

Intrinsic and extrinsic drivers of recruitment across the distribution range of a seed-dimorphic herb

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Received: 16 November 2016 / Accepted: 1 February 2017 / Published online: 9 February 2017
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Abstract Recruitment of new individuals, through germination and seedling survival, is a key process for short-lived plants. Here, we analyzed intraspecific variation in recruitment across the latitudinal range of *Plantago coronopus*, a widespread herb that produces both large basal seeds with a mucilaginous coat and small apical seeds without coat. We experimentally tested the effects of seed traits and water availability on recruitment, by using seeds from a wide environmental stress gradient from N Africa to N Europe. Our experiments were carried out in controlled environmental conditions and in dunes where the species naturally occurs. Water shortage decreased seed germination and seedling survival for all populations, showing the importance of water supply for *P. coronopus*. Basal seeds showed higher and faster germination rates than apical seeds. Since among-population variation in seed mass was not related to potential germination rate, it is the mucilaginous coat rather than size difference that likely drives the

differential success between seed morphs. Seed mass positively affected seedling survival instead, but only in controlled conditions with regular water supply. An experiment in a dune showed indeed that the highest survival corresponded to the local population and not the one with the largest seeds. Our results demonstrate that both intrinsic and extrinsic factors drive inter-population variation in the early life stages of this short-lived plant, allowing it to adapt across the environmentally heterogeneous distribution range. Gathering information on intraspecific variation in recruitment-related traits will help us to understand and predict plant responses in a context of climatic change.

Keywords Environmental stress · Intraspecific variation · Germination · Mixospermy · Seedling survival · Seed size

Introduction

Intraspecific variation in key life-history traits and vital rates is receiving growing attention, as it may increase species niche width, alter species interactions, and affect adaptation to changing environments (Bolnick et al. 2011; Doak and Morris 2010; Vilellas et al. 2015). In plants with short life cycles, where individual fitness relies to a large extent on a single or few successful reproductive events, seed germination, emergence timing, and seedling survival constitute some of the most critical processes (van Groenendael

Communicated by Thomas A. Nagel.

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and Slim 1988; Silvertown et al. 1996; Picó et al. 2003; Verdú and Traveset 2005). Due to its key role in plant performance, recruitment is expected to vary among populations as a consequence of environmental heterogeneity. In widespread species, where environmental conditions may vary geographically, the necessary recruitment for population persistence will depend on the successful combination of fecundity, germination, and seedling survival at each particular location across the species distribution range. Many studies have analyzed variation in seed and seedling performance across taxa (e.g., Jurado and Westoby 1992; Jakobsson and Eriksson 2000; Pivatto et al. 2014), or within populations in one or more species (e.g., Vaughton and Ramsey 2001; Baraloto et al. 2005; Lönnberg and Eriksson 2013). However, information about recruitment traits in multiple populations across significant parts of species ranges is less frequent (Murray et al. 2004; Yakimowski and Eckert 2007; De Frenne et al. 2009). Patterns of among-population variation in critical recruitment traits remain indeed poorly known, even though such variation may increase species resilience and ultimately reduce the risk of extinction in the face of environmental change (Cochrane et al. 2015).

Besides the effects of environmental conditions, seed mass has often been investigated as one of the main drivers for germination and seedling performance. Some studies across and within species have found, in general, positive effects of seed mass on plant performance in these early processes of the life cycle (Westoby et al. 1992; Chapin et al. 1993; Lönnberg and Eriksson 2013), but others did not find consistent patterns (e.g., Larson et al. 2016). Also, Moles and Westoby (2006) argued that early advantages of larger seeds may dilute in later life stages. On the other hand, other characteristics apart from seed size, such as seed shape or coat traits, may have an important role in early plant performance (Harper and Benton 1966). In this context, species with heteromorphic seeds provide an interesting case of study. The presence of seeds with different characteristics gives plants an opportunity to overcome possible limitations to recruitment associated with unpredictable, stochastic environmental conditions (Imbert 2002), such as ruderal or highly variable habitats (Yang et al. 2012).

