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Effect of Simulated Parent-Created Microenvironmental Conditions on Germination of *Retama sphaerocarpa* (L.) Bois. Seeds

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Abstract

Parent plants of woody species can create special microenvironmental conditions in their neighbourhood that modify factors such as light intensity, litter accumulation or nutrient levels. These conditions may be beneficial or not for their seeds to germinate, depending on the species strategy. As a N-fixing species, *Retama sphaerocarpa* can exert its influence on soil nitrogen levels as well as over light intensity. Moreover, adult plants understorey constitute a refuge for many herbaceous species, which can strongly compete with recently-established *R. sphaerocarpa* seedlings. Our objective was to test if the effect of parent-created microenvironment is positive for *R. sphaerocarpa* seed germination under different meteorological conditions. Previously scarified seeds were used for the experiment, set to germinate in two different phytotrons, at 14°C and 19°C (simulating temperature conditions of early and late arrival of autumn rains), under full light and shade, and with three levels of KNO₃. All factors considered (temperature, light intensity and nitrate levels) had significant effects in both final germination percentage and germination speed. The results seem to confirm our initial hypothesis about the favourable conditions provided by parent plants for *R. sphaerocarpa* seeds' germination. The effects on germination speed suggest that, under adult plant canopies, seedlings could have at least an initial advantage in their competition with seedlings of herbaceous species of the understorey, and the interactive effect between light and nitrate points to a colonisation strategy of open zones for this species.

Introduction

Adult plants of trees and shrubs in arid and semi-arid environments sometimes play an important role facilitating the establishment of other plant species, mainly herbs (McAuliffe, 1988; Franco & Nobel, 1989; Silvertown & Wilson, 1994; Pugnaire *et al.*, 1996a; Pugnaire *et al.*, 1996b; Moro *et al.*, 1997a; Moro *et al.*, 1997b). This effect may be mediated by amelioration of extreme climatic conditions (Valiente-Banuet & Ezcurra, 1991; Vetaas, 1992), greater availability of nutrients (Callaway *et al.*, 1991; Gutiérrez *et al.*, 1993; Moro *et al.*, 1997b) or greater availability of water (Dawson, 1993; Joffre & Rambal, 1993), together with an increase in the soil seed bank (Aguar & Sala, 1994; Moro *et al.*, 1997b). This facilitation process makes woody species understorey and surroundings a zone of high biomass and species diversity, constituting the so called "fertile islands" (García-Moya & McKell, 1970; Garner & Steinberger, 1989).

Retama sphaerocarpa (L.) Boissard shrublands are an example of this kind of ecosystems in which woody components constitute "fertile islands". This species dominate wide regions in central and southern Spain. The facilitation effect, together with its resistance to extreme weather conditions (especially to water stress), its great development of the radical system and its N-fixing capabilities, make *R. sphaerocarpa* a good species for restoration and revegetation projects. Moreover, these shrublands constitute a very interesting silvo-pastoral system, created and maintained by herbivores, analogous to the "Dehesas" and "Montados" but at a smaller scale: medium-large size herbivores and *Quercus* sp. trees vs. small mammals and shrubs (Gómez Sal *et al.*, 1999). This potential interest contrasts with the little knowledge available about the expansion mechanisms of this plant. It is known, although it has not been quantified, that part of the pods are wind-dispersed, and also that seeds can be dispersed by

some herbivores, mainly rabbits, that eat the pods when they have little else to feed upon (see also Izhaki & Ne'eman, 1997). However, the greatest densities of *R. sphaerocarpa* seeds and seedlings have been found under the canopy of adult plants (Gómez & Hódar, 1997; Lopez-Pintor unpublished data). The effect of parent plants on *R. sphaerocarpa* seed germination is also unknown. Adult shrubs can exert its influence on many environmental factors; light intensity and soil nitrogen levels can be considered the most important ones. Under the canopy, the reduction in light intensity ameliorates water and heat stress, and N-fixation and the decomposition of litter provides a nutrient enriched environment. These conditions have a facilitating effect on herbaceous vegetation, which in turn makes *R. sphaerocarpa* understorey (at least a priori) a rather unsuitable place for its sexual regeneration, because if seeds are to germinate in it, seedlings will have to compete strongly with herbaceous plants coming up at the same time.

