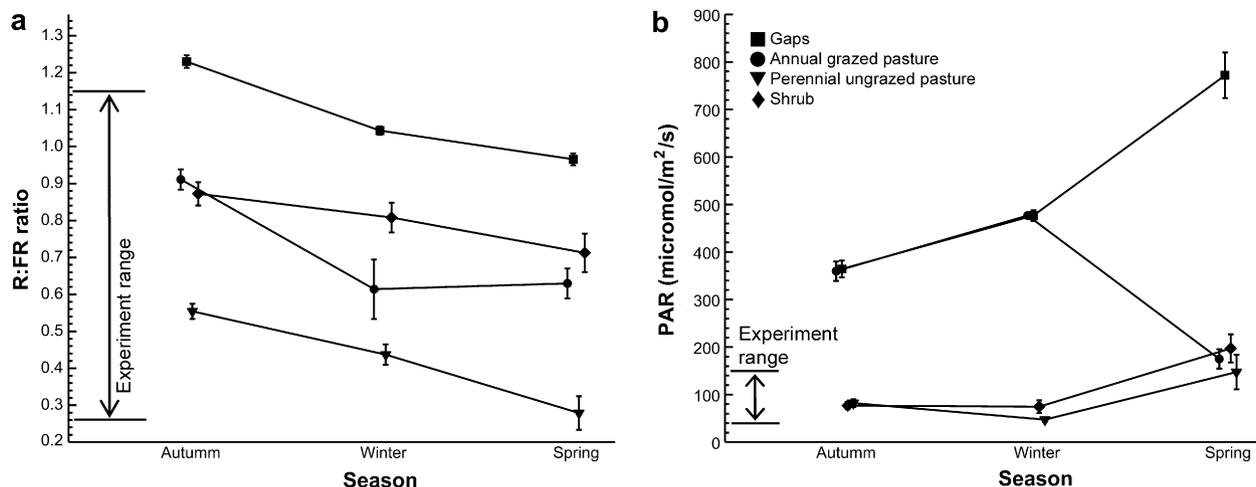
Fig. 1. Seasonal changes in a) red:far-red ratio (R:FR) and b) Photosynthetically Active Radiation (PAR; μmol/m²/s) at ground level in the main grassland microhabitats potentially experienced by seeds and seedlings (annual grazed pasture, shrub, perennial ungrazed pasture and gaps) in the study site. Data are mean ± 1SE for the 2005–2007 period.

then left in the germination chambers for two more weeks. Viability of non-germinated seeds was pressure checked.

The germination counts yielded two parameters: percentage of germination (calculated over viable seeds) and T50 (days required to reach 50% of total germination).

Two way-ANOVAs were performed to test the effects of light quality and quantity on germination percentage and T50 as response variables. In the case of light quality, R:FR ratio was used as a fixed factor with 5 levels. In the case of light quantity, PAR was used as a fixed factor with 2 levels. In all cases, species response to grazing (Status) was used as a fixed factor with two levels (*increasers*, *decreasers*) and species were nested within the grazing status, because the species could not be the same for the 2 grazing status levels (Zar, 1999). *S. purpurea* was excluded from these analysis due to its low germination rate (less than 10% in all the treatments, see Fig. 3).

Germination percentage was arc sine transformed and T50 was square root transformed to achieve normality and homocedasticity assumptions. All the analyses were run with the SPSS v14.0 package (SPSS Inc., Illinois, USA).

3. Results

3.1. Light quality and quantity under field conditions

Spatial and temporal patterns of light conditions at ground level were found in the study area (Fig. 1). The R:FR ratio was higher in gaps and lower in perennial ungrazed pasture. Annual grazed pasture and microhabitats beneath the dominant shrubs showed intermediate values for this parameter. In all microhabitats, a decrease in the R:FR ratio over time was observed with the lowest values recorded in spring. In contrast, PAR values increased from autumn to spring in all microhabitats except for the annual grazed pasture. The maximum values were observed for gaps and annual grazed pasture. Perennial ungrazed pasture and microhabitats beneath shrubs presented very low values of PAR. The value of this parameter in annual grazed pasture converged towards the former microhabitats in spring.

3.2. Effects of light quality on germination

There was a significant interaction between grazing status and light quality in the two-way ANOVA model for germination

percentages (4 d.f., $F = 25.70$, $p < 0.001$). *Decreaser* species were not influenced by R:FR ratio in their germination percentages, while *increaser* species underwent a significant reduction in their germination percentages, particularly at low R:FR ratios (Fig. 2).

