



## Changes in rainfall amount and frequency do not affect the outcome of the interaction between the shrub *Retama sphaerocarpa* and its neighbouring grasses in two semiarid communities

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### ABSTRACT

We evaluated the net outcome of the interaction between the shrub *Retama sphaerocarpa*, our target plant, and different herbaceous neighbours in response to changes in the magnitude and frequency of rainfall events during three years. The experiment was conducted in natural and anthropogenic grasslands dominated by a perennial stress-tolerator and ruderal annual species, respectively. In spite of the neutral or positive effects of neighbours on water availability, neighbouring plants reduced the performance of *Retama* juveniles, suggesting competition for resources other than water. The negative effects of grasses on the photochemical efficiency of *Retama* juveniles decreased with higher water availabilities or heavier irrigation pulses, depending on the grassland studied; however, these effects did not extend to the survival and growth of *Retama* juveniles. Our findings show the prevalence of competitive interactions among the studied plants, regardless of the water availability and its temporal pattern. These results suggest that positive interactions may not prevail under harsher conditions when shade-intolerant species are involved. This study could be used to further refine our predictions of how plant–plant interactions will respond to changes in rainfall, either natural or increased by the ongoing climatic change, in ecosystems where grass–shrubs interactions are prevalent.

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### 1. Introduction

The study of the dynamics of plant–plant interactions along gradients in water availability has been a major topic in dryland ecology during the past decade (e.g. Brooker et al., 2008; Pugnaire et al., 2011). The relationship between plant–plant interactions and water stress gradients is particularly complex in arid and semiarid environments (Goldberg and Novoplansky, 1997; Holmgren et al., 1997), that experience marked, and sometimes erratic, fluctuations in water availability (Miranda et al., 2011; Schwinning and Sala, 2004). The natural temporal dynamics of water availability is likely to be affected by the global changes in climate in semiarid environments, with forecasted reductions in the amount of rainfall and increases in the frequency of high

intensity showers in the Mediterranean Basin (IPCC, 2007). Temporal changes in rainfall availability should be considered, therefore, in any study of plant–plant interactions and community dynamics in water-limited ecosystems. This is necessary to be able to better predict the response of plants to natural and future changes in rainfall patterns (Miranda et al., 2011; Tielbörger and Kadmon, 2000).

Grass–shrub interactions are particularly instructive for studying the effects of these rainfall patterns on the outcome of plant–plant interactions because the two growth forms differ markedly in their distribution and abundance, root architecture, and water acquisition strategies (Sala et al., 1989; Scholes and Archer, 1997). While grasses tend to use the water derived from small rainfalls more efficiently, shrubs generally perform better after continuous and large rainfall events, which recharge deeper soil profiles (Sala et al., 1989; Schwinning and Sala, 2004). These grass–shrub interactions are thus likely to be affected by the reduction in rainfall amount and the increases in the frequency of large rainfall events that are predicted under future climate change scenarios. Altered

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rainfall will also likely affect the degree of niche partitioning and enhance coexistence among the two groups (Ogle and Reynolds, 2004). Additionally, and in spite of their differential use of water sources, facilitation and competition between grasses and shrubs does exist (e.g. Soliveres et al., 2012; Tielbörger and Kadmon, 2000) either mediated by water or by other resources such as light or nutrients (Holmgren et al., 1997; Scholes and Archer, 1997). These grass–shrub interactions might also be sensitive to alterations in water availability; for example, longer summer droughts reduce the recruitment of shrub species (López et al., 2008), and grasses may foster the survival and recruitment of shrub seedlings under moderate, but not extreme, drought conditions (Anthelme et al., 2007; Maestre and Cortina, 2004). The potential responses of these interactions to changes in rainfall amount and frequency may cause abrupt shifts in the sign of grass–shrub seedlings interactions and in the communities dominated by these plant types. However, while the response of grass–shrub interactions across contrasting water regimes is relatively well studied (reviewed in Brooker et al., 2008; Pugnaire et al., 2011), the response of these interactions to larger and multiple level gradients in temporal patterns and abundance of current or future rainfall is poorly understood (Miranda et al., 2011; Tielbörger and Kadmon, 2000). The study of responses across such multi-level gradients is needed in order to improve our predictions and therefore theoretical models of the relationship between plant–plant interactions and abiotic stress (Lortie, 2010).

In this study, we aimed to test the response of grass–shrub interactions to water pulses differing in amount or frequency in two semiarid communities from central Spain: a natural *Stipa tenacissima* L. steppe (hereafter called “natural grassland”) and an annual-dominated grassland located in a motorway slope (hereafter called “anthropogenic grassland”). Studies focussing on both natural and novel ecosystems can provide insights that allow us to improve predictions of the response of plant communities to differing water regimes (Brooker, 2006). Our focal target species was the leguminous shrub *Retama sphaerocarpa* (L.) Boiss. (hereafter *Retama*) and our focal neighbour species were the stress-tolerator tussock grass *S. tenacissima* (syn. *Macrochloa tenacissima* (L.) Kunth.) in the natural grassland, and several ruderal annual species in the anthropogenic grassland. The study of the factors affecting *Retama* establishment is of particular interest because it allows us to improve our knowledge of plant community dynamics and restoration in semiarid Mediterranean environments. In these environments, *Retama* is a keystone species, due to its positive effects on soil fertility (e.g. Caravaca et al., 2003) associated with facilitative effects on other plant species (Pugnaire et al., 1996a). We manipulated the amount and frequency of available water to create a gradient in water stress, and tested the following hypotheses: i) Both *Stipa* and annual species will have positive effects on the performance of *Retama* seedlings due to their microclimatic amelioration (Goldberg and Novoplansky, 1997; Holmgren et al., 1997); ii) *Stipa* and annual species will differ in their effect on *Retama* seedling survival under heavy water shortage. Specifically, *Stipa* could reduce *Retama* seedling survival as the increased competition for water might outweigh the positive environmental buffering promoted by shade in this ecosystem (Holmgren et al., 1997; Maestre and Cortina, 2004). Conversely, as annuals die during summer, their positive effects on *Retama* seedling survival will persist under the driest conditions because of the lack of strong competition and the positive effects expected from the shade produced by their dry tissues (Soliveres et al., 2012); and iii) Less frequent but heavier irrigation events will reduce competition between *Retama* and both *Stipa* and annual species due to the water reaching deeper soil layers and promoting niche segregation (Ogle and Reynolds, 2004; Sala et al., 1989).

## 2. Material and methods

### 2.1. Study area

Both the natural and anthropogenic grasslands selected for this study are located in the centre of the Iberian Peninsula (about 19 and 44 km South from Madrid [Spain] for the anthropogenic and natural grasslands, respectively; see Appendix A in the Supplementary material for the exact location) and share the same climate and soil type. The climate is semiarid Mediterranean, with an average annual precipitation and temperature of 388 mm and 14 °C, respectively, and with a strong summer drought (Aranjuez weather station; 1994–2005 period; Marqués et al., 2008). Both communities are located on gypsum-rich soils, classified as *Xeric Haplogypsid* (Marqués et al., 2008), although in the anthropogenic grassland the original substrate has been altered by the mixture with gravel and components from external sources during the construction of the motorway (García-Palacios et al., 2010). Vegetation in the natural grassland is an open steppe dominated by *S. tenacissima*, with a perennial plant cover of 24%. Vegetation in the anthropogenic grassland is dominated by annuals, with a mean cover of 75% and with *Bromus rubens* L., *Bromus diandrus* Roth., and *Medicago sativa* L. as the most abundant species (16, 14 and 14% of the total cover, respectively; García-Palacios et al., 2010). Hereafter we refer to these as herbaceous annuals for simplicity.

### 2.2. Experimental design

In December 2006, 176 two-year old *Retama* juveniles, with a mean height of  $27 \pm 2$  cm, were hand planted in each site in  $20 \times 20 \times 20$  cm holes. All plants were watered with 0.5 l of water when planted, to enhance establishment. These juveniles were obtained from a nursery in central Spain (viveros Bárbol, Madrid) and were grown in Forest Pot 300 containers (Nuevos Sistemas de Cultivo S.L., Girona Spain) with a volume of 300 ml and a depth of 18 cm. We randomly assigned these juveniles to two different microsites: “Neighbour” and “Open”. Because of the heterogeneous patch-interpatch structure of the natural grassland, and the homogenous herbaceous cover of the anthropogenic grassland, these microsite types were defined differently in the two ecosystems. Neighbour microsites were located: 1) upslope and adjacent to *Stipa* tussocks of ca. 1 m width and over 80 cm height (<15 cm from the edge of the north face of the tussock, where facilitative effects of this species on target shrubs have been found, e.g. Maestre et al., 2003) in the natural grassland, and 2) in a vegetation patch of 50 cm diameter in the anthropogenic grassland. The patch consisted of several annual species forming a vegetation cover of 75–100% (in spring) with a height of approx. 40 cm. These were either located in bare ground areas at least 80 cm away from any perennial plant (natural grassland), or placed in sites where all aboveground vegetation within circles of 80-cm diameter surrounding the target seedling was clipped monthly (anthropogenic grassland). We acknowledge that we could not prevent competition of their roots for water just by clipping the aboveground material on neighbouring grasses. However, we could not remove roots because of the important effect that this might have on soil infiltration and therefore on our watering treatment. Moreover, with repeated aerial clipping, non-resprouter species were effectively removed and, eventually, the treatment should also importantly reduce the reserves and resprouting ability of resprouter species. Hence, we believe that our treatment effectively reduced competition between herbaceous plants and our target species and that root competition should be negligible within our Open microsites.

Because of the high density of rabbits observed at both study sites (S. Soliveres pers. obs.), and to avoid seedling predation, juveniles

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