In Mediterranean environments, meteorological fluctuations constitute a key factor in the dynamics of plant communities (Peco, 1989). In fact, these fluctuations have been considered the main cause of inter-annual changes in the floristic composition of annual grasslands (Talbot & Biswell, 1942; Pitt & Heady, 1978). Time of arrival of the first effective autumn rains has been demonstrated to be decisive during the regeneration phase of these grasslands. Early autumn rains followed by a period of well distributed rains can give herbaceous seedlings higher probabilities of survival, as they would have more time to develop before winter comes (Espigares & Peco, 1993). However, a dry period following germination after the first rains can kill many of the seedlings (Espigares & Peco, 1995), thus eliminating potential competitors. The earlier the first autumn rains arrive the more likely these dry periods are to occur. Therefore, an appropriate combination of parent-created microenvironmental conditions and time of arrival of the first autumn rains could promote *R. sphaerocarpa* seeds germination in such a positive way that the apparently negative effect of the understorey (i.e. higher abundance of herbaceous competitors) would be overcome.

The objective of this paper was to test if the main factors controlled by the parent plant in its neighbourhood (light intensity and soil nitrogen levels), together with temperature regime (simulating early and late arrival of autumn rains), had any effect on *R. sphaerocarpa* seed germination.

Materials and methods

Plant material

During the summer of 1995, pods of *Retama sphaerocarpa* were collected from a mature shrubland located in Fresno del Torote (Central Spain, 40°35'N, 3°25'W), on alluvial soils of Quaternary terraces with sandy-loam texture. The climate is dry Mediterranean with an annual mean precipitation of 450 mm and a mean annual temperature of 13.5°C. Pods were dried and stored in the darkness until the beginning of the experiment. *R. sphaerocarpa* seeds, like other leguminous shrubs of the Iberian Peninsula such as *Genista* or *Cytisus*, have a physical dormancy (Baskin & Baskin, 1989) due to their impermeable seed coat. Once this physical barrier is overcome, seeds germinate readily (Catalan Bachiller, 1991). Therefore, after manual extraction from the pods, seeds were scarified with the help of a pair of pincers, with which an incision was made on them, at the opposite side of the embryo (Pérez Fernández, 1996). One thousand and eighty seeds treated in this way were distributed in groups of 10. Each group was placed in a 9 cm diameter Petri dish on a bed composed of a layer of hydrophilic cotton and filter paper on top.

Experimental design

Three factors were controlled: temperature, light and nitrogen. For the temperature treatment two phytotrons were simultaneously used, one at a temperature of 19°C, approximate average temperature of early autumn conditions in the zone, and the other at 14°C, approximate average temperature of late autumn conditions. Day length was 12 h and light intensity was 205.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Previous data on PPFD (Photosynthetic Photon Flux Density) measured outside and inside shrub canopy showed that the overall reduction in light intensity caused by adult *R. sphaerocarpa* individuals was approximately 60-70%. As in other experiments dealing with the effect of shade on germination and growth of seedlings (e.g. O'Connor, 1995; Franco-Pizaña *et al.*, 1996; Tanouchi, 1996), we used shade cloth of the required light intensity amortigation (i.e. 70%) for the light treatment, providing shade to half of the Petri dishes. For the nitrogen treatment three KNO₃ solutions were used: control (only distilled water), low (10.72 mmol/l), and high (21.45 mmol/l). These concen-

trations were calculated from an average value of available nitrogen in acid soils of Central Spain of 30 $\mu\text{g/g}$ of soil, and using maximum field capacity data from *R. sphaerocarpa* shrubland soils (Estalrich, 1994). Increasing concentrations of nitrogen simulated the natural gradient of nitrogen in soil from the outside to the *R. sphaerocarpa* understorey. These concentrations are within the range normally used in germination tests, 0-50 mmol/l (Karssen & Hilhorst, 1992). The experimental design was a 2x2x3 completely randomised, giving a total of 12 treatment combinations, with 9 replications per treatment, yielding a final total of 108 Petri dishes. At the beginning of the experiment, all Petri dishes were moistened with 20 ml either of distilled water or nitrate solution, and remoistened if necessary to avoid desiccation. The experiment was laid out in December 1996, and followed daily during 40 days. Every germinated seed in every Petri dish was noted down and removed. A seed was considered germinated when at least 3 mm of radicle had emerged.