There was also a significant species × light quality treatment interaction (28 d.f., $F = 2.67$, $p < 0.001$). All the four analysed *increasers* had seeds showing reduced germination in low R:FR ratios (Fig. 3). *H. glabra* presented approximately 50% less germination from 0.86 to 0.59 R:FR levels than the 1.00 level, and even less in 0.24 (Fig. 3).

Amongst the *decreasers*, *A. castellana* and *S. scabriflora* showed a significant effect of light quality on their germination percentages (Fig. 3). *A. castellana* germination was never lower than 90%, but ANOVA and *post hoc* Tukey analysis detected a significant difference between 0.86 and 0.59 R:FR ratio levels. *S. scabriflora* always showed germination percentages below 50% and a significant
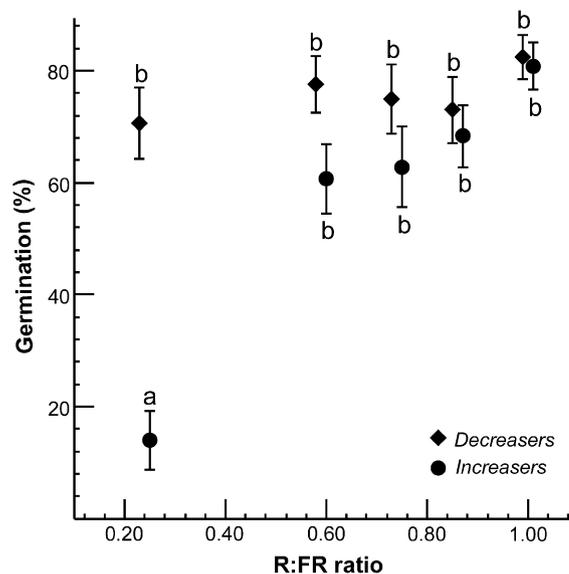

Fig. 2. Germination percentages (mean ± 1SE) for nine Mediterranean grassland species of known grazing status (*increasers*, *decreasers*) across a gradient of red:far-red (R:FR) ratio. Letters above each bar show significant differences between groups ($p < 0.05$). *Spergularia purpurea* was excluded due to its low germination rate in all the treatments (see Fig. 3).
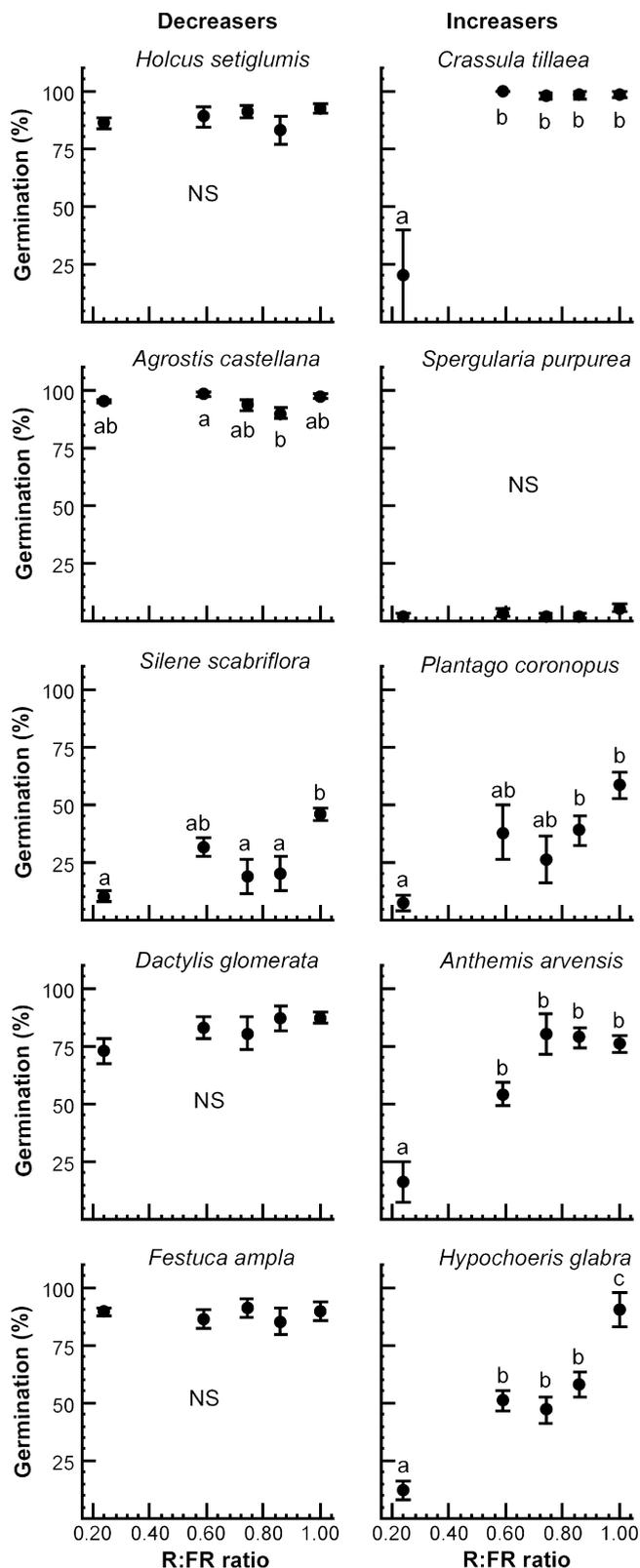
Fig. 3. Germination percentages (mean ± 1SE) for each of the ten Mediterranean grassland species of known grazing status across a red:far-red (R:FR) ratio gradient. Letters above each bar show significant differences between R:FR treatments ($p < 0.05$; NS = Non-significant effect).

