

Colonization processes in semi-arid Mediterranean old-fields

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Abstract

Semi-arid Mediterranean ecosystems undergo a slow process of secondary succession after disturbance which is dependent on rainfall. We tested the hypothesis that colonization of abandoned lands in semi-arid SE Spain was slowed down by seed dispersal and species-specific responses to climatic variability. In field and glasshouse experiments we analysed germination of the two main colonizer species, their appearance in the field as seedlings, their relationships with climate and the resulting population structure. Seed germination of the two dominant legume species, *Anthyllis cytisoides* and *Retama sphaerocarpa*, was enhanced by scarification, but triggered in the field by temperature and rainfall, respectively. There was no evidence of allelopathic effects affecting germination in the field. Population structure reflected high inter-annual variability in shrub establishment, which was related to rainfall in spite of self-thinning and other processes that modeled current shrub numbers. Colonization of abandoned lands in semi-arid, Mediterranean environments in SE Spain seems to be primarily limited by seed dispersal, but also affected by climatic variability, which produced temporally separated recruitment events.

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1. Introduction

Succession after disturbance is controlled by seed availability, as scarcity of propagules may limit succession more than local ecological processes (Zobel et al., 2000; Foster, 2002). In Mediterranean ecosystems, the species pool after disturbance is determined by both the pre-disturbance community and the surrounding vegetation (Milton, 1995), so that composition of the emerging community is a function of both local and regional processes whose relative influence vary with time (Mouquet et al., 2003). Agricultural practices over centuries have limited availability of propagules of some perennial species, influencing thus the rate and course of secondary succession after land abandonment (Bonet, 2004). In arid environments, in addition, irregular rainfall and extreme conditions slow down processes and make succession look like arrested (Fowler, 1986).

Cessation of agriculture in the semi-arid south-east region of Spain in past decades led to a patchy environment where almost monospecific stands of early colonizer species like *Anthyllis cytisoides* L. or *Retama sphaerocarpa* (L.) Boiss. are still part of the landscape several decades after abandonment (Puigdefábregas et al., 1996; Haase et al., 1997). Both species are part of more mature, late successional communities, but for long time they remain monospecific. This may be due to a number of reasons. Either there is a seed dispersal limitation (Huston, 1999; Foster, 2002) so that seeds of one species do not reach stands of the other species; or seeds do reach other stands but do not establish because of predation (Willott et al., 2000a, b; Hensen, 2002) or do not germinate due to allelopathy or other soil conditions (Chaves and Escudero, 1997). Finally, seedlings may not establish because of adverse weather or because seedlings are eliminated by competition or herbivory (Milton, 1995; Huston, 1999; Zobel et al., 2000; Rey-Benayas et al., 2002).

Here we test whether colonization was limited by seed dispersal, the effect of climate on seedling emergence, and the frequency of *A. cytisoides* and *R. sphaerocarpa* establishment. We hypothesized that seeds of one species would readily germinate outside their own stand, and that weather would induce interspecific differences in germination rate and establishment. We also expected recruitment to occur in temporally separated events. These hypotheses were tested in experiments where we analysed germination rate in laboratory and in the field, the appearance of seedlings in the field to check for inter-annual variations and the effect of weather and, finally, population structure in 25-year-old plots to test the result of all the above factors combined.

2. Methods

2.1. Field sites and species

The study area is stretching north-east at the foot of Sierra de los Filabres range near Tabernas (Almería province, Spain, 37°08'N, 2°22'W, 490 m elevation); it is composed of broad valleys, small hills and mountains to 2000 m. The underlying rock is myscaschist. The mean annual rainfall is ca. 230 mm, i.e. near the lower limit tolerated by continuous sclerophyllous forest or scrub. The vegetation has suffered from severe human impact for thousands of years, and the natural vegetation is unknown. It was probably dominated by small trees or tall shrubs. Some remnants of *Quercus rotundifolia* Lam. persist on the top of the mountains and some slopes in the study area, plantations of *Pinus halepensis* Mill. were established successfully on others, and many olive yards are found on the rolling valley

floors. The study site is typical of areas formerly used for arable crops, but abandoned in the latter part of the 20th century.

The tall, burning-resistant tussock grass *Stipa tenacissima* L. dominates rocky sites, and eventually spreads onto old-fields. However, the earliest colonizers are herbs and low shrubs, notably *Artemisia barrelieri* Besser (Haase et al., 1997). Soon one or both of the legumes *A. cytisoides* or *R. sphaerocarpa* invade. *Anthyllis* is a 0.5–1.0 m tall shrub with a fairly dense canopy, while *Retama* is 2–4 m tall with a straggling open canopy. The dispersal units of these species are seeds and pods, respectively. The seeds of *Anthyllis* are 0.2×0.3 mm and mean dry mass is 1–4 mg; while those of *Retama* are around 3×6 mm and weigh 90–100 mg. They are dispersed chiefly by wind, secondarily by water, and occasionally by animals.

R. sphaerocarpa is a drought-deciduous, nitrogen-fixing shrub with evergreen photosynthetic stems which occurs in the Mediterranean part of northern Africa and in the Iberian Peninsula. Its roots reach up to 30 m deep (Haase et al., 1996) and sustain the physiological activity of the canopy for most of the year (Haase et al., 1999). It has a conspicuous understory vegetation of annual and perennial species, which affects soil fertility (Pugnaire et al., 1996; Pugnaire and Lázaro, 2000). *Retama* seeds are covered by a hard coat and usually germinate in winter (January–February). *A. cytisoides* is a summer-deciduous shrub found throughout the south-eastern Iberian Peninsula where it colonizes disturbed soils. Unlike *Retama*, its root system does not reach deep water sources and hence is more sensitive to water shortages (Haase et al., 2000). It is used as livestock fodder (Barroso et al., 1995), although its quality is rather low (Robledo et al., 1991). *A. cytisoides* replaces earlier colonizers on abandoned lands on phyllites and schists, and forms dense stands (up to 10,000 plants ha^{-1} ; Haase et al., 1997) that last for decades (Gutiérrez, 2000). A high mortality and subsequent thinning of shrub clumps may result from intraspecific competition for water (Haase et al., 1997).

2.2. Germination rate

The germination rates of seeds were determined in laboratory tests. Seeds of *Anthyllis* and *Retama* were collected from mature fruits in the field in June and August 1995, respectively. Samples of *Retama* seeds that remained in the canopy in November 1995 were also collected. To test for the effect of seed age in *Retama*, seeds gathered in the summer of 1993 were included in the experiment. Seeds were scarified by rubbing them gently with fine quartz sand in a mortar for either 30 or 90 s. Seeds were then placed in the dark at room temperature (15–18 °C) on wet filter paper in petri dishes and germination (emergence of a 1-mm root) was recorded every week for about 4 months. Three replicates of 25 seeds each were used to test time to germination in scarified and untreated seeds.

2.3. Sowing experiments

In March 1996, twelve 25×25 cm quadrats were randomly distributed in gaps in two stands occupied either by *Anthyllis* or *Retama* and in a mixed stand. Six quadrats were sown with 100 untreated *Anthyllis* seeds and six with 50 *Retama* seeds, all collected the summer before and kept in paper bags at room temperature. Every quadrat of *Anthyllis* was placed near a quadrat of *Retama*, so that they shared the same micro-climate. Quadrats were checked every 2 weeks for seedling emergence for 1 year. In January 1996 ten 250-ml

samples of soil from a depth of 3 cm from each of the stands where the sowing experiment was done were spread in 2-cm deep trays and brought to a glasshouse where they were watered regularly and checked weekly for seedling appearance during 5 months.

2.4. Seedling emergence

Natural seedling appearance in the field was monitored in two stands, one dominated by *Anthyllis* and another by *Retama*, in spring 1993, 1994, 1996 and 1997, as well as the number of *Retama* seeds on the soil surface. Field work was interrupted in 1995 so that there are no data available for that year. In the mostly flat *Retama* stand on the valley floor, we established three transects oriented N–S and two E–W. In the *Anthyllis* stand, occupying a 10° slope on an alluvial fan facing east, all five transects were oriented E–W following the direction of the slope. In each transect, we sampled the understory of 10 mature shrubs nearest to a straight line as well as their between-canopy gaps. For understory sampling, we used 10 × 10-cm quadrats under *Anthyllis* shrubs (mean canopy diameter 0.66 ± 0.03 m, 0.54 ± 0.01 m in height) and 25 × 25-cm quadrats under *Retama* shrubs (2.14 ± 0.11 m in diameter, 1.93 ± 0.72 m height). They were positioned in each of the four aspects under the shrub canopy, ca. 0.5 m from the trunk in *Retama* and 5–10 cm in *Anthyllis*. Seedlings in canopy gaps and *Retama* seeds on the soil surface were sampled by throwing four times a quadrat (25 × 25 cm in *Anthyllis* stands and 50 × 50 cm in *Retama* stands) on ten gaps between shrubs along the transect line. Percent cover of shrubs was calculated by the interception method, and shrub density was estimated from the number of shrubs in each transect expressed on a per-area basis.

Temperature and rainfall during the sampling years were recorded by an automatic weather station which integrated a radio network data acquisition system (cf. Puigdefábregas et al., 1996; Ordiales et al., 2001). The weather station has a sampling period of 20 s, averaging and storing data at 10 min intervals (5 min for rainfall data).

2.5. Establishment patterns

Long-term patterns of shrub establishment were analysed on non-disturbed, recently abandoned (<25 years) in the Serrata hills near Tabernas, Almería (Spain) in which we assumed population structure would mirror colonization processes in absence of human intervention. Three stands dominated by *Anthyllis* and three by *Retama* were selected on the same soil type (eutric cambisols, FAO 1998) and similar physiognomy, differing only slightly in the time of abandonment. Three 25 × 25 m plots were established in each stand, including >50 *Anthyllis* or *Retama* individuals. The shrubs were harvested; in the lab, 10 mm long segments of the trunk were obtained with an electrical saw near the root-shoot junction. Segments were polished and cleaned of debris with compressed air, which provided a trustable method for ageing the shrub. Each time, rings were counted along three different radii and, if there were discrepancies, the mean was taken as the most likely shrub age.

2.6. Statistical analyses

Differences among years and position in seedling emergence in experimental plots were tested by 2-way ANOVA using the Statistica 6.0 software (Statsoft 2001). Differences

among years in seed numbers were tested by one-way ANOVA. Data were log-transformed prior to statistical analysis. We used multiple linear regression with the best subset selection method to determine the climatic variables that significantly predicted seedling appearance in gaps. We used rainfall (annual, autumn, and in the period September–January) and temperature (annual mean, and mean and minima for autumn and September–January) with mean values of transect per year.

Patterns of shrub establishment in our field area were related to climate variables of the Tabernas series provided by the Spanish Instituto Nacional de Meteorología. Relationships between climatic variables and population structure were tested by linear regression analysis using Statistica.

3. Results

3.1. Germination rate

The percentage of germination for untreated *Anthyllis* seeds was very low, but mechanical scarification of the testa significantly increased seedling emergence to near 50% (Fig. 1a). Scarifying the seeds for 90 s rather than 30 s did not increase the percentage of germination. *Retama* had a higher germination rate without scarification (24%, Fig. 1a), but the length of scarification treatment had a significant effect on the proportion of germinated seeds, reaching a maximum at 90 s. The 1-year-old seeds gave a higher rate of germination than the 3-year-old seeds (Fig. 1b). Seeds of *Retama* that remained in the canopy over the winter had a very low germination rate (8%).

3.2. Sowing experiments

Near 80% of the *Retama* seeds sown in both pure *Anthyllis* or *Retama* stands, and in areas where the two species grew together, germinated within 2 months (Table 1). By contrast, the germination rate of *Anthyllis* was low and similar to that of untreated seeds in the laboratory, with mean rates not significantly different among stands (near 4%).

Few seedlings of either *Anthyllis* or *Retama* appeared in soil samples taken from its own stand, but not in those of the other species. Only in soils from the mixed stand did appear seedlings of both species, but numbers were low and did not allow for statistical tests (data not shown).

3.3. Spatial and temporal distribution of seedlings

Canopy cover in stands dominated by *Anthyllis* was $44 \pm 3\%$, with a density of ca. 3000 plants ha^{-1} . In *Retama* stands, average plant cover was $47 \pm 2\%$ and density ranged from 212 to 516 plants ha^{-1} , with a mean of 409 ± 56 shrubs ha^{-1} .

There was a big difference in the density of *Anthyllis* seedlings emerging on gaps and in the understory of shrubs (Table 2), often several times higher in the understory, particularly in 1993. The number of seedlings varied significantly with canopy aspect (Table 3). Northern and southern aspects had the highest and lowest numbers of seedlings, respectively, the other two aspects in between.

In *Retama* stands, the number of seedlings under the canopy was generally similar to that in gaps (Table 2). The number of seeds recorded in gaps was much higher than the

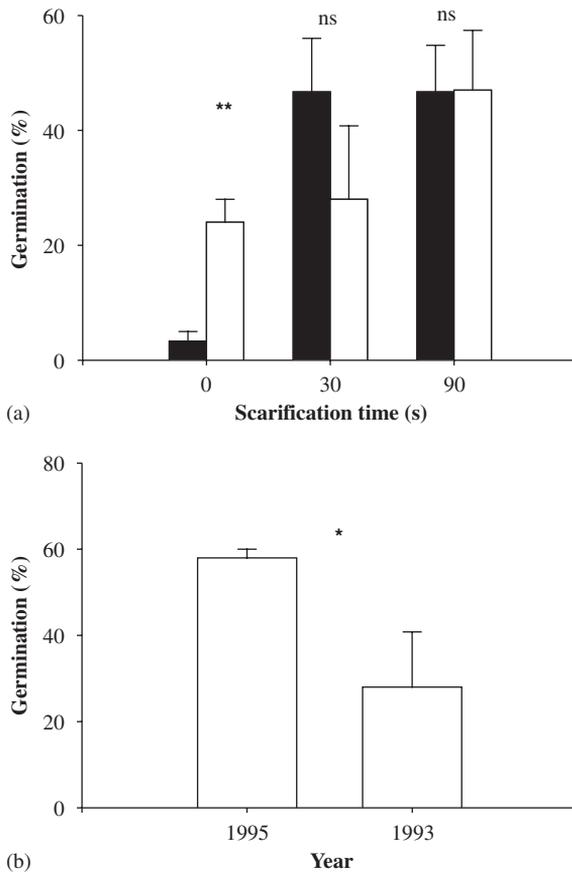


Fig. 1. Germination rate of 1-year-old *Anthyllis* (solid bars) and *Retama* (clear bars) seeds after scarification for 30 and 90 s with quartz sand (a), and of *Retama* seeds collected in 1993 and in 1995 after 30 s scarification (b). Data are mean values ± 1 S.E. Significant differences (*t*-test) given by ** (0.01) and * (0.05); ns, not significant.

Table 1
 Germination rate of *Anthyllis* and *Retama* seeds sown in stands dominated by each species and in a mixed stand

	Germination rate (%)	
	<i>Anthyllis</i>	<i>Retama</i>
<i>Anthyllis</i> stand	4.0 ± 1.4	78.3 ± 7.9
<i>Retama</i> stand	3.3 ± 1.5	86.3 ± 8.3
Mixed stand	1.3 ± 0.8	80.3 ± 4.7
<i>P</i>	0.105	0.240

Numbers are means ± 1 standard error (*n* = 6). Significance of differences (ANOVA) given by *P*.

number of seedlings, and there was no correlation between the two values. The number of *Retama* seedlings under the canopy did not vary significantly with aspect (Table 3).

There were great differences among years in the number of seedlings of both species appearing in gaps and of *Retama* seeds on the soil surface. Weather conditions during the

Table 2
Number of *Anthyllis* and *Retama* seedlings and of *Retama* seeds per m² of soil surface

	<i>Anthyllis</i>		<i>Retama</i>		<i>Retama</i> seeds
	Gaps	Understorey	Gaps	Understorey	Gaps
1993	11.2 ± 1.8	144.5 ± 11.5	1.9 ± 0.7	3.9 ± 1.1	35.3 ± 9.0
1994	15.3 ± 4.1	20.0 ± 4.1	0.0 ± 0.0	0.0 ± 0.0	16.0 ± 8.9
1996	24.2 ± 2.8	51.5 ± 8.5	6.2 ± 1.0	4.8 ± 0.7	29.5 ± 4.4
1997	9.9 ± 1.1	31.5 ± 8.5	5.8 ± 1.2	10.6 ± 1.7	59.9 ± 4.5
<i>P</i>					
Position	0.01		0.44		—
Year	0.02		0.04		<0.001
<i>P</i> × <i>Y</i>	0.31		0.07		—

Numbers are means ± 1 standard error (*n* = 5). Significance of differences (2-way ANOVA for seedlings and one-way ANOVA for seeds) given by *P*.

Table 3
Average number of *Anthyllis* and *Retama* seedlings per m² at different aspects under the shrub canopy of each species in the period 1993–1997

	North	South	East	West	<i>P</i> <
<i>Anthyllis</i>	100.9 ± 9.3 ^c	23.8 ± 9.1 ^a	69.8 ± 9.0 ^{bc}	52.9 ± 9.4 ^b	0.001
<i>Retama</i>	4.4 ± 0.4 ^a	3.9 ± 0.3 ^a	5.4 ± 0.5 ^a	4.9 ± 0.5 ^a	0.78

Numbers are means ± 1 standard error (*n* = 20). Values in a row followed by the same superscript letter are not statistically significant (at *P* < 0.05, Tukey test). Significance of ANOVA given by *P*.

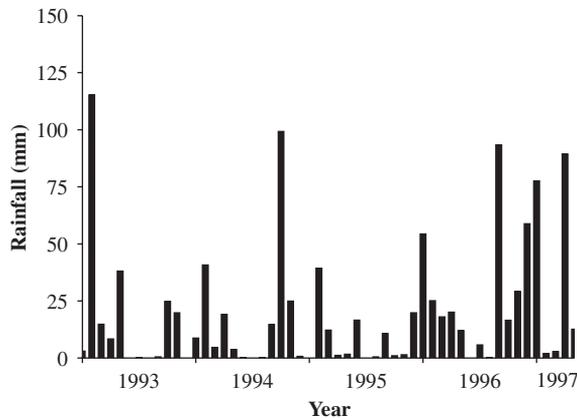


Fig. 2. Monthly rainfall distribution in the Tabernas, Almeria region during the period of seedling monitoring in the field (1993–1997).

monitored period showed the high variability characteristic of arid zones (Fig. 2). For instance, a relatively wet year (1992–1993) with 294 mm rainfall was followed by a drier year (112 mm in 1993–1994). Mean temperatures varied significantly between 1992 and

1997, and were decoupled from total rainfall. Absolute minimum temperatures in winter ranged from 2.6 °C in 1997 to 5.7 °C in 1996, and absolute maximum temperatures ranged between 24.9 and 27.2 °C. Precipitation was also irregularly distributed between September and June; in most years autumn rainfall was concentrated in October–November, whereas spring rainfall was randomly distributed (Fig. 2).

The number of *Anthyllis* seedlings found in gaps increased in the 1993–1996 period and decreased in 1997. On the contrary, the highest number of *Retama* seedlings appeared in 1996 and 1997, with no seedlings observed in 1994 (a very dry year) and few in 1993 (Table 2). The number of *Retama* seeds in gaps also differed significantly among years (Table 2).

The number of seedlings of one species found in the other community was negligible (<0.01%).

The two species differed in the climatic factors that were correlated with seedling appearance. A high proportion in the variance of *Anthyllis* seedling emergence in gaps was explained by the average minimum temperature in September–December, i.e. the months preceding germination (seedling density = $1.8T_{\min}$, $R_{\text{adj}}^2 = 0.66$, $P < 0.0001$). The number of *Retama* seedlings recorded in gaps over the 4 years of monitoring was best explained by annual rainfall and minimum temperature between September and January, i.e. the period preceding germination (seedling density = $0.034\text{Rainfall} - 0.049T_{\min}$, $R_{\text{adj}}^2 = 0.815$, $P < 0.0001$).

3.4. Population structure

The first *Retama* shrubs established in our plots in 1986. During the following 12 years, recruitment varied from 0 to 11 shrubs per year (Fig. 3). *Anthyllis* successfully started colonization in 1982 and established afterwards more regularly than *Retama* (Fig. 3).

The number of *Anthyllis* shrubs between 1983 and 1994 depended on the annual rainfall (Fig. 4a) but the variance explained was small (33%), showing that other factors influenced the current number of shrubs. In *Retama*, the average number of established individuals

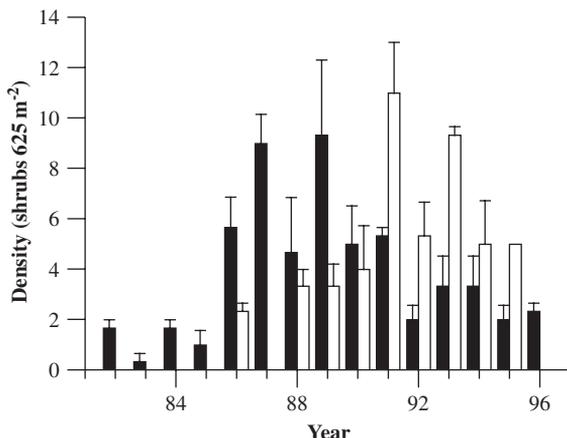


Fig. 3. Yearly distribution of *Anthyllis* (solid bars) and *Retama* (clear bars) shrubs in 25 × 25 m plots in the 1983–1997 time period. Data are mean values ± 1 S.E.

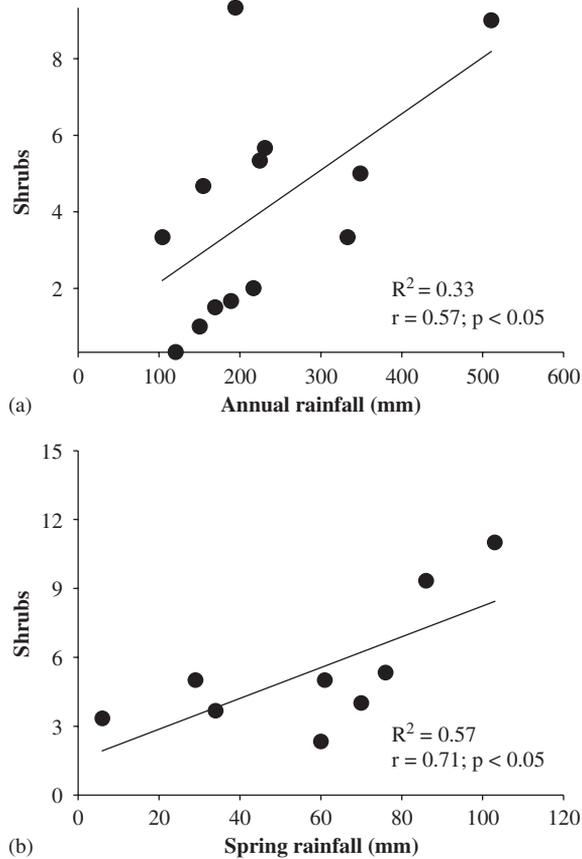


Fig. 4. Relationships between rainfall (September–August) and the mean number of *Anthyllis* (a) and *Retama* (b) shrubs established in our plots each year between 1983 and 1997.

between 1983 and 1994 was significantly related to annual rainfall, but the strongest correlation was with spring rainfall (Fig. 4b). Water availability in spring explained over 50% of *R. sphaerocarpa* establishments in spite that rainfall between February and May represented only 30% of the mean annual precipitation.

4. Discussion

Our data show that coexisting, close-related species may widely differ in their responses to climate, being population dynamics governed by species-specific environmental triggers. Thus, while seedling appearance in *Anthyllis* mostly depended on minimum autumn temperatures, in *Retama* it depended on temperature and rainfall. Secondly, these data suggest that succession in abandoned semi-arid lands in SE Spain may be limited by seed dispersal, as seeds are unavailable outside their stands and there are no constraints on germination, and by rainfall, that produces temporally separated recruitment events.

4.1. Germination triggers

Both species had low germination rates, consequence of the physical dormancy imposed by a thick testa (Ibañez and Passera, 1997; Baskin and Baskin, 1998). However, the small increase in germination rate of *Anthyllis* after scarification suggests also a physiological dormancy. In both species the delayed germination led to seed accumulation in the soil, forming a locally permanent seed bank characteristic of many leguminous shrubs in Mediterranean ecosystems (Pérez-Fernández et al., 2001) which is critical for species inhabiting unpredictable environments (e.g. Venable and Lawlor, 1980).

Differences in seedling emergence between the understory and gaps may be due to seed availability, but also suggest that several factors affect germination and recruitment. The higher germination in northern and eastern aspects under *Anthyllis* points to water as a main germination trigger when the temperature regime is adequate. By contrast, the number of seedlings under *Retama* shrubs was similar in all aspects, perhaps because the dense understory buffered against climatic factors (Pugnaire et al., 2004). In gaps, the number of seedlings was unrelated to the number of seeds, suggesting that processes like daily temperature fluctuations are needed to soften the seed coat (Vazquez-Yanes and Orozco-Segovia, 1982; Van Assche et al., 2003). In spite of the large number of seedlings under the mother plant canopy, there were never clusters of shrubs. Understories provide a suitable environment for establishment, where water and nutrients availability are high (Pugnaire et al., 1996, 2004), but seedlings in the understory of the mother plant die soon because of competition with herbs, excessive shade, grazing, or pathogens (e.g. Wenny, 2000).

Seeds that remained on the canopy in winter showed a lower germination rate, suggesting that most of them were unsound or underdeveloped.

4.2. Seed dispersal

Allelopathic effects, which may delay colonization by other species, have been detected in some Mediterranean shrublands (e.g. Chaves and Escudero, 1997). In our plots, however, germination of seeds of one species in stands occupied by other species was not impeded, suggesting that the lack of establishment could be rather due to dispersal limitations. Dispersal of *Anthyllis* and *Retama* is mainly by wind and secondarily by water. Occasionally, these species are dispersed by animals like sheep and rabbits, and Malo and Suárez (1996) showed that livestock and wild animals naturally spread *Anthyllis* seeds while increasing their germination rate. Rabbits also spread *R. sphaerocarpa* seeds, but pellets are usually left on latrines where they rarely germinate, or seedlings die soon because of the chemical conditions. As a result, dispersal in these species is mainly airborne, with seeds reaching few meters from the mother plant by primary dispersal, and water or wind may scatter them a few more meters. Thus, the distance from remnant individuals to newly available patches and seed predation by ants and rabbits (Willott et al., 2000a, b; Hensen, 2002) may limit colonization, explaining why seeds may not be found outside stands occupied by these species.

4.3. Distribution of seeds and seedlings

The number of *Retama* seeds on the soil surface varied significantly among years, as did the number of *Anthyllis* and *Retama* seedlings. Seed germination in these two species seem

to be controlled by different climatic factors, as the number of *Anthyllis* seedlings appeared between 1993 and 1997 depended on the minimum autumn temperatures while the numbers of *Retama* seedlings were a function of rainfall and minimum temperatures. Because *Anthyllis* germinates in December, temperature would be the main control of germination. For *Retama*, though, seeds germinate in February when winter is over and the main limitation would be water. Thus, germination triggers seem to fit the life history of these two species.

The pace of succession appears to be limited also by climatic variability, affecting both germination and establishment. It is critical for seedlings to root deep enough to reach moist soil horizons in the 4–5 months period between germination and the onset of the summer drought. Unlike *Anthyllis*, *Retama* did not establish every year, showing both species a high inter-annual variability which is common in arid systems (Grice and Westoby, 1987). Most of the variation found was explained by rainfall. However, the weakness of the correlation between rainfall and the number of individuals established each year (Fig. 4) suggests that other factors such as herbivory or competition affect the observed shrub numbers. Although low, the variability explained by rainfall alone is higher than for other species and ecosystems (e.g. Milton, 1995), perhaps because this is a notably dry environment.

In summary, by analyzing the cycle of reproduction from seeds to mature plants we showed that succession in abandoned lands in semi-arid SE Spain is slow because of (1) the scarcity of propagules, driven in part by life-history strategies and seed dispersal traits, and (2) climatic factors that control germination and establishment of the long-living dominants. Because population dynamics is strongly modulated by rainfall and temperature, climatic change could induce important changes in plant communities of SE Spain.

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