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Morphological variability in propagules of a desert annual as a function of rainfall patterns at different temporal and spatial scales

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Summary

1. Organisms living in highly variable environments have to display integrated strategies to deal with both systematic and random variation occurring at different temporal and spatial scales. Two predictions were tested by analysing geographic-scale patterns of seed size and seed retention (serotiny) in *Chorizanthe rigida*, a strict winter desert annual that delays seed dispersal and releases propagules after rainfall events: (i) adaptation to systematic environmental cues occurs by means of changes in morphology, and (ii) within-individual variation in seed size allows a differential response to rainfall cues: while some seeds germinate rapidly others are retained for future rainfall events.

2. We quantified morphological variation and performed germination experiments on *C. rigida* propagules (involucres + achenes) from six populations distributed throughout the Mojave and Sonoran deserts covering: (i) a systematic, west-to-east, winter-to-bi-seasonal (summer and winter) precipitation gradient and (ii) a winter-rain unpredictability gradient inferred from long-term climatic data.

3. The propagule retention structure (i.e. base area of the pedicel) of *C. rigida* individuals experiencing bi-seasonal rainfall is double the size of those that have evolved under a strict winter rainfall regime, showing that populations living in bi-seasonal environments have higher seed retention, which allows them to avoid releasing seeds to a summer rainfall cue.

4. Within-individual variance of propagule size varied significantly between populations and was correlated with winter rainfall variability in each site.

5. Germination varied as a function of propagule size; smaller seeds germinated more readily than larger seeds. Increased variability in propagule size might result in a more variable germination response.

6. Under common experimental conditions germination varied significantly among sites and was negatively correlated with mean winter effective precipitation, suggesting that propagules from populations in drier sites have lower germination moisture thresholds.

7. *Synthesis.* *C. rigida* propagules have larger bases in deserts with biseasonal rainfall, which allows them to avoid seed release during summer rainfall cues, and display within-individual seed variance associated to rainfall unpredictability, a trait often interpreted as a bet-hedging strategy. Our study provides empirical evidence of an integrated strategy that allows to cope with both random and systematic rainfall variation.

Key-words: delayed dispersal, plant biomechanics, rainfall variability, seasonal cues, seed size, serotiny

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Introduction

Organisms have to cope with both predictable and unpredictable environmental conditions occurring at different temporal and spatial scales (Roff 2002; Simons 2011). However, there is little empirical evidence on how species respond to environmental variation that includes both a predictable and a random signal (Halkett *et al.* 2004; Wong & Ackerly 2005). Due to their low and sporadic rainfall, deserts are inherently variable and unpredictable environments (Noy-Meir 1973), yet desert rainfall is not completely unpredictable and there is both a systematic component and a random component to precipitation patterns. Desert regions do have seasonal precipitation patterns, for example, in North America, the Mojave Desert has mostly winter precipitation while the Sonoran Desert has bimodal precipitation with peaks in both winter and summer (Sheppard *et al.* 2002; Loik *et al.* 2004; Reynolds *et al.* 2004). Furthermore, intraseasonal rainfall variation within a desert results in some sites that have more variable and less reliable winter precipitation than in other sites (Ezcurra & Rodrigues 1986).

Large-scale rainfall variation within entire desert regions provides an opportunity to test hypotheses on how organisms adapt to gradients of predictable and unpredictable environmental conditions. On the one hand, winter annuals need to avoid germinating in response to summer rainfall when high temperatures would be fatal, and, on the other hand, they face the problem of successfully completing their life cycle within a short and unpredictable growing season (Mulroy & Rundel 1977; Gutterman 1993; Gutterman, Shem-Tov & Gozlan 1998). While avoiding summer germination demands a systematic response, the unpredictability of winter rains imposes a classical bet-hedging problem: if all seeds germinate with the first rain and this rain event is not followed by sufficient rainfall, all seedlings will die and the fitness of the mother plant will fall to zero (Childs, Metcalf & Rees 2010; Reed *et al.* 2010). In order to maximize long-term fitness, in highly unpredictable environments only a fraction of an individual's cohort should germinate so that one failed season will not be irreversibly harmful for the individual, even if the expected fitness during good years is reduced (Cohen 1966; Philippi 1993; Simons 2011; Gremer & Venable 2014).

