Acta Oecologica 36 (2010) 74–79

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

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

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ARTICLE INFO

Article history:
Received 7 May 2009
Accepted 5 October 2009

Keywords:
Grassland plants
High irradiance response
Red:far-red ratio
Seeds
Herbivory
Light environment
Community dynamics

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.

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).

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doi:10.1016/j.actao.2009.10.005

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 *increaser*s *vs decreaser*s (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 $\mu mol/m^2/s$. The five abovementioned 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 $\mu mol/m^2/s$ 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