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Spreading recruitment over time to cope with environmental variability

Rita Braza · María B. García

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

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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

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 mucopolysacharid 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 Straight 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^2)	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^2) 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 losts, 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 generalised 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

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

295 The germination of basal and apical seeds in the
296 hand sowing experiment was examined in terms of
297 overall rates over the study period (g_b and g_a,
298 respectively) and the proportion of seedlings (origi-
299 nating from each type of seed) that germinated late
300 (g_{bl} and g_{al}, respectively). Because, in these analyses,
301 we are only interested in the intrinsic differences of
302 dimorphic seeds, only the type of seed was consid-
303 ered as a fixed factor in the GLMMs (binomial error
304 and logit link function used), while population and
305 year were included as random factors.

Results

Overall emergence and survival

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

317 When both spatial and temporal variations were
318 included in the model, the spatial differences found
319 above disappeared (Table 2). The rate of emergence
320 was more variable across years in A-m (CV: 145%)
321 than in the other two perennials (CV for P-c and P-m:
322 74 and 83%, respectively; Fig. 1 left bottom row).
323 Seedling survival was also very variable across years
324 (Fig. 1 middle bottom row), including the possibility
325 of no survival at all in dry years (04–05 in A-m and
326 P-m). The perennial population, P-m, was the most
327 variable one for survival, with a coefficient of
328 variation of 89%, whereas A-m and P-c had values
329 of 77 and 55%, respectively.

Emergence timing and survival

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

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

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

Seed heteromorphism and emergence timing

348 Apical seeds germinated in a significantly lower
349 proportion than basal seeds, irrespective of popula-
350 tion and year ($g_a = 20\%$, $g_b = 57\%$; $N = 48$ pots;
351 $F = 46.54$; $P < 0.0001$). Only 2% of seedlings
352 originating from basal seeds appeared late in the
353 season (average of the two populations and years)
354 compared with 9% of apical seeds ($N = 44$;
355 $F = 19.09$; $P = 0.0003$).

356 To estimate the proportion of early and late
357 emergents in the field coming from basal and apical
358 seeds we used the recruitment at the P-c population
359 and the 2 years of hand sowings, which corresponded
360 to a rainy (03–04) and a dry (04–05) year (it could not
361 be estimated in the A-s population because emer-
362 gence was incomplete for the second year after
363 vandalization). The probability of early-emerging
364 seedlings to come from basal and apical seeds was
365 estimated straightforward from the proportion of each
366 kind of seed released by mother plants ($P_b = 0.92$
367 basal seeds and $P_a = 0.08$ for apical ones, Braza
368 et al. in press) and germination rates early in the
369 season (results from hand sowings each year; Fig. 3).
370 The proportion of new seedlings later in the season
371 (late emergents) coming from each type of seed,
372 however, will depend not only on the specific
373 germination rate of each kind of seed later in the
374 season each year (for example $g_{bl03–04}$ would corre-
375 spond to the germination of basal seeds late in the
376 03–04 year), but also on their availability in the soil
377 after early germination ($1 - g_{be03–04}$). According to
378 that, the vast majority of seedlings found in the field
379 after the first autumn rains come from basal seeds
380 (95–98%, depending on the year; Fig. 3). Later in the
381 season, however, the source of new emerged