Empirical evidence on the adaptive value of cued-germination and bet-hedging traits has mostly focused on plants forming seed banks in the soil, but less is known about above-ground seed banking in desert annuals. Serotinous annuals retain seeds in their dry skeleton after they die, releasing a fraction of seeds each time it rains (Evenari, Shanan & Tadmor 1971). The retention of mature seeds within the maternal plant has been interpreted as a dispersal strategy of adaptive significance in randomly fluctuating arid ecosystems as it reduces risk by spreading seed dispersal over time, playing the same role that delayed germination plays in the soil seed bank of other desert annuals (Venable & Lawlor 1980; Ellner & Shmida 1981;

Kamenetsky & Gutterman 1994; van Rheede van Oudtshoorn & van Rooyen 1999). Moreover, bet-hedging models have shown that seed size can also constitute a bet-hedging trait and that increasing environmental unpredictability should result in higher seed size variation as this trait has an important effect on seedling survival (Olofsson, Ripa & Jonzén 2009). Widely distributed serotinous plants in deserts with different degrees of climatic variability constitute an ideal system to test the ideas behind adaptations to environmental cues and environmental unpredictability as these plants retain their seed cohort thus allowing the quantification of offspring variation within an individual.

We investigated how propagule morphology and germination are related to rainfall patterns in the desert spineflower *Chorizanthe rigida*, a serotinous winter annual found across the Sonoran and Mojave Deserts of North America. This plant retains seeds within its spiny, lignified dead skeletons for several years, and its seeds are dispersed by rainfall events. Involucres (i.e. dispersal structure formed by three-bracts holding one achene) are held on to the branch by a hygrochastic-tissue base that swells and softens when wet, allowing seed detachment caused by the pounding of raindrops. Non-detached involucres remain attached to the plant as the lignified tissues re-dry (Martínez-Berdeja *et al.* 2014; Fig. 1). In sites that receive monsoon rains, *C. rigida* faces the challenge of retaining seeds when the summer rains arrive to avoid dispersing seeds to the false summer moisture cue, and it has to cope with winter rainfall unpredictability as well. In this paper, we describe geographic patterns of involucre morphology and germination ability in *C. rigida* in search for empirical evidence of adaptive responses to rainfall unpredictability via serotiny and seed size variation. Our predictions were that (i) plants growing in deserts with summer-rain pulses

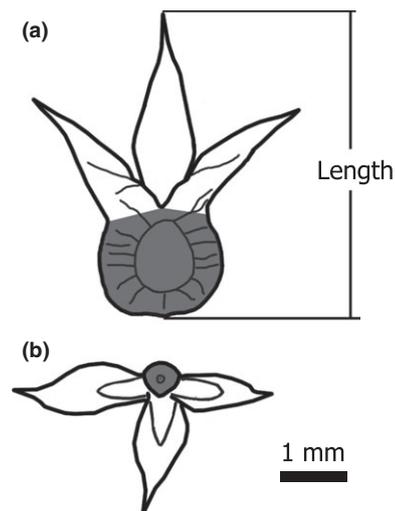


Fig. 1. Frontal view showing propagule size (mm², in grey) and involucre length (mm) (a), and basal view of *Chorizanthe rigida*'s involucres showing base area (mm², in grey) (b).

should show a different involucre morphology leading to a lower ease of release when facing a summer rain and (ii) that within-individual variance in propagule traits associated with successful establishment should increase with the unpredictability of winter rainfall.

