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Natural selection on seed size through the life cycle of a desert annual plant

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Abstract. Under stressful circumstances, seed size has important consequences for germination, survival, and reproductive success; all of these are important components of plant fitness. This study investigates the relationship between seed size and fitness in the Sonoran Desert winter annual *Dithyrea californica*. This species represents a unique opportunity to study natural selection on seed size in the wild due to a serendipitous detail of its life history: the seed coat remains attached and unchanged to the root throughout its life. It is thus possible to excavate the root and measure the seed size that originated each plant. We measured the relationship between seed size and germination by comparing seed sizes of germinated and dormant seeds in the field over four consecutive years. We also measured the effect of seed size on survival and reproductive success using data from censuses of plant mortality and fecundity of survivors, relating survival and fecundity to the size of their initial seed size, and the number of conspecific neighbors. Larger seeds had a higher probability of germination than smaller seeds. Plants originating from larger seeds had higher survival rates and higher fecundity than plants originating from smaller seeds. The amount of precipitation had a beneficial effect on plant fecundity and influenced seed-size survival selection. Plant competition decreased plant fecundity but not survival, creating a detrimental environment for plants only to grow and reproduce. This is the first study to show empirical evidence of seed-size selection throughout the whole life cycle in a natural setting. Further, maternal provisioning has benefits that persist into adulthood, and environmental interactions are important in determining survival and fecundity.

Key words: *Dithyrea californica*; environmental influence; fitness; intraspecific competition; seed size; selection in the wild.

INTRODUCTION

Seed size is a key trait that has important fitness consequences throughout the plant's life cycle. Due to better maternal provisioning, plants from larger seeds often have a competitive advantage over plants derived from smaller seeds in terms of germination (Roach 1987, Winn 1988), survival (Stanton 1984, Dalling and Hubbell 2002, Moles and Westoby 2004a, b, 2006, Susko and Cavers 2008), growth, and reproduction (Winn 1988, Mojonner 1998). In environments where mortality due to resource limitation or competition is high, it might be advantageous to produce a few large seeds rather than many smaller seeds. On the other hand, smaller but more numerous seeds have an advantage in fecundity (Muller-Landau 2010), and might be better at dispersing and colonizing new habitats (Skarpaas et al. 2011). For instance, early successional species tend to have small seeds, suggesting that a reduced size might be beneficial in dispersing and avoiding competition (Turnbull et al. 1999).

Seed-size selection might be determined by the finite amount of resources available. Baker (1972) surveyed seed size in the California flora and found that larger seeds are more likely to be found in drier habitats. This led him to conclude that seed size is an adaptation to cope with drought. Baker proposed that larger seed size would allow seedlings to develop larger roots and therefore obtain access to water more readily than small seeds, which is better in dry environments (c.f. Jurado and Westoby 1992, Leishman and Westoby 1994b, Kidson and Westoby 2000, Hallett et al. 2011). In more mesic sites, light and nutrients might be more likely to influence seed-size selection than water availability. Early studies in the British flora reveal that larger seeds tend to be found in more shaded habitats (Salisbury 1942, 1974, Thompson and Hodgkinson 1998). Critical resources affecting competition vary among environments, and might be driven by light or nutrients in wet environments and water in dry environments.

Environmental factors that influence seed-size selection in desert plants might not operate equally on different life history stages. Seed-size selection operating through survival in the desert is likely to be more influenced by water availability than by competition

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with neighboring plants because plants in early stages have not yet developed extensive root systems or foliage capable of depleting neighbors' resources (Tevis 1958, Beatley 1967, Inouye et al. 1980). On the contrary, seed-size selection operating through fecundity is more likely to be affected by both water availability and competition because their effects would directly reflect seed provisioning and therefore seed size. It is currently unknown whether water availability has a stronger effect than competition on either survival or fecundity. Whereas high water availability is expected to relieve the selective pressures on seed size early in the life cycle, subsequent competition is likely to be greater and there may be more competition at higher water availability.