Table 2 Results of the GLMMs

	Spatial variability					Temporal variability				
	n	Fixed factors	F	Random effects	Variance estimate	n	Fixed factors	F	Random effects	Variance estimate
Seedling emergence	203	Population	11.07***	Plot	0.5 (0.21)	720	Population	0.82	Year	1.15 (0.62)
				Quadrat	0.39 (0.06)				Plot	0.68 (0.17)
									Quadrat	0.53 (0.05)
Seedling survival	176	Population	30.83***	Plot	0.42 (0.19)	536	Population	0.75	Year	4.93 (2.9)
				Quadrat	0.54 (0.14)				Plot	0.87 (0.31)
									Quadrat	0.83 (0.17)
Late emergence	172	Population	4.37*	Plot	0.14 (0.08)	552	Population	1.46	Year	1.36 (0.79)
				Quadrat	0.49 (0.13)				Plot	0.68 (0.29)
									Quadrat	1.56 (0.2)
Survival of late emergents	841	Emergence time	40.45***	Plot	1.05 (0.49)	266	Emergence time	1.67	Year	1.04 (1.28)
		Population	17.77***	Quadrat	0.39 (0.24)				Plot	1.18 (0.71)
		Interaction	0.2						Quadrat	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 levesl are shown (* 0.05 < P < 0.01; *** P < 0.0001). For random effects, the covariance parameter estimate and standard error are shown in *parenthesis*
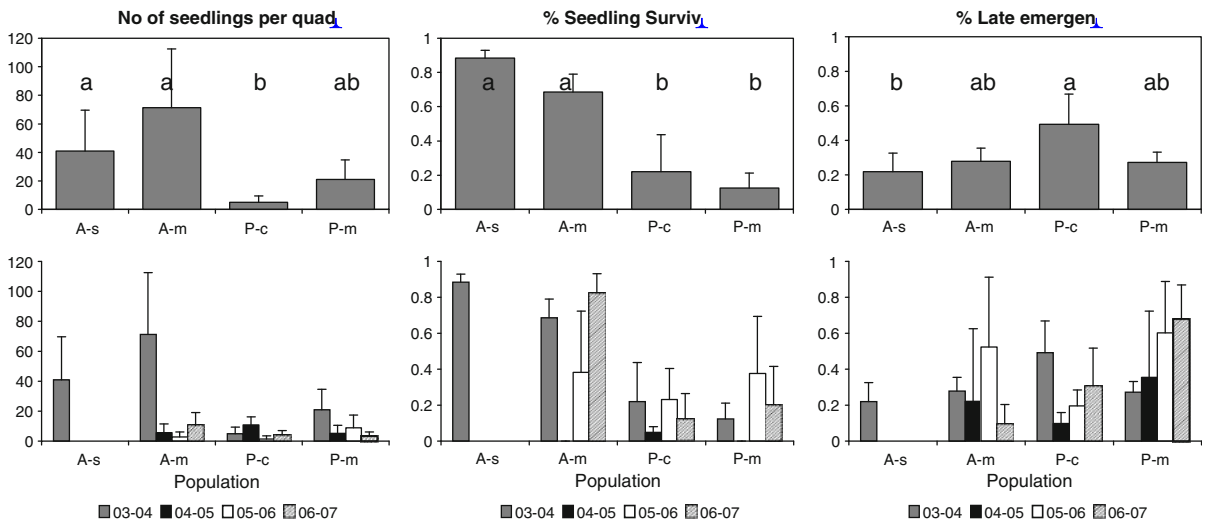
Fig. 1 Components of recruitment in the four populations of *P. coronopus* studied (*A-s* annual shrubland, *A-m* annual marsh, *P-c* perennial coast, *P-m* perennial mountain) in the rainy year (2003–2004; *upper row* of histograms; different *letters* indicate post-hoc significant differences among populations after Bonferroni correction), and across 4 years (*bottom row*). *Lines on bars* correspond to standard deviations of the means
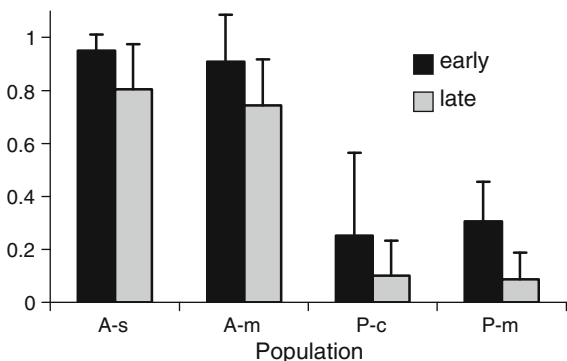

Fig. 2 Survival of early- and late-emerged seedlings in the four populations of *P. coronopus* studied (*A-s* annual shrubland, *A-m* annual marsh, *P-c* perennial coast, *P-m* perennial mountain) in a rainy year (2003–2004)