In this study, we experimentally analyze the variation in recruitment in multiple populations across the latitudinal range of the widespread herb *Plantago*

coronopus. This species is a common, short-lived plant in North Africa and Europe, showing high variability among populations in life-history traits and demographic rates at different spatial scales (Waite and Hutchings 1982; Braza et al. 2010; Villellas et al. 2013). In addition, *P. coronopus* shows seed dimorphism (whereby fruits produce large basal and small apical seeds) combined with mixospermy (presenting a mucilaginous coat, but only in basal seeds; Dowling 1933). A previous study showed large effects of water and nutrient stress on seed traits and seed production across the species latitudinal range (Villellas and García 2013), mainly by increasing the abundance, size, and mucilage production of basal seeds. Additional work on *P. coronopus* has shown the influence of those seed traits on posterior germination and seedling survival, such as positive effects of seed mass for plants emerging from basal seeds (Koelewijn and Van Damme 2005), or higher germination rates in basal than in apical seeds (Schat 1981; Braza and García 2011), but results were limited to local or regional scales. Our goal here is to analyze spatial variability in recruitment at a continental scale in response to water stress, evaluating the potential intrinsic and extrinsic factors driving each recruitment component.

More specifically, we first looked for differences in germination between dimorphic seeds, and between experimental treatments with different levels of water availability. We expected to find higher performance in basal than in apical seeds across the whole environmental and geographical range. Second, for the (most abundant) basal seed type, we explored whether the variability in seed size recorded across the species latitudinal range affects germination and seedling survival under different levels of water supply. Our null hypothesis was that seed size has a general positive effect on individual performance. Finally, we searched for differences in seedling survival between the local and foreign populations in a transplant experiment carried out in a sand dune, with the expectation of the highest persistence in the local population.

Materials and methods

Study species

Plantago coronopus L. (buck's horn plantain, Plantaginaceae) is a short-lived herb with a variable

lifespan, from 1 (annual) to 5 yr. It is common around the Mediterranean Basin and also spreads from North Africa to NW Europe, mainly along the Atlantic coast (Hultén and Fries 1986; Fig. 1), occurring in a variety of habitats like sand dunes, cliffs, shrublands, or human-disturbed areas. This study is restricted to the most common subspecies *Plantago coronopus* ssp. *coronopus*, which can be distinguished by the morphology of the bracts (Chater and Cartier 1976), and which will hereafter be referred to as *P. coronopus*.

Each individual produces several spikes with wind-pollinated flowers. Each fruit produces in turn two types of seeds in variable number: up to four large basal seeds, and one or no small apical seeds. Basal seeds further differentiate morphologically and functionally from apical ones by (i) possessing a mucilaginous coat that facilitates water absorption (Dowling

1933) and (ii) showing faster and higher germination rates (Schat 1981; Braza and García 2011). Thus, basal seeds seem to perform better than apical ones in habitats or situations of low water or resource supply. Seed germination mainly occurs in autumn, but a small percentage may take place later in spring, both for the basal and apical morphs (Braza and García 2011).

Seed collection and experiments

Seeds were collected from nine populations across most of the latitudinal range of *P. coronopus*, from North Africa to North Europe (Table 1; Fig. 1). All populations contained thousands of individuals. In each population, a minimum of 15 reproductive individuals were randomly chosen, and their spikes

Fig. 1 Location of populations of *Plantago coronopus* sampled in the study (black dots). The distribution range of the species, according to Hultén and Fries (1986), is highlighted in gray (including coastal outlines). See Table 1 for population acronyms