Despite the seminal early ideas of Baker and Salisbury, the study of the adaptive significance of seed size has involved mostly greenhouse or pot experiments (Cideciyan and Malloch 1982, Leishman and Westoby 1994a, Bonfil 1998, Eriksson 1999) and macroecological comparisons of the distribution and functional correlates of species with different seed size (Moles et al. 2004, Moles and Westoby 2004a, b, 2006, Moles et al. 2005). Some studies have tried to add more realism by mixing greenhouse experiments with field experiments but have not gone beyond the seedling stage (Marshall 1986, Leishman and Westoby 1994b, Benard and Toft 2007). Exploration of the fitness consequences of seed size in natural field settings including fecundity selection is rare (Wulff 1986, Mojonier 1998). In fact, some studies have proposed that seed-size effects do not extend into adulthood (Cideciyan and Malloch 1982, Winn 1988, Houssard and Escarre 1991, Susko and Lovett-Doust 2000), ignoring the effects of seed size on fecundity.

In this paper, we describe a study of the ecological mechanisms of natural selection on seed size during the life cycle of a desert annual plant, *Dithyrea californica* Harvey (Brassicaceae). Our objective was to look for empirical evidence of the consequences of seed size on fitness in a natural setting, and to describe how environmental interactions influence seed-size selection. We performed a multiyear demographic study in the field, following individual plants from germination to seed set. We then related performance to the size of the seed from which each individual germinated. Specifically, we examined whether seed size has an influence in early stages of the plant such as germination and survival, and whether those influences extend into adulthood as expressed by fecundity. This study is the first to our knowledge to document the fitness consequences of seed size through the entire life cycle, using plants naturally germinated in the field and in a variety of environmental conditions. In this study, we take advantage of a serendipitous detail of the natural history of *Dithyrea californica* seeds, which enables us to document the fitness consequences of seed size through the whole life cycle, in the field under a variety of environmental conditions. Since *D. californica* grows in sandy soils and the seed coat remains attached and

unchanged to the root throughout its life, it is possible to easily excavate and recover the seeds that originated individual plants.

We hypothesize that (1) plants originating from larger seeds will germinate faster and have higher survivorship than plants originating from smaller seeds; (2) seed-size effects will not persist into adulthood; and (3) water availability and intraspecific competition will exert opposite selective pressures on seed size.

METHODS

Study species

Dithyrea californica Harvey (Brassicaceae) is a self-incompatible desert winter annual plant that is widespread in semi-stabilized sand dune habitats in the Lower Colorado River Basin subdivision of the Sonoran Desert (Felger 2000). Germination typically occurs in the fall and depends on the timing of rains. There are limited data available on this species, but, based on information on other winter annuals from the region (Bowers 1996, Felger 2000), germination usually occurs in November/December, and occasionally happens as early as September and, rarely, as late as March. Reproduction usually occurs from late February to early April. Each flower produces a two-lobed fruit that eventually separates into two single-seeded mericarps. This flattened fruit with two round lobes is responsible for the common name, "spectacle pod."

We will use "seed" to refer to the mericarp, which consists of a single seed with associated ovarian tissue and which functions ecologically as the unit of dispersal and germination. This mericarp has a thick and persistent ring, the diameter of which is a good metric of seed mass (simple linear regression, $r = 0.432$, $P < 0.0001$; Appendix: Fig. A1). Seedlings germinate through the persistent ring, which usually stays attached to the root for the entire life of the plant (Fig. 1). This provides an efficient way to measure the size of the seed long after germination.

Field data collection

The experiments were conducted in semi-stabilized dune habitats at three sites within the Lower Colorado River Basin subdivision of the Sonoran Desert: Sierra del Rosario (32°9'57.85" N, 114°7'15.46" W) and Sierra Blanca (31°34'21.04" N, 113°29'27.96" W) in Sonora, México; and Coachella Valley Preserve (33°48'35.60" N, 116°19'56.45" W) in California, USA (see Table 1). The vegetation in these sites is dominated by a mixture of dune creosote bush (*Larrea divaricata* var. *arenaria*) and white bursage (*Ambrosia dumosa*). A diverse flora of ephemeral plants, including *D. californica*, germinates in years with favorable winters, and flowers in the spring (Felger 2000, Bowers 2005).

