



Spatial segregation of plant species caused by *Retama sphaerocarpa* influence in a Mediterranean pasture: a perspective from the soil seed bank

A. López-Pintor*, T. Espigares and J.M. Rey Benayas

Dpto. Interuniversitario de Ecología, Universidad de Alcalá. Fac. Ciencias, 28871-Alcalá de Henares, Madrid, Spain; *Author for correspondence (e-mail: antonio.lopezpintor@uah.es; phone: +34 91 885 5091; fax: +34 91 885 4929)

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Abstract

Retama sphaerocarpa is a leguminous shrub whose important role in the semi-arid regions of south-eastern Spain has already been assessed: shrub canopies reduce light intensity, and thus evapotranspiration; also their extensive radical system take water and nutrients from great volumes of soil, concentrating them in the understorey. Consequently, subcanopy vegetation benefits from these facilitation processes, increasing its productivity. However, these shrublands have been rarely studied at a broader scale, i.e. as a savannah-like system composed of a variable number of shrubs scattered in a herbaceous matrix. As the microenvironmental conditions associated to the understorey are rather different from those of the open spaces among shrubs, species composition of the herbaceous matrix is expected to change accordingly. Thus, *R. sphaerocarpa* would be an important and still unknown source of spatial heterogeneity to the system. Our main purpose was to evaluate, through the soil seed bank, the heterogeneity in the herbaceous community induced by this shrub species. Soil samples were collected around adult shrubs from three positions relative to the canopy: near the centre of the shrubs, at the edge of the understorey, and completely outside the canopy. Floristic composition was evaluated by germination under greenhouse conditions. The results show that each position has a different floristic composition, characterised by a group of different species. The herbaceous species associated with the external position have functional traits which enable them to resist water stress and herbivore pressure, such as hairs, CAM metabolism, early flowering, horizontal growth or tiny stature. The species associated with the central position lack those traits, and are more competitive in more mesic environments, rich in nitrogen. The lowest number of seedlings and species was found in the internal position, suggesting that in our study the facilitation process may have less importance for community dynamics due to less stressful environmental conditions.

Introduction

In arid and semiarid ecosystems, trees and shrubs are known to exert a very important influence upon the herbaceous layer (Vetaas 1992; Belsky and Canham 1994; Rhoades 1997). Their deep roots explore great volumes of soil in search for water and nutrients, which they accumulate and afterwards release into their surroundings (Tiedemann and Klemmedson 1977; Belsky et al. 1989; Weltzin and Coughenour

1990; Frost and Edinger 1991; Rhoades 1997). Processes like hydraulic lift (Dawson 1993; Emerman and Dawson 1996), rainfall concentration via stemflow (Thurrow et al. 1987; Nívar and Bryan 1990; Ko and Reich 1993; Haworth and McPherson 1995), and microclimatic amelioration (Tiedemann and Klemmedson 1977; Belsky et al. 1989; Georgiadis 1989; Jackson et al. 1990; Ko and Reich 1993), contribute to a higher microbial activity (Rhoades 1997), making the understorey of woody species a site of

high nutrient availability. Many plant and animal species take refuge in these sites (Archer et al. 1988), providing easily decomposable material that enhances the effects of woody plants. For these reasons they are known as 'fertility islands' (García-McKell and McKell 1970). In this way trees and shrubs play an important role in the generation of spatial heterogeneity in these environments.