Materials and methods

STUDY SYSTEM

The spineflower (*Chorizanthe rigida*, Polygonaceae) is a short, erect desert annual, 2–10 cm high. It has a single main taproot and stout stems covered by stiff, spiny bracts. As the stem grows, the soft, long-petioled basal leaves are shed and give place to linear, rigid bracts (or cauline leaves) with a terminal spiny awn that becomes hard and thorn-like with age. The single flowers, with a diminutive perianth, are subtended by a three-segmented involucre with hard spiny bracts (Fig. 1). The fruit is a single achene, or 'seed', that matures inside the involucre. Flowering lasts from March to May and plants mature and produce seeds at the end of the spring season (April–May). *C. rigida*'s dispersal propagule is formed by the achene surrounded by the involucral bracts, which are shed from the plant as a single unit. The plant has no active seed-release mechanism, the pedicel tissue of the involucre softens with moisture, and the involucre gets detached by the pounding of rain drops (Martínez-Berdeja *et al.* 2014). Once released, seeds germinate inside the involucre and seedlings emerge in the winter season (December–February). Some seeds germinate near the mother plant while others are dispersed by run-off. We have not observed seeds germinating while the involucre is still attached to the mother plant. After the rain events end, the pedicels of the undetached involucre harden again as the plant skeleton re-dries. This plant has a 1300-km-wide latitudinal span, ranging from Baja California's Central Desert (lat. 29°N) to the Great Basin in Nevada (lat. 40°N) and is common in the Mojave and Sonoran deserts, especially in desert pavements (Felger 2000; Baldwin *et al.* 2002).

SAMPLING

Individuals were collected from six populations distributed along two precipitation gradients: a West-to-East precipitation gradient, going from winter-rain to bi-seasonal (summer and winter) deserts; and a North-to-South winter precipitation gradient with varying predictability. One population was sampled in the eastern Mojave Desert at the Mojave Desert National Preserve, California, located in the Clark Mountains Wilderness Area. Five populations were sampled in the Sonoran Desert: one was located in the Arizona Upland subdivision of the Sonoran Desert in Organ Pipe National Monument, Arizona, while the other four populations were sampled in the Lower Colorado Valley subdivision of the Sonoran Desert in Ocotillo Wells State Vehicular Recreation Area in California; the Pinacate Biosphere Reserve in Sonora, Mexico; Valle de Las Tinajas in Baja California, Mexico, and in Calamajué, Baja California, Mexico (Fig. 2, Table 1). Plants belonging to the 2009–2010 growth season were collected once the plants were dry, in summer 2010.

MORPHOMETRIC MEASUREMENTS

Sixty spineflower individuals (10 per population) were soaked in water for 10 min to facilitate detachment of the involucre. Involucre sampling design was as follows: within an individual plant, three to four involucre were obtained from nodes of the different branches (i.e. tertiary, secondary and central), and this sampling