Seedlings emerge roughly 4–10 days following the first precipitation event of the season. Thus we marked seedlings of *D. californica* 10 days after the first precipitation event (while seedlings were in the cotyle-

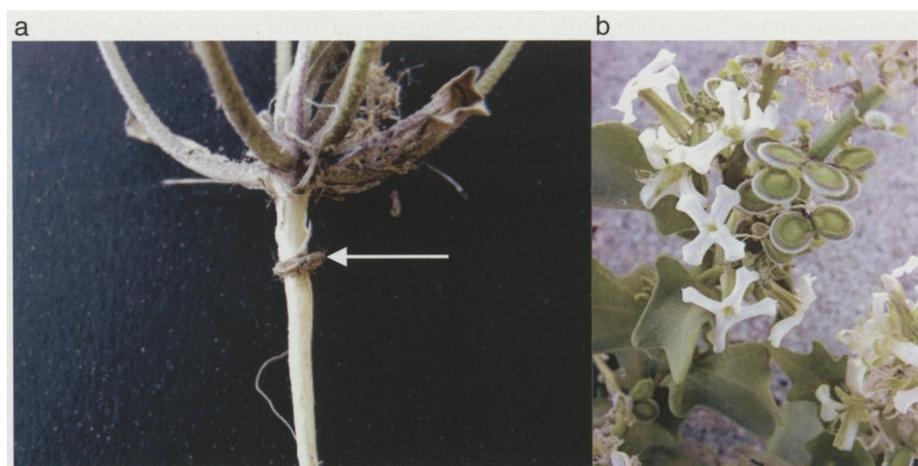


FIG. 1. (a) An adult *Dithyrea californica* plant showing its special feature: the persistent seed ring used in this study, and (b) flowers and siliques still attached to the mother plant. Photo credits: Martha M. Gómez and Calflora.

don stage) and kept track of individual plants during the 1991 and 2008–2012 growing seasons. We followed them until the end of reproduction, and collected the adult plants to measure fecundity. For each collected plant, we measured the diameter of the persistent seed ring as well as the number of seeds produced. Precipitation data were taken from weather stations (in Mexico, Texas Electronics TR-525I tipping bucket rain gauge [Dallas, Texas]; in USA, Western Regional Climate Center [data available online])⁵ located at the study sites. For every individual, we counted the number of neighbors by species in a 10 cm radius from the focal plant. This area is thought to correspond roughly to the resource depletion zone for an annual plant the size of *D. californica* (Silander and Pacala 1985). In our analyses, we used intraspecific density as a covariate because we found that plants from the same species compete more strongly than plants from different species. In our models, there was a slight gain of variance explained using intraspecific density rather than all species combined. This is presumably because *Dithyrea californica* is a “big” annual with larger leaves and roots than most of the rest common ephemerals occurring as neighbors.

Germination studies

To test whether the probability of germination is associated with seed ring diameter, we compared the ring diameters of randomly chosen germinated and non-germinated seeds in the field. Estimates for the sizes of germinated seeds were obtained by measuring persistent seed ring diameters of germinated seedlings. Germinated seedlings were marked and their number of neighbors counted until we reached 150 seedlings, however data on some individuals was lost due to lack of ring diameters, or premature senescence; ending up with an unbalanced

