

Seed Bank and Understorey Species Composition in a Semi-arid Environment: The Effect of Shrub Age and Rainfall

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Understorey vegetation in patches of Retama sphaerocarpa shrubs in semi-arid environments is dependent on the overstorey shrub life history. Community structure changes with shrub age as a result of physical amelioration of environmental conditions by the canopy and organic matter accumulation in the soil. We investigated the effect of the canopy on understorey species diversity in the field and its relationships with the soil seed bank under 50 shrubs from 5 to 25+ years old, and compared species composition in the field in a wet and a dry year. Species composition of the soil seed bank under R. sphaerocarpa shrubs did not differ significantly with shrub age, but seed density increased as the shrubs aged. In the field, community composition changed with shrub age, increasing species richness in a process that depended on the amount of spring rainfall. Our results suggest that the soil seed bank is rather uniform and that the shrub canopy strongly selects which species appear in the understorey. There were seeds of many species present under both young and old shrubs but which only established under old shrubs. This showed dispersal was not limiting species abundance and suggested that the canopy was an important sorting factor for species present in the understorey. Less frequent species contributed the most to patch diversity, and rainfall effectively controlled species emergence. Understorey community composition depended on multiple interspecific interactions, such as facilitation by the shrub and competition from neighbours, as well as on dispersal processes. Facilitation in this environment is a key feature in the structuring of plant communities and in governing ecosystem functioning. © 2000 Annals of Botany Company

Key words: Community structure, competition, dispersal, facilitation, species composition, rainfall variability, *Retama sphaerocarpa*, seed bank, semi-arid environments.

INTRODUCTION

Soil seed banks are important components of vegetation dynamics affecting both ecosystem resistance and resilience. In arid ecosystems seed banks are characterized by high spatial and temporal variability (Thompson, 1987; Rundel and Gibson, 1996), and are particularly affected by spatial patterns of vegetation (Guo et al., 1998). Patches under shrubs accumulate large seed banks (Aguiar and Sala, 1997) because of the high seed output of clumped vegetation, the trapping of wind-dispersed seeds, the protection from predators, and possibly deposition by birds using the shrubs as perches (Keeley, 1987; Mull and MacMahon, 1996). Seed accumulation is higher in the centre of the patch and decreases towards the edges (Moro et al., 1997b; Guo et al., 1998). The high seed availability, along with its long persistence in the soil (Inouye, 1991; Rundel and Gibson, 1996) make understorey habitats areas of high plant diversity in dry ecosystems.

In semi-arid environments indirect, positive interactions between overstorey and understorey plants are common (McAuliffe, 1988; Aguiar *et al.*, 1992; Vetaas, 1992; Soriano *et al.*, 1994; Callaway, 1995; Franco-Pizaña *et al.*, 1996; Pugnaire *et al.*, 1996*a*), and facilitation is a key process by which many species broaden their distribution range,

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increasing productivity and species diversity on a regional scale (Pugnaire *et al.*, 1996*b*). The shrub canopy affects understorey species composition in several ways. Withinpatch gradients of radiation and temperature interact with gradients of litter accumulation and nutrient distribution (Moro *et al.*, 1997*b*) to create a varied environment where many different species find their optimum. Processes such as mineralization of organic matter show a spatial variability within the patch, affecting resource availability within very small distances (Moro *et al.*, 1997*b*).

In these patches the effect of the canopy changes with shrub age (Archer *et al.*, 1988; Callaway and Walker, 1997), and both the physical protection offered by the canopy and soil organic matter and nutrients increase with time (Pugnaire *et al.*, 1996b). As canopies age, gradients of biomass production and species distribution appear in the understorey (Moro *et al.*, 1997*a*), where stress-tolerant species show up towards the edge of the projected canopy area while more mesic species are found well inside the canopy.