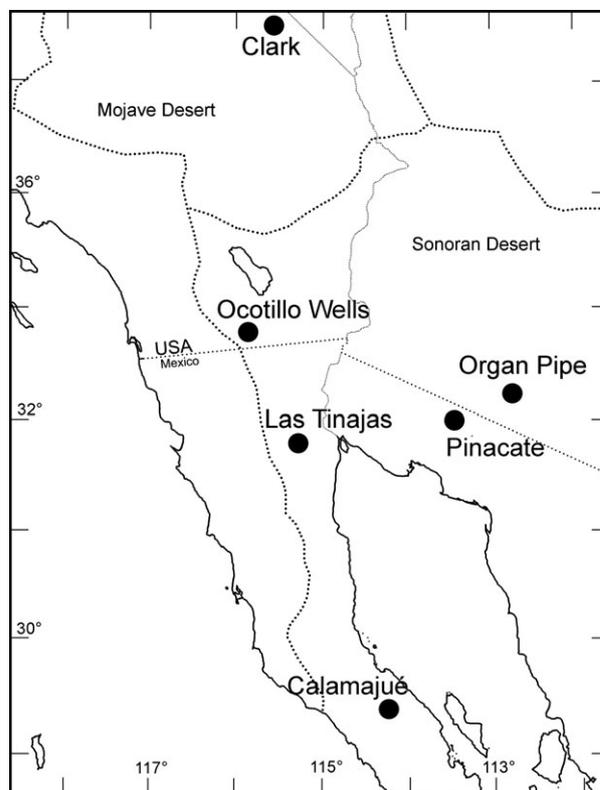


Fig. 2. Collection sites of *Chorizanthe rigida* populations in the Sonoran and Mojave desert regions (see Table 1 for location details).

was repeated at three plant levels (level 1 being the closest to the root and level 3 the one closest to the plant's tip). Because the branching pattern of these plants is determinate, there was no difference between sites in the proportion of involucre produced within different branches. The size of the plant's canopy (mm) and the branch position and level from which each involucre was collected were recorded. A total of 27–36 involucre were collected from each individual plant. Involucre images (frontal and base views, Fig. 1) were obtained using a dissecting microscope and a digital camera. The following morphometric variables were measured from the involucre images: (i) the size of the seed receptacle in the involucre (referred hereafter as 'propagule size'), measured as the projected area of the involucre's central 'belly'; (ii) involucre length, measured from the top of the central bract of the involucre to the base; and (iii) cross-sectional area of the involucre pedicel (referred hereafter as 'base area'). Areas were defined with points marked using a custom program made in MATLAB 7.5 with Image Processing Toolbox 6.0 (MathWorks, Natick, MA, USA). In order to analyse seed traits within the progeny of each single individual, the identity of the parental individuals was maintained in all morphometric measurements and subsequent analyses. We obtained the mass of propagules (involucre containing an achene) from a subsample ($n = 160$) of involucre and found a highly significant allometric correlation between propagule size and mass of the achene ($r = 0.70$; $F = 142.9$; d.f. = 1, 158; $P < 0.0001$) verifying that the morphometric variable propagule size could be used as a proxy for achene mass (referred hereafter as 'seed size').

GERMINATION EXPERIMENT

With seeds from the same sampled populations, we conducted two separate germination trials to examine the germination behaviour

Table 1. Field locations of collection sites for *Chorizanthe rigida* and nearest weather stations used for the analysis

Collection sites	Coords.	Elev. (m)	Weather station, locations and dates	Coords.	Elev. (m)
Clark Mountains Wilderness Area	35°31'32"N/115°35'19"W	1065	Mojave, CA 1948–2001	35°03'N/118°10'W	834
Organ Pipe National Monument	32°07'49"N/112°45'56"W	550	Organ Pipe Cactus Nat. Monum., AZ 1949–2009	31°57'N/112°48'W	512
Ocotillo Wells State Vehicular Recreation Area	33°09'14"N/116°09'40"W	156	Borrogo Desert Park, CA 1942–2013	33°13'N/116°24'W	245
Las Tinajas, Baja California	31°49'48"N/115°11'29"W	21	San Felipe, BC 1949–2010	31°02'N/114°50'W	20
Pinacate Biosphere Reserve, Sonora	31°51'49"N/113°26'46"W	322	Sonoyta, Sonora 1949–2011	31°52'N/112°51'W	398
Calamajué, Baja California	29°29'11"N/114°17'18"W	480	Chapala, BC 1971–2000	29°29'N/114°22'W	640