number of germinated seedlings per year. The sizes of non-germinated seeds were obtained by collecting 125 soil samples each of four consecutive years at the end of the germination season at the same locations as the germinated seedlings. Each soil sample covered a 314 cm² soil surface and was collected to a depth of 10 cm in the same area as the seedlings. Soil samples were sieved with a 1-mm sieve that efficiently captures all seeds while allowing all sand particles to fall through. Diameters of these ungerminated viable seeds were measured in the lab with digital calipers. Viability was determined by visually inspecting and poking them under a dissecting microscope to determine that they were filled and not rotted (cf. Pake and Venable 1996). All plants measured belonged to a single cohort since they were flagged shortly after the first and only germination flush. We tested for significant differences in germination probability as a function of seed diameter using year as a nominal covariate with a generalized linear model regression assuming a binomial distribution of germination (germinated vs. not-germinated) and a logit link using the glm function in the R package stats (R Development Core Team 2008). We are not interested in the effect of year except to control for it. This is because, while the seed bank was consistently measured on a standard number, area and volume of samples, seedling number was not, so year differences are difficult to interpret.

Survival studies

To test whether individuals originating from larger seeds had higher survivorship than individuals from smaller seeds, randomly chosen seedlings were flagged 10 days after germination-triggering rain and visited periodically until the death of all seedlings. At each census, dead plants were excavated and the persistent seed ring was recovered to measure its diameter. The study was conducted in Sierra del Rosario in 2011 and

⁵ <http://www.wrcc.dri.edu/>

TABLE 1. Years and sites where seed-size selection was measured in the field as well as the different amounts of precipitation used in the study.

Site and year	Germination-triggering rain (mm)	Growing-season rain (mm)	Stage measured
Rosario 1991	†	70.6	R
Rosario 2008	45	†	G
Rosario 2009	22	†	G
Rosario 2010	40	96.5	G, R
Rosario 2011	23	29	G, S
Coachella 2011	†	38.6	R
Sierra Blanca 2012	†	115	S, R

Note: Stages are germination (G), survival (S), and reproduction (R).

† Data not needed for the analysis.

Sierra Blanca in 2012. These sites have broadly similar sand dune habitats. We used an ANCOVA with the *lm* function in the R package stats to determine the relationship between time to death and seed ring diameter, using the number of conspecific neighbors and the site-year as covariates.

Fecundity studies

To determine whether plants originating from larger seeds produced more seeds than plants from smaller seeds, plants were collected at the end of reproduction and their persistent seed rings as well as the number of seeds produced were measured. Data were analyzed as the number of seeds produced as a function of seed ring diameter, the number of conspecific neighbors, and site-year with a multiple linear regression using the *lm* function in the R package stats. We performed a priori linear contrasts on site-years in relation to the amount of growing-season rain as the differences from the mean of growing-season rain so we could relate differences in site-years to differences in growing-season rain. The number of seeds produced was natural log transformed to homogenize residual variance and meet the assumptions of the general linear model.

RESULTS

Seed-size-dependent germination

The probability of germination was positively associated with seed ring diameter (generalized linear model binomial, $P = 0.01$; Table 2), indicating that larger seeds have a higher probability of germination than smaller seeds. In the range of 3.8–5.8 mm seed diameter, a millimeter of increase in seed diameter raises the probability of germination by ~8%.

Seed-size-dependent survival

Seed ring diameter was positively correlated with time to death, such that plants originating from larger seeds survived longer than plants from smaller seeds (ANCOVA; $P = 0.0001$; Table 3, Fig. 2). Main effects of site-year were not statistically significant ($P = 0.14$; Table 3). The interaction between seed diameter and site-year was statistically significant, implicating that that the effect of seed diameter on time to death was stronger in the wetter site-year Sierra Blanca in 2012 than drier site-year in Rosario in 2011 ($P = 0.04$; Fig. 2, Table 3). Each unit of increase in seed diameter corresponds to five more days of survival on average in Rosario in 2011 and eight days in Sierra Blanca in 2012. The effect of the number of conspecific neighbors was not statistically significant ($P = 0.59$; Table 3).

Seed-size-dependent reproductive success

Plants originating from larger seeds had higher fecundity than plants from smaller seeds (multiple linear regression, $P < 0.0001$; Table 4, Fig. 3). For every millimeter increase in seed diameter, fecundity increased by 24%. The number of conspecific neighbors had a detrimental effect on the number of seeds produced ($P < 0.0001$). For an increase in one neighbor within a patch, fecundity decreased by 13%. A priori linear contrasts included in site-years were positively correlated to fecundity ($P < 0.0001$) so that a centimeter increase in growing-season rain resulted in a 38% increase in seed production. The interactions of seed diameter with site-year and competition were not statistically significant. This does not support our hypothesis that competition or growing-season rain would influence seed-size selection.

TABLE 2. Probability of germination as a function of seed diameter and years (from 2008 to 2011) in Sierra del Rosario.

Independent variable	<i>B</i>	Deviance	Residual deviance	<i>P</i>
Seed diameter	0.32	6.104	1116.1	0.01
Year	0.58	86.245	1029.8	<0.0002
Model χ^2	92.35			
Pseudo R^2	0.14			
<i>N</i>	844			

Notes: Column *B* lists partial logistic regression coefficients. *N* is the number of seeds.

TABLE 3. Time to death (d) as a function of seed diameter (mm), site-year, and the number of conspecific neighbors.

Independent variable	Estimate	SE	P	R ²
Seed diameter (mm)	5.22	1.331	0.0001	0.02
Seed diameter × site-year	2.78	1.348	0.04	0.01
Competition	1.24	2.266	0.59	0.001

DISCUSSION

Dithyrea californica provides a unique opportunity to document seed-size selection in the wild. Our data suggest that there are significant positive effects of seed size on fitness throughout the life cycle, suggesting positive directional selection during the years we measured. Plants originating from larger seeds had a higher probability of germination, survived longer, and produced more seeds than their smaller counterparts, indicating that higher maternal investment to individual offspring increases per seed fitness. Biotic and abiotic interactions played an important role influencing fitness. Intraspecific competition had a detrimental effect on fecundity but not on survivorship. Our data indicated that water availability had a beneficial effect on fecundity and influenced seed-size survival selection.

Seed diameter enhanced the probability of germination. Larger seeds in this species might inherently germinate more than smaller ones. This is important from ecological and evolutionary perspectives because differential germination of different sized seeds could set the stage for subsequent seed-size selection each growing season. Larger germination-triggering rain events are expected to translate into a longer window of moist conditions suitable for germination than smaller rain events, potentially allowing smaller seeds to germinate, thereby increasing the population variation in seed size of germinated seedlings. It is important to emphasize that a higher probability of germination does not necessarily translate into higher fitness since post-germination environmental conditions will ultimately determine the fate of individuals and lower germination is sometimes favored by natural selection.

Seed diameter also had effects on survival such that plants germinating from larger seeds survived longer than plants originating from smaller seeds. The significant seed diameter by year/site interaction indicates that seed-size selection operating through survival had different strengths in the two year-sites we measured it. Seed-size survival selection was stronger during the wet site-year of Sierra Blanca in 2012 (115 mm of rain) than in the dry site-year of Rosario in 2011 (23 mm of rain). This result is counterintuitive given that we expected water availability to relax seed-size selection. Some of the variables that explained significant amounts of fitness variation nevertheless had low predictive capacity. We attribute this to the many sources of environmental heterogeneity that create unexplained fitness variance when measuring natural selection in a completely wild setting.

Intraspecific competition did not impact time to death, contrary to our expectations but consistent with previous studies with desert annual plants from the Sonoran and Mohave deserts (Tevis 1958, Beatley 1967, Inouye et al. 1980). Apparently, size differences resulting from competition that affect fecundity play a lesser role in pre-reproductive mortality. If plants die at early stages, they might be too small to experience competition for light, nutrients or water from their neighbors as they have smaller depletion zones and lesser nutrient requirements than adult plants that have more biomass and thus more photosynthetic needs.

The analysis of fecundity selection demonstrated that seed-size effects indeed extend beyond the juvenile stage into adulthood, affecting the number of seeds produced. Specifically, water availability and intraspecific competition exerted opposing effects on fecundity. Water availability had a positive effect on the amount of seeds produced by creating a good environment fueling growth and reproduction. However, we did not find evidence that water availability relaxed seed-size selec-

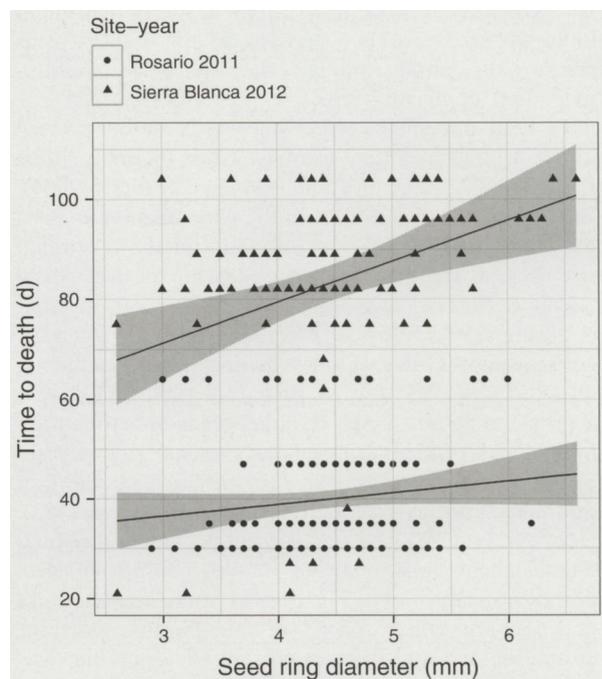


FIG. 2. Time to death (d) for plants as a function of seed ring diameter (mm). Black diamonds represent the dry site-year Rosario 2011, and black triangles represent the wetter site-year Sierra Blanca 2012. Lines represent the linear fit for both years with ANCOVA. Shaded areas around the lines are 95% confidence intervals, $n = 262$ plants.

TABLE 4. Number of seeds produced as a function of seed diameter (mm), competition, and precipitation.

Independent variable	Estimate	SE	P	R ²
Seed diameter	0.22	0.046	<0.0001	0.14
Competition	-0.14	0.014	<0.0001	0.08
Site-year	0.32	0.022	<0.0001	0.22

Note: Competition represents number of conspecific neighbors.

tion through fecundity. Intraspecific competition has a detrimental effect on reproductive success but did not change the strength of selection operating through fecundity differences.

It is not clear how these results would generalize to a more mesic plant species. The pulsed nature of water availability in desert systems and precipitation differences between years play a major role in determining fitness our study. We must be cautious in trying to extrapolate our results to other environments where water is not the main limiting variable as it is in deserts. In moist environments, light or nutrients might be the selective pressures that mediate seed-size selection, at least in short lived plants. In plants with different life histories from *Dithyrea californica*, such as perennials, the effect of seed size might be more relevant to survival selection rather than to fecundity selection given that their reproductive success is spread through the a longer life cycle.

Seed-size selection in *D. californica* might not be always unidirectional toward larger seeds. Seed dispersal and seed predation are other selective forces that might influence seed size but perhaps favor smaller seeds creating a conflict though the life cycle. Within-individual conflicting selective pressures on seed size have been documented previously in relation to seed dispersal and seedling establishment (Schupp 1995, Parciak 2002, Alcantara and Rey 2003, Gomez 2004). In *Olea europea* var. *silvestris* the gape opening of seed dispersers exerts a selective pressure on the maximum size of seeds that can be dispersed, while post-dispersal selective events, such as seedling survival, present opposing selective forces (Alcantara and Rey 2003). In *Quercus ilex*, Gomez (2004) demonstrated conflicting selective pressures due to predators preferring larger acorns and an advantage of larger seeds in germination timing and percentage, seedling survival and growth. These conflicts may result in variable seed-size selection or even stabilizing selection (Nelson and Johnson 1983). However, none of these studies went beyond the seedling establishment stage, ignoring possible conflicting selection during adulthood. The present study demonstrates that seed-size effects extend beyond the juvenile stage into adulthood and for that reason, we argue that it is critical to measure selection across the whole life cycle.

The seed-size selection dynamics measured in the present paper are those acting on the offspring. Maternal effects on offspring provisioning can also influence the evolution of seed size and are actually thought to create a parent-offspring conflict because

selection on mothers operates through the number of offspring as well as their individual fitnesses. Thus selection on mothers is thought to favor an optimal offspring size while selection on offspring will tend to favor larger seeds. Extending this study for at least two consecutive generations would allow us to compare the fitness consequences of seed size from the mother and offspring standpoints and complete the whole life cycle (Donohue 2009).

Directional selection is the most common form of selection in wild populations (Kingsolver and Diamond 2011); however, given its transient nature, strong directional selection is somewhat rare (Kingsolver et al. 2001). Several different scenarios might occur for annual plants with a persistent seed bank such as the winter annuals from the Sonoran Desert. For instance, plant competition, which depends on the seed bank density, will be dictated by the amount of germination-triggering rain and the amount of growing-season rain in recent years, which may be responsible for a buildup in

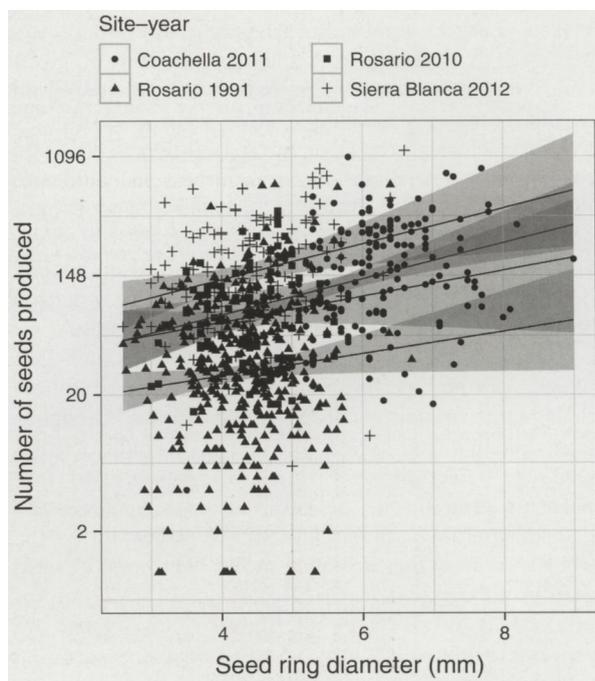


FIG. 3. Number of seeds produced as a function of seed diameter in Rosario 1991 and 2010, Coachella 2011, and Sierra Blanca 2012. The fitted lines represent the slopes of seed ring diameter on the number of seeds produced in different site-years, analyzed with ANCOVA. Shaded areas represent 95% confidence intervals, $n = 771$ plants.

density. A wet previous year (or several sequential wet years) will build up the soil seed bank available for germination in a given year so that competition will be high even if there is only a little germination rain in the current year. Likewise, a prolonged multiyear drought will result in the decay of the seed bank. A good rain event at the beginning of next growing season would have very different outcomes on seed-size selection in these two different scenarios due to differences in competitive densities.

Investigations of temporal variation in natural selection in wild populations shed light on the nature of evolutionary change, the maintenance of genetic variation and the dynamics of local adaptation in natural populations (Siepielski et al. 2009). Our unique system provides insights into the adaptive nature of seed size by identifying important relationships between seed size and components of fitness through the vegetative and reproductive cycle of *D. californica*. We have demonstrated that seed-size effects go beyond early life stages and can ultimately affect fecundity. Thus we recommend including measures of fecundity in studies of seed-size selection. Our study also incorporates a great amount of realism by studying selection in a population of naturally germinated plants in the field, with natural patterns of competition and stage-specific precipitation. Our multiyear data sets the stage for further hypothesis testing on the selective dynamics of seed size through the life cycle.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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