

## Recruitment in a Mediterranean annual plant community: seed bank, emergence, litter, and intra- and inter-specific interactions

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A small-scale field study was conducted to explain seedling emergence and recruitment of reproductive individuals in a four-year-old Mediterranean annual plant community. The analyzed levels were populations, functional types, and total number of individuals in the community. We hypothesized that the number of germinable seeds positively affects the number of emerged seedlings, which positively affects the number of reproductive individuals. We hypothesized as well that litter mass, biomass of established adults, and number of non-conspecific emerged seedlings negatively affect the numbers of emerged seedlings and reproductive individuals. The results supported our multivariate causal explanation of plant recruitment, although concordances with the initial hypotheses were more frequent at the community level. The effect of the number of germinable seeds on the number of emerged seedlings was found to be robust only at the community level. At the population level, this relationship did not have a consistent tendency and depended on species identity and range of seed density experienced. Litter had negative effects on total number of individuals in the community, and usually non-significant effects at the population level. Litter effects were found to be inversely related to seed mass, and sharper cotyledons did not improve seedling emergence likely by favoring litter mat penetration. Interactions among plant species appeared not to have any effect on seedling emergence and survival, and had positive effects on certain populations. Biomass of established adult plants exerted no influence on seedling emergence and survival, probably due to their low abundance in this community during the germination period. Results permitted the inference of the main stages in the recruitment process and causal factors. They provided evidence for the greater importance of germination and emergence in comparison with seedling survival to insure reproductive recruitment in this community.

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Recruitment of reproductive individuals in plant communities is influenced by multiple interacting factors which can be arranged in a number of sequential and distinct stages. Numerous studies have addressed the issue of recruitment in relatively simple conditions under experimental constraints (see Harper 1977, Fenner and Kitajima 1999, Fenner 2000 for extensive reviews). However, it is necessary to approach the subject by

testing multiple causal factors within a community context under field conditions.

Recruitment of reproductive individuals of annual plants depends chiefly on the abundance of germinable seeds, and emergence and survival of seedlings. Abundance of germinable seeds has been found to be a key factor, particularly in early successional phases (Moore 1980). Under such dynamical conditions, species com-

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position of the seed bank and vegetation usually are quite similar (Leck and Graveline 1979, Levassor et al. 1990, Lavorel and Lebreton 1992). The relationship between the density of germinable seeds and the number of emerged seedlings is not simple because seed density can affect emergence rate through various mechanisms such as accumulated respiratory CO<sub>2</sub> (Knapp 1954, Mack and Harper 1977) or facilitation to break the soil crust (Gutterman 1993).

Biotic and abiotic factors can affect recruitment of populations at one or more of three consecutive stages (germinable seeds, seedling emergence and seedling survival) through direct or indirect effects. Established adult plants usually negatively affect all three stages (Gorski et al. 1977, Silvertown 1980, Tyler and Dantonio 1995). Density of conspecific and non-conspecific seedlings mainly exert negative effects on seedling emergence and survival as well (Fenner and Kitajima 1999). Seedling mortality risk is initially constant but turns density dependent above a threshold of seedling density (Harper and McNaughton 1962, Yoda et al. 1963). Pathogens and herbivores may also negatively affect germinable seeds (Crist and Friese 1993, Reader 1993) and seedlings (Mack and Pyke 1984, Neher et al. 1992, Hanley et al. 1996). Litter accumulation usually influences all stages by changing the physical, chemical and biological microenvironment of seeds and seedlings (Facelli and Pickett 1991a, Reader 1993, Bosy and Reader 1995). Weather conditions affect germinable seed bank composition and seedling emergence and survival, and these effects are species dependent (Espigares and Peco 1993, Peco and Espigares 1994). Thus, the nature and extent of hazards that individuals have to overcome during the establishment process determine recruitment of species in the community.

Functional traits such as seed mass and cotyledon shape may modify the relative role of the different factors conditioning population recruitment. For example, smaller seeds are associated with lower emergence and/or survival under more competitive situations (Gross and Werner 1982, Winn 1985, Burke and Grime 1996). Seed mass also affects the vulnerability to seed predators (Thompson 1986), and seed mass and seedling shape affect the ability of the seedlings to penetrate the litter mat (Keever 1973, Sydes and Grime 1981, Tao et al. 1987, Molofsky and Augspurger 1992). Large-seeded species may have an advantage when establishing in the presence of ground cover such as litter or previously established plants, whereas small-seeded species may have an advantage in the presence of seed predators (Reader 1993). Some authors (Grime 1979, Reader 1993) have suggested that the combined effects of ground cover and seed predation hinder predictions about the real consequences of seed mass. Grouping species according to their functional traits allows us to test the influence of these traits in species recruitment.

In this study we conducted a one-year small-scale field experiment in a four-year-old Mediterranean annual plant community. The main objective was to explain seedling emergence and recruitment of reproductive individuals at three hierarchical levels: (1) population, (2) functional types, and (3) total number of individuals in the community. The specific objectives of our study were: (1) to infer causal explanations mediated through germinable seed bank, litter abundance, and intra- and inter-specific interactions among seedlings, (2) to analyze the influence of two functional traits (seed size and cotyledon shape) on recruitment, and (3) to determine the critical stages for recruitment of reproductive individuals in the community.

## Methods

### Study site

The study was conducted at "El Encín" experimental farm (Instituto Madrileño de Investigación Agraria y Alimentaria, IMIA) located in Alcalá de Henares (Central Spain, 40° 35' N, 3° 25' W). Elevation is 565 m. Climate is semi-arid continental Mediterranean. Mean annual temperature is 13.1°C. Mean monthly temperatures range from 4.6°C in December to 23.1°C in July. Mean annual precipitation is 410 mm. Precipitation is characterized by a high year-to-year fluctuation in timing and amount, and by a pronounced summer drought. Main rainfall periods are autumn and, to a lesser extent, spring. The study year was slightly drier than usual (391 mm), and it started to rain in November.

The study area is located on Quaternary alluvial terraces with a flat topography and soils with a clay content of approx. 26.4% and pH = 8.1. Potential vegetation is an *Ulmus minor* forest, which was totally transformed into arable land hundreds of years ago. Currently, plant communities are dominated by annual species including grasses such as *Hordeum murinum* L., *Trisetum paniceum* (Lam.) Pers., *Lophocloa cristata* (L.) Hyl., and forbs such as *Papaver rhoeas* L. and *Hypocoum procumbens* L. All these species have similar adaptation features, i.e., opportunistic annual strategy (Fernández Alés et al. 1993). Reproductive individuals chiefly die at the beginning of the summer drought (July) and their biomass is accumulated as litter. This occurs for all species except for late-summer species which remain alive until October–November. Germination is concentrated to the main autumn rainfall period (Espigares and Peco 1993). Species pass the winter as seedlings or juveniles, and grow very fast to the adult stage during the spring rains. Mean aboveground net primary production is 611 g m<sup>-2</sup> yr<sup>-1</sup>.

## Experimental design

A 0.5-ha field was split into 18 plots of 11 m × 14 m. A nine-point grid was set in each plot, and four randomly selected points were used as sampling sites. The laborious task of monitoring emergence and survival of all seedlings from all species in the field restricted both the feasible number of sampling sites and replicates at each one. Each of the 72 chosen sites was sampled as follows:

(1) A 10 cm × 10 cm × 8 cm deep soil sample was collected in the autumn (September 1995) to determine the germinable seed bank in a glasshouse (*sensu* Thompson and Grime 1979). Samples were collected immediately before the start of the precipitation period in order to minimize differences in germinable seeds between glasshouse and field samples. The glasshouse was a transparent glass shelter where temperature and light were close to outdoor conditions. The density of germinable seeds was determined in four subsamples per soil sample. Each subsample was placed in the top part of 10-cm deep and 25-cm<sup>2</sup> round pots on a 5-cm deep layer of vermiculite, separated by a fine layer of gauze. The soil subsamples were watered regularly from November onwards. Seedlings were identified, counted and removed throughout one year. This period was considered sufficiently long since most seeds in this type of community germinate during the first year (Levassor *et al.* 1990). Four pots with sterile soil were placed in the glasshouse in order to determinate potential seed rain but no seeds from outside the soil samples were detected.

(2) A 10 cm × 10 cm field quadrat was sampled to count the number of emerged seedlings and the survival of individuals until reproductive age. This counting was assisted by mapping individuals on photographs with a periodicity of 10 d during the first four months (September–December), and then every month during the following seven months because emergence rate was much lower. Deaths were registered at every phenological stage: cotyledon, seedling (fewer than six leaves including cotyledons), juvenile (6 to 10 leaves), adult (> 10 leaves), and reproductive individuals (adult with flowers or fruits).

(3) A 10 × 10 cm quadrat was sampled in order to estimate dry-mass of litter and dry-mass of biomass of late-summer species at the beginning of the germination stage. Biomass of late-summer species reflects abundance of established adult plants at the germinable stage.

The three sets of samples that were taken at every site were located 10 cm from each other. One hundred seeds of every species were collected in the study area in order to estimate the average dry mass per seed. Species were sorted according to two functional traits, seed mass and cotyledon shape, into the following

functional types: small-seeded (< 0.1 mg), medium-seeded (0.1 mg–1 mg), large-seeded (> 1 mg), sharp cotyledon, and flat cotyledon (Appendix 1). Medium-sized and large-sized herbivores (rabbits, hares and sheep) were fenced out during the experiment.

## Data analyses

We used two approaches. A prioristic structural equation modeling (SEM) procedure was used in order to test the causal hypotheses for the recruitment of reproductives at the population and functional type levels. SEM is a powerful statistical technique when a prioristic causal model is specified and the model, including direct and indirect effects, results in a complex system (Mitchell 1992, Albert *et al.* 2000, Escudero *et al.* 2000). This technique is also useful in the case of studies under field conditions where experimentation is not feasible (Palomares *et al.* 1998). For the community level, we used a stepwise multiple regression procedure because, as stated by Wootton (1994), it is a suitable approach when there are very few direct and indirect effects involved in the explanatory model.

The hypothetical causal model for a given population and functional type describes how variables are *a priori* causally linked in terms of direct and indirect effects (Fig. 1). We hypothesized the following: 1) the number of germinable seeds positively affects the number of emerged seedlings, which 2) positively affects the number of reproductive individuals. Furthermore, 3) litter mass, 4) biomass of late-summer species, and 5) number of non-conspicuous emerged seedlings affect the numbers of emerged seedlings and reproductive individuals. We expected a negative effect of litter in this community in concordance with Monk and Gabrielson (1985), who found pioneer species are more negatively affected by litter than late successional species. We expected as well a negative effect of non-conspicuous seedlings and of established plants (*i.e.* late-summer species biomass in our study), since the absence of competition from neighbor individuals is a common requirement for germination and seedling survival (Silvertown 1980, Fenner 1985). However, we considered that abundance of established adults affect seedling emergence and does not affect seedling survival in the studied community because late-summer species die before the seedling growth period. Finally, we hypothesized that 6) the negative effects of non-conspicuous germinable seeds are mainly indirect through the number of non-conspicuous emerged seedlings due to inter-specific competition. We tested this model for the 12 most frequent species in the community. They were present in at least 33 sampling sites, the most frequent being found in all 72 sampled sites (Appendix 1; Table 1A).

In order to analyze the influence of some functional traits on species recruitment, we grouped all species in the community according to seed size and cotyledon shape. Two additional hypotheses were included in the model: 7) large-seeded species are less limited than small-seeded species by litter accumulation, biomass of late-summer species, and number of non-conspecific seedlings. Larger seeds give rise to larger seedlings, and this translates into an advantage to overcome negative effects exerted by litter (Molofsky and Augspurger 1992) and competition (Leishman and Westoby 1994). 8) Sharp cotyledon species are less influenced by litter accumulation than flat cotyledon species as a sharp shape favors penetration of the litter mat (Sydes and Grime 1981).

The null hypothesis of the causal models is that the observed and predicted variances and covariances are equal, assuming that the empirical data were generated by the causal processes specified by the models (Shipley 1999). If the calculated probability under the null hypothesis is small (below  $P < 0.05$ ) then one must conclude that the null hypothesis is false, i.e. the observed data were unlikely to have been generated by the hypothetical causal process and the causal hypothesis must be rejected. If the null model is not rejected, we have no good statistical reason to reject the hypothesized causal models, and it remains as a potential explanation. Because the assumptions of the Chi-square test can result from inadequate statistical power (Mitchell 1993), we also used the Normed Fit Index (NFI) (Bentler and Bonnett 1980) and the Goodness-of-Fit Index (GFI) (Tanaka 1987). Values above 0.90 in both indices indicate good practical fit (Mitchell 1992). It is generally accepted to use the NFI and GFI indexes as an alternative to the Chi-square test to assess the degree of fit of causal models when data may depart from multivariate normality and sample sizes are small (Tanaka 1987, Bollen 1989, Loehlin 1992, Mitchell

1993, Palomares et al. 1998, Albert et al. 2000, Escudero et al. 2000).

Standardized partial regression coefficients were calculated to estimate the sign and strength for individual paths in the model (Mitchell 1993, Petraitis et al. 1996). We used multivariate Wald tests to assess the significance of these standardized partial regression coefficients. The unexplained variation ( $U_i$ ) of the three dependent variables in the path model (numbers of germinable seeds, emerged seedlings, and non-conspecific emerged seedling) was estimated as  $U_i = (1 - R_i^2)^{1/2}$ , where  $R_i$  is the squared multiple correlation (Mitchell 1993). Computations of the structural equation models were performed using PROC CALIS (SAS Institute 1996). Statistical analyses on count data were computed using log-transformed data,  $\log(x + 1)$ .

We used backward stepwise multiple regressions for exploring the effects of number of germinable seeds, late-summer species biomass, and litter mass on the emergence of total number of individuals in the community, and the effects of number of emerged seedlings and litter mass on the total number of reproductive individuals. At this community level, the explanatory models have fewer interactions because the potential effects of non-conspecific germinable seeds and emerged seedlings were left out. In the final models, standardized partial regression coefficients measured the relative importance of each variable.

Finally, we estimated species composition similarity among germinable seeds, emerged seedlings and reproductive individuals at each sampling site. Whittaker (1952) index of community association was chosen because it is responsive to less abundant species in communities heavily dominated by very few species. A value of 0 indicates completely different species composition, while 1 indicates the same species in the same proportions.

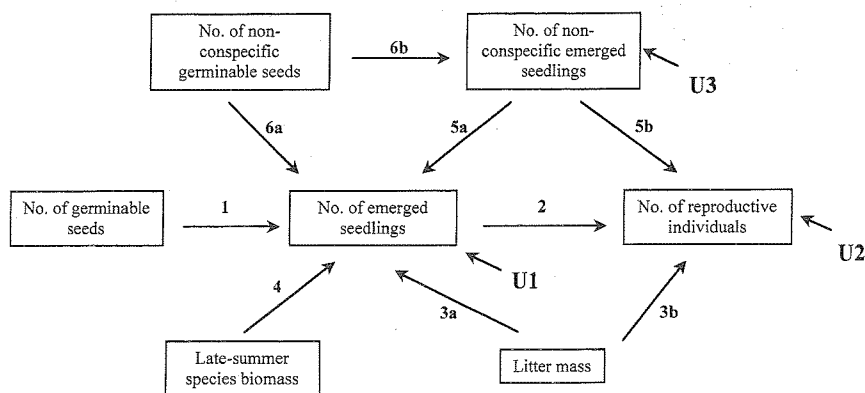


Fig. 1. Path diagram of the hypothetical causes of recruitment of reproductive individuals in a Mediterranean annual plant community at the population and functional type levels. Arrows show causal effects of one variable on another. Path numbers match hypotheses explained in the text (Data analysis section) and path coefficients in Table I. Numbers of emerged seedlings and reproductive individuals of the analyzed species and number of non-conspecific seedlings are dependent variables. The unexplained variation of dependent variables is denoted by  $U_i$  (see text for additional explanations).

Table 1. Results of the structural equation modeling performed A) on the eleven most abundant species found in the studied community and B) on the functional types. For every species and functional type we indicate 1) number of observations (*n*), 2) model fit parameters (Chi-square test, Normed Fit Index (NFI), and Goodness-of-Fit index (GFI), 3) standardized partial regression coefficients of paths, and 4) unexplained variance of dependent variables ( $U_1$ , emerged seedlings;  $U_2$ , reproductive individuals; and  $U_3$ , non-conspecific emerged seedlings). For paths we indicate hypothesis number in Fig. 1 and nomenclature is as follows: NGS: number of germinable seeds, NES: number of emerged seedlings, NRI: number of reproductive individuals, LM: litter biomass, LSEB: late-summer species biomass, NNCGS: number of non-conspecific germinable seeds, and NNCES: number of non-conspecific emerged seedlings.

	<i>n</i>	Model fit				Path coefficients										Unexplained variance						
		Chi-square	GFI	NFI		1	2	3a	3b	LM-NRI	4	LSEB-NES	5a	5b	6a	6b	NNCGS-NES	NNCGS-NCES	$U_1$	$U_2$	$U_3$	
A) Plant species																						
<i>Papaver rhoeas</i>	72	0.29	0.98	0.97	0.35*	0.68*	-0.1	-0.11	0.06	0.1	0.19*	0.02	0.52*	0.93	0.66	0.85						
<i>Hordeum murinum</i>	63	0.05*	0.95	0.8*	-0.06	0.62*	0.11	-0.11	-0.16	-0.01	0.07	-0.02	0.47*	0.98	0.78	0.88						
<i>Hyecoum procumbens</i>	62	0.14	0.96	0.95	0.25*	0.96*	0.01	0.02	0.13	0.03	0.02	-0.27*	0.46*	0.93	0.28	0.89						
<i>Trisetum panicum</i>	54	0.14	0.95	0.96	0.62*	0.97*	-0.09	-0.04	-0.02	0.03	0.02	0.09	0.43*	0.72	0.19	0.92						
<i>Papaver hybridum</i>	46	0.11	0.94	0.81*	0.16	0.63*	-0.08	-0.04	-0.15	0.07	0.09	-0.07	0.5*	0.97	0.76	0.86						
<i>Herniaria glabra</i>	38	0.06	0.92	0.76*	0.3*	0.3*	0.15	0.1	-0.01	0.57*	0.15	-0.17	0.6*	0.82	0.91	0.80						
<i>Lamium amplexicaule</i>	37	0.19	0.94	0.93	-0.45*	0.92*	-0.29*	0.05	-0.05	0.18	-0.01	-0.31	0.36*	0.74	0.36	0.93						
<i>Sisymbrium irio</i>	36	0.35	0.93	0.91	0.53*	0.52*	-0.15	-0.22	-0.1	0.5*	0.04	-0.17	0.63*	0.70	0.79	0.78						
<i>Descurainia sophia</i>	35	0.15	0.93	0.76*	-0.29*	0.52*	-0.17	0.01	-0.12	0.07	-0.04	-0.02	0.38*	0.92	0.86	0.93						
<i>Anacyclus clavatus</i>	34	0.24	0.94	0.9	-0.48*	0.84*	-0.1	-0.08	0.06	0.15	-0.07	-0.12	0.49*	0.87	0.53	0.87						
<i>Lophoclaena crataea</i>	33	0.3	0.94	0.95	0.27	0.98*	-0.01	-0.02	0.22	0.11	0.02	-0.01	0.42*	0.94	0.17	0.91						
B) Functional types																						
Sharp cotyledon species	72	0.005*	0.93	0.87*	0.5*	0.87*	-0.19*	-0.12*	0.04	0.07	0.04	0.14	0.34*	0.77	0.39	0.94						
Flat cotyledon species	72	0.007*	0.94	0.91	0.29*	0.7*	-0.2*	-0.21*	-0.13	0.09	0.06	-0.005	0.58*	0.91	0.61	0.82						
Small-seeded species	72	0.02*	0.95	0.92	0.51*	0.8*	-0.23*	-0.15*	0.03	0.07	-0.16*	0.1	0.33*	0.80	0.52	0.94						
Medium-seeded species	72	0.05*	0.96	0.95	0.46*	0.9*	-0.17	-0.1*	-0.02	0.36*	-0.07	-0.34*	0.52*	0.78	0.39	0.85						
Large-seeded species	72	0.04*	0.96	0.91	0.11	0.82*	0.08	-0.11	0.04	-0.1	0.09	-0.04	0.52*	0.98	0.58	0.85						

\*  $P < 0.05$ .

## Results

Overall, our explanatory models explained the recruitment of reproductive individuals at three hierarchical levels. At the population level, the hypothesized multivariate causal model was accepted (Chi-square Goodness-of-Fit tests were not significant at  $P < 0.05$ ) for ten out of the twelve most frequent species. These species accounted for 83.1% of germinable seeds, 78.1% of emerged seedlings, and 70.2% of reproductive individuals of a pool of 56 species. When we considered functional types, the Chi-square tests rejected the hypothesized models (tests were significant), though the Goodness-of-Fit Index was always  $\geq 0.90$ , indicating a good degree of fit of models to field data. At the community level, stepwise regressions were highly significant ( $P < 10^{-6}$ ) and accounted for 32.3% of the variance in the case of the number of emerged seedlings and 72.9% in the case of the number of reproductive individuals.

### Population level

The hypothesized model did not apply for *Chenopodium album* because this species did not emerge under field conditions (501 individuals emerged in the glasshouse and only one in the field). For the eleven remaining frequent species, the Chi-square test revealed that the model was only rejected for *Hordeum murinum* (Table 1A). The NFI index also suggested a weak degree of fit of the model for *Papaver hybridum*, *Herniaria glabra* and *Descurainia sophia*. The mean unexplained variance for the eleven species was 86% (ranging from 70% to 98%) for the number of emerged seedling and 57% (ranging from 17% to 91%) for the number of reproductive individuals.

The relationship between numbers of germinable seeds and emerged seedlings was largely species dependent. Four species had a significant positive relationship, three species had a significant negative relationship, and five species were indifferent. The number of emerged seedlings of all populations was positively related to the number of reproductive individuals. Some species had a high path coefficient ( $> 0.9$ ) because of the high survival rate of the seedlings. The number of non-conspecific germinable seeds exerted a significant negative effect on seedling emergence of *Hyecoum procumbens*. The number of non-conspecific seedlings did not have any negative effect on the numbers of emerged seedlings and reproductive individuals. Surprisingly, it exerted a significant positive effect on the number of emerged seedlings of two species (*Herniaria glabra* and *Sisymbrium irio*), and on the number of reproductive individuals of one species (*Papaver rhoeas*). Biomass of late-summer species did not affect the number of emerged seedlings of any population.

Despite the general negative relationships between litter and the numbers of emerged seedlings and reproductive individuals, only the emergence of *Lamium amplexicaule* showed a significant negative relationship with litter abundance.

### Functional traits

The type with sharp cotyledons had a tighter relationship between the numbers of germinable seeds and emerged seedlings and between the numbers of reproductive individuals and emerged seedlings (Table 1B). The type with sharp cotyledons suffered less negative effects of litter on seedling survival. The unexplained variations for numbers of emerged and reproductive individuals were greater for the flat cotyledon type than for its sharp cotyledon counterpart.

Litter effects were related to seed mass. The greater the seed mass, the smaller the negative effect of litter on numbers of emerged seedlings and reproductive individuals (Table 1B). The effects of the number of emerged seedlings of other seed type were also related to seed mass: the greater the seed mass, the smaller negative effects of number of emerged seedlings of the other type. The unexplained variance for number of emerged seedlings was greater for the large-seeded species type than for the small- and medium-seeded species types. The unexplained variance for number of reproductive individuals was similar in all three seed mass types.

### Community level

A mean of 8663 seeds/m<sup>2</sup> emerged from the seed bank in the glasshouse, 6283 seedlings/m<sup>2</sup> emerged in the field, and 3007 individuals/m<sup>2</sup> reached the reproductive stage. Mean rate of seedling emergence was 72.5% and of seedling survival was 47.9% per sampling site. Mean species composition similarity (Whittaker index) between emerged seedlings and reproductive individuals was high (71.1%) and greater than between germinable seeds and emerged seedlings (49.8%).

The relationships between the numbers of germinable seeds and emerged seedlings and between the numbers of reproductive individuals and emerged seedlings were

both positive (Table 2). Litter negatively affected the numbers of emerged seedlings and reproductive individuals, and biomass of late-summer species did not have any significant effect.

## Discussion

### Factors conditioning seedling emergence

Abundance of germinable seeds did not always satisfactorily predict seedling emergence of species, although it did so at the community level. At the population level, the relationship between the numbers of germinable seeds and emerged seedlings largely depended on species identity. The results of only four out of the twelve most abundant species were consistent with our hypothesis and showed a significant positive relationship between these numbers. Four species are few if we take into account that most species of the community are annuals and early successional species (Moore 1980) and the high frequency and size of available gaps (Peco et al. 1998). Three species showed a significant negative relationship, suggesting that the number of germinable seeds may exert a negative effect on seedling emergence. Density-dependent negative effects of conspecific seeds on germination were also found by Speer and Tupper (1975) and Froud-Williams and Ferris (quoted by Fenner 1985: 101). However, the exact effect of seed abundance on germination may depend on the actual density range experienced. In our study, the negative effects occurred in the case of the species with less seed density in the seed bank (a maximum density of 10 seeds/100 cm<sup>2</sup>), pointing to a statistical artifact. Null and positive effects occurred for similar seed ranges (maximum densities of 125 and 116 seeds/100 cm<sup>2</sup>, respectively). Further experimentation is necessary to ascertain the processes underlying these findings. Researchers usually find that the number of conspecific seeds does not modify the emergence rate (Harper 1977, Baskin and Baskin 1998, Fenner 2000), and sometimes can produce positive effects, e.g. an abundant seed pool facilitates seedling emergence by breaking the soil crust (Gutterman 1993).

Our study pointed to neutralism as the major type of relationship between seeds of different species. The

Table 2. Results of the stepwise multiple regressions used to explain A) the total number of emerged seedlings and B) the total number of reproductive individuals in the plant community. Only significant variables are reported. Adjusted,  $R^2$  are 0.32 and 0.73, respectively. Standardized partial regression coefficients, standard errors and  $P$ -values are indicated.  $n = 72$ .

Effect	Standardized partial regression coefficient	Standard error	$P$ -value
A) No. of emerged seedlings			
No of germinable seeds	0.45	0.099	0.00002
Litter mass	-0.3	0.099	0.003
B) No. of reproductive individuals			
No. of emerged seedlings	0.75	0.067	0.0000001
Litter mass	-0.24	0.067	0.0005

number of non-conspecific germinable seeds did not affect seedling emergence except for *Hypocoum procumbens*. This species showed a negative effect, suggesting resource competition or allelopathy interactions during the seed stage. Again, researchers usually find that the number of non-conspecific seeds does not modify the emergence rate of a given species (Harper 1977, Baskin and Baskin 1998, Fenner 2000).

We did not find any negative effect of the number of non-conspecific seedlings on seedling emergence of a given species. These results are not consistent with our initial hypothesis that inter-specific competition may play a relevant role by reducing seedling emergence. Aguiar et al. (1992) also found that a partial reduction of competition had no significant effect on the number of emerged *Bromus pictus* seedlings. Experiments by Peco and Espigares (1994) with Mediterranean annual pasture species under laboratory conditions yielded similar results. Competition effects of neighbors on seedling emergence are mainly reported in communities with a dense canopy produced by the established plants (Gorski et al. 1977, Silvertown 1980). Our explanation is that seedling canopy was not dense enough to promote competitive effects and to enforce seed dormancy. In our study two species (*Herniaria glabra* and *Sisymbrium irio*) showed positive effects from non-conspecific seedlings, an evidence for potential facilitation processes during the emergence stage in this community.

Litter abundance had little effect on seedling emergence at the population level. Despite the general negative trends, only the emergence of *Lamium amplexicaule* showed a significant negative relationship with litter abundance. This result is not consistent with our initial hypothesis that litter accumulation after summer drought should have an influence on emergence in this community. A similar amount of litter to that found in our study (ranging from 49 to 663 g of dry mass/m<sup>2</sup>) affected annual species density in field and laboratory studies of other authors (Facelli and Pickett 1991b, Boserup and Reader 1995). Litter can reduce seed germination and/or restrict shoot extension (Reader 1993). In our study, litter exerted a greater negative effect on seedling emergence at the level of the total number of individuals in the community. The negative effect of litter on seedling emergence was inversely related to seed mass, in agreement with our initial hypothesis and Keever (1973), Tao et al. (1987), Facelli and Pickett (1991b), Reader (1993), Boserup and Reader (1995). This result supports the hypothesis that the amount of seed reserves plays some role in preventing negative effects of litter on emergence in this community. Functional types with different cotyledon shape (flat and sharp) revealed similar negative effects of litter abundance on emergence. Sharper cotyledons did not favor litter mat penetration and seedling emergence, in contrast to Grime (1979), Sydes and Grime (1981). The physical

structure of litter in forest habitats may exert greater mechanical impedance.

Finally, in contrast to our initial hypothesis, previous established plants of late-summer species in autumn exerted no effect on seedling emergence at the studied levels. This effect was probably due to their low abundance in the study area (a mean of 27 g/m<sup>2</sup>).

### Factors conditioning seedling survival

All populations and the total number of individuals in the community yielded a positive relationship between the numbers of emerged seedlings and reproductive individuals. Mean species composition similarity between these numbers was high. Thus, community composition at the reproductive stage was determined right after germination in autumn. Heady (1958) also found this pattern in annual Mediterranean pastures in California.

Inter-specific interactions appeared not to have important negative effects on seedling survival of individual species. The number of non-conspecific seedlings only had significant effects on the density of reproductive individuals of *Papaver rhoeas*, and this effect was positive. This result is not consistent with our initial hypothesis and previous studies that found density-dependent negative effects from non-conspecific seedlings (Aguilera and Lauenroth 1993, Kolb and Robberecht 1996). Our result does, however, concur with those of Silander and Pacala (1985), Peco and Espigares (1994), who found no significant effects of competition on seedling survival of annual species under laboratory conditions. Most studies reporting negative effects of seedling density on plant performance address growth, weight or reproductive success, but not seedling survival. Our study hints that high plasticity of annuals impedes strong mortality under competition conditions, and individuals reach the reproductive stage smaller in size. In Mediterranean annual plant communities seedling emergence is concentrated to the autumn period under conditions of abundant resources (mostly water and space), thus suffering little competitive pressure. An exception was the small-seeded species type, which showed that the number of non-conspecific seedlings has negative effects on the number of reproductive individuals. This suggests that seed reserves again may play some role in supporting inter-specific competition in this community.

Litter abundance had little effect on seedling survival at the population level, in spite of the general negative trend. These results are consistent with our initial hypothesis that litter can reduce seedling survival only at the community level (Herman and Chilcote 1965, Fowler 1986). Litter effect depended on seed size: large-sized seeds did not suffer significant negative effects. This result is also consistent with our initial hypothesis

Table 3. Summary of results and consistency with posed hypotheses of factors affecting a) seedling emergence and b) seedling survival in a Mediterranean annual plant community.

	Hypothesized effects		Population		Functional type		Total number of individuals	
	Results	Consistency	Results	Consistency	Results	Consistency	Results	Consistency
a) Seedling emergence	Positive	For four sp.	All positive except for large-seeded sp.	Yes	Yes except for large-seeded sp.	Positive	Yes	
Germinable seed bank	Negative	For one sp.	No effect except for one sp.	No	No effect except for medium-seeded sp.	-	-	
Emergent seedlings of non-conspecific sp.	Negative	No	Neutral and positive effects	No	No effect except for medium-seeded sp.	-	-	
Late-summer species biomass	Negative	No	No effect	No	No effect	No effect	No	
Litter	Negative	For one sp.	No effect except for one sp.	Yes	Negative effect except for large- and medium-seeded sp.	Negative	Yes	
b) Seedling survival	Positive	Yes	All positive	Yes	Yes	Positive	Yes	
Emergent seedlings	Negative	No	Neutral and positive effects	No	No effect except for small-seeded sp.	-	-	
Emergent seedlings of non-conspecific sp.	Negative	No	No effect	No	All negative except for large-seeded sp.	Negative	Yes	
Litter								

that seed reserves also ameliorate negative effects of litter on seedling survival (Black 1958).

### Concluding remarks: balance of factors affecting reproductive recruitment

Overall, the results of this study supported our explanatory models of recruitment, and allowed us to infer the main stages and causal factors affecting recruitment of reproductive individuals. Results provide evidence for the importance of early stages of establishment (emergence) as compared to seedling survival to determine community floristic composition. Our results concurred with those of Bartolome (1979) and Rice (1989), who found high seedling mortality in Mediterranean annual plant communities in California. However, this high mortality affected little the proportion of species, likely because it was primarily influenced by density-independent biotic and abiotic factors.

Concordances with the path initial hypotheses were more frequent at the community level as compared to the population level (Table 3). We conclude the following from our study. 1) In agreement with widely accepted hypotheses described in the literature for annual plant communities, we found further evidence for the positive relationship between the number of reproductive individuals and emerged seedlings at the population and community levels. There is as well a positive relationship between the numbers of germinable seeds and emerged seedlings at the community level. 2) At the population level, we found a variety of relationships (positive, negative and neutral) between the numbers of germinable seeds and emerged seedlings. 3) We found a possible case of inter-specific competition between seeds, a type of interaction also hardly described in the literature. 4) Litter exerted negative effects on seedling emergence and survival. Large-sized seeds reduced litter effects and sharper cotyledons did not improve emergence and survival. 5) In contrast to our initial hypothesis, established plants at the germination stage did not affect seedling emergence. 6) The number of non-conspecific seedlings did not negatively affect emergence and survival at the population level, except for the small-seeded species type. For some species we found evidence of facilitation processes during the seedling survival period.

Finally, we suggest two major reasons that affected the degree of fit of the explanatory models and that might account for some of the unexplained variation. 1) Seed banks (Thompson 1986, Dessaint et al. 1991) and litter distribution (Facelli and Pickett 1991a) are extremely spatially heterogeneous in this type of communities, and by necessity it was not possible to estimate litter abundance, germinable seed bank, and emerged seedling density at the same sampling point. 2) Soil samples were 8 cm deep, and likely included seeds that



germinated under glasshouse conditions but that would not have germinated under field conditions (Baskin and Baskin 1998).

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Appendix 1. Relative frequency of the 56 species encountered at the studied field and their biological traits. The twelve species selected for structural equation modeling are in bold. Seed mass was classified as small (< 0.1 mg), medium (0.1 mg–1 mg) and large (> 1 mg). Nomenclature follows Tutin et al. (1964–1981).

Species	Relative frequency	Cotyledon shape	Seed mass
<i>Papaver rhoeas</i> L.	100.0	Flat	Small
<i>Hordeum murinum</i> L.	87.5	Sharp	Large
<i>Hypocoum procumbens</i> L.	86.1	Sharp	Large
<i>Trisetum paniceum</i> (Lam.) Pers.	75.0	Sharp	Small
<i>Chenopodium album</i> L.	68.1	Flat	Medium
<i>Papaver hybridum</i> L.	63.9	Flat	Medium
<i>Herniaria hirsuta</i> L.	52.8	Flat	Small
<i>Lamium amplexicaule</i> L.	51.4	Flat	Medium
<i>Sisymbrium irio</i> L.	50.0	Flat	Small
<i>Descurainia sophia</i> (L.) Webb ex Prantl in Engl. & Prantl.	48.6	Flat	Small
<i>Anacyclus clavatus</i> (Desf.) Pers.	47.2	Flat	Small
<i>Lophochloa cristata</i> (L.) Hyl.	45.8	Sharp	Small
<i>Stellaria media</i> (L.) Vill	43.1	Flat	Medium
<i>Vulpia ciliata</i> Dumort	31.9	Sharp	Medium
<i>Polygonum aviculare</i> L.	30.6	Sharp	Large
<i>Veronica hederifolia</i> L.	30.6	Flat	Large
<i>Galium parisiense</i> L.	29.2	Flat	Medium
<i>Veronica polita</i> Fries	29.2	Flat	Medium
<i>Cerastium glutinosum</i> Friesa	27.8	Flat	Small
<i>Hirschfeldia incana</i> (L.) Lagr.-Foss.	27.8	Flat	Medium
<i>Sonchus oleraceus</i> L.	20.8	Flat	Medium
<i>Bromus rubens</i> L.	19.4	Sharp	Large
<i>Fumaria parviflora</i> Lam.	18.1	Sharp	Large
<i>Lactuca serriola</i> L.	18.1	Flat	Medium
<i>Filago pyramidata</i> L.	16.7	Flat	Small
<i>Arenaria serpyllifolia</i> L.	15.3	Flat	Small
<i>Cardaria draba</i> (L.) Desv.	15.3	Flat	Large
<i>Fumaria officinalis</i> L.	13.9	Sharp	Large
<i>Capsella bursa-pastoris</i> (L.) Medicus	12.5	Flat	Small

## Appendix 1. (Continued)

Species	Relative frequency	Cotyledon shape	Seed mass
<i>Chondrilla juncea</i> L.	11.1	Flat	Medium
<i>Holosteum umbellatum</i> L.	11.1	Flat	Small
<i>Petrorhagia dubia</i> (Rafin) G. López & Romo	11.1	Flat	Medium
<i>Cardus bourgeanus</i> Boiss & Reuter	9.7	Flat	Large
<i>Veronica arvensis</i> L.	9.7	Flat	Small
<i>Adonis aestivalis</i> L.	8.3	Sharp	Large
<i>Amaranthus albus</i> L.	6.9	Flat	Medium
<i>Campanula erinus</i> L.	6.9	Flat	Small
<i>Lolium rigidum</i> Gaudin	6.9	Sharp	Large
<i>Silene nocturna</i> L.	6.9	Flat	Medium
<i>Crepis vesicaria</i> L.	5.6	Flat	Small
<i>Bromus tectorum</i> L.	5.6	Sharp	Large
<i>Erodium ciconium</i> (L.) L'Her	5.6	Flat	Large
<i>Trigonella polyceratia</i> L.	5.6	Flat	Medium
<i>Linaria</i> sp.	4.2	Flat	-
<i>Taraxacum</i> sp.	4.2	Flat	-
<i>Bromus maximus</i> Desf.	1.4	Sharp	Large
<i>Centaurea melitensis</i> L.	1.4	Flat	Large
<i>Diptotaxis eruroides</i> (L.) DC	1.4	Flat	Medium
<i>Diptotaxis virgata</i> (Cav.) DC	1.4	Flat	Small
<i>Geranium molle</i> L.	1.4	Flat	Large
<i>Lithospermum arvense</i> L.	1.4	Flat	Large
<i>Linaria hirta</i> (L.) Moench	1.4	Flat	Medium
<i>Portulaca oleracea</i> L.	1.4	Flat	Medium
<i>Vicia cracca</i> L.	1.4	Hypogeal	Large
<i>Vicia peregrina</i> L.	1.4	Hypogeal	Large
Forbs unknown	15.3	Flat	-