Data analysis

To examine the effect of the factors considered on both the number of seedlings produced and the speed of germination, three parameters were calculated for each Petri dish: final percentage of germination, number of days the first seed took to germinate, and day in which half the final percentage of germination was reached. Upon these parameters multifactor ANOVAs were performed. Percentage data, not following a normal distribution, were transformed to the arc tan(x). The germination profile of the seeds of each Petri dish was calculated by noting the accumulated number of seeds germinated in each week. These 108 profiles were classified using a profile attribute index (Faith *et al.*, 1985), and the UPGMA ('Unweighted Pair-Group Method using Asymmetric Averages') flexible sorting strategy ($\beta=0.0$) as the clustering method, available in the PATN package (Belbin, 1987).

Results

The ANOVA performed on final percentage of germination data showed significant main effects of temperature, no effect of light intensity and nitrogen, and interactive effects of light and nitro-

gen on germination of *R. sphaerocarpa* seeds (Table 1). The percentage of germination was significantly lower at 14°C ($83.33\% \pm 1.31$) than at 19°C ($87.04\% \pm 1.31$) (LSD test, $p=0.05$). Light intensity had only a significant effect when combined with nitrogen (Fig. 1): without KNO_3 the final percentage of germination was significantly higher in the shade treatment; when KNO_3 is added, maximum germination level was reached in the full light treatment.

The classification of the germination profiles yielded two groups: fast germinating and slow germinating profiles. The former were those with short time lag between the beginning of the experiment and the first germination, and the latter were those with longer time lag. The multifactorial ANOVA performed on time lag data showed significant effects of temperature and light intensity, and no effect of nitrogen (Table 2). At 19°C seeds germinated sooner than at 14°C. The number of days until the first germination was 4.01 ± 0.11 at 19°C and 5.38 ± 0.11 at 14°C (LSD test $p<0.01$). When exposed to full light seeds germinated later than under shade (time lag of 4.40 ± 0.11 days in shade and 5.00 ± 0.11 with full light) (LSD test, $p<0.01$). There were no interactions between any of the factors.

In relation to the time when half the maximum percentage of germination was attained, the ANOVA showed significant effects for all the factors considered, together with interaction between temperature and light intensity (Table 3). The effect of nitrate was negative both in low and high concentrations, making seeds reach half their final germination percentage later than in absence of KNO_3 (day 8.92 ± 0.33 against day 7.37 ± 0.33) (LSD test, $p<0.01$). There were no significant differences between treatments with low and high nitrate concentration. The interaction between light intensity and temperature caused an accelerated germination of *R. sphaerocarpa* seeds (Fig. 2): while at 14°C light intensity had no significant effect on germination speed, at 19°C half the final germination percentage was reached more than 2 days sooner in shade than in full light. Both factors alone had similar effects, shade and higher temperature treatments accelerating germination (day 7.51 ± 0.27 vs. day 9.02 ± 0.27 in the first case, day 7.86 ± 0.27 vs. day 8.67 ± 0.27 in the second).