of the achenes inside the involucre (as it gets dispersed in the wild) and of the naked achenes. To test for the effect of the involucre on germination, six involucre were obtained from nodes of the central, secondary and tertiary branches to include different sizes (two small, two intermediate, and two large; Table S1 in Supporting Information). In total, 720 involucre were used from 20 individuals from the six populations. The propagules (involucre with the seed contained within the bracts) were put on trays (31 cm × 21 cm × 3 cm) filled up with soil that was watered to field capacity. Afterwards, trays were covered with germination paper (Anchor Regular Weight Seed Germination Paper, 38 lb) before sowing to be able to count seedlings and record germination with precision. Seeds were sprayed with a copper solution to prevent fungal growth. Trays were put in growth chambers (Percival Model MB-60, number 8-152-10) at 22 °C with a 12/12 h photoperiod and were watered weekly with 350 mL (corresponding to 5 mm of precipitation in the field) for 1 month, until 20 mm of simulated rainfall (the median amount of January precipitation in the regional deserts) had been reached. Germination was scored as the emergence of the radicle from the involucre and was recorded every 2 days until the end of the month.

To examine the achene germination behaviour, achenes were extracted from small, intermediate and large involucre from individuals in five *C. rigida* populations ($n = 196$ achenes, we did not have enough seeds from Organ Pipe for this experiment). Germination trials followed the same methodology described in the previous paragraph. Achenes were followed for 2 weeks, until 10 mm of simulated rainfall had been supplied (the experiment was performed in 2 weeks because similar germination percentages to the first germination experiment were reached during this period). Germination was scored as the emergence of the radicle from the achene and was recorded every 2 days until the end of the second week. Seeds were stored in dry, dark conditions in the laboratory at 20 °C and were not given any temperature treatment before the germination trials. The experiment was conducted in May 2014 (seeds of *C. rigida* often endure more than 4 years in the field within the dry maternal tissues).

A subsample of involucre and achenes ($n = 278$) was weighed to obtain the masses of the whole propagule and the achene, to verify that our propagule size category (large, intermediate, and small) implied differences in reproductive investment. Both propagule mass and achene mass increased significantly with increasing propagule size category ($F = 271.1$, d.f. 2, $P < 0.0001$ for propagule mass, and $F = 73.9$, d.f. 2, $P < 0.0001$ for achene mass; Table S1).

CLIMATOLOGICAL ANALYSIS

Long-term precipitation and temperature data were obtained from the weather stations [from NOAA in the US and from SMN (*Servicio Meteorológico Nacional*) in Mexico] nearest to the sampled *C. rigida* populations. We only used climate data recorded between 1942 and 2013; not all stations had records for the complete period, but on average we included 56 years of data (Table 1). The weather stations were located in the following sites: Mojave, California; Borrego Desert Park, California; San Felipe, Baja California; Chapala, Baja California; Organ Pipe Cactus National Monument, Arizona; Sonoyta, Sonora (Table 1).

Because of the species' long latitudinal span, temperatures – and hence evaporative demand – can differ considerably from one site to another. In order to correct for different evaporative demands, we divided each monthly precipitation value by Walter's potential evapotranspiration (PET) estimate for that month ($PET = 2 T$, where T is the monthly mean temperature; Walter 1968), to get a measure of effective moisture available for the plants. For example, an effective precipitation (EP) value of 0.3 for a given month indicates that the precipitation that fell during that month covered only 30% of the plant's estimated water demand. Before doing this transformation, we validated Walter's model by regressing pan evaporation data (Evaporation data from SMN weather stations, data set included the same years as precipitation data) as a proxy of PET, against Walter's estimated PET for the four different weather stations within the study region that have evaporation data (Sonoyta: $r^2 = 0.88$; San Agustín: $r^2 = 0.89$; San Felipe: $r^2 = 0.92$; and San Luis Gonzaga: $r^2 = 0.81$; $P < 0.0001$ in all cases). When the altitude of the weather station differed from that of the site, mean temperature values were corrected by elevation, assuming an adiabatic gradient of 0.8 °C for each 100 m.

