

# Spreading recruitment over time to cope with environmental variability

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**Abstract** Seedling establishment is one of the most vulnerable life cycle stages, and a key component for the population dynamics in short-lived plants. In unpredictable environments, timing of emergence is critical for the success of plant performance, and different adaptive bet-hedging strategies have evolved to reduce the risk of failure in recruitment. In this study we describe the spatio-temporal pattern of seedling emergence (overall rate and timing) and survival in four contrasting Mediterranean habitats for *Plantago coronopus*, a small herb with dimorphic seeds. We then explore the importance of spreading germination within years, as well as the role of the two types of seeds from a broader temporal perspective. Populations strongly differed for all recruitment components analyzed in a given year, but this spatial differentiation diluted when a longer period was considered. Apical (smaller) seeds germinated later and in a significantly lower proportion than basal (larger) seeds. Both late emergents and seedlings from apical seeds had lower survival probability in a rainy year. However, our results suggest that in a population

having the lowest production of apical seeds, late emergents coming from apical seeds may constitute a large fraction of yearly recruitment and that their performance was non-significantly different from that of early emergents over the 4-year study period. This study provides evidence of the importance of two related traits (spreading seedling emergence through time by producing dimorphic seeds) as bet-hedging strategies to cope with environmental unpredictability. This is at least partly accomplished by increasing the potential of recruitment in favourable years, instead of buffering such important process in extremely bad years.

**Keywords** Annual and perennial populations · Bet-hedging · Mediterranean · *Plantago coronopus* · Seed dimorphism · Seedling survival

## Introduction

Seedling establishment is a critical stage in the life cycle of plants. It determines the number of individuals entering the next generation, which has important consequences for the demography and evolutionary ecology of the species (Kitajima and Fenner 2000). The importance of recruitment for species' persistence, however, varies among organisms with different longevities (Silvertown et al. 1993; García et al. 2008). Many short-lived species strongly depend on

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the short-term success of recruitment, because in the absence of a persistent seed bank, failure of seedling establishment can result in local extinction.

Seedling recruitment is also one of the most vulnerable life cycle stages, and often the stage most intimately linked to environmental conditions (Fenner 1987). It has been demonstrated that biotic and abiotic factors strongly affect plant performance during this stage through variation in soil resources, light, drought, pathogens, herbivory or neighbours (de Jong and Klinkhamer 1988; Ostfeld and Canham 1993; Herrera 2002; Gustafsson and Ehrlén 2003). Because environmental factors might also vary during the season, timing of emergence is critical for the success of seedling performance (Verdú and Traveset 2005). The larger size reached by early emerging seedlings may entail benefits in terms of increased survival advantages in competitive situations (Dyer et al. 2000), or in arid and Mediterranean environments where species must survive drought periods (Escudero et al. 1999). On the other hand, interactions with negative environmental factors might also be longer for early emergents too, which would favour late emergence (Weekley et al. 2007). Thus, the optimal time of emergence will depend on the particular set of environmental conditions influencing seedling performance at each site.

Recruitment may also vary considerably in time, and strong temporal variation in vital rates like recruitment has important consequences for life-history evolution and population dynamics (Real 1980; Tuljapurkar 1989; Boyce et al. 2006). Under such situation, natural selection usually favours mechanisms that spread the risk of reproduction through time in what is known bet-hedging strategies (Philippi and Seger 1989). Spreading germination within a year, or among several years (through a permanent seed bank) is an example of adaptive bet-hedging strategies (Cohen 1966; Evans et al. 2007; Venable 2007). Although these strategies may be suboptimal in ‘average’ years, they protect parental fitness from extremely bad years (Mathias and Kisdi 2002).