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)
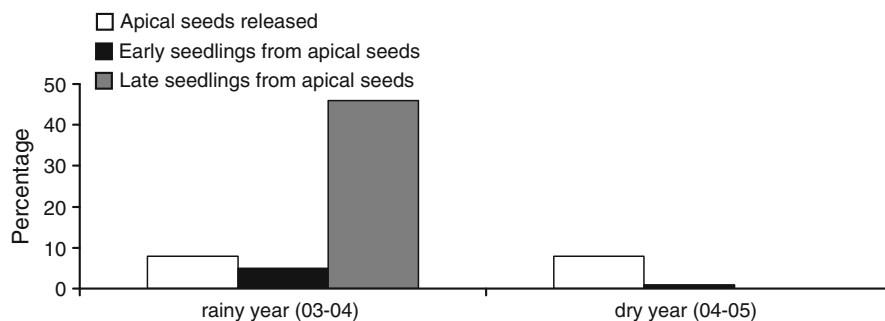
419 same period as in annuals, but also (mainly) during
420 the summer, increasing survival differences between
421 annuals and perennials. In contrast to the association
422 between recruitment components and life history
423 reported here, pre-dispersal reproductive components
424 of this species do not seem to be associated to life
425 history (fruit set, seeds per fruit, seed weight,
426 proportion of apical seeds or total seed production
427 per plant; Braza et al., in press). Thus, pre- and post-
428 dispersal variables are not necessarily coupled and
429 driven by the same factors in this widespread plant.
430 Nevertheless, this study shows that the recruitment
431 components change from year to year to the extent
432 that temporal fluctuation may dilute any fingerprint of
433 the life history.
434 The population of the annual life form fluctuated
435 more in time than the two perennials for seedling
436 emergence, while it was one perennial population
437 which fluctuated most for seedling survival. This is
438 not a surprising pattern, since seedling emergence
439 and survival, as well as the advantages of an early or
440 late emergence, have been found to be highly variable
441 within species in space and time (Battaglia 1996;
442 Ibáñez and Schupp 2001; Gómez-Aparicio et al.
443 2005). Strategies to cope with temporal unpredict-
444 ability are expected to be of high importance because
445 strong temporal variation in vital rates like recruit-
446 ment has important consequences for life-history
447 evolution and population dynamics (Real 1980;
448 Tuljapurkar 1989; Boyce et al. 2006). Under such
449 conditions, short-lived plants like *P. coronopus* are
450 expected to evolve risk-spreading strategies because
451 reproduction occurs only once or twice in their
452 lifetime (Rees 1994).
453 There is a large amount of literature predicting or
454 documenting the advantages of seed dimorphism as
455 one of such strategies in disturbed or variable
456 environments. Different kinds of seeds may offer a

457 wider ecological window in terms of seed bank,
458 delayed germination, higher tolerance to stressful
459 conditions, or higher dispersability (see, for example,
460 Imbert 2002; Redondo-Gómez et al. 2008). Seed
461 dimorphism also allows populations to fit better local
462 environments by adjusting different proportions of
463 dimorphic seeds (Venable et al. 1987; Cheptou et al.
464 2008), and may have a profound effect on the life
465 cycle and population regeneration in the successive
466 years (Mandak and Pysek 2005).
467 Our results suggest two traits representing bet-
468 hedging strategies in *P. coronopus*, which seem to be
469 related: the distribution of seedling emergence over
470 the season, and the production of two kinds of seeds.
471 Both late emergence and the production of apical
472 seeds could be interpreted as suboptimal traits. Late-
473 emerged seedlings showed disadvantage in terms of
474 survival compared to early emergents for all the four
475 populations in a rainy year. Emerging late, however,
476 could not be considered disadvantageous under a
477 long-term perspective, given that the differential
478 success of early- and late-emerged seedlings in a
479 given year disappeared in the coastal population.
480 Thus, spreading germination within a year in that
481 case, like spreading it among several years (through a
482 permanent seed bank), can be considered an example
483 of adaptive bet-hedging strategies (Cohen 1966;
484 Evans et al. 2007; Venable 2007).
485 According to our model that combines both kinds
486 of seeds and their respective germination rates and
487 emergence timing, apical seeds could constitute an
488 important source of the late emergents even in
489 populations where apical seeds are produced in a
490 very reduced proportion compared to others (P-c;
491 Braza et al., in press). Germination is a fast process in
492 this species, given that seeds do not need a dormancy
493 period, and a couple of days of humidity are enough
494 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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