The herbaceous layer responds to the wide variety of microenvironments created by the woody plants, changing its species composition and abundance (Scifres et al. 1988; Pieper 1990; Fuhlendorf and Smeins 1997). The spatial heterogeneity in the distribution of nutrients, water, and insolation turns into a mosaic of herbaceous species that often results in high beta-diversity (McNaughton 1983; Belsky 1990; Vetaas 1992; Belsky and Canham 1994). Mediterranean pastures, mainly dominated by annual species, are reported to have high diversity (Naveh and Whittaker 1979). Several factors seem to contribute to the co-existence of so many species, with climatic fluctuations (Pineda et al. 1987; Peco 1989; Peco and Espigares 1994; Espigares and Peco 1995) and the long history of human exploitation (Marañón 1986) as the most important. The transformation of Mediterranean woods into savannah-like systems for domestic herbivores could be one of the main processes involved in the last factor. The opening of dense woods would turn the relatively continuous understorey conditions into a mosaic of open pasture and understorey conditions. The new system, with selected individuals scattered in a matrix of herbaceous vegetation, would have increased spatial heterogeneity due to the intermingling of those situations.

The effect of trees and shrubs upon the associated pastures is rather conspicuous. Firstly, in the contrast between species composition and abundance in open spaces and the internal regions of the understorey (González Bernáldez et al. 1969; Alonso et al. 1981; Rico and Puerto (1988–1989); Marañón and Bartolome 1993; López-Pintor 2001). Secondly, the herbaceous community also varies with aspect: the southward side of the understorey is similar in species composition to the open spaces but different from the northward side (Rico and Puerto (1988–1989); López-Pintor 2001). Wild and domestic herbivores (deer, sheep, cattle) can modulate and further enhance the spatial heterogeneity, favouring some species and decreasing the abundance of others by differential consumption and dispersal. Their habitat selection also plays an important role in both ecosystem func-

tion and heterogeneity maintenance, via redistribution of nutrients in faeces (Escudero et al. 1985; De Miguel 1989; Gómez Sal et al. 1992; De Miguel et al. 1997). The spatial integration of these factors, understorey conditions and herbivore activity, originates patches characterised by the predominance of either of them. Different groups of herbaceous species would be favoured in these patches, depending on their functional traits. For example, greater abundance of species with mechanisms to avoid herbivory in the open spaces, or without specific adaptations to high evapotranspiration conditions under woody species canopies.

Retama sphaerocarpa (L.) Boiss. is a leguminous shrub now in expansion in central and southern Spain due to cropland abandonment, originating shrublands where it is the dominant woody species. This shrub has been shown to exert an important influence upon its understorey (Pugnaire et al. 1996a, 1996b; Moro et al. 1997a, 1997b). Its canopy ameliorates the microenvironmental conditions by reducing temperature and insolation extremes. It also provides nutrients to the understorey via litterfall. The vegetation growing under the canopy benefits from all these processes, increasing its productivity. Furthermore, it has been demonstrated that *R. sphaerocarpa* benefits from the higher biomass under its canopy, showing that the interaction can be even mutualistic (Pugnaire et al. 1996a).

Pugnaire et al. (1996b) have already shown, for *R. sphaerocarpa* shrublands of south-eastern Spain, that the floristic composition of the herbaceous layer under the canopy changes with shrub age and from the centre towards the canopy border (Moro et al. 1997b; Pugnaire and Lázaro 2000). But the spatial heterogeneity of the understorey continues towards the external positions, with a mosaic of different microenvironmental conditions depending on aspect (northward side vs. southward side of the shrubs), distance to the canopy and herbivore activity (López-Pintor 2001). Therefore, each patch along this gradient would favour a different combination of herbaceous species, depending upon their functional traits. The spatial integration of these patches, from the understorey towards the open spaces among shrubs, would depict a herbaceous layer with a relatively high β -diversity. This broader scale perspective, considering *R. sphaerocarpa* shrublands as savannah-like systems composed of a variable number of shrubs scattered in a herbaceous matrix, is still rare in the bibliography (but see Gómez Sal et al. (1999)). Accordingly, the

spatial heterogeneity originated by the shrubs at this scale, including the open spaces among individuals, is still unknown.

The objective of this work is to study the spatial heterogeneity induced by *R. sphaerocarpa* shrubs upon the herbaceous community, evaluated through its soil seed bank, along the entire gradient from the open spaces to the centre of the shrubs. We hypothesised that this shrub-generated gradient induces a change in the herbaceous community, and that the functional traits of the predominant species may change accordingly. The two types of functional traits considered were those related to water stress resistance and herbivory avoidance.

Material and methods

The site selected for this study was a mature shrubland near the river Torote, central Spain (40.3°50' N, 3.2°48' W). Its climate is dry, continental Mediterranean (13.5 °C mean annual temperature; 450 mm/yr mean annual precipitation). The site was almost flat, with soils of alluvial origin and sandy-loam texture. The main herbivores are rabbits, with a population of intermediate density (4–5 rabbits/ha for Madrid Province). There are no domestic herbivores.

In this area, three adult shrubs of *R. sphaerocarpa* were selected for sampling. To avoid misleading effects of shrub age they had similar canopy dimensions (3.0–3.5 m of diameter), as there is a strong correlation between canopy size and age (Pugnaire et al. 1996b). Three different sampling positions were established, corresponding to concentric bands around the canopy centre and defined from the centre as follows (Figure 1): internal (20–50 cm), border (110–140 cm), external (250–300 cm). Soil seed bank samples were collected at the beginning of autumn, 14 8 × 8 cm soil cores from each position, regularly distributed around the shrubs. These samples included the 3 upper cm of the soil, where the main part of the seed bank is contained. Samples were placed in germination pots (8 × 8 × 10 cm), prepared as follows: they were filled with vermiculite up to 7 cm, on top of which a cotton gauze was laid to separate the substrate from the soil sample. The total number of pots was 126 (3 shrubs × 3 positions × 14 samples). They were initially watered to field capacity and put to germinate under greenhouse conditions. Subsequent watering was provided when needed. All seedlings were identified to species level. Nomenclature follows Tu-

tin et al. (1968–1980). The experiment was followed until mid-summer (8 months), when no more seedlings appeared. The soil seed bank of our study site is mainly composed of species with a transient seed bank (Ortega et al. 1997), which germinate in autumn. Of them, only some species keep a small percentage of viable seeds in spring. The possible errors committed by using this methodology would be basically quantitative, not qualitative. Moreover, Malo (2000) has reported that, when studying seed banks of central Spain with this methodology, the greatest errors are committed if it is applied on samples coming from a different source than soil (e.g., dung). Under these conditions, germination experiments are valid when studying the spatial segregation of species (i.e. when qualitative accuracy is more important than quantitative).

A Non-Metric Multidimensional Scaling (NMS) was performed upon the resulting 60 species × 126 samples matrix, to explore the main variation trends in the floristic composition of the soil seed banks. Sorensen index was used to calculate the distance matrix. A series of ANOVAs was performed to test the effect of position in *R. sphaerocarpa* understorey on the number of species and total number of seedlings. To explore the preference of the most frequent species, i.e., present in at least 10% of the samples, for a given position in the understorey, Kruskal-Wallis tests were performed due to the non-normality of species abundance data. Finally, χ^2 analyses were used to detect relationships between species preferential location and the presence of the functional traits considered. We focused on two groups of traits, related to water stress and to herbivory, two of the main characteristics of the Mediterranean ecosystems in the Mediterranean Basin. The former group includes the presence of woolly/hairy leaves, Crassulacean Acid Metabolism, and early flowering. The latter group includes horizontal growth/basal rosette and tiny stature. All of these traits have been previously related to each group by many authors (e.g., Rossiter (1966) and Gómez Sal et al. (1986), Espigares and Peco (1995), Lamberts et al. (1998), Blondel and Aronson (2000), Díaz et al. (2001)). Several authors have reported early flowering as an adaptation to water stress avoidance (Bennington and McGraw 1995; Ehrman and Cocks 1996; Del Pozo et al. 2000; Meyre et al. 2001); others have shown its relationship to herbivory avoidance (Hadar et al. 1999; Juenger and Bergelson 2000). For all analyses STATISTICA (Statsoft, Inc. 1993) was used.

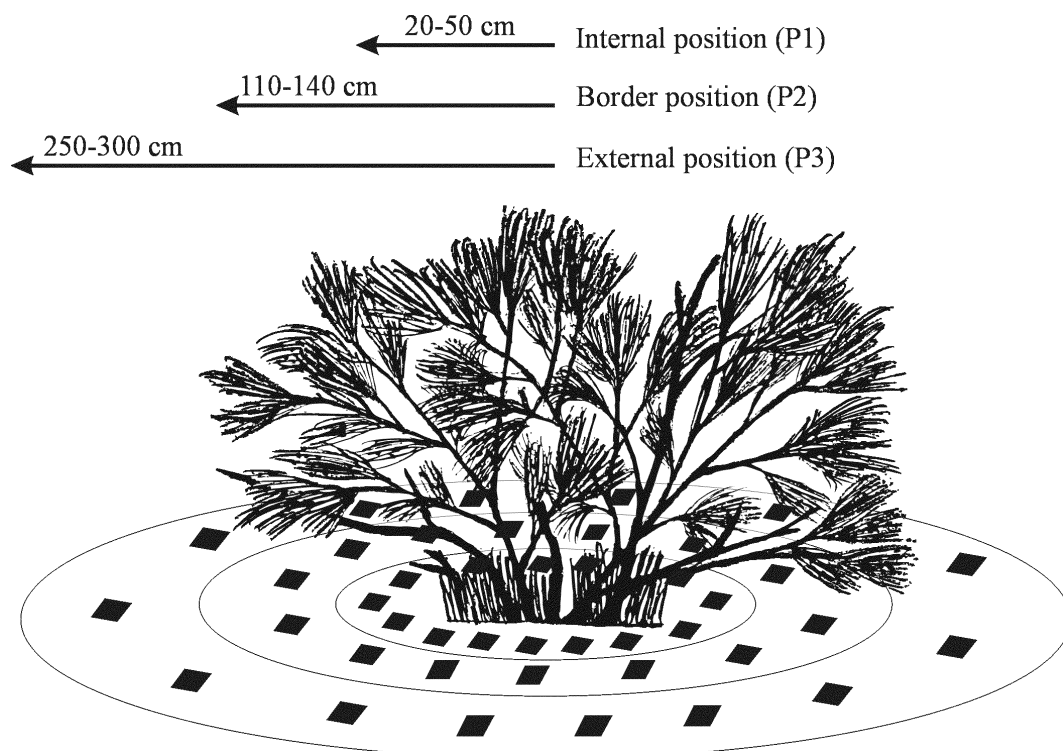


Figure 1. Sketch of sampling design, with the three positions considered defined as concentric bands around the shrub centre.

Results

The NMS performed on the floristic data revealed that the species composition of the soil seed banks is greatly influenced by *R. sphaerocarpa* shrubs (Figure 2). The first axis of this ordination clearly shows the changes in floristic composition of the soil seed banks along the gradient from the internal position under the shrubs to the open spaces among shrubs. The ANOVA performed upon Axis 1 coordinates for each sample showed significant differences ($F = 181.03$, $p < 0.0001$) for the different positions in relation to *R. sphaerocarpa* canopy. That is, each position was significantly different in species composition from the others.

Thirty species, those appearing in at least 10% of the samples, were selected for the analysis of preferential position in the canopy. The Kruskal-Wallis tests indicated that 7 species reached their maximum abundance in the internal samples, 4 species in the border position, and 14 species in the external samples (Table 1). Only for 5 species no significant relationship between abundance and position in the understorey was found.

χ^2 analyses used to test the associations between species spatial segregation and the presence of functional traits to cope with water stress and herbivory, showed significant results for both kinds of traits ($\chi^2 = 6.03$, $p = 0.0141$ and $\chi^2 = 5.95$, $p = 0.0147$, respectively). Among the species associated with the open areas predominate those with adaptations to water stress (85.71% vs. 14.29%) and herbivory (71.43% vs. 28.57%). On the contrary, in the centre of the canopy species that lack these characteristics are more abundant (83.33% vs. 16.67% for water stress related traits; 100% vs. 0% for herbivory related traits, respectively).

The ANOVAs performed on the number of seedlings and species ($F = 86.57$ and $F = 19.0$, respectively; $p < 0.0001$ for both) showed that the influence exerted by *R. sphaerocarpa* individuals is also quantitative. The total number of seedlings was far lower in the centre of the canopy than in the external position (mean \pm SD: 46.5 ± 15.94 vs. 135.1 ± 54.03 seedlings per pot, respectively, Figure 3a). Similarly, the number of species germinating in the internal position was lower than in the external position (mean \pm SD: 9.55 ± 1.9 vs. 12.57 ± 2.26 species per pot, respectively, Figure 3b). The correlation analysis

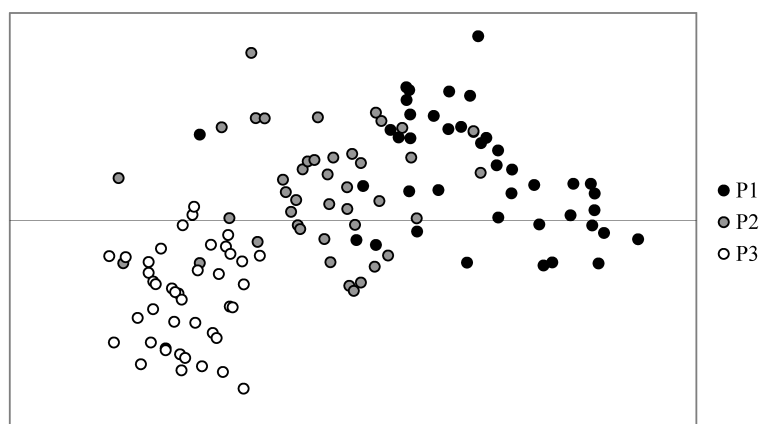


Figure 2. Results of the NMS performed upon species abundance data for the three positions in the understory. P1 = internal position; P2 = border position; P3 = external position.

showed a positive relationship between species richness and seedling emergence ($r = 0.437$, $p < 0.0001$, $n = 126$).

Discussion

Our results illustrate the importance of *R. sphaerocarpa* in shaping the spatial heterogeneity of these shrubland pastures. The NMS showed that the soil seed bank of the herbaceous community changes its floristic composition from the centre towards the open spaces, being different in each of the three positions considered in relation to shrub canopy. Thus, the reported change in the herbaceous community from the centre to the edge of the canopy by Pugnaire et al. (1996b) and Pugnaire and Lázaro (2000) extends farther outside the understory, towards the open spaces, and is already present from the very beginnings of the community. The processes involved in the genesis of this heterogeneity are widely known for another woody species in different parts of the world, including the Iberian Peninsula (Tiedemann and Klemmedson 1977; Montoya 1982; Thurow et al. 1987; Belsky et al. 1989; Ko and Reich 1993; Haworth and McPherson 1995). There is the physical effect of the canopy, reducing light intensity, ameliorating temperature extremes, and concentrating rainfall towards the centre of the understory through stemflow. Depending on the climatic conditions, their effect as wind traps can also be of great importance in the system dynamics (Kellman 1979; Bernhard-Reversat 1982; Reichman 1984; Escudero et al. 1985; Guo et al. 1998; Chambers 2000). Several of these processes

have already been demonstrated for *R. sphaerocarpa*. In this case, the differences between understory and open pasture conditions are further enhanced by the positive effect over the soil nutrient content exerted by this species, as (Pugnaire et al. 1996a, 1996b; Moro et al. 1997a, 1997b) have shown for *R. sphaerocarpa* shrublands of south-eastern Spain, and López-Pintor (2001) for those of central Spain, with more mesic environmental conditions. In the context of the savannah-like systems such as those formed by this shrub species, the final picture one gets is that of a matrix of open area conditions, interspersed with island-shaped patches of quite different biotic and abiotic characteristics. The herbaceous species respond to the different set of conditions of open areas, border zone and understory adjusting their abundance and causing even a spatial segregation of species. In spite of the fact that more spatial heterogeneity could be expected in the herbaceous community of open areas, our results highlight the sharp contrast between them and the understory, as the dispersion of samples in the NMS is quite similar for the three positions considered. The heterogeneity in the herbaceous matrix created by the influence of woody species is widely known for other Mediterranean formations (González Bernáldez et al. 1969; Pineda et al. 1981; Rico and Puerto 1988, 1989), as well as for tropical savannahs (e.g., Skarpe (1992) and Vetaas (1992), Belsky and Canham (1994)).

The overall change in floristic composition among the three positions considered in the *R. sphaerocarpa* understory, is further illustrated by the spatial segregation in the herbaceous community, showed by the significantly higher abundance of some species in

Table 1. Results of Kruskal-Wallis analyses on species preference for the three positions in the understorey of *R. sphaerocarpa*.

Species	Hairy/woolly leaves	CAM	Early flowering	Horizontal growth/basal rosette	Tiny stature	Position	p
<i>Aphanes microcarpa</i>	1	0	0	0	1	P3	***
<i>Crassula tillaea</i>	0	1	0	0	1	P3	***
<i>Crepis capillaris</i>	1	0	0	1	0	P3	***
<i>Erophila verna</i>	0	0	1	0	1	P3	*
<i>Filago pyramidata</i>	1	0	0	0	0	P3	***
<i>Herniaria hirsuta</i>	1	0	0	1	0	P3	**
<i>Mibora minima</i>	0	0	1	0	1	P3	***
<i>Sagina apetala</i>	0	1	0	0	1	P3	***
<i>Sedum caespitosum</i>	0	1	0	0	1	P3	***
<i>Spergularia rubra</i>	1	0	0	1	0	P3	***
<i>Trifolium suffocatum</i>	0	0	0	0	1	P3	***
<i>Trisetum loeflingianum</i>	1	0	0	0	0	P3	***
<i>Tuberaria guttata</i>	1	0	0	0	0	P3	***
<i>Veronica arvensis</i>	0	0	0	0	0	P3	*
<i>Capsella bursa-pastoris</i>	1	0	0	1	0	P2	***
<i>Plantago lagopus</i>	1	0	0	1	0	P2	**
<i>Polycarpon tetraphyllum</i>	0	0	0	0	0	P2	***
<i>Vulpia spp.</i>	0	0	0	0	0	P2	***
<i>Arenaria serpyllifolia</i>	0	0	0	0	0	P1	**
<i>Calendula arvensis</i>	0	0	0	0	0	P1	**
<i>Galium parisiense</i>	0	0	0	0	0	P1	***
<i>Geranium molle</i>	1	0	0	0	0	P1	***
<i>Stellaria media</i>	0	0	0	0	0	P1	***
<i>Urtica urens</i>	0	0	0	0	0	P1	***
<i>Retama sphaerocarpa</i>			Not	considered		P1	**
<i>Cerastium semidecandrum</i>			Not	considered		—	ns.
<i>Erodium cicutarium</i>			Not	considered		—	ns.
<i>Heliotropium europeum</i>			Not	considered		—	ns.
<i>Herniaria glabra</i>			Not	considered		—	ns.
<i>Trisetum paniceum</i>			Not	considered		—	ns.

* p < 0.05

** p < 0.01

*** p < 0.001.

P1 = internal position

P2 = border

P3 = external position.

each position. The samples corresponding to the open areas among the shrubs are characterised by species with functional traits related to water stress, herbivory, or both. *Filago pyramidata*, *Crassula tillaea*, *Sagina apetala*, *Sedum caespitosum* or *Erophila verna* belong to the first group. Hairy/woolly leaves, CAM metabolism, and early flowering, are functional traits providing these species adaptation to avoid or reduce damage produced by the high irradiation and evapotranspiration conditions of open areas (Rossiter 1966; Bennington and McGraw 1995; Espigares and Peco 1995; Ehrman and Cocks 1996; Lamberts et al.

1998; Meyre et al. 2001). Other species (e.g., *Herniaria hirsuta*, *Mibora minima*, *Spergularia rubra* or *Trifolium suffocatum*) have horizontal growth/basal rosette or are very small, traits adapted to herbivore grazing and trampling (Gómez Sal et al. 1986; Blondel and Aronson 2000; Díaz et al. 2001), more frequent and intense in open areas. These two groups of traits are closely related in Mediterranean ecosystems, and tend to appear together because mechanisms to avoid dessication are also useful for herbivory avoidance (Naveh 1975). In contrast, the inner positions in the understorey are characterised by spe-

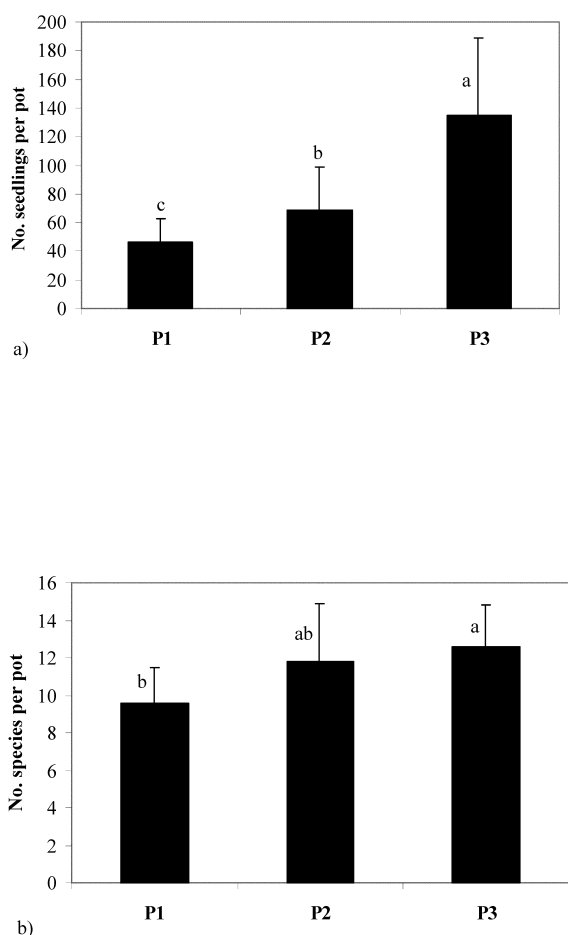


Figure 3. Graph of means for: a) number of seedlings; b) number of species, for the three positions considered in relation to shrub canopy. Different letters associated to the means indicate statistically significant differences (LSD test, $p < 0.05$). P1 = internal position; P2 = border position; P3 = external position.

cies, such as *Arenaria serpyllifolia*, *Geranium molle*, *Stellaria media* or *Urtica urens*, that lack these traits. In addition to this fact, they are considered as nitrophilous species, showing their greatest abundance in nitrogen-rich environments such as the *R. sphaerocarpa* understoreys (Rivas-Martínez 1975, 1978). Overall, these characteristics would make them more competitive in understorey conditions than in open areas, and they would take refuge in the central zones of the canopies. Without these microenvironments, the abundance of this group of species in the system would be very low. Finally, the canopy border would represent an intermediate zone, for which only a few species (*Capsella bursa-pastoris*, *Polycarpon tetraphyllum*, *Plantago lagopus* or *Vulpia* spp.) show preference over the other two positions. This group in-

cludes species with and without traits associated to water stress resistance and herbivory avoidance.

We must highlight the case of *R. sphaerocarpa* seedlings, more abundant in the internal position (Table 1). Based on a germination experiment, López-Pintor et al. (2000) proposed that this species would have a germination niche towards the centre of the shrubs. Seed accumulation from the parent plant and an enhanced microbial activity (Moro et al. 1997b) due to adult facilitation (which would accelerate seed coat degradation) may explain this. Most of these seedlings, however, will die probably because of competition with herbaceous plants or predation by insects within the first year (Haase et al. 1996; Espigares et al. 2001).

Our results show a significant increase in the number of seedlings from the centre of the canopy towards the open spaces among the shrubs (Figure 2a). However, Moro et al. 1997b found, in shrublands located in south-eastern Spain, a decrease in the abundance of seedlings from the intermediate position in the understorey towards the edge. They interpreted this greater abundance of seedlings towards the internal zones of the canopy in terms of a wind-trap effect of the shrubs. The canopies would act as physical barriers, trapping wind-borne particles, including seeds. This effect has been reported for other woody plants in different arid and semi-arid environments of the world (Kellman 1979; Bernhard-Reversat 1982; Escudero et al. 1985), and results in a greater seed accumulation in the soil of the understorey compared to the open spaces among individuals (Reichman 1984; Guo and Berry 1998; Chambers 2000). Our contrasting results can be attributed to the different climatic and stress conditions between our study site and that of Pugnaire et al. (1996b), Moro et al. (1997b) and Pugnaire and Lázaro (2000), central and south-eastern Spain. In arid environments, with a relatively high proportion of bare soil, seeds and mineral particles are more easily carried by the wind, and therefore the effect of physical barriers has a greater importance than in more mesic, less stressful environments (Reichman 1984). The higher precipitation of central Spain in relation to south-eastern Spain (450 mm vs. 259 mm, respectively), and the higher associated vegetative cover, would reduce the importance of wind as an agent of transport and accumulation of seeds. Therefore, the amount of seeds in the central areas of the canopy would be lower.

Species richness decreased towards the internal positions of the understorey (Figure 2b). This result

is consistent with those of Moro et al. (1997b), who found increasing richness towards the canopy border. As these authors stated, the competitive exclusion resulting from the proliferation of species better adapted to the greater availability of water and nutrients towards the centre, due to facilitation effects, would be responsible for this effect. The positive correlation between species richness and abundance suggests that the seed bank under the canopy would depend more on seed production than on the input of wind-borne seeds.

Wind is not the only mechanism of secondary dispersal in arid and semiarid environments. Animals play a key role in the redistribution of seeds (Reichman 1984; Guo 1996), affecting both density and horizontal distribution of species seed banks. Foraging, microhabitat, and deposition preferences of different animals, such as rodents, ants and birds, have specific consequences on the seed bank (Pulliam and Brand 1975; Whitford 1978; Reichman 1979), and therefore upon the herbaceous community. In our study, the relatively high density of rabbits (*Oryctolagus cuniculus*) is probably an important factor affecting the spatial heterogeneity of the seed bank. This species has different microhabitat preferences for feeding, social activities, and pellet dropping, resulting in a considerable spatial heterogeneity in the herbaceous community (López-Pintor 2001). The importance of rabbits on the dynamics of Mediterranean ecosystems, from which it is native, still has to be quantified.

As an overall conclusion, it can be stated that *R. sphaerocarpa*, like other woody species in arid and semiarid savannah-like ecosystems, constitutes a key factor in the structure of the herbaceous community. They create patches with especial conditions in a matrix of open areas, of high insolation and evapotranspiration, and with potentially high herbivore activity. These patches have milder environmental conditions and are nutrient enriched. Thus, the canopies would act as a refuge for those species lacking functional traits associated to water stress resistance and herbivory avoidance. These species would be rare in the herbaceous community otherwise. Therefore, its β -diversity would increase at ecosystem level due to the island-shaped areas of different species composition created by the shrubs. Herbivores may further contribute to the spatial heterogeneity of these savannah-like systems through habitat selection and the spatial segregation of their activities.

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