The proportion of summer precipitation was calculated by dividing the June–August EP by the annual total EP. The two sites that had less than 3% summer EP were classified as winter-rain locations (Clark and Las Tinajas), while all other sites, which had more than 8% of summer EP, were classified as having a bi-seasonal rainfall distribution. Summer precipitation in San Felipe, the nearest weather station to the Las Tinajas site, is 8% of the annual total EP. The Las Tinajas site, however, is located in the rainshadow of Las Tinajas range (500 m in elevation), where the summer monsoon coming from the south-east rarely reaches. By analysing paired weather stations in the peninsula placed on both the east and west side of ranges like Las Tinajas, we calculated that a 500-m-high range can intercept as much as 70% of incoming monsoonal precipitation, leaving only 30% to fall on

the western rainshadow slope (Ezcurra, Mellink & Martínez-Berdeja). For this reason, we corrected the amount of summer precipitation for Las Tinajas by reducing the San Felipe summer rainfall by 70% and estimated that monsoon rainfall in this station is c. 2.4% of the annual total. Finally, in order to get an estimate of the unpredictability of winter rainfall in each site, we calculated the interannual coefficient of variation ($cv = \text{variance}/\text{mean}$) of total winter effective precipitation.

STATISTICAL ANALYSES

A total of 1921 involucre from 60 individuals were sampled for the morphometric experiment (Las Tinajas, 316; Clark, 336; Organ Pipe, 317; Ocotillo Wells, 321; Calamajué, 314; and Pinacate, 317). In order to improve normality in the error distribution and linearity in the trait responses, morphometric variables (propagule size, involucre length, and involucre base area) were log-transformed before analysis. For models with multiple predictors (ANCOVAs and multiple regressions), we selected the best model using both the values of partial F -tests and Akaike Information Criterion (AIC). All analyses were performed using the R v.3.0.1 (R Development Core Team 2013).

We used an ANCOVA design (by means of the LM function in R) to test whether involucre base area differed as a function of seasonal rainfall pattern. Our dependent variable was involucre base area (mm^2), and our independent variables were precipitation pattern (fixed factor with two categories: winter vs. bi-seasonal) and three covariates, including (i) plant canopy width, (ii) branch hierarchy where each involucre was found (central, tertiary, secondary) and (iii) involucre length. Site was included as a fixed effect nested within precipitation pattern, and individual plants were nested within site. Bartlett's test was performed to verify homogeneity of variances.

To analyse the effect of site on propagule size, we used a linear model with seed size as our dependent variable and two main effects: sites and individuals nested within sites. Thus, we were able to partition the observed variance in propagule size into three sources (i) between sites (i.e. among populations), (ii) within sites (within populations) and (iii) within individuals. We were not able to test for differences in mean propagule size between sites because the model failed Bartlett's test for homogeneity of variances, indicating that the variances in seed size differed significantly between sites. We then used linear regression to test whether there was a relationship between mean within-individual variance in propagule size at each site with the coefficient of variation of winter effective precipitation at the site.

The effect of propagule size and seed size on seed germination was analysed using a generalized linear model for proportions (logistic model by means of the GLM function in R with logit link) with the proportion of (i) germinated propagules and (ii) germinated seeds as dependent variables and two factors as predictors: (i) size of the propagule or seed (a factor with three levels, small, intermediate and large) and (ii) site (a categorical factor with six site categories for the propagule germination experiment and five for the seed germination experiment). Finally, the effect of winter rainfall on total germination at each site was analysed using a logistic regression model with the proportion of germinated seeds as the dependent variable and winter precipitation as predictor, measured as (i) mean winter effective precipitation and (ii) the frequency of months in which rainfall exceeds evapotranspiration.

Results

INVOLUCRE BASE AREA AND RAINFALL SEASONALITY

There was a significant effect of precipitation pattern (winter vs. bi-seasonal) on involucre base area: Populations experiencing almost exclusively winter precipitation had a

significantly ($P < 0.0001$) smaller base than those under a bimodal rainfall distribution pattern (Fig. 3, Table S2). Two within-individual covariates (branch hierarchy and involucre length) were related to the area of the involucre base (Table S2). There was a significant, but quantitatively small ($r^2 = 0.004$), effect of the plant's canopy width on the involucre's base area (Table S2). Some interaction terms were also significant, but their contribution was quantitatively negligible ($r^2 < 0.001$ in all cases, Table S2). The final model included the effect of precipitation pattern, branch hierarchy and involucre length (cumulative $r^2 = 0.80$) as predictors of involucre base area (Table S2). The variances of the involucre bases did not differ significantly among sites, except for Calamajué, a site on the southern edge of the species' distribution had variation in base area significantly larger than the rest.