However, community dynamics in the understorey also interacts with facilitation by the canopy in addition to other environmental factors such as rainfall (which is one of the major factors affecting overall plant productivity in arid environments), vegetation dynamics and seed banks. In these environments both perennial and annual species accumulate seeds in the soil but the distinction between permanent and transient seed banks (Baskin and Baskin, 1998) is weak, as the extent of germination depends on rainfall. As the soil moisture threshold for germination varies among species (Pake and Venables, 1996), rainfall variability strongly affects community composition. Some annual species may not be present for years in the standing vegetation, but population persistence is secured throughout unfavourable years by dormant seeds that eventually germinate when conditions are adequate. Rainfall unpredictability is the underlying factor causing the huge soil seed banks found in arid environments (Cohen, 1966; Philippi, 1993).

In this study we quantified the soil seed bank in patches of *Retama sphaerocarpa* (L.) Boiss. shrubs of different age, and compared these data with field observations of understorey species composition in a moist and a dry year. We hypothesized that: (1) as community composition varies along a gradient of shrub age, the understorey seed bank should also differ among the shrubs; and (2) changes in species composition should be larger in communities under young shrubs than under old shrubs in years of low rainfall because of their different facilitative effect.

MATERIALS AND METHODS

Field site

The field site is located at the bottom of the Rambla del Saltador valley in the Almería province, Southeast Spain (37°08'N, 2°22'W, 630 m altitude)—a place known as Rambla Honda with a semi-arid climate (described by Puigdefábregas et al., 1996). The temperature is mild, with a warm season from June to September and a cool season from December to March. Mean temperature in the measured 9 year period was 15.8°C, and rainfall averaged 256 mm with widely irregular inter- and intra-annual distributions. The valley bottom is filled with poorly assorted alluvial detritus with low water holding capacity, and low organic matter and nutrient concentrations. It is occupied by an open shrubland of R. sphaerocarpa, a leafless leguminous shrub with a very deep root system (Haase et al., 1996b). Overall, shrubs are distributed at random, but detailed spatial analysis shows that small shrubs are clumped, medium-sized shrubs are distributed at random, and large shrubs are regularly distributed (Haase et al., 1996a), suggesting a competition process increasing with shrub size. Patches of vegetation around R. sphaerocarpa shrubs in this habitat strongly contrast with almost bare soil between shrubs (Pugnaire et al., 1996b). The facilitation effect of overstorey shrubs over understorey vegetation is caused by feedback processes leading to an increase in organic matter, nutrients (particularly N and P) and fine soil particles (Pugnaire et al., 1996b). The mineralization rate under the canopy is much higher than in surrounding gaps, and microenvironmental conditions are ameliorated in the understorey (Moro et al., 1997a).

Experimental design

We selected 50 shrubs, randomly distributed in a mixed age-class stand on the floodplain of the Rambla Honda, and grouped them into five age intervals: 5–10 years (n = 8), 10·1–15 years (n = 18), 15·1–20 years (n = 9), 20·1–25 years (n = 8), and >25 years (n = 7). Canopy age was estimated from a known linear regression of age with branch diameter (L. Gutiérrez, unpubl. res.) using the basal diameter of the thickest branch, assumed to be the oldest of the shrub, because *R. sphaerocarpa* shrubs coppice easily and it is difficult to age the shrubs non-destructively.

Soil seed banks were estimated by seedling appearance. Although this method only shows the viable fraction of the actual seed bank, it is a convenient way to compare soils with similar conditions (Brown, 1992; Kitajima and Fenner, 1999). Soil from the upper 3 cm was sampled at an intermediate point between the canopy edge and the centre in September 1996, and bulked from four thoroughly mixed subsamples (one for each of four aspects, except for very small shrubs) which represented a total 50 cm² of soil surface per shrub.

Polyethylene pots were filled with a mixture of vermiculite and perlite (1:1), on top of which was placed a volume of natural soil of each of the 50 samples, equivalent to 150 ml of dry soil (bulk density changes significantly with shrub age; Pugnaire *et al.*, 1996*b*). Between autumn and early summer pots were kept outdoors under a rain shelter and watered every other day with deionized water. A commercial nutrient solution was added every month. Flowering individuals were extracted as soon as they were identifiable, keeping soil disturbance to a minimum.

In the spring of 1996, at the time of maximum plant diversity, the floristic composition including annual and perennial species in the understorey of the same shrubs was recorded, and compared with that observed in 1994. Species nomenclature followed Castroviejo *et al.* (1986–1999, vols. 1–8); otherwise, Tutin *et al.* (1964–1983).

Climatic data were obtained from the Rambla Honda data base (cf. Puigdefábregas *et al.*, 1996) recorded by an automatic weather station.

Significant changes in species frequency with time were determined by regression analysis. We applied a multivariate analysis (detrended correspondence analysis, DCA) using PC-ORD (MjM Software Design, Gleneden Beach, OR, USA) to the field and seedbank datasets, and plotted the first axis (representing the main vegetation gradient) against shrub age to assess changes in understorey community composition with time.

RESULTS

Germination of annual species in the seed bank experiment commenced in October 1996, soon after the first watering. Flowering started in January and continued until June, with different species flowering at different times. Altogether, we identified 86 species in our 50 soil samples, ranging from seven to 23 species per sample. Per age class, the total number of species was highest (65) in the 10–15 year-old class and lowest (39) in the 20–25 year range. Nevertheless,

TABLE 1. Number of species and seedlings m^{-2} emerging from the soil seed bank under R. sphaerocarpa shrubs, diversity
(H'; Shannon-Wiener) and evenness $(J'; Pielou)$ indexes applied to the seed bank, and species richness in the understorey of
shrubs in the field in spring 1994 and 1996

Age class	Soil seed bank				No. of species in the field	
	No. of species	Seedlings m^{-2} (×10 ³)	H′	J′	1994*	1996
Ι	15.7 ± 0.7	12.0 ± 1.2	$2\cdot 3 \pm 0\cdot 1$	0.57 ± 0.02	8 ± 1	17 ± 1
II	15.3 ± 0.8	13.8 ± 1.4	2.2 ± 0.1	0.54 ± 0.02	9 ± 1	23 ± 1
III	17.3 ± 1.5	12.9 ± 1.4	2.3 ± 0.1	0.56 ± 0.03	18 ± 1	39 ± 2
IV	15.1 ± 1.8	17.5 ± 2.7	2.2 ± 0.1	0.50 ± 0.04	20 ± 2	37 ± 3
V	17.8 ± 5.5	21.2 ± 4.1	2.1 ± 0.1	0.49 ± 0.07	19 ± 1	40 ± 2

* Pugnaire et al., 1996b.

Values are average by age class ± 1 s.e. (n = 7-18).

TABLE 2. Contribution of seeds to the soil seed bank at the two extremes of the shrub chronosequence (average of age class + 1 s.e.)

	Proportion of seeds in the seed bank				
	Class I	Class V	b	F	Р
Decrease with age					
Rostraria pumila	12.7 ± 1.6	4.8 ± 2.5	-0.97	42.3	0.007
Logfia clementei	7.3 ± 3.4	0.0 ± 0.0	-0.92	16.34	0.027
Loeflingia hispanica	6.9 ± 5.4	0.0 ± 0.0	-0.89	12.58	0.038
Leysera leyseroides	0.9 ± 0.9	0.6 ± 0.4	-0.98	62.11	0.004
Lasiopogon muscoides	0.3 ± 0.3	0.0 ± 0.0	-0.86	8.77	0.059
Increase with age					
Silene decipiens	11.7 ± 5.6	20.0 ± 8.2	0.885	10.83	0.046
Asphodelus tenuifolius	0.3 ± 0.3	15.6 ± 6.6	0.953	29.9	0.012
Capsella bursa-pastoris	0.3 ± 0.3	7.9 ± 2.9	0.992	176.55	0.0009
Sisymbrium erysimoides	0.0 ± 0.0	5.9 ± 4.3	0.903	13.26	0.035
Bromus rubens	0.9 ± 0.9	3.8 ± 3.5	0.73	9.35	0.015
Erodium malacoides	0.0 + 0.0	0.6 + 0.4	0.908	14.15	0.033

Slope (b) and significance of the regression against time of those species which significantly changed their abundance in the soil seed bank.

the average number of species per age class was similar (15-17) even though the number of seedlings m⁻² (seed density) significantly increased with shrub age (Table 1), reaching values of over 21 000 plants m⁻². Species diversity (Shannon-Wiener index) did not change with age because of changes in the evenness index (Table 1) that showed dominance processes of some species under older shrubs. Several species decreased in the seed bank as shrubs aged, while other species increased their proportion within the seed pool (Table 2).

Some species that were present in the field were not in our seed bank samples. Species such as *Aegilops triuncialis* may have completed their life cycle by the time we surveyed the understorey, while stress-tolerant species like *Ifloga spicata* or *Sisymbrium erysimoides*, typically found in gaps between shrubs, may have simply been too rare under shrubs to show up in our subsamples. However, we obtained seedlings of species which were rare in the understorey (e.g. forbs and perennial species), suggesting that the number of species not picked up by our sampling could be small. In addition, rare and perennial species may require special conditions to germinate. We obtained, though, seedlings of shrubs like Anthyllis cytisoides with natural low germination rates, but other species may have not germinated within our experimental time period. In contrast, in our seed bank determinations we obtained 19 species that were present under only a small fraction of shrubs (less than 10 %), again suggesting that our method would detect less frequent species.

A total of 106 species was identified in the field in 1996 (see Appendix), ranging from 12 to 51 under individual shrubs. The average species richness increased from 17.5 per shrub in the first (youngest) age class to 40 in the last (oldest) age class (Table 1) and the total number of species per age class increased from 42 to 95, the two oldest classes having only 77. This implies an overall increase in both the average and total number of species under each shrub in 1996 compared to 1994 (Table 1), the latter being a drier year in which only 62 species were recorded and when the total number of species increased from 21 in the youngest to 48 in the oldest class. A number of species (19) increased in frequency in the understorey as the shrub aged (Table 3), while others did not show a significant trend; none of them decreased significantly.

 TABLE 3. Slope and significance of the regression against time for species which significantly increased their abundance along the shrub chronosequence in the field

Species	b	R^2	F	Р
Andryala ragusina	0.924	0.853	17.4	0.025
Asphodelus tenuifolius	0.935	0.875	20.9	0.019
Avena barbata	0.955	0.911	30.7	0.011
Avena sterilis	0.988	0.975	119.7	0.001
Carlina corymbosa	0.922	0.850	17.0	0.025
Carrichtera annua	0.911	0.830	14.6	0.031
Cirsium arvense	0.882	0.778	10.5	0.047
Daucus durieua	0.983	0.966	85.1	0.002
Geranium molle	0.892	0.795	11.6	0.042
Hordeum leporinum	0.956	0.915	32.2	0.010
Juncus bufonius	0.882	0.778	10.5	0.047
Lamarckia aurea	0.913	0.833	14.9	0.030
Lolium rigidum	0.935	0.875	20.9	0.019
Malcolmia africana	0.903	0.816	13.3	0.035
Malva parviflora	0.918	0.843	16.2	0.027
Medicago truncatula	0.919	0.844	16.2	0.027
Papaver pinnatifidum	0.955	0.912	31.0	0.011
Reseda undata	0.967	0.934	42.9	0.007
Vulpia hispanica	0.935	0.875	20.9	0.019

We believe the decrease in the number of species in the two oldest classes was caused by dominance processes, as some of the late-coming species strongly occupied understorey space obstructing the establishment of other species.

Of the species identified in 1996, 22 were found exclusively in the soil seed bank, 42 only in the field, and 64 in both. Differences in the number of species between field and greenhouse were largest in older classes (Table 1).

Multivariate analysis (DCA) showed important differences between understorey communities with shrub age, both in the actual field vegetation and in the seedbank (Fig. 1). Change with age in species composition was better explained in the field ($r^2 = 0.64$) than in the seedbank ($r^2 = 0.46$).

Differences in climatic conditions may account for the different number of understorey species in both years. A drought period ended in 1994, totalling 122.2 mm rainfall between September 1993 and May 1994, of which only 77 mm fell between January and May. By contrast, rainfall between September 1995 and May 1996 totalled 162.3 mm, of which 129 mm fell between January and June 1996. The total number of species found in the understorey paralelled rainfall, with 62 and 106 species, respectively, in 1994 and 1996. Proportionally, differences between both years were most marked under the second and third age classes than under the two oldest classes (Table 1).

DISCUSSION

Our data indicate that age-related community dynamics in shrub understoreys are not driven by changes in the seed bank. In contrast to field observations, where species richness increased under the oldest *R. sphaerocarpa* shrubs (Table 1), the number of species in the soil seed bank was highly consistent across shrub ages (Table 1). However, seed density increased with shrub age and the abundance of

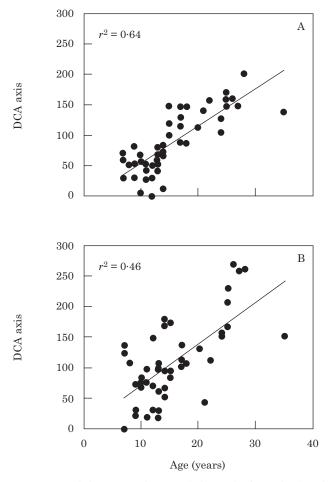


FIG. 1. Detrended correspondence analysis (DCA) first axis plotted against shrub age in field vegetation (A) and in the seed bank (B). Points represent individual communities.

several species in the seed bank varied with time (Tables 1 and 2). Many species occurred as seeds under young and old shrubs, but only recruited under old shrubs. This shows that dispersal was not limiting species abundance, and suggests that the canopy effect was an important sorting factor for species appearing in the understorey, as shown by differences in community composition between the field and the seedbank (Table 1).

The average species richness and diversity index of the seed bank remained roughly constant throughout the shrub age chronosequence, again suggesting that dispersal did not limit species appearance in the understorey.

Differences between seed bank determinations and actual vegetation are not uncommon (e.g. Khan, 1993; Bertiller and Aloia, 1997; Marañón, 1998), and may be attributed to environmental variability and the inertial effect of the soil seed bank which buffers against quick changes in species composition (Fenner, 1985; Pake and Venables, 1996). In our case, however, differences between potential and actual community composition appeared to be affected by both interspecific interactions, such as facilitation by the shrub, and dispersal processes (Pugnaire *et al.*, 1996*a*, *b*).

Differences in species composition between field communities and seed bank estimates were mainly caused by less frequent species, like weeds and ruderals (Pugnaire *et al.*, 1996*b*) Seeds of small stress-tolerant species found mainly in gaps between shrubs contributed the most to the species pool emerging from the soil seed bank, where 17 species contributed 80% of the total seed count, but other more mesic, shade-tolerant species were often under-represented in the seed bank, perhaps because their adult population was smaller.

Physical amelioration offered by the *Retama* canopy led to an increase in the number of understorey species found in the field in both years, wet and dry (Pugnaire *et al.*, 1996*a*; Moro *et al.*, 1997*b*). As the shrubs grew older and larger, their facilitative effect was greater (Pugnaire *et al.*, 1996*b*), and more species established under the canopy (Table 1), increasing their number over two-fold between the youngest and oldest shrubs in both years. An increase was also caused by the higher availability of water in 1996, and both effects combined (facilitation plus higher rainfall) to give a five-fold increase in the number of species found in the understorey of *R. sphaerocarpa* in 1996 (Table 1).

In relative terms, the facilitative effect was more important in older than in younger shrubs during the dry year, and the number of species did not increase as much in the former as in the latter during the wet year (Table 1) because of the smaller buffering effect of younger shrubs. This result agrees with the hypothesis that positive interactions are more important when abiotic stress is stronger (Bertness and Callaway, 1994), which in our field site translates into larger herb populations and higher community stability through time.

The pattern of seed distribution enhances vegetation patchiness in this semi-arid ecosystem because herbs and litter retain seeds during lateral movements across the soil surface (Aguiar and Sala, 1997). Vegetation patches act as a sink for resources, either actively through root absorption of water and nutrients (Hook et al., 1991; Gutiérrez et al., 1993; Belsky, 1994; Burke et al., 1995), or passively accumulating wind-blown dust and litter (Barth and Klemmedson, 1982; Garner and Steinberger, 1989; Pugnaire et al., 1996b), in a feedback process that reinforces vegetation heterogeneity (Wilson and Agnew, 1992; Agnew, 1997). Nutrient dynamics in these patches is increased (Moro et al., 1997b) as well as diversity and productivity (Pugnaire et al., 1996a, b), in a way that highlights the importance of vegetation patches in modifying the ecological processes in semi-arid environments.

We could ask whether patch colonization by more competitive species is limited by dispersal or by environmental (biotic and abiotic) conditions (Tilman, 1994), because seeds may differ in their ability to reach a patch but their establishment is influenced by the canopy (offering an ameliorated environment) and by competition from preexisting species. Seeds of many species were found under both young and old shrubs, but only recruited under old shrubs. This shows that dispersal was not limiting species abundance, and suggests that the canopy effect was an important sorting factor for species appearing in the understorey. Transects in patches under old shrubs show hierarchical orders of species from the centre to the edge caused by strong gradients under the canopy (Pugnaire *et al.*,

1996b; Moro et al., 1997b), and the species show competitive ability trading off against colonizing ability (Tilman, 1997) as early colonizers are competitively displaced to the edges by later-coming species. The same result in the proportion and number of species arises from soil bank analyses, pointing to the fact that understorey community composition depends on multiple interspecific interactions, such as facilitation by the shrub, competition from neighbours, and dispersal processes. In summary, community dynamics under R. sphaerocarpa understoreys was not driven solely by changes in the soil seed bank, but also by biotic interactions. Facilitation was a key factor in structuring plant communities and governing ecosystem functioning. Retama sphaerocarpa shrubs greatly increased species diversity at local and regional scales, and contributed to ecosystem stability, overriding climatic fluctuations proper of semi-arid environments.

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APPENDIX

Euphorbia helioscopia

Species present in the field in 1996

Aegilops ovata Aegilops triuncialis Alvssum minus Anacyclus clavatus Andrvala ragusina Anthyllis cytisoides Artemisia barrelieri Asphodelus tenuifolius Asterolinon linum-stellatum Atractylis cancellata Atractylis humilis Avena barbata Avena sterilis Brachypodium distachyon Bromus diandrus Bromus rubens Calendula tripterocarpa Capsella bursa-pastoris Carlina corvmbosa Carrichtera annua *Centaurea melitensis* Centaurea sp. Chenopodium murale Cirsium arvense *Clypeola jonthlaspi* Convolvulus althaeoides Cynodon dactylon Dactylis glomerata Daucus durieua Desmazeria rigida Diplotaxis ilorcitana Echium sp. Erodium chium Erodium cicutarium Eryngium campestre Eryngium ilicifolium

Foeniculum vulgare Galium spurium Geranium molle Hedypnois cretica Helianthemum ledifolium Herniaria fontanesii Hordeum leporinum Hypochoeris glabra Juncus bufonius Legurus ovatus Lamarckia aurea Lathyrus sp. Lavandula multifida Leontodon hispidulus Leontodon longirrostis Levsera levseroides Limonium thouinii Linum strictum Lobularia libyca Loeflingia hispanica Logfia clementei Logfia minima Lolium rigidum Lycocarpus fugax Malcolmia africana Malva parviflora Marrubium vulgare Matthiola parvifora Medicago minima Medicago truncatula Neatostema apulum Notoceras bicorne **Ononis** ornithopodioides Ononis viscosa Orobanche sp.

Papaver hybridum Papaver pinnatifidum Paronchya agentea Paronichya suffruticosa Piptatherum miliaceum Plantago afra Plantago lagopus Polycarpon tetraphyllum Reichardia intermedia Reichardia tingitana Reseda undata Rostraria pumila Rumex bucephalophorus Rumex induratus Scabiosa monspeliensis Senecio linifolius Shismus barbatus Silene colorata Silene decipiens Silene littorea Silene portensis Silene tridentata Sonchus oleraceus Sonchus tenerrimus Spergularia rubra Stipa capensis Thymus baeticus Tolpis barbata Trifolium scabrum Trigonella polyceratia Urospermum picroides Vallantia muralis Volutaria lippii Vulpia hispanica