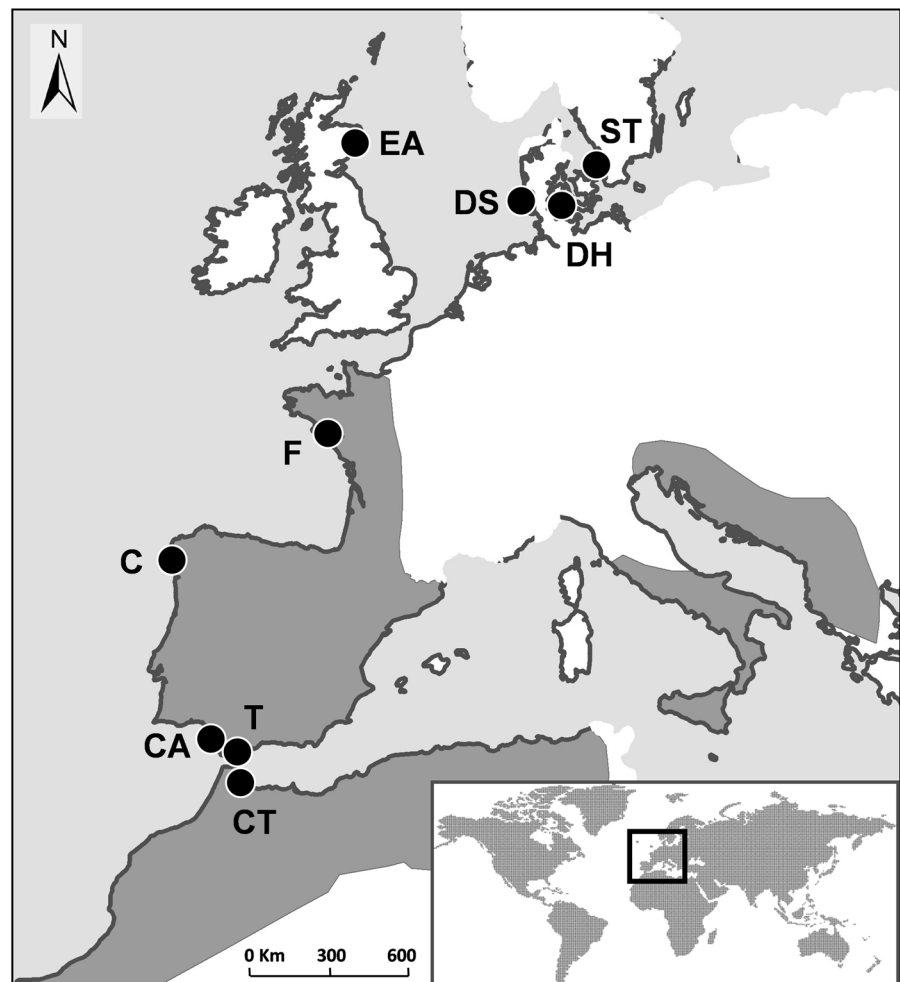


Table 1 Location of populations of *Plantago coronopus* in the study

Population	Location	Coordinates
CT	Ceuta, Spain	35°54'N, 05°21'W
T	Tarifa, Spain	36°02'N, 05°38'W
CA	Camposoto, Spain	36°25'N, 06°13'W
C	Corrubedo, Spain	42°33'N, 09°01'W
F	Pen Bron, France	47°18'N, 02°30'W
DH	Helnaes, Denmark	55°08'N, 09°59'E
DS	Skallingen, Denmark	55°29'N, 08°15'E
ST	Torekov, Sweden	56°23'N, 12°38'E
EA	Aberdeen, Scotland	57°20'N, 01°55'W

were collected in paper envelopes and later kept in a dry environment until usage for experiments. In the laboratory, seeds from all individuals within each population were pooled.

Three germination experiments were performed (Table 2): two with high water availability in the greenhouse (GerF in moist filter paper and GerS in sand substrate), and one with lower water availability in a sand dune where the species naturally occurs (GerD). In GerF experiment, seeds were sown in Petri plates with filter paper (25 seeds per plate, 4 plates per population and seed type). They were daily watered throughout the experiment, so that they were always in contact with water. In GerS, seeds were sown in small pots of water-resistant paper filled with sand (5 seeds per pot, 150 pots per population; only basal seeds used due to a natural scarcity of apical ones) that were in permanent contact with water through small holes in their lower part. In GerD, seeds were sown in October

in cell trays filled with sand and buried at ground level in Sand dune 1 in Tarifa, southern Spain (25 seeds per cell, 8 cells per population and seed type), mimicking as much as possible the natural process of recruitment. Trays were watered only the first day in this case, before and after sowing, just to ensure seeds remained attached to the substrate. For GerF and GerS experiments, germination of individual seeds was daily monitored for 14 and 21 days, respectively. For GerD experiment, final germination was checked after 26 days. Differences in experiment duration respond to increasing time needed for germination with increasing environmental stress. Still, GerD experiment might have partially underestimated final germination values, as some emergence after several months of sowing has been reported elsewhere (2 and 9% of seedlings coming from basal and apical seeds, respectively, were late emergent; Braza and García 2011). However, the relative behavior of basal and apical seeds should not have been affected, considering the clear differences found in our study among both types (see Results).