THE VARIANCES OF PROPAGULE SIZE AND WINTER RAINFALL

There were significant differences in the variances of propagule size among sites (Bartlett's $K^2 = 180.6$, d.f. = 5, $P < 0.0001$). The nested ANOVA showed that within-individual sum of squares of propagule size accounted for more than 90% of within-site variation, indicating that variation in seed size within each site is a result of variation in propagule size within the individual plants. In some sites, individuals produced propagules that were highly variable in size, while in other sites, the variation in propagule size within the individuals was significantly lower. The variation observed in propagule sizes within individuals at each site was significantly correlated with the coefficient of variation of winter effective precipitation of the site ($r = 0.88$, $P = 0.02$; Fig. 4).

PROPAGULE SIZE AND GERMINATION

We found a significant and negative relationship between propagule size and germination in all sites except Ocotillo

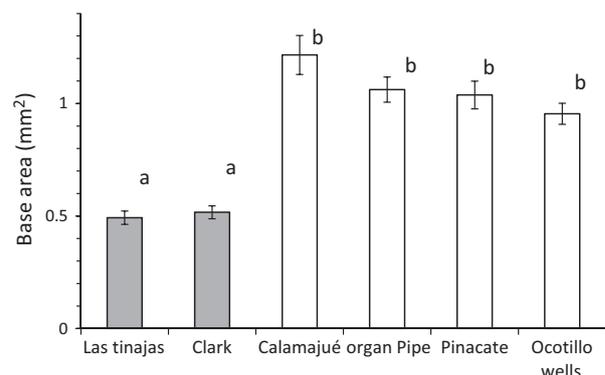


Fig. 3. Involucre base area (mm^2 , $\bar{x} \pm \text{SE}$) in each study site. Same letters above bars indicate sites that do not differ significantly. Sites with winter rains only (Las Tinajas and Clark; grey bars) have significantly smaller involucre bases than bi-seasonal sites with summer showers (Calamajué, Organ Pipe, Pinacate, and Ocotillo Wells; white bars).

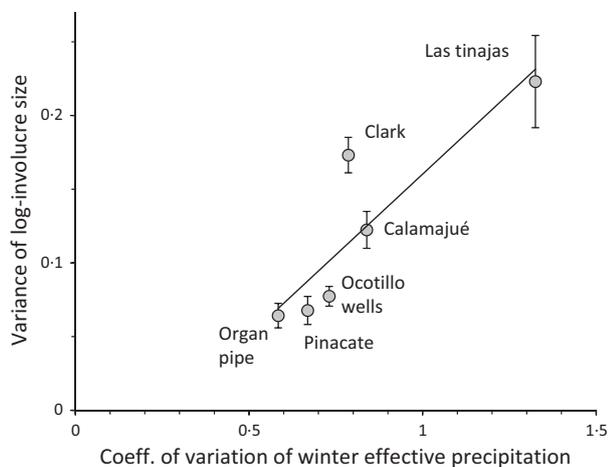


Fig. 4. Correlation between the variance of log-transformed propagule size and precipitation variability (measured as the coefficient of variation of winter effective precipitation) for the six study sites ($r = 0.88$, d.f. 4, $P = 0.02$).