Mediterranean ecosystems show a high ecological variability in space and time: in space, as several different types of habitats can be found in areas of Mediterranean climate; in time, because of high temporal unpredictability, particularly in the amount and seasonal pattern of precipitation, alternating dry

and rainy years. Mediterranean regions are therefore suitable systems to explore the consequences of spatio-temporal variations in recruitment patterns, and on the adaptive strategies of the flora to mitigate such variation. They have been the focus of several recruitment studies (see for example Herrera et al. 1994; Gómez-Aparicio et al. 2005; Lázaro et al. 2006), but herbs have received considerably less attention than woody plants (but see Vilà and Lloret 2000; Garrido et al. 2007).

In this study we use a widespread herb mainly distributed around the Mediterranean region (*Plantago coronopus* L.), as a model system to explore seedling recruitment in heterogeneous and unpredictable environments. *P. coronopus* is a small herb occurring in a wide variety of habitats, and the life cycle can be either annual or short-lived perennial (Chater and Cartier 1976). Seedling emergence occurs from autumn to March, usually in terms of subsequent cohorts associated with rainfall. *P. coronopus* has dimorphic seeds because fruits may contain two types of seeds that differ in size, shape, and ecological behaviour (Dowling 1933). Seed heteromorphism is considered a bet-hedging strategy because it spreads offspring in space (through differential dispersal) and/or time (through differential germination), covering a wider number of possible environmental scenarios, and reducing the risk of parental investment (Imbert 2002).

Here we describe the spatio-temporal patterns of seedling emergence and survival in contrasting Mediterranean habitats, and ask the following questions:

- (1) Is the observed spatial variability of recruitment components consistent among years?
- (2) Is temporal variation in seedling emergence within seasons advantageous?
- (3) Do the two types of seeds differ in recruitment characteristics? If so, in which way can a mixed strategy be beneficial?

## Materials and methods

### Study species

*Plantago coronopus* L. subsp. *coronopus* (Plantaginaceae), the most widespread subspecies across the

species geographic range (Hultén and Fries 1986), is a small herb with leaves arranged in one to a few rosettes. Flowering starts in March in annual populations, and lasts until the plant dies in May–June. The age of adult plants in these populations can thus vary from 1 to 6 months. Flowering occurs later in perennial populations (June–July), where in most individuals do not flower in their first year.

Adult plants produce several inflorescences with numerous flowers arranged into dense spikes. Fruits are capsules containing two types of seeds: large basal (up to four, with a thick mucopolysaccharid coat), and small apical seeds (zero or one per fruit, with a much thinner coat). The coat of basal seeds becomes mucilaginous when in contact with water or humidity, making them stick to soil surface, and helping roots to penetrate the soil (Dowling 1933; Schat 1981). Apical seeds, on the contrary, seem to be released together with the capsule lid, which may facilitate dispersal by wind or water (Dowling 1933).

Populations and study years

Four populations in the southern part of the Iberian Peninsula located in contrasting environments were selected for the study: shrubland (s), marsh (m), coastal dune (c) and mountain meadow (m) (Table 1). In two of them, individuals behave as annuals (A; thereafter named as A-s and A-m, attending the habitat), while, in the other cases, they are perennials (P; thereafter named as P-c and P-m). The climate of the region is typically Mediterranean: with little temperature fluctuations, 4 months of summer drought (June–September), rainy winters with high inter-annual variability in amount, and seasonal distribution of precipitation. The annual populations occur at sites that experience more extreme temperatures and lower precipitation than the perennial ones (Table 1). One of the perennial populations (P-m) has a particularly wet microclimate because of its position in the mountain facing the Strait of Gibraltar, where fogs are very frequent.

This study lasted from autumn 2003 until summer 2007. In the following, years will be named with the last two digits of the 2 years involved in the growing season (for example, 03–04 lasts from September 2003 until August 2004). Years were classified as ‘rainy’ (03–04), ‘dry’ (04–05) or ‘average’ (05–06 and 06–07) according to their total precipitation relative to the average for the last 30 years at the

**Table 1** Geographic location, main environmental characteristics and sampling variables of the four populations of *P. coronopus* studied in the southern part of the Iberian Peninsula

Population	Life history	Location (m asl)	Habitat	Min–Max temperature (°C)	Yearly precipitation (mm)	No. plots monitored (m of the sides)	No. quadrats (10 × 10 cm <sup>2</sup> )	No. early/late emergents labelled in 03–04
A-s	Annual	37°15' N 6°13' W (42)	Shrubland	11–25	558	6 (0.4 × 0.4)	24	112/98
A-m	Annual	36°53' N 6°17' W (2)	Marsh	12–24	578	6 (0.4 × 0.4)	24	105/128
P-c	Perennial	36°02' N 5°38' W (1)	Coastal dunes	15–20	845	3 (1 × 4)	130	112/98
P-m	Perennial	36°06' N 5°32' W (730)	Foggy mountain	11–19	1,045	5 (1 × 1)	25	86/102

meteorological station closest to the respective population. Quartiles of the distribution were used to classify dry, average and rainy years.

### Sampling method

Monitoring of seedlings started in the autumn 2003. It was carried out in several small quadrats (10 × 10 cm) randomly selected within larger plots. The number and size of plots, as well as the number of quadrats, differed among populations according to seedling density (Table 1). Populations were repeatedly visited over four growing seasons (every 4–6 weeks during the first year of study, and three times per year in the following years), and the number of new seedlings was counted in each quadrat. The total number of emerging seedlings per quadrat in a year will hereafter be named ‘overall emergence’. ‘Survival’ was estimated as the proportion of seedlings reaching the onset of the seasonal reproductive period at each population (March for annuals, and June for perennials), regardless of whether they flowered or not. ‘Timing of emergence’ was classified as early if seedlings germinated right after the first autumn precipitations (October–November) and late when the first autumn precipitations recorded later. A total of 7,951 seedlings were monitored during the study.

About 100 early- and 100 late-emerging seedlings were individually labelled in each population in the autumn 2003, and followed until they died (Table 1). To avoid extensive labelling in the field and their accidental losses, in the autumns of 2004–2006, we monitored the fate of seedlings located in the quadrats containing only one kind of seedling (early or late emergents). The A-s population was destroyed during the second year of study, and was removed from the analysis of temporal variability.

Differences in the timing of emergence between the two types of seeds were examined in field sowing experiments. In October 2003 and 2004 (rainy and dry years, respectively) we sowed basal and apical seeds in one annual (A-s) and one perennial (P-c) population. Groups of 100 or 50 seeds (basal or apical seeds, respectively) were released on sterilized soil within permeable pots randomly placed among plots. A total of 4,000 seeds (800 basals and 200 apicals in each population and year) were used for this experiment. Pots were checked three times: after the first

autumn precipitations to record early emergents (November), and during the winter (February) and the spring (April), to record late emergents.

### Data analysis

Variation in overall emergence, seedling survival and proportion of seedlings emerging late among the four populations was examined in a good (rainy) year (03–04), the only period where data were available from all the studied populations. Population was considered a fixed factor, while plots within population, and quadrats within plots, as random effects. When significant differences among populations were detected, post-hoc comparisons were conducted (with Bonferroni correction) to find out which populations differed. Analyses were conducted by fitting generalized linear mixed models (GLMMs) to the data with the GLIMMIX procedure of SAS 9.2. In each case, we chose the error distribution and the link function that best fitted our data: poisson error and log link function for seedling counts (overall emergence), and binomial error and logit link function for binary response variables or proportions (survival, and proportion of late emergence).

Differences among populations in overall emergence, seedling survival, and proportion of seedlings emerging late were explored again including the 4 years of study, although only three populations were used (the A-s was vandalized in the second year of monitoring). To do so, year (nested within population) was included as another random factor into the previous GLMMs, as it was considered another source of variation affecting recruitment within populations. On the other hand, the coefficients of variation (CV) of the three recruitment components above mentioned were also calculated for comparison.

Individually labelled seedlings in 2003 were used to test for the differences in survival between early and late emergents. We included emergence period, population and their interaction as fixed factors in GLMMs. Plots within populations and quadrats within plots were considered as random factors. In order to explore to what extent results were consistent over time, we compared survival of early and late emergents across 4 years in the P-c population, the only one with quadrats containing only early or late seedlings in the 4 years of monitoring (04–05 was the

driest year in the decade and the emergence was very reduced compared to 03–04). In this model, year was considered as another random factor.

The germination of basal and apical seeds in the hand sowing experiment was examined in terms of overall rates over the study period ( $g_b$  and  $g_a$ , respectively) and the proportion of seedlings (originating from each type of seed) that germinated late ( $g_{bl}$  and  $g_{al}$ , respectively). Because, in these analyses, we are only interested in the intrinsic differences of dimorphic seeds, only the type of seed was considered as a fixed factor in the GLMMs (binomial error and logit link function used), while population and year were included as random factors.

## Results

### Overall emergence and survival

Our first model tested differences in the amount of seedling emergence and survival among the four contrasted habitats studied in a rainy year (03–04). Populations significantly differed in overall emergence (range 5–70 seedlings per quadrat) and seedling survival (Table 2; Fig. 1 left and middle upper row). On average, seedling emergence in annual populations was twice as high as in perennial ones, and also had much higher survival rates.

When both spatial and temporal variations were included in the model, the spatial differences found above disappeared (Table 2). The rate of emergence was more variable across years in A-m (CV: 145%) than in the other two perennials (CV for P-c and P-m: 74 and 83%, respectively; Fig. 1 left bottom row). Seedling survival was also very variable across years (Fig. 1 middle bottom row), including the possibility of no survival at all in dry years (04–05 in A-m and P-m). The perennial population, P-m, was the most variable one for survival, with a coefficient of variation of 89%, whereas A-m and P-c had values of 77 and 55%, respectively.

### Emergence timing and survival

The proportion of seedlings emerging late also varied significantly among localities (Table 2; Fig. 1 right upper row). In a rainy year (03–04), most of the emergence took place after the first autumn rains, so

that less than 30% could be considered as late emergents (except in P-c where the proportion of early and late emergents was equal). This pattern was not consistent among years (Fig. 1 right bottom row, Table 2). Overall, the proportion of late emergents ranged between 10 (A-m in 06–07, and P-c in 04–05) and 68% (P-m in 06–07) of the yearly emergence.

In the rainy 03–04 year, late emergents had a significantly lower survival than early emergents (Table 2; Fig. 2). When several years were considered in the P-c population, however, this effect of timing disappeared (Table 2).

### Seed heteromorphism and emergence timing

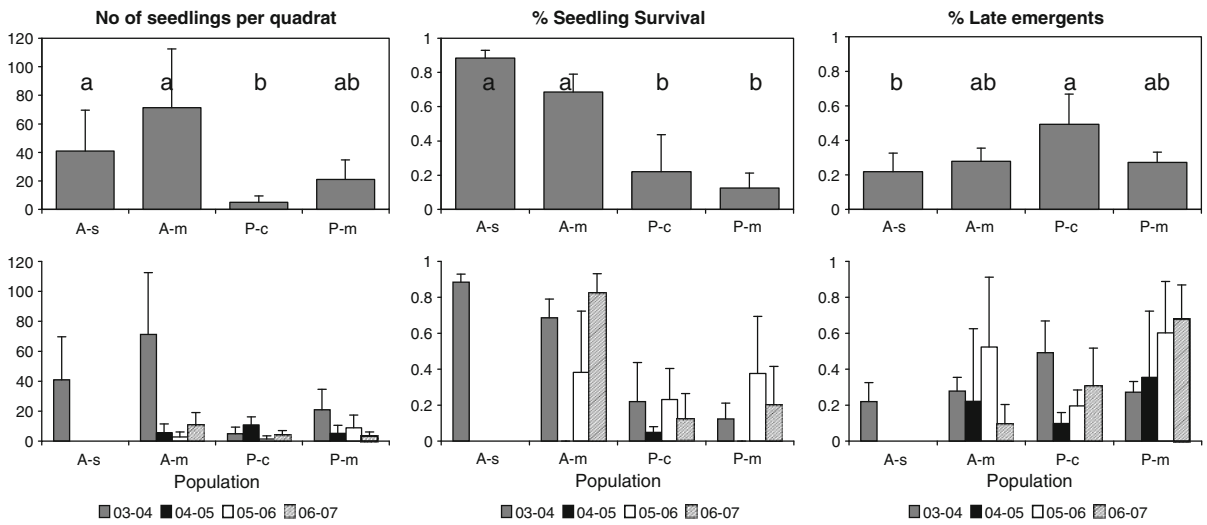
Apical seeds germinated in a significantly lower proportion than basal seeds, irrespective of population and year ( $g_a = 20\%$ ,  $g_b = 57\%$ ;  $N = 48$  pots;  $F = 46.54$ ;  $P < 0.0001$ ). Only 2% of seedlings originating from basal seeds appeared late in the season (average of the two populations and years) compared with 9% of apical seeds ( $N = 44$ ;  $F = 19.09$ ;  $P = 0.0003$ ).

To estimate the proportion of early and late emergents in the field coming from basal and apical seeds we used the recruitment at the P-c population and the 2 years of hand sowings, which corresponded to a rainy (03–04) and a dry (04–05) year (it could not be estimated in the A-s population because emergence was incomplete for the second year after vandalization). The probability of early-emerging seedlings to come from basal and apical seeds was estimated straightforward from the proportion of each kind of seed released by mother plants ( $P_b = 0.92$  basal seeds and  $P_a = 0.08$  for apical ones, Braza et al. in press) and germination rates early in the season (results from hand sowings each year; Fig. 3). The proportion of new seedlings later in the season (late emergents) coming from each type of seed, however, will depend not only on the specific germination rate of each kind of seed later in the season each year (for example  $g_{bl03-04}$  would correspond to the germination of basal seeds late in the 03–04 year), but also on their availability in the soil after early germination ( $1 - g_{be03-04}$ ). According to that, the vast majority of seedlings found in the field after the first autumn rains come from basal seeds (95–98%, depending on the year; Fig. 3). Later in the season, however, the source of new emerged

**Table 2** Results of the GLMMs

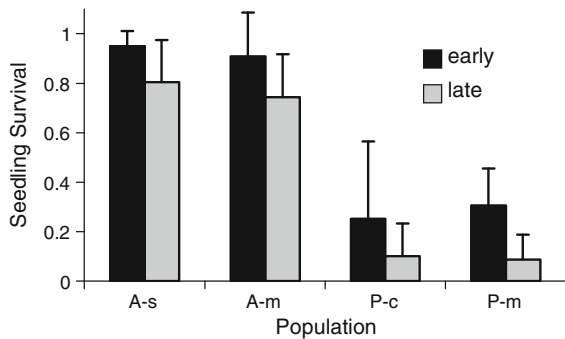
	Spatial variability				Temporal variability					
	<i>n</i>	Fixed factors	<i>F</i>	Random effects	Variance estimate	<i>n</i>	Fixed factors	<i>F</i>	Random effects	Variance estimate
Seedling emergence	203	Population	11.07 <sup>***</sup>	Plot Quadrat	0.5 (0.21) 0.39 (0.06)	720	Population	0.82	Year Plot Quadrat	1.15 (0.62) 0.68 (0.17) 0.53 (0.05)
Seedling survival	176	Population	30.83 <sup>***</sup>	Plot Quadrat	0.42 (0.19) 0.54 (0.14)	536	Population	0.75	Year Plot Quadrat	4.93 (2.9) 0.87 (0.31) 0.83 (0.17)
Late emergence	172	Population	4.37 <sup>*</sup>	Plot Quadrat	0.14 (0.08) 0.49 (0.13)	552	Population	1.46	Year Plot Quadrat	1.36 (0.79) 0.68 (0.29) 1.56 (0.2)
Survival of late emergents	841	Emergence time Population Interaction	40.45 <sup>***</sup> 17.77 <sup>***</sup> 0.2	Plot Quadrat	1.05 (0.49) 0.39 (0.24)	266	Emergence time	1.67	Year Plot Quadrat	1.04 (1.28) 1.18 (0.71) 1.01 (0.33)

Spatial variability was tested by comparing seedling emergence, survival, and late emergents across a rainy year (03–04), in a total of *n* quadrats randomly placed in four populations, and survival of *n* late emergents. Temporal variability was tested over 4 years of study in three populations (A-m, P-c and P-m) for seedling emergence and survival, and one population (P-c) for survival of late emergents (*n* indicates the number of quadrats monitored). For fixed factors, *F*, statistic and the significance levels are shown (\* 0.05 < *P* < 0.01; \*\*\* *P* < 0.0001). For random effects, the covariance parameter estimate and standard error are shown in *parenthesis*



**Fig. 1** Components of recruitment in the four populations of *P. coronopus* studied (A-s annual shrubland, A-m annual marsh, P-c perennial coast, P-m perennial mountain) in the rainy year (2003–2004; upper row of histograms; different letters indicate

post-hoc significant differences among populations after Bonferroni correction), and across 4 years (bottom row). Lines on bars correspond to standard deviations of the means



**Fig. 2** Survival of early- and late-emerged seedlings in the four populations of *P. coronopus* studied (A-s annual shrubland, A-m annual marsh, P-c perennial coast, P-m perennial mountain) in a rainy year (2003–2004)

seedlings can vary dramatically depending on the precipitation (Fig. 3). In the dry year, no late emergent would come from apical seeds, while in the rainy year, the proportion of late emergents would be almost balanced between both types of seeds (46% of the apical ones).

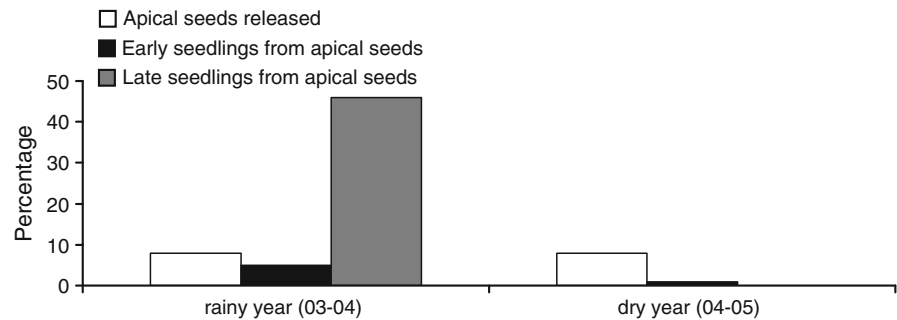
**Discussion**

Recruitment is a crucial process for short-lived plants, and our study on *P. coronopus* shows that

nearby localities dramatically differ in the density of emerged seedlings, timing of emergence, as well as in the probability of survival in a given year. The results also show that among-population differences are not consistent among years. This highlights the importance of long-lasting fieldwork studies to make generalizations about recruitment patterns and their variability in space and time, and to understand local adaptation in traits related to germination.

Some spatial differences seem to be associated with the life form. According to the classic life-history theory, annual life forms would be favoured in environments where the probability for a seed to become a flowering plant within one season is greater than the probability for an adult to survive to another flowering season, whereas perennials would be favoured when the contrary occurs (Charnov and Schaffer 1973; Roff 1992). Our results agree with these predictions. At least in favourable years, annuals had higher recruitment success (in terms of seedling emergence and survival) than perennials. Moreover, perennial populations have to survive for one or two harsh summers to become adults. As drought is one of the main causes of seedling mortality in Mediterranean ecosystems (Manzaneda et al. 2005; Garrido et al. 2007; Giménez-Benavides et al. 2007; Rodríguez-Pérez and Traveset 2007), seedling mortality may occur not only during the

**Fig. 3** Proportion of apical seeds produced in the inflorescences of P-c population, and early and late emergents estimated to come from them in two contrasted years (see text for further details)



same period as in annuals, but also (mainly) during the summer, increasing survival differences between annuals and perennials. In contrast to the association between recruitment components and life history reported here, pre-dispersal reproductive components of this species do not seem to be associated to life history (fruit set, seeds per fruit, seed weight, proportion of apical seeds or total seed production per plant; Braza et al., in press). Thus, pre- and post-dispersal variables are not necessarily coupled and driven by the same factors in this widespread plant. Nevertheless, this study shows that the recruitment components change from year to year to the extent that temporal fluctuation may dilute any fingerprint of the life history.

The population of the annual life form fluctuated more in time than the two perennials for seedling emergence, while it was one perennial population which fluctuated most for seedling survival. This is not a surprising pattern, since seedling emergence and survival, as well as the advantages of an early or late emergence, have been found to be highly variable within species in space and time (Battaglia 1996; Ibáñez and Schupp 2001; Gómez-Aparicio et al. 2005). Strategies to cope with temporal unpredictability are expected to be of high importance because strong temporal variation in vital rates like recruitment has important consequences for life-history evolution and population dynamics (Real 1980; Tuljapurkar 1989; Boyce et al. 2006). Under such conditions, short-lived plants like *P. coronopus* are expected to evolve risk-spreading strategies because reproduction occurs only once or twice in their lifetime (Rees 1994).

There is a large amount of literature predicting or documenting the advantages of seed dimorphism as one of such strategies in disturbed or variable environments. Different kinds of seeds may offer a

wider ecological window in terms of seed bank, delayed germination, higher tolerance to stressful conditions, or higher dispersability (see, for example, Imbert 2002; Redondo-Gómez et al. 2008). Seed dimorphism also allows populations to fit better local environments by adjusting different proportions of dimorphic seeds (Venable et al. 1987; Cheptou et al. 2008), and may have a profound effect on the life cycle and population regeneration in the successive years (Mandak and Pysek 2005).

Our results suggest two traits representing bet-hedging strategies in *P. coronopus*, which seem to be related: the distribution of seedling emergence over the season, and the production of two kinds of seeds. Both late emergence and the production of apical seeds could be interpreted as suboptimal traits. Late-emerged seedlings showed disadvantage in terms of survival compared to early emergents for all the four populations in a rainy year. Emerging late, however, could not be considered disadvantageous under a long-term perspective, given that the differential success of early- and late-emerged seedlings in a given year disappeared in the coastal population. Thus, spreading germination within a year in that case, like spreading it among several years (through a permanent seed bank), can be considered an example of adaptive bet-hedging strategies (Cohen 1966; Evans et al. 2007; Venable 2007).

According to our model that combines both kinds of seeds and their respective germination rates and emergence timing, apical seeds could constitute an important source of the late emergents even in populations where apical seeds are produced in a very reduced proportion compared to others (P-c; Braza et al., in press). Germination is a fast process in this species, given that seeds do not need a dormancy period, and a couple of days of humidity are enough to activate root emergence in basal seeds. Thus,



apical seeds could play an important role in local recruitment through delayed emergence, besides the theoretical advantages of long distance dispersal. Bet-hedging strategies, despite not being optimal in most conditions, are thought to be advantageous in some circumstances, protecting parental fitness from extremely bad years (Mathias and Kisdi 2002). In our particular case of study, however, the role of apical seeds (and therefore of late emergents) was higher in the good year than in the bad year in the perennial population where it was investigated, contributing significantly to that year's cohort.

The high unpredictability of seasonal precipitation, and the irreversible effects of droughts in the Mediterranean climate, constitutes severe ecological scenarios for seedling settlement, having dramatic consequences for short-lived herbs. This study provided evidence of the importance of bet-hedging strategies like spreading seedling emergence through time by producing dimorphic seeds, to cope with such limitations. In *P. coronopus*, an organism totally dependent on precipitation to reproduce or to simply survive, this is at least partly accomplished by increasing the potential of recruitment in favourable years instead of buffering such important process in extremely bad years.

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