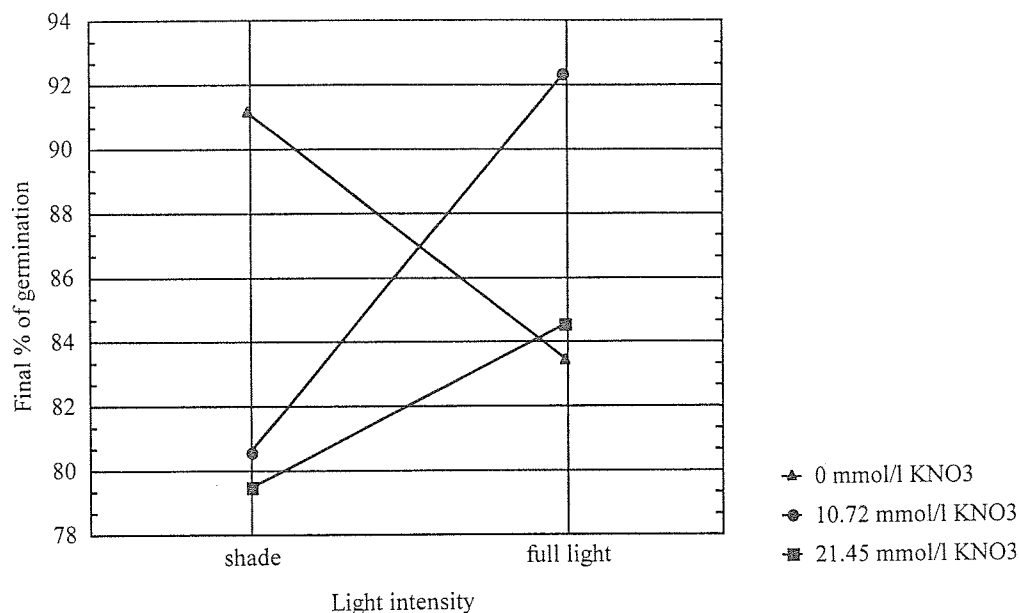


Fig. 1. Interaction between light intensity and [KNO₃] on final percentage of germination. (LSD test, $p < 0.001$)

Table 1. Table of three-factorial ANOVA performed on final germination percentage. n.s. = no significant differences (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Source	d.f.	SS	F	p
Temperature	1	0.000009	3.99	*
Light intensity	1	0.000008	3.41	n.s.
[KNO ₃]	2	0.000006	2.46	n.s.
Temperature*Light intensity	1	0.000000	0.13	n.s.
Light intensity*[KNO ₃]	2	0.000018	7.72	***
Temperature*[KNO ₃]	2	0.000000	2.03	n.s.

Table 2. Table of three-factorial ANOVA performed on time lag data (days between the beginning of the experiment and first germination) (n.s. = no significant differences; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Source	d.f.	SS	F	p
Temperature	1	50.70	70.20	***
Light intensity	1	9.48	13.13	***
[KNO ₃]	2	1.79	2.47	n.s.
Temperature*Light intensity	1	0.04	0.05	n.s.
Light intensity*[KNO ₃]	2	0.84	1.17	n.s.
Temperature*[KNO ₃]	2	0.62	0.86	n.s.

Table 3. Table of three-factorial ANOVA performed on day in which half the final germination percentage was reached (n.s. = no significant differences; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Source	d.f.	SS	F	p
Temperature	1	17.38	4.43	*
Light intensity	1	61.69	15.72	***
[KNO ₃]	2	23.21	5.91	***
Temperature*Light intensity	1	26.91	6.86	**
Light intensity*[KNO ₃]	2	7.64	1.94	n.s.
Temperature*[KNO ₃]	2	2.19	0.56	n.s.

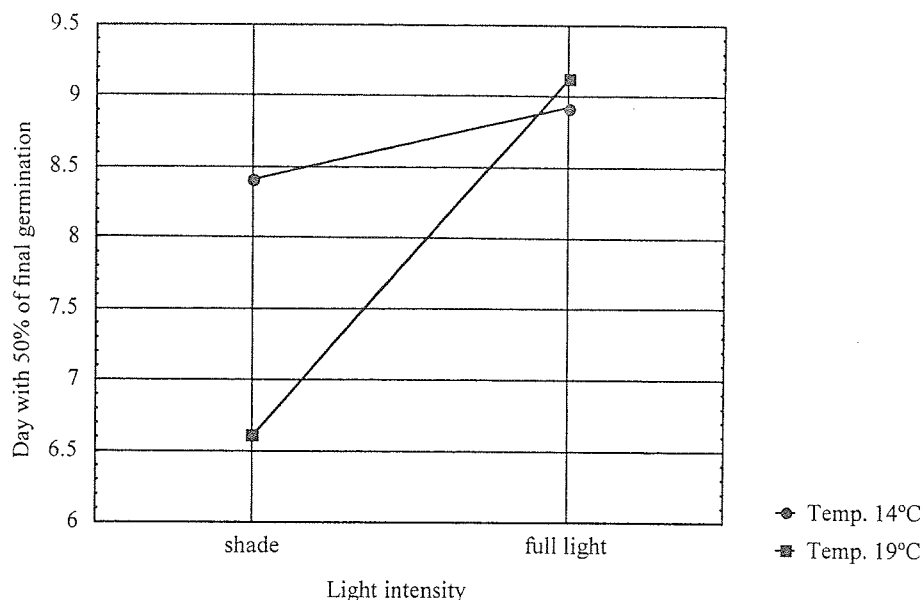


Fig. 2. Interaction between light intensity and temperature on the day in which half the final percentage of germination is reached. (LSD test, $p=0.01$)

Discussion

Our results point that adults of *Retama sphaerocarpa* seem to exert an influence over their seeds germination through the control of some important factors such as light intensity and the amount of available nitrogen in the soil.

In general terms, nitrate induced a negative response on *R. sphaerocarpa* seed germination, except for its interaction with light intensity, which will be discussed later. Increasing nitrate concentration produced a reduction in germination speed and, although marginally not significant, also in the final percentage of germination. These results are consistent with those of Pérez Fernández (1996), though our nitrate concentrations were lower. Influence of this form of nitrogen on germination has been widely studied and found to be positive, promoting germination (in general) within a range of 0–50 mmol/l (e.g. Probert *et al.*, 1987; Hilhorst & Karssen, 1989; Pons, 1989; Mekki & Leroux, 1991; Bouwmeester & Karssen, 1992; Karssen & Hilhorst, 1992; Bouwmeester & Karssen, 1993; Thanos & Rundel, 1995). Supra-optimal concentrations would inhibit germination (Karssen & Hilhorst, 1992). In our case, even low concentrations (10.72 mmol/l KNO_3) had negative effects, indicating that seeds of this species have a very low tolerance to nitrate, except when com-

bined with high light intensity. At first sight, the relatively high levels of nitrate in *Retama sphaerocarpa* understorey (Pugnaire *et al.*, 1996b; Moro *et al.*, 1997a; Moro *et al.*, 1997b) would make it a very unsuitable place for seeds of this species to germinate. However, as Pons (1989) demonstrated, other plants growing at the same time take soil nitrate actively, reducing its availability in their neighbourhood. At the time of *R. sphaerocarpa* seeds germination there would be many seeds of herbaceous species also in the process of germination or seedlings already growing. Thus, most probably nitrate levels in the vicinity of *R. sphaerocarpa* seeds would be lower than in the absence of neighbours.

As regards to light intensity, shade enhanced germination speed, measured both as days before first germination and day in which half the final germination percentage was attained. Bernardes *et al.* (1996) and Tremblay *et al.* (1996) found also positive effects of shade on germination of *Bactris gasipaes* and *Acer rubrum* respectively. This was attributed to improved moisture conditions, together with a reduction in soil temperatures in the first case. Owens *et al.* (1995) and O'Connor (1995) interpreted similar findings in field experiments also in terms of reduced soil desiccation. In our case, effects of light intensity are real effects as Petri dishes allow a better control of moisture con-

ditions than field trials, and care was taken to remoisten them when they showed signs of desiccation. We consider, therefore, our results as a direct response of seeds to light intensity, which suggests that shade provided by adult individuals may promote accelerated *R. sphaerocarpa* seed germination.