($\chi^2 = 7.8$, d.f. 2, $P = 0.02$). After a month of watering 5 mm per week (totalling 20 mm of simulated precipitation, or an EP value of 0.45), germination in small propagules was significantly higher than in the larger ones, with medium propagules having intermediate germination values (Fig. 5). In the Ocotillo site, we found a significant interaction effect between site and propagule size ($\chi^2 = 23.1$, d.f. 10, $P = 0.003$) and in contrast with all other sites, larger propagules had significantly more germination than the smaller ones (0.48 ± 0.08 vs. 0.23 ± 0.07 , respectively; $P = 0.02$).

After receiving a cumulative total of 20 mm of water, we found significant differences in propagule germination between sites ($\chi^2 = 112.3$, d.f. 5, $P < 0.0001$). The differences in observed germination between sites were significantly but negatively related to the mean winter effective rainfall of each site (logit regression model: $\chi^2 = 48.1$, d.f. 1, $P < 0.0001$; Fig. 6) and to the frequency of winter months in which rainfall exceeds evapotranspiration (logit model: $\chi^2 = 63.1$, d.f. 1, $P < 0.0001$), two measures of the general winter rainfall conditions.

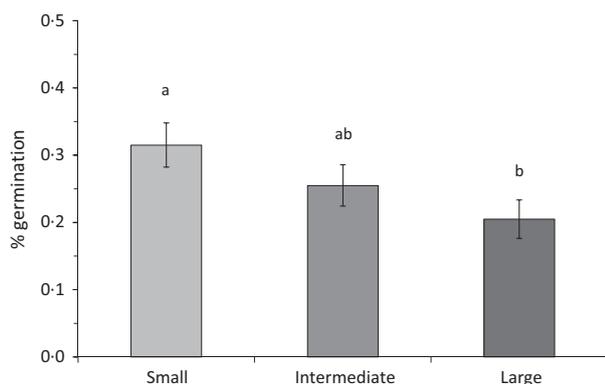


Fig. 5. Per cent germination of small, intermediate and large involucres (different letter labels indicate significant differences between groups at $P < 0.05$).

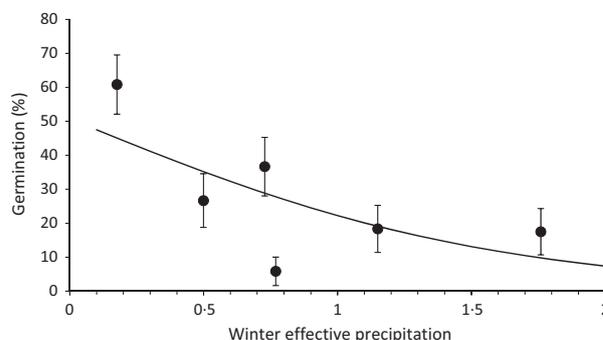


Fig. 6. Logistic regression model between per cent germination and mean winter effective precipitation at each site ($r^2 = 0.35$; $\chi^2 = 48.1$, d.f. 1, $P < 0.0001$).

In contrast with whole propagules, we did not find a significant effect of seed size on bare-achene germination after 2 weeks of watering 5 mm per week (totalling 10 mm of simulated precipitation) and we did find a significant effect of site ($\chi^2 = 19.9$, d.f. 4, $P = 0.0005$) on germination. These results suggest that the observed differences in propagule germination within each site are given by the involucre encasing the achene or seed.

Discussion

THE SUMMER MONSOON: ADAPTATION TO BI-SEASONAL RAINFALL PATTERNS

The base area of involucres in spineflower plants growing in sites with summer rainfall was significantly larger than those in winter-rain sites. The twofold difference in base areas from the small-based involucres at Clark and Las Tinajas compared to the broad-based involucres in Ocotillo Wells, Organ Pipe, Pinacate and Calamajué suggests that different populations of *C. rigida* have evolved biomechanical characteristics adapted to local rainfall seasonality patterns. Biomechanical experiments performed on this species confirmed that larger pedicels require more force for detachment and that weathering and repeated wetting lowers the involucres' breaking force (Martínez-Berdeja *et al.* 2014).

Monsoon rains reach the Sonