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Original article

Natural variation of fecundity components in a widespread plant with dimorphic seeds

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ABSTRACT

The number and size of seeds are the basis of the quantity and quality components of female reproductive fitness in plants, playing a central role in the evolutionary ecology of life history diversification. In this study we show and analyze the natural variability of several fecundity variables (fruit set, seed production per fruit, seed size, total seed production per plant, and proportion of small seeds) in *Plantago coronopus*, a widespread, short-lived herb with dimorphic seeds. The structure of such variability was examined at the individual, population (eight locations with different environments within the same region), and life history levels (annual vs perennial), and correlated to soil fertility. There was no divergence associated to the life history for any of the variables studied. Total seed production (the quantity component of female fitness) was correlated with maternal resources, while the size of the large mucilaginous, basal seeds, and the proportion of the small apical seeds (quality component) were more associated to environmental resources. Thus, internal and external resources shape different fitness components, maximizing seed production, and fitting the size and proportion of different kind of seeds to local conditions irrespective of life history. *P. coronopus* illustrates the versatility of short-lived widespread plants to combine fecundity traits in a flexible manner, in order to increase fitness at each of the many possible habitats they occupy over heterogeneous environments.

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1. Introduction

The reproductive success of any organism depends on the number and long-term success of its offspring, that is, the quantity and quality components of reproductive fitness. Resource limitation, however, creates trade offs between those fitness components that might be solved in different ways depending on the selective pressures dominating at different ecological scenarios (Roff, 1992).

In plants, the most important female fitness components are seed number and seed size. Seed size is considered a good estimator of the quality and future success of offspring because many studies have demonstrated its positive relationship with germination rates, seedling survival, or establishment (e.g. Jakobsson and Eriksson, 2000; Moles and Westoby, 2004). Life history theory predicts a unique optimal seed size for each species in response to a set of selective pressures (Smith and Fretwell, 1974; Harper, 1977). There is, however, abundant empirical evidence

showing that seed size, as well as seed number, can vary considerably among and within individuals, populations, and species (Michaels et al., 1988; Méndez, 1997; Halpern, 2005). The effect of the mother plant size on the number of offspring has been widely documented (Herrera, 1991; Sletvold, 2002), while the causes for intraspecific variation in seed size seem to be more complex. Positional effects within plants, branches, inflorescences and flowers, and among individual differences in genetic constitution or resource availability, are some plausible causes (McGinley et al., 1987; Venable, 1992; Platenkamp and Shaw, 1993).

Seed size may also be related to the local environment. For example, it has been proposed that larger seeds would be more advantageous in shaded, dry, poor places, or under high competition. They would result in larger seedlings capable of getting resources faster, competing better, and being more resilient to limiting environmental factors such as drought or herbivory (Westoby et al., 1992; Leishman et al., 2000). It has also been suggested that producing seeds of different sizes can be an evolutionary stable strategy in spatially or temporally heterogeneous habitats (Geritz, 1995), with the smaller seeds being more successful in good places or years, and larger seeds in bad sites. A particular case of intra-individual variability in seed size is seed

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heteromorphism: two or more discrete types of seeds (in size, shape or physiology) are produced by the same mother plant, each one usually with different dispersal capacity and germination requirements (Venable, 1985). It is considered a bet-hedging strategy because it reduces the risk of parental investment: offspring are distributed in space (through differential dispersal) and/or time (differential germination timing), covering a wider array of possible environmental scenarios (Imbert, 2002).

Variability in reproductive components has also been related to different life history strategies. Interspecific comparisons have shown that plants with longer reproductive life spans tend to have larger seeds (Silvertown, 1981; Moles et al., 2004), supporting the classical idea that short-lived plants (*r* strategists) tend to produce higher number of smaller seeds than long lived plants (Piánka, 1970). Because annuals occur more often in variable and unpredictable habitats, it has also been proposed that seed heteromorphism, as a form of bet-hedging, should be more common in annual than in perennial plants (Mandák, 1997).