Two experiments of seedling survival were performed with basal seeds (Table 2): one including regular water supply in an open common garden (with sand substrate; SurS) and one exposed to water stress in a sand dune where the species naturally occurs (SurD). Both SurS and SurD experiments were performed in early spring (April). In SurS, seeds were sown in wooden planters filled with sand (compartments of 30 × 30 cm; 25 seeds per compartment, 4 compartments per population). Seeds were regularly watered until germination, and germinated seedlings that remained alive after one week (onset of

Table 2 Experiments performed with *Plantago coronopus*

Experiment	Conditions	Populations	Sample size	Duration
GerF	Greenhouse (filter paper)	T, C, F, DS, ST, EA	100 Bsd, 100 Asd	14 d
GerS	Greenhouse (sand)	T, C, F, DS, ST, EA	750 Bsd	21 d
GerD	Sand dune 1	T, C, F, DH, ST, EA	200 Bsd, 200 Asd	26 d
SurS	Common garden (sand)	CT, T, CA, C, F, DS, ST, EA	22 Bsl	14 m
SurD	Sand dune 2	T, C, F, DS, ST, EA	290 Bsl	15 m

Experiment names refer to process investigated (Ger = germination; Sur = seedling survival) and environmental conditions used (F = filter paper substrate, greenhouse; S = sand substrate, greenhouse/common garden; D = Dune). The greenhouse and the open common garden are situated in Zaragoza (Spain), Sand dune 1 is located in Tarifa (South Spain), and Sand dune 2 in Laxe (North Spain). Sample size refers to the number of basal (Bsd) and apical (Asd) seeds used per population, or the number of seedlings coming from basal (Bsl) seeds per population. The duration of the experiment is reported in days (d) or months (m). In SurS, mean sample size across populations is shown

experiment) were watered daily the first week and then weekly the following two months. Seedling survival was registered 14 months after the onset of the experiment. In SurD experiment, seedlings from GerS experiment were transplanted within pots to Sand dune 2 (Laxe, northern Spain), completely opening the lower part of the pots to allow normal root growth and water diffusion. Only two seedlings were maintained per pot, to minimize seedling competition, and 145 pots per population were transplanted. Seedlings were watered only the day of the transplant. In the first year of the experiment (3 months after the transplant), we counted the number of leaves and measured leaf length in a random subset of 200 individuals from all populations. Seedling size was estimated by multiplying the number of leaves by leaf length (see also Vilellas et al. 2013). Finally, survival was recorded for all the individuals 15 months after the transplant.

Seed mass

Basal and apical seed mass values were obtained from a previous study, where we weighed eight groups of 25 seeds of each type per population (due to the small size of seeds; Vilellas and García 2013). For the present study, we used mean values per population. In a preliminary analysis, we tested for differences in seed mass among populations with analyses of variance, by using the values from the 25-seed groups (*aov* function, *stats* package, R Development Core Team 2011). Populations showed significant differences in seed mass both for basal ($F_8 = 56.84$, $p < 0.001$) and apical seeds ($F_8 = 5.42$, $p < 0.001$), which supported the use of average population values.

Data analysis

To analyze the effects of seed type and experimental condition on the final germination percentages, we performed Generalized Linear Mixed Models (GLMMs) with a binomial error distribution (*glmer* function, *lme4* package in R). A simple GLMM with an intercept and the random effect of population was compared by likelihood ratio test against models with the additional fixed effect of seed type (basal or apical), experimental condition (GerF, GerS or GerD) or both (*anova* function, *stats* package in R). Tukey's pairwise comparisons were then performed to analyze the differences between levels of the fixed effects (*glht*

function, *multcomp* package in R). Additional likelihood ratio tests were performed separately for basal and apical seeds to test for the effect of seed mass.

To analyze in detail differences in the temporal pattern of germination between seed types in the GerF experiment, we used the Cox proportional hazards model (Scott et al. 1984; McNair et al. 2012). The Cox model belongs to the so-called time-to-event analyses, which are based on the distribution of germination times of individual seeds. Specifically, we tested for differences between basal and apical seeds in the hazard function, which informs about how likely it is that a seed that has not germinated by time t will germinate shortly after t (McNair et al. 2012). The model included a random factor of population.

To analyze the effects of basal seed mass on early survival in SurS, we performed Generalized Linear Models (GLMs) with a binomial error distribution (*glm* function, *stats* package in R). A simple GLM with an intercept was compared by likelihood ratio test against a model including the effect of seed mass. Finally, we tested for local adaptation in the transplant experiment SurD. To do so, we analyzed differences in survival between populations after 15 months, by means of a GLM with a binomial error distribution and Tukey's pairwise comparisons. For the subset of plants in SurD whose size was measured, we analyzed the effect of seed mass and seedling size on survival. A simple GLM with an intercept and the random effect of population was compared by likelihood ratio test against a model including also the effect of seed mass and seedling size.

Results

Seed germination

Significant differences in final germination percentages were detected between seed types and between experimental conditions, since the model for germination including both factors showed the lowest AIC and BIC values and a significant p value (Table 3). Basal seeds showed higher final germination percentages than apical seeds both in the greenhouse (GerF) and in Sand dune 1 (GerD; Fig. 2). Also, for both seed types, germination was higher under high moisture conditions in the greenhouse (filter paper and sand; GerF and GerS) than in natural conditions (GerD),

Table 3 Analyses of the effects of seed type, experimental conditions, and seed mass in final germination percentages

Analysis	Df	AIC	BIC	logLik	<i>p</i>
All seeds					
Intercept	2	1687.18	1689.98	−841.59	
Seed type	3	1118.35	1122.56	−556.18	<0.001
Experiment	4	437.07	442.67	−214.53	<0.001
Seed type + experiment	5	307.15	314.16	−148.58	<0.001
Basal seeds					
Experiment	4	198.56	202.12	−95.28	
Seed mass + experiment	5	199.55	204	−94.775	0.315
Apical seeds					
Experiment	3	96.82	98.27	−45.41	
Seed mass + experiment	4	98.73	100.67	−45.36	0.768

For all seeds, a simple generalized linear mixed model with an intercept and the random effect of population is compared by likelihood ratio test against models with the additional fixed effect of seed type (basal or apical), experimental condition (filter paper in greenhouse, sand substrate in greenhouse, or Tarifa sand dune) or both. Additional likelihood ratio tests are performed separately for basal and apical seeds, to test for the effect of seed mass

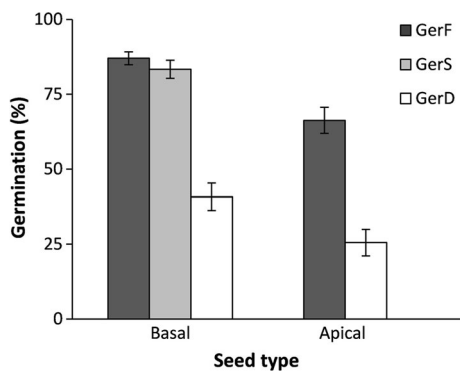


Fig. 2 Final germination in *Plantago coronopus* for basal and apical seeds in three experimental conditions. GerF (dark gray) = greenhouse, filter paper; GerS (light gray) = greenhouse, sand; GerD (white) = Sand dune 1 (see also Table 2). Bars represent mean population values \pm standard errors

with similar values between the two experimental conditions in the greenhouse (Fig. 2). Tukey's pairwise comparisons revealed significant differences in germination between apical and basal seeds ($p < 0.001$), between GerD and GerF ($p < 0.001$), and between GerD and GerS ($p < 0.001$), but not between both greenhouse experiments with regular water supply (GerF and GerS; $p = 0.813$). In the analysis of the temporal pattern of germination in the greenhouse (GerF), basal seeds germinated significantly earlier than apical ones, and showed higher final germination percentages (Fig. 3; Cox proportional

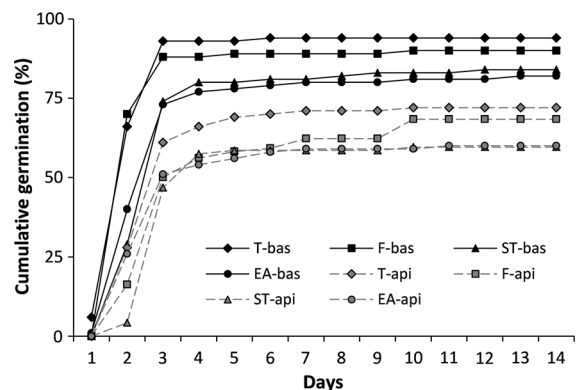


Fig. 3 Cumulative germination of basal (black solid line) and apical (gray dashed line) seeds in filter paper in *Plantago coronopus* during 14 days (experiment GerF). Results are shown only for four populations for clarity (T: diamonds; F: squares; ST: triangles; EA: circles), but the remaining populations (C and DS) show a similar pattern. See Table 1 for population acronyms

hazards model: $\chi^2 = 146.5$, d.f. = 1, $p < 0.001$). Finally, seed mass did not have a significant effect on final germination percentage across the different experimental conditions, neither in basal nor in apical seeds (Table 3; Fig. 4a, b). Overall, the experimental condition (with different levels of water availability) determined germination rates of both kinds of seeds irrespective of seed size, and apical seeds germinated less and later than basal ones even in the conditions of the highest water supply.

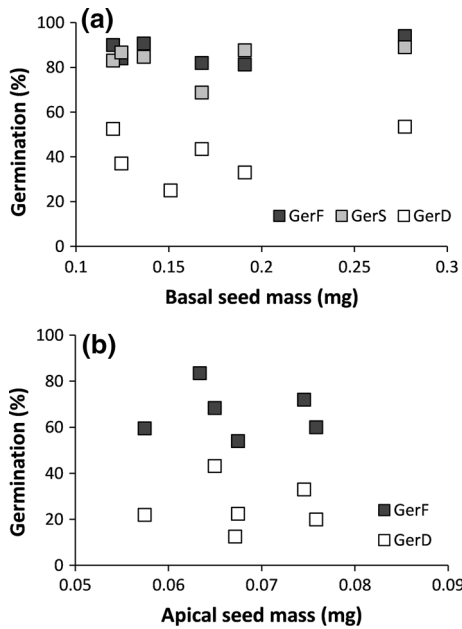


Fig. 4 Relation between basal (a) and apical (b) seed mass and final germination in *Plantago coronopus*. Final germination percentages are given for three experimental conditions (as in Fig. 2)

Seedling survival

Survival after ca. 1 year was much higher in the open common garden with low water stress (SurS) than under natural conditions in a sand dune (SurD; compare Fig. 5a, b), showing again the importance of water availability in the early phases of *P. coronopus* life cycle. In the common garden, survival was positively correlated with seed mass (Table 4; Fig. 5a). In the transplant experiment under natural conditions in the sand dune, Tukey’s pairwise comparisons revealed significant differences in survival between populations (Fig. 5b), suggesting local adaptation: the local population (C) showed the highest survival, and another Iberian population naturally growing ca. 900 km away (T) showed the second highest survival. The high performance of population C in the sand dune, compared to the other populations, contrasts with results in the common garden, where C shows moderate survival levels (29% of survival, while four other populations showed values between 40 and 80%). In contrast with results from the common garden experiment, survival in the dune was not

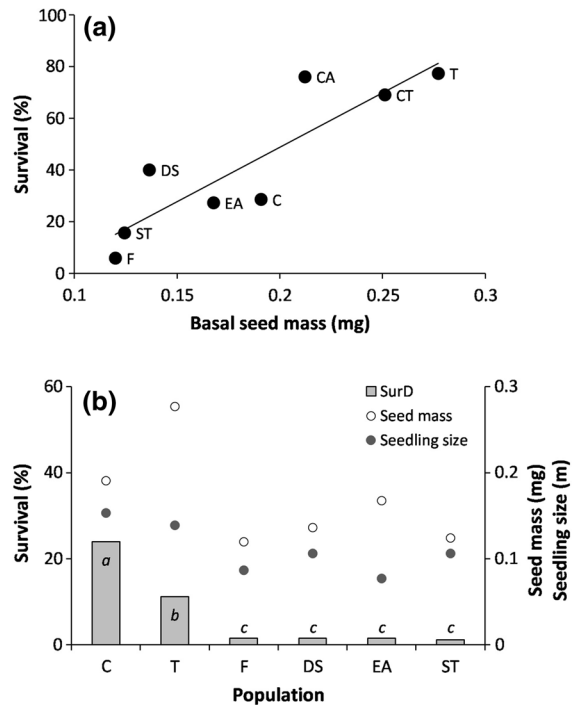


Fig. 5 Seedling survival of *Plantago coronopus* in an open common garden (a SurS experiment) and in a transplant experiment in Sand dune 2 (b; SurD), in relation with basal seed mass and seedling size. In b, C is the local population (see Table 1 for population acronyms), and populations sharing a letter do not differ significantly in survival, according to post hoc analyses (see Methods)

Table 4 Analyses of the effects of seed mass and seedling size in survival percentages in an open common garden (SurS experiment) and in a transplant experiment in Sand dune 2 (SurD)

Analysis	Df	AIC	BIC	logLik	p
SurS					
Intercept	1	85.02	85.10	-41.51	
Seed mass	2	39.53	39.69	-17.76	<0.001
SurD					
Intercept	2	263.90	270.54	-129.95	
Seed mass	3	265.60	275.57	-129.80	0.584
Seedling size	3	254.46	264.43	-124.23	<0.001

In SurS, a simple generalized linear model with an intercept is compared by likelihood ratio test against a model with the additional effect of seed mass. In SurD, a generalized linear mixed model with an intercept and the random effect of population is compared against models with the additional effect of seed mass and seedling size

correlated with seed size, although it was correlated with early seedling size (Table 4; Fig. 5b).

Discussion

The way species' life-history traits are shaped, and their importance for the life cycle, is crucial to understand population persistence through time. However, not many studies have explored such variability over a significant part of species distribution ranges or environmental gradients (but see, e.g., Kalisz and Wardle 1994; Angert 2009; Joshi et al. 2001; Doak and Morris 2010). *Plantago coronopus* is an interesting study species in this context because it exhibits an unusual spatial variation in quantitative and qualitative reproductive traits, including the particular combination of seed dimorphism and mixospermy. Previous observational studies on this taxon have shown important spatio-temporal variation in some life-history traits and processes at both regional and continental scales (Braza et al. 2010; Braza and García 2011; Villellas and García 2013). In this paper, we have experimentally analyzed the spatial variability and the drivers of germination and seedling survival along most of the species' latitudinal gradient finding that variation in recruitment can be explained by a combination of intrinsic and extrinsic factors.

Evidence from previous studies suggests that water availability has played a critical role in the life-history evolution of *P. coronopus*. For example, drought increases biomass allocation to reproduction more intensively in annual than in perennial forms (Hansen et al. 2013), and seed mass and the ratio of basal to apical seeds are correlated to a precipitation gradient across Europe (Villellas and García 2013). Likewise, in the present study, we found that the large spatial variation in recruitment recorded across the species distribution range has been shaped by water availability. We found indeed that germination rates are positively associated to water availability, irrespective of seed type, and that high moisture may trigger germination very quickly (>50% germination after 3 days; see also Schat 1981). In addition, seedling survival was also substantially higher under artificial water supply than in natural conditions in the dune. This finding might explain why some populations of *P. coronopus* occurring in drier habitats have shifted from perennial to annual life cycles, as a way to avoid

a prolonged exposure of individuals to harsh conditions (van Kleunen 2007; Braza and García 2011).

For a species that frequently occurs in environments that are spatially or temporally patchy, or subject to unpredictable climatic conditions, seed dimorphism constitutes a bet-hedging strategy that may increase overall recruitment success (Venable 1985; Imbert 2002; Brändel 2007). By producing different types of seeds, plants can spread the risk of recruitment failure in space (through differential dispersal ability) and/or time (through differential germination timing). Interestingly, this bet-hedging strategy can be adjusted to local conditions by regulating the number, proportion, and size of each kind of seed (Villellas and García 2013), or by evolving fast if environmental conditions change, as demonstrated by Cheptou et al. (2008) in fragmented landscapes. Apical seeds in *P. coronopus* show a worse per capita performance than basal ones, at least in terms of germination (Fig. 2), but they require lower resource investment, which potentially allows a higher offspring production under resource constraints. In addition, the higher dispersal capacity of apical seeds by wind or water due to their lower mass and a lack of a sticky mucilaginous coat (Dowling 1933; Schat 1981; Kuiper and Bos 1992) may be an essential strategy in open and disturbed habitats. Finally, there is a delay in germination timing in apical seeds (Fig. 3). Such delay, which is more pronounced in natural conditions and which has been shown to increase overall seedling recruitment (Braza and García 2011), constitutes a temporal bet-hedging mechanism that increases the chances of population persistence. A number of studies have dealt so far with factors involved in *P. coronopus* germination (e.g., Kuiper and Bos 1992; Shem-Tov et al. 1999; Luciani et al. 2001), and the differential behavior of both seed morphs found here agrees with the previous work (Schat 1981; Braza and García 2011), but this is the first time that a consistent pattern is found across populations at a large spatial scale and highly contrasted environments.

The literature shows conflicting results regarding the influence of seed size in recruitment, with some examples of weak or unclear effects (van Mólken et al. 2005; Lönnberg and Eriksson 2013; Larson et al. 2016). In our study, the higher germination rates found in basal compared with apical seeds seem to be due to the presence of a mucilaginous coat in the former,

rather than to differences in size between seed morphs. This is supported by an absent effect of seed size on germination rates in either of the seed types (and a larger variation in size between basal seeds of the different populations than between seed morphs; Villellas and García 2013). The importance of the mucilage in germination may be explained through its role in holding the seed attached to the soil once moistened, thus facilitating the radicle penetration into the particles. Such effect on radicle behavior was observed in an experiment including basal seeds freed from their mucilaginous coat (Dowling 1933). Other advantages have also been attributed to the mucilage, such as protection from seed predation and soil erosion, and even facilitation of DNA repair in arid environments (see, e.g., Grubert 1974; García-Fayos et al. 2010; Yang et al. 2012). However, these benefits might take place in nature but less likely in our controlled experimental conditions, especially inside the greenhouse. Apart from the mucilaginous coat, additional hypotheses not tested here could help to explain differences in germination between seed morphs. For example, both types might present different dormancy or germination requirements of temperature or light conditions, but we lack such information from the literature. On the other hand, apical seeds are frequently found in nature attached to the capsule lid, which reduces germination rates (Dowling 1933, Schat 1981), but apical seeds in our study were released from the capsule. In the absence of additional information, we can at least conclude that the mucilaginous coat is partially responsible for the differential behavior in germination between seed morphs. Given its likely role in drought tolerance, it constitutes another way of adaptation to local environmental conditions in *P. coronopus*.

The lack of relationship between seed size and germination success in either of the experimental condition contrasts with the positive relationship between seed size and seedling survival in our common garden study. This outcome suggests that the “seed coat benefit” for germination is later replaced by a “seed size nutrient-supplier effect” on survival during the early plant stages. However, we did not find such an effect in the harsher dune experiment, indicating that the benefits of the internal nutrient supply lose importance in natural conditions of stress. In such conditions, traits other than seed size or seed nutrient supply seem to determine seedling

size and ultimately survival, probably in relation with specific biotic or abiotic factors. In fact, our results suggested the presence of local adaptation in the species, since the local plants from N Spain showed the highest survival and the second highest survival corresponded to the population from S Spain. The latter is less phylogenetically related to the local population than the population from France (Berjano et al. 2015), and also occurs in the Iberian Peninsula. Thus, it probably has a better overall preadaptation to the array of environmental conditions of the experimental site, such as the high climatic seasonality.

Overall, the present study has shown that the two main components of recruitment, germination and seedling survival, are key life-history processes that respond to both intrinsic and extrinsic (environmental) factors. Water availability has a fundamental role in species performance in the early stages of the life cycle, but other factors such as seed dimorphism, seed mass, and the degree of local adaptation may have important consequences for the ultimate fate of individuals. Previous work highlighted that environmental gradients alone are not reliable predictors of species variation in recruitment (Cochrane et al. 2015). In fact, our study supports that only a good knowledge of the general life history and ecological strategies of plants, together with information about the intrinsic and extrinsic drivers of intraspecific variation in recruitment, will allow us to understand and predict species behavior in a context of environmental change.

Acknowledgements This study was funded by the Spanish Ministry of Science and Innovation through two National Projects (CGL2006-08507; CGL2010-21642) to M.B.G. and a scholarship (FPU) to J.V. We would like to thank R. Braza for seed material from France and Morocco, A. Adsuar, M. L. Dehesa, J. M. Olesen, C. Pérez and A. Taboada for assistance in the field and laboratory, and F. Ojeda for help in the field and valuable comments on the manuscript. Two anonymous reviewers provided useful suggestions for improving the final article.

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