In general, increasing temperature promotes germination, both of woody (e.g. Young *et al.*, 1991; Bai *et al.*, 1995; Thanos & Rundel, 1995; Demel Teketay, 1996; Williams *et al.*, 1996) and herbaceous species (e.g. Bouwmeester & Karssen, 1992; Plummer & Bell, 1995; Thanos & Rundel, 1995; Altom & Murray, 1996; Tort, 1996), up to an optimum beyond which germination is inhibited. This optimum depends on the species. To this point, our results show nothing new. The really interesting point is the interaction between light intensity and temperature, factors simulating parental influence and climatic conditions (early/late autumn conditions in our case), respectively. Both seeds of Mediterranean grasslands and *R. sphaerocarpa* germinate in autumn (Espigares & Peco, 1993; Gómez & Hódar, 1997). The temperature at which this germination occurs depends on the time of arrival of first effective rains. Espigares & Peco (1993) showed that most species in these pastures responded positively to early autumn conditions, having in general higher germination percentage and germination speed. In addition, it is well known that differences of a few days in the emergence of seedlings can have negative consequences for later seedling survival when they compete for resources with previously-emerged competitors (Harper, 1961; Black & Wilkinson, 1963; Cook, 1979; Gross, 1980; Miller, 1987). In this context, our results suggest an interesting hypothesis: the combination of parental influence (shade) and early arrival of autumn rains could benefit *R. sphaerocarpa* seedlings by giving them some competitive advantage through faster germination. Moreover, since the sooner autumn rains come the more probable would be a drought period afterwards, this beneficial effect could be greater, as these kind of events could kill part of *R. sphaerocarpa* seedling competitors (Espigares & Peco, 1995). If there is a relationship between seed size and resistance to stress periods (Harper, 1977; Leishman & Westoby, 1994), this species would be better prepared to survive these droughts than most herbaceous species because of its bigger seeds. An indication of this process could be the relatively

high number of seedlings found under the canopy of adult plants compared to the open zones around them (Gómez & Hódar, 1997).

Another question to be discussed is the remarkable interaction found between light intensity and nitrate levels. Even though our nitrate concentrations had a detrimental effect on germination, when combined with high light intensity, it caused an increase in the final germination percentage. This interaction has been found by other authors (Probert *et al.*, 1987; Hilhorst & Karssen, 1989; Hilhorst & Karssen, 1990; Karssen & Hilhorst, 1992; Thanos & Rundel, 1995). Pons (1989) interpreted this interaction as a gap detection mechanism of high ecological importance. Plants actively growing give shade to their surroundings and take nitrate from the soil, depleting its levels. In this context, the ability to detect simultaneously light and nitrate levels – both indicating presence or absence of competitors – and respond to them would constitute an invaluable mechanism to avoid competition. The presence of this mechanism in *Retama sphaerocarpa* seems to indicate that this species has also a strategy of colonising open spaces. Its seeds lack a specialised mechanism of dispersion, pods falling directly from the adult plant or being taken away by the wind. In some cases *R. sphaerocarpa* seeds have been found in rabbit pellets (López-Pintor, pers. obser.), as is the case with another *Retama* species (Izhaki & Ne'eman, 1997). It would not be strange that, after the pellet is disintegrated, the seed found itself in a microenvironment with relatively high levels of nitrogen compounds and high levels of light, which would favour its germination. In fact, there seems to be evidence of *R. sphaerocarpa* seedling recruitment in abandoned rabbit dropping-places (Gómez & Hódar, 1997).

It can be argued that, although statistically significant, the differences we have found in both final germination percentage and germination speed measures are small enough to be considered biologically meaningful. In relation to germination speed, Espigares & Peco (in preparation) have demonstrated that, in Mediterranean annual grasslands, delays of a few days in seedling emergence can raise the mortality of seedlings that emerge following a critical point, after which the interactions between individuals begin to affect their survival. Moreover, despite our temperature treatment considered a difference of half the range of Espigares & Peco (1993) (5°C vs. 10°C), we still have found significant differences.

To conclude, it is remarkable the difference between open sites and understorey in relation to the mechanism by which *R. sphaerocarpa* seeds germination is favoured. In open sites, greater final germination percentages are promoted, while in the understorey it is faster germination what is promoted. The former could be due to the presence of a few or no competitors and the more variable environmental conditions, that would make more advantageous having a greater number of seedlings (to increase survival probabilities of any of them). The high levels of potential competition in the understorey could make more advantageous faster germination and establishment than a higher number of seedlings.

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