These evolutionary predictions, and their relationship to environmental variables, are best tested in species occurring at large geographical areas or heterogeneous ecological scenarios. In this paper we study the intraspecific natural variation of a number of female reproductive components (fruit set, seeds per fruit, seed size, total seed production per plant, and proportion of different kind of seeds) in a widespread short-lived plant species with annual and perennial forms and dimorphic seeds, *Plantago coronopus* L. (buck's horn plantain, Plantaginaceae). Besides its broad geographic range, it occurs in very different habitats, including roadsides, natural marshlands, dry sand dunes, and moist mountain and coastal meadows. Its variability in life history and occurrence in different habitats provides a unique opportunity to explore the sources of natural variation in fecundity components. Ascertaining these patterns are necessary for further exploration on the causes and consequences of fecundity patterns, and ultimately, for determining selective scenarios and their adaptive value through proper experimental designs.

We test if, as expected, bigger seeds are associated with longer life spans, or places with lower resources or prompting higher competition. Likewise, we expect a more pronounced seed heteromorphism in annual life form, because iteroparity already constitutes a bet-hedging strategy in perennials. Our ultimate goal is to explore which factors are molding seed number and size in a short-lived widespread species occurring in such a variety of habitats, which in turn are related to its capacity to behave more as a colonizer or a locally adapted plant.

2. Materials and methods

2.1. Study species

P. coronopus is a very polymorphic species that occurs from northern Morocco and the Iberian Peninsula to East Asia, and reaches the North of Europe through a narrow strip along the Atlantic coast (Hultén and Fries, 1986). The subspecies *coronopus*, the one used in this study, is the most widespread as it occurs throughout most of the geographic range. There are annual and perennial forms in separate populations (Chater and Cartier, 1976).

Individual plants produce one to a few rosettes, and reproductive individuals bear several inflorescences with wind-pollinated flowers densely arranged in spikes. Each single fruit may contain up to 5 seeds: four are large, cylindrical-shaped, and located in the basal part of the ovary, while the remaining seed (not always present) is smaller, more angulated, and located in the upper part of the ovary (separated from the basal ones by a thin layer of placental tissue;

Dowling, 1933). Besides differences in the position, abundance, size and shape, basal seeds have a thicker coat than apical ones. In contact with moisture, the coat becomes a mucilaginous matrix that sticks the seed to soil surface, helping roots to penetrate into the soil (Dowling, 1933; Schat, 1981). By contrast, apical seeds have a much thinner coat, and seem to be released together with the capsule lid, which could assist them to either float or fly further away (Dowling, 1933). Such dimorphism offers the advantage of both antitelechory (large, mucilaginous seeds when moistened; mixospermy) and long-distance dispersal (apical seeds).

2.2. Study populations

Eight populations (four annuals, four perennials) were selected in the southern part of the Iberian Peninsula, an area of Mediterranean climate where *P. coronopus* grows in different habitats (Fig. 1, Table 1). The climate of the region is typically Mediterranean: mild mean monthly temperatures, rainy autumns and winters, four months of summer drought, and an important interannual variability in precipitation. There are, however, important within regional differences in annual mean rainfall and seasonal variation in monthly mean and extreme temperatures (populations in Table 1 constitute an example of such variability). This variation is usually linked to elevation, and distance from the sea. One of the studied populations, for example, is located in the forest gaps of a community rich in relict species, with a particularly wet microclimate where fogs are frequent because of its position in the mountain facing the Strait of Gibraltar (P-m, see below).

Perennial populations are mostly located on sandy soils, in the coastal dunes or close to the sea (0–12 km away; Fig. 1). Two populations were on bare poor soils (P-c and P-c2), and another two in habitats where competition should be strong (P-w and P-m). Annual populations are located more inland (Fig. 1), on sandy (A-s) and clay (A-r, A-m, A-m2) soils with variable organic matter content, and salinity (Table 1). They suffer lower minimum and higher maximum average temperatures, and lower precipitation, than perennial populations. Smaller individuals, and higher plant densities, are typical of annual compared to perennial populations (Table 1).