difference between 1.00 R:FR level and all other levels with the exception of 0.59 (Fig. 3).

T50 was affected by grazing status (1 d.f., $F = 195.56$, $p < 0.001$). *Increasers* germinated faster than *decreasers* (2.72 ± 0.15 SE *vs* 5.70 ± 0.19 SE; Fig. 4). Status × R:FR treatment was also significant for T50 (4 d.f., $F = 3.27$, $p = 0.013$). *Increasers* showed an increment in germination speed at 0.24 R:FR ratio level, whereas for *decreasers*, this did not change at any of the levels (Fig. 4). Species × R:FR treatment interaction was not significant (28 d.f., $F = 1.24$, $p = 0.204$).

3.3. Effects of light intensity on germination

Photosynthetically active radiation (PAR) had a net effect on germination percentages (1 d.f., $F = 5.27$, $p = 0.025$). Seeds under 100% PAR conditions had lower germination than those under 30% PAR conditions (73.95 ± 4.42 SE *vs* 81.77 ± 2.86 SE; Fig. 5). There were no significant differences between grazing status (1 d.f., $F = 0.18$, $p < 0.676$). No significant interactions with status (1 d.f., $F = 0.32$, $p = 0.576$) or with species (7 d.f., $F = 1.18$, $p = 0.328$) were detected for germination percentage.

T50 was affected by PAR (1 d.f., $F = 11.06$, $p = 0.001$). Seeds at 30% PAR germinated faster than seeds at 100% PAR (4.42 ± 0.30 *vs* 5.47 ± 0.40). Grazing status also showed significant differences (1 d. f., $F = 91.36$, $p < 0.001$). *Increasers* germinated faster than *decreasers* (3.43 ± 0.30 SE *vs* 6.16 ± 0.29 SE; Fig. 6). There were no significant interactions between PAR and grazing status (1 d.f., $F = 0.42$, $p = 0.522$), or with species (7 d.f., $F = 1.43$, $p = 0.207$) factors for T50.

4. Discussion

The tests support the main hypothesis of the study: germination of grazing *increasers* was significantly affected by light quality, whereas germination of grazing *decreasers* was not. *Increasers* inhibited their germination at low R:FR ratios, showing their potential ability to avoid germination under highly competitive conditions. This concurs with the field evidence for grazing induction of seed germination by phytochrome detection observed in
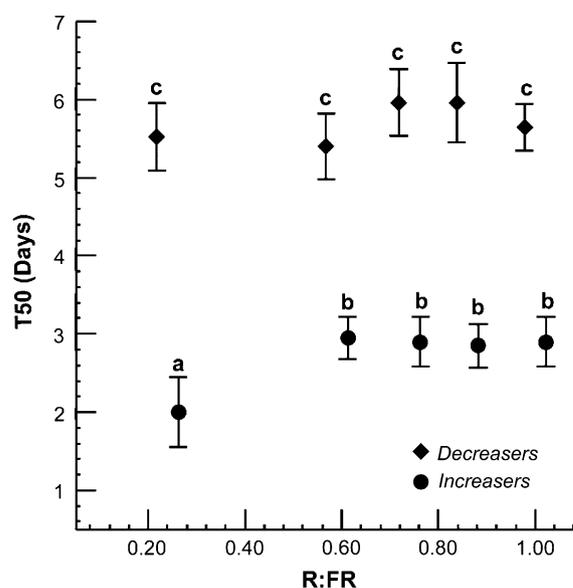

Fig. 4. Time to 50% germination (T50, mean ± 1SE) for nine Mediterranean grassland species of known grazing status (*increasers*, *decreasers*) across a red:far-red (R:FR) ratio gradient. *Spergularia purpurea* was excluded due to its low germination rate in all the treatments (see Fig. 3).
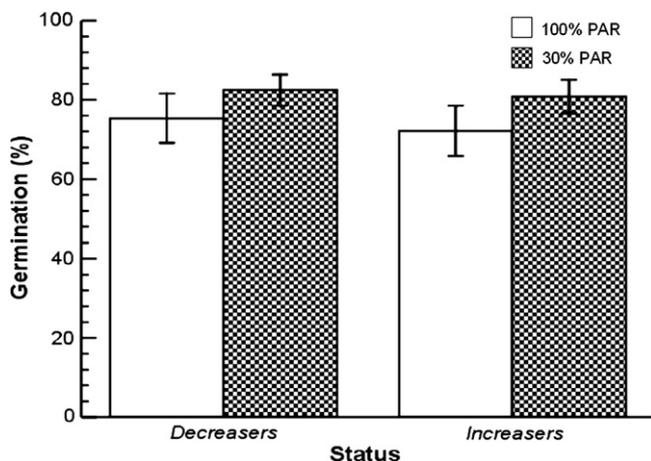
Fig. 5. Germination percentages (mean ± 1SE) for nine Mediterranean grassland plant species of known grazing status in two PAR treatments (100% PAR, 30% PAR). *Spergularia purpurea* was excluded due to its low germination rate in all the treatments (see Fig. 3).

Lolium multiflorum (Deregibus et al., 1994). Furthermore, germination was found to be faster in *increasers* than in *decreasers*, particularly at low R:FR ratios (Fig. 4). This result may also be a response of seeds from grazed pasture species to reduce competition when green shade is detected. Our results therefore suggest that the species with a phytochrome-mediated R:FR germination response may have been positively selected by grazing.

The intensity of the inhibition response by germination of *increasers* to low R:FR ratios depends on the species. Germination of at least one of the *increasers*, *H. glabra*, was inhibited at a high R:FR ratio level (0.86) (Fig. 3), however on average, there was a moderate but significant decrease of germination at a 0.24 R:FR ratio. This inhibition was lower than that one detected by Batlla et al. (2000), who found that two weed species were able to detect subtle changes in the R:FR ratio, inhibiting their germination even at a 0.95 R:FR ratio.

However, field conditions can modify these light responses. Water stress can enhance germination inhibition at high R:FR ratios (Niedzwiedzsiegien and Lewak, 1989) and temperature can change seed sensitivity to the R:FR ratio (Yirdaw and Leinonen, 2002). Furthermore, higher irradiance can also increase the inhibitory effects of the far-red light components (Górsky and Górska, 1979). Nonetheless, the sensitivity found for *increaser* species in our
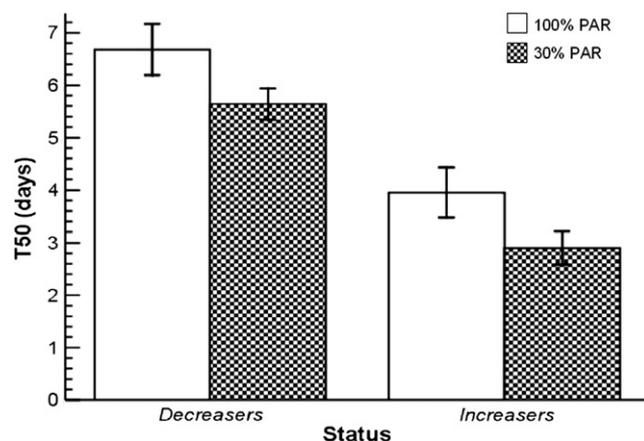
experiment seems sufficient to respond to the R:FR ratios in abandoned pastures under natural conditions during autumn, the main germination period, and can be used to explain why these species decrease or even disappear from Mediterranean grasslands when grazing ceases.

The seeds of all selected species showed lower germination at 100% than at 30% PAR (125 ± 15.92 SE and 37.5 ± 4.77 SE μmol/m^2/s, respectively). This result supported our hypothesis concerning the predominance of high irradiance response (HIR) in all Mediterranean grassland species, regardless of their grazing status. This mechanism has been described by many authors as preventing germination in places or times that are unfavourable for seedling establishment (Górsky and Górska, 1979; Pons, 2000). This response lends weight to the idea that in Mediterranean ecosystems, the inhibition of germination by high photon flux densities plays an important role in avoiding high mortality rates under the high temperatures and dry conditions in summer, immediately after seed release (Thanos et al., 1991). In the present study, T50 was affected by PAR (Fig. 6). All selected species germinated faster at 30% PAR, and *increaser* species germinated quicker than *decreasers*. The scope of our experiment in the analysis of irradiance responses of species of different grazing status is limited by the few PAR levels used in the experiment, a result of space limitations in the growth chambers. Although the range of PAR values in our experiment seems to be smaller than the range detected under field conditions in gaps and annual grazed pasture (Fig. 1), these PAR values were recorded 5 cm above ground level in the field (see photo/radiometer limitations in Methods) and the values experienced by seeds at ground level were probably lower, given that many seeds are partially covered by dry plant matter during this period of the year. However, the results do show that these two PAR levels were sufficiently different to reveal differential effects of light intensity on germination, which concur with the HIR hypothesis predictions. Testing at higher irradiance levels would provide more clear-cut differences and would be necessary to test the HIR hypothesis.

Another possible limitation of our experiment is the phylogenetic bias in the chosen species. The ideal choice would have been a balanced group of species from similar phylogenetic groups in both grazing response groups (*increasers* and *decreasers*). However, in our study there were more grasses than forbs in the *decreaser* group. Looking at Fig. 3, in addition to the grazing response groups, phylogeny also seems to predict seed response to R:FR, showing that grasses do not have a response while forbs do. In order to check whether the detected response could be attributed to phylogeny, a bibliographic search was conducted for studies using multiple species that might have documented the germinative response of herbaceous species to R:FR, only yielding one case (Jankowska-Blaszczuk and Daws, 2007). These authors analysed the impact of R:FR ratios on the germination of 27 temperate forest herbs in relation to shade tolerance, seed mass and persistence in the soil. We compiled a table for a set of 36 species, including those in this study (12 grasses and 24 forbs), and found no association between the type of response to R:FR and phylogeny (Chi-squared: 0.57, $p = 0.45$). Given that there were more perennials amongst the decreasers in our grazing response group, we tested the relation between lifespan (annuals *vs* perennials) and response to R:FR, and once again found no significant association (Chi-squared: 1.89, $p = 0.17$). In this case, however, we did find a trend, albeit non-significant, for a larger number of annual species to show a germinative response to R:FR than in the case of perennials (77.7 *vs* 48%). This germinative response mechanism might be linked to a tendency detected by other authors in which the annual plant trait seems to be associated with grazing (McIntyre et al., 1995; Vesk et al., 2004; de Bello et al., 2005), although the issue requires further investigation.

Fig. 6. T50 (mean ± 1SE) for nine Mediterranean species of known grazing status in two PAR treatments (100% PAR, 30% PAR). *Spergularia purpurea* was excluded due to its low germination rate in all the treatments (see Fig. 3).

The results of this study confirm that grazing is a selective force for species with phytochrome-mediated germination. Given its involvement in gap colonization, herbivory-caused disturbance seems to select for such species. Grassland plant community composition is thus controlled by herbivores, not only via direct impact on individual plants, but also by indirect effects induced by changes in the light environment of seeds. Germination control via light quality seems to be one of the reasons for the lower abundance of grazing *increasers* in abandoned grasslands. Other reasons such as resistance to defoliation may help to explain the lower or null abundance of grazing *decreasers* in grazed pastures (Del-Val and Crawley, 2005). However, further field experiments, including the combination of additional factors that influence germination and seed viability such as temperature, animal ingestion and water availability, are needed to understand the relative importance of phytochrome-mediated germination in the composition of grassland communities. Also, the potential influence of growth form and phylogeny should be analysed in other systems using different combinations of phylogenetic groups and growth forms within the *increaser* and *decreaser* groups.

Acknowledgements

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