2.3. Sampling

In each population, 20–30 inflorescences were collected at random in the fruiting period (spring for annuals, summer for perennials), each one from a different plant, and separated at least 1 m. Each inflorescence was examined under the binocular microscope, and the total number of flowers and fruits was counted and used to calculate fruit set as the ratio number of fruits : initial number of flowers. In a sample of about 30 fruits evenly distributed along the spike, ranging from 10% to 100% of total number in each inflorescence (very large to very small inflorescences respectively), the number of basal and apical seeds was counted, and the proportion of apical seeds calculated. The average weight of basal seeds was determined from sets of 10–30 seeds gathered in each of 10–25 plants (depending on seed availability from each individual plant; some mothers did not produce enough small seeds as to get a minimum of 10 to be weighted).

To account for the effect of maternal resources on the reproductive components, the entire plants were collected in a subsample of four populations representative of the two life histories and contrasted habitats (A-s, A-m, P-c, P-m). Rosettes were dried at 60 °C until constant weight, and subsequently weighed to include plant biomass as a covariable in our analysis. The number of inflorescences, the length of the spikes, and the

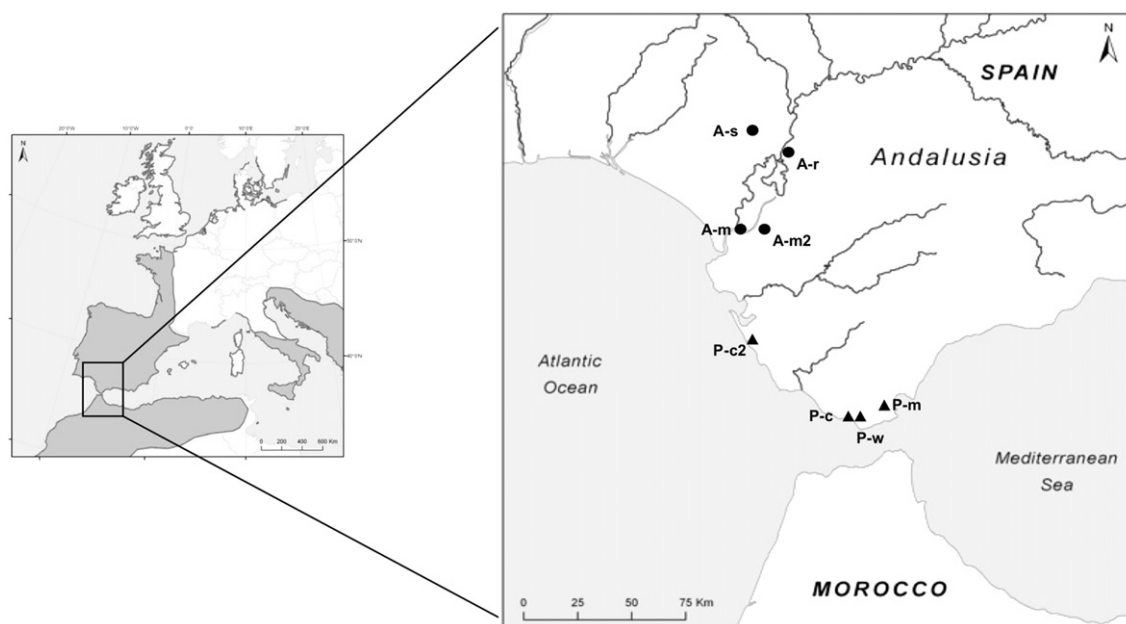


Fig. 1. Location of the eight populations of *Plantago coronopus*, four annual (A-) and four perennial (P-), studied in southern Spain. Shaded area: overall distribution in Europe and N Africa.

average fruit set and seed production per fruit, were used to estimate the total output of seeds per individual plant.

Finally, 5 cores of soil (10 cm deep) were collected in each population studied, to analyze electric conductivity (ratio 1:5 of soil in water), percentage of organic matter, and Nitrogen (Headnes, 1984). The content of cores was pooled before conducting soil analyses, to get one value per population.

2.4. Data analysis

The effect of life history on the reproductive components (fruit set, number of seeds per fruit, proportion of apical seeds, and seed weight) was analyzed by fitting generalized linear mixed models (GLMMs). Life history was considered as a fixed factor, and populations and individual plants (nested within populations) as random effects. Degrees of freedom were estimated using the Satterthwaite's method. Variance estimates of random effects indicate the amount of variability of the reproductive components at each level (population or individual; Littell et al., 1996) for comparison within each life history class (annual, perennial), the factor of our interest. We used the eight populations for this purpose.

The effect of individual biomass in all the same reproductive components plus the total seed production per plant were also analyzed with a GLMM, adding the log-plant biomass as

a covariable in the subset of four populations. The slope of the regression for total seed production against plant biomass was also calculated for each population.

In both GLMMs we used the error distributions and link functions that best fitted our data: binomial distributions and logit link functions for fruit set and proportion of apical seeds, and normal distributions and identity link functions for average number of seeds per fruit, total number of seeds per plant (log transformed) and weight of basal seeds. All the models were performed using the GLIMMIX procedure in SAS 9.2.

Differences between life histories for the three soil properties measured were tested by one-way Anova. The relationship between population average values of reproductive components and soil variables (organic matter, Nitrogen content) in the eight locations examined, was tested by Spearman correlation.

3. Results

Fruit set was high in all the populations examined, ranging between 75% (P-m) and 100% (A-r; see also Fig. 2). No significant differences were found between life histories in the proportion of flowers setting fruit (Table 2). Mean number of seeds per fruit ranged between 2.3 (P-c) and 3.8 (A-m2), although the difference

Table 1

Location and environmental characteristics of the studied populations. Density was calculated from the content of plants in a minimum of 4 square meters. Climatic data have been taken from the Digital Climatic Atlas (<http://opengis.uab.es/wms/iberia/mms/index.htm>). See text for further details on how on soil properties were determined.

Population	Life history	Location (m.a.s.l.)	Habitat	Plant density (m ²)	Average biomass s.d. of adult plant (gr)	Min-Max yearly temperature (°C)	Yearly precipitation	Main soil component	% Organic matter in soil	% Organic Nitrogen in soil	Conductivity mS/cm
A-s	Annual	37°15'N 6°13'W (42)	Shurbland	3614	0.064 ± 0.12	11–25	558	sand	0.75	0.036	0.04
A-r	Annual	37°11'N 6°04'W (3)	rivershade			12–24	582	clay	2.42	0.158	0.021
A-m	Annual	36°53'N 6°17'W (2)	marsh	1560	0.097 ± 0.13	12–24	578	clay	2.46	0.193	2.99
A-m2	Annual	36°56'N 6°08'W (1)	marsh			12–24	560	clay	1.91	0.155	1.71
P-c	Perennial	36°02'N 5°38'W (1)	coastal dunes	20	3.926 ± 2.97	15–20	845	sand	0.09	0.005	0.04
P-c2	Perennial	36°25'N 6°13'W (0)	coastal dunes			14–22	622	sand	0.41	0.015	0.08
P-w	Perennial	36°02'N 5°38'W (2)	wetland			15–20	845	sand	1.88	0.103	0.15
P-m	Perennial	36°06'N 5°32'W (730)	foggy mountain	107	0.834 ± 0.69	11–19	1045	sand	2.92	0.183	0.24

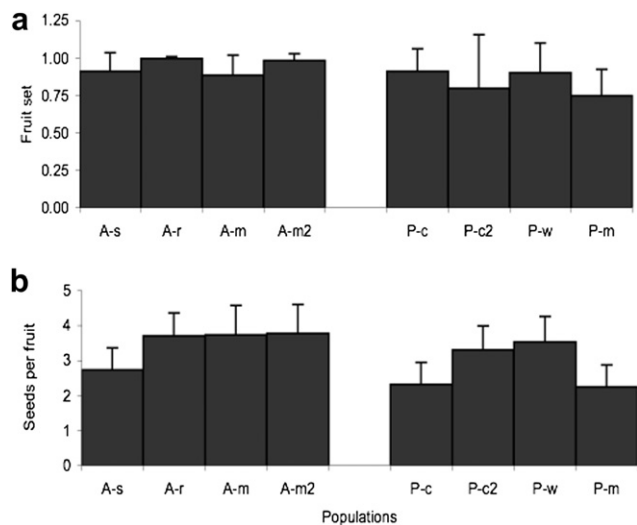


Fig. 2. Reproductive success of *Plantago coronopus* in the studied populations, in terms of a) fruit set (fruit to flower ratio) and b) average number of seeds per fruit. Lines on bars correspond to ± 1 s.d.; A: annuals, P: perennials.

between annuals and perennials (Fig. 2) was not statistically significant either (Table 2).

All the populations examined produced apical seeds, ranging from 9.0% (P-c) to 21.0% (P-m) of the total number of seeds produced. There was a negative relationship between the size of basal seeds and the average number of seeds per fruit ($R^2 = 0.52$; $P = 0.04$; $N = 8$, population average values used). Annuals had slightly smaller basal seeds and produced a lower proportion of apical seeds (Fig. 3), but differences between life histories were not significant in any case (Table 2).

The effect of plant biomass on reproductive fitness components was tested in a sample of two annual and two perennial populations. A negative effect was found on the proportion of apical seeds (independently of the life history; Table 2). Plant biomass had no significant effect neither on fruit set nor on average number of seeds per fruit, however it was the most important factor explaining total seed production (Table 2). The amount of seeds per plant of annuals (average \pm s.d.: 257 ± 596 and 902 ± 1148 in A-s and A-m respectively) and perennials (2185 ± 2051 and 2984 ± 3694 in P-c and P-m respectively) was not significantly different (Table 2). Nevertheless, the relationship between biomass and total seed production (the slope of the regression, β coefficient [95% CI]) was much higher in annuals (A-s: $12.3 [10.0–14.1]$, A-m: $9.0 [6.5–11.4]$) than perennials (P-c: $1.1 [0.7–1.5]$, P-m: $3.4 [2.6–4.1]$).

Table 2

Results of the generalized linear mixed models (GLMM) for the reproductive variables studied. For fixed factors, the *F* statistics and degrees of freedom (numerator and denominator) are shown; the sign indicates the direction of significant effects. For random effects, values correspond to the covariance parameter estimate and standard error (in brackets). Significance levels: **: $0.01 < p < 0.001$; ***: $p < 0.001$.

		Fruit set	Seeds per fruit	Total seeds per plant	Seed weight	Proportion of apical seeds
Regional sampling 8 populations	<i>Fixed factors</i>					
	Life history	1.79 _{1,5,73}	2.31 _{1,6,06}		0.22 _{1,6,09}	0.11 _{1,6,26}
	<i>Random effects</i>					
	Pops	3.84 (2.45)	0.33 (0.20)		0.004 (0.002)	0.08 (0.05)
Plants	5.07 (0.62)	0.10 (0.05)		0.0007 (0.0003)	0.19 (0.06)	
Deeper sampling 4 populations	<i>Fixed factors</i>					
	Life history	1.14 _{1,2,12}	0.35 _{1,2,05}	0.08 _{1,2,11}	0.54 _{1,2,03}	1.20 _{1,2,22}
	Biomass	0 _{1,7,54}	1.93 _{1,109,6}	(+) 53.93 _{1,110} ***	0.68 _{1,93,1}	(-) 9.98 _{1,45,66} **
	<i>Random effects</i>					
Pops	0.02 (0.17)	0.92 (0.94)	1.50 (1.55)	0.01 (0.01)	0.17 (0.19)	
Plants	1.90 (0.35)	0.0004 (0.05)	0.26 (0.13)	0.0004 (0.0003)	0.007 (0.05)	

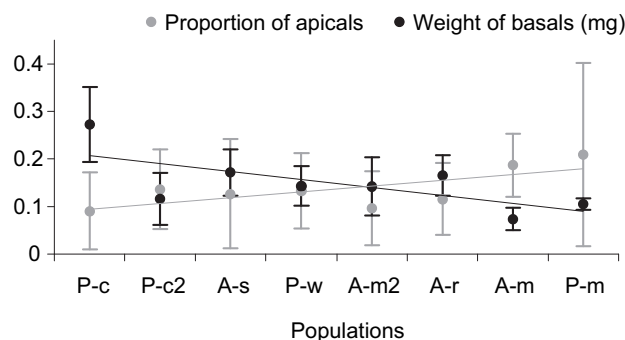


Fig. 3. Proportion of apical seeds per plant (grey dots), and average weight of basal seeds, the most abundant within fruits (black dots). A: annuals, P: perennials. Lines on bars correspond to ± 1 s.d. Populations on the X axis follow an increasing gradient soil organic matter.

The variance component at the individual level was higher than at the population level for fruit set. For the remaining variables examined (seeds per fruit, seeds per plant, seed weight, and proportion of apical seeds), the highest variance component was found at the population level (random effects, Table 2).

Life history groups did not significantly differ with respect to any of the three soil properties examined (one-way ANOVA for Organic matter, Nitrogen, and conductivity; $p > 0.12$ always). The content of organic matter in soil (similar results were obtained for N) was marginally significantly correlated to the size of basal seeds (Spearman $\rho = -0.67$; $P = 0.07$; $N = 8$), and proportion of apical seeds (Spearman $\rho = -0.69$, $P = 0.06$, $N = 8$).

4. Discussion

Our study showed a wide variability of different components of female fecundity in a small area of a species which spans a huge latitudinal and longitudinal range. This may help to understand the ability of *P. coronopus* to settle down in heterogeneous environments over large areas, and also its success to get established as an alien in other continents (see for example <http://plants.usda.gov/java/profile?symbol=PLCO3>; <http://florabase.dec.wa.gov.au/browse/profile/7297>).

4.1. Fecundity patterns and life history

The lack of clear divergences associated to the life history suggests that the lifespan has little to do with the reproductive performance of this plant (except obviously for the number of reproductive events and therefore the lifetime seed production, not

explored in this study). The highest amount of variability in the reproductive components examined in *P. coronopus* is usually held among populations, and this population differentiation seems to respond better to some environmental factors than to the annual or perennial way of life.

The lack of differences between life histories for fruit set fits well previous findings reported in the extensive review of Sutherland (1986), who could not find that annuals were more successful than perennials. The number of seeds per fruit, and the size of seeds, did not differ between life histories either, but a trade off between both variables emerged at the population level. This result is similar to the negative correlation between seed weight and number of seeds per capsule found in a dataset of 30 *Plantago* species (Primack, 1978). Several studies have also shown a similar trade off when exploring the relationship between seed size and number within individuals (Lalonde and Roitberg, 1989; Vaughton and Ramsey, 1998), life forms (Shipley and Dion, 1992), or communities (Jakobsson and Eriksson, 2000). Our study showed that such trade off operates not only at the genus, species or individual level, but also at the population level within species, thus providing a mechanistic explanation for those multi-scale patterns.

4.2. Seed heteromorphism

Larger basal seeds are produced in poor, sandy soils (A-s, P-c), where they are expected to have a clear advantage by producing larger roots able to get faster to water table and other scarce resources (Westoby et al., 1992). These places are also the ones where lower proportion of apical seeds occurs. The thicker mucilaginous coat of basal seeds (the most abundant ones) constitutes an antitelechory system to assist germination (Gutterman and Shem-Tov, 1996), which should play a central role in dry soils with scarce resources. On the other hand, smaller basal seeds and a higher proportion of apical seeds are found in richer soils (A-m) or more humid places (P-m, higher rainfall, Table 1). Lesser reserves stored in basal seeds, and a thinner mucilaginous coat of apical ones, would make seeds more dependent on humidity and/or other soil resources to germinate and get established.

The germination rate of basal seeds is higher than the apical ones (from *in situ* hand sowings, Braza and García, in press). On the other hand, Koelewijn and Van Damme (2005) demonstrated that smaller seeds of *P. coronopus* produced smaller seedlings in the glasshouse, and tended to germinate and survive to a lesser extent under the same field conditions. Taken together, these results suggest that the population differentiation responds to the trade off of producing as many seeds as possible, but assuring first their long-term viability (larger seeds in poor places), which probably constrains the number of apical seeds developed in ovaries. The type and weight of seeds in this species seem to be controlled primarily by local external factors, not necessarily those determining the kind of life history possible at each place.

The ecological pattern combining seed dimorphism and mixospermy found in *P. coronopus* agrees with findings in other plants. Higher amounts of slime have been found in populations of other dimorphic species of Asteraceae occurring in drier habitats (Kreitschitz and Vallès, 2007). Also, in some heteromorphic or amphicarpic species, a higher abundance of the larger morph has been recorded in unfavourable places or years (Koller and Roth, 1964; Baker and O'Dowd, 1982; Mandák and Pyšek, 1999). Seed heteromorphism is a feature typical of unpredictable environments and disturbed habitats (Imbert, 2002), where the existence of two or more morphs offers a larger range of opportunities for germination, seedling survival, and dispersal (Imbert, 2002; El-Keblawy, 2003; Carter and Ungar, 2003; Mazer and Lowry, 2003; Dyer, 2004; Brändel, 2007; Wei et al., 2007).

The amplitude of the ecological window provided by two seed morphs can also be adjusted through selection by regulating the abundance of each one. In a dimorphic short-lived compositae producing achenes with and without a specialized dispersal mechanism (*Crepis sancta*), the observed spatial pattern seems to be the result of rapid evolution against the less efficient morph for wind dispersal in patches originated by habitat fragmentation (Cheptou et al., 2008). In *P. coronopus*, the size of basal seeds, and the proportion of apical seeds, are related variables that seem to be responding to selective forces to adjust better their different functionality to external resources (soil richness and/or water availability). Phenotypes maximizing fitness at each local environment through their quality component (seed size and seed dimorphism), would have been favoured over time, a sign of local adaptation. Further experimental work will elucidate the existence of such operating system, but the patterns shown point out to this possibility.

4.3. Quantitative component of fitness

Likewise the quality component of fitness, the quantity component does not seem to be driven by life history. Annuals tend to be smaller than perennials but have a higher investment in seeds than perennials (deeper slope for the total seed crop as biomass increases). The enormous variety of plant sizes occurring within all populations of *P. coronopus* does not probably allow to find significant differences of seed production between both life histories. Maternal resources constitute the best predictor of seed output, and among-population variability is the main source of variation for total seed production across the contrasted life histories and habitats examined. Thus, this widespread species holds a high variability of sizes independently of the kind of life cycle, producing as many seeds as possible according to the biomass of each individual plant. Our observations along the whole latitudinal range of the species over the years suggest that *P. coronopus* is subjected to metapopulation dynamics, especially in disturbed places and extreme environmental conditions. High variability within and among populations seems a good premise for a mobile or colonizing species immersed in a metapopulation system, where plasticity should be favoured over local adaptation (Sultan and Spencer, 2002).

4.4. Concluding remarks

This study has shown that, irrespective of life history, maternal and environmental resources are the factors best explaining natural variability in number and size (in terms of weight of basal seeds, and frequency of apical ones) of offspring in *P. coronopus*, contributing in different ways to shape the dynamics of a common and generalist plant species. Maternal and environmental resources modulate different aspects of the quantity and quality components of fecundity. This combination of drivers, together with the capacity to make short (annual) or longer (perennial) life cycles at different environments, provides a widespread plant with the necessary flexibility to maximize reproductive output at each of the many possible habitats it occupies along its wide geographic range, resulting in an overwhelming variation of reproductive traits at all levels (individuals, populations, life histories, and habitats). Documenting this variation, and its potential evolutionary outcome, is a requisite for predicting how species would accommodate a scenario of rapid global changes, for which these kind of species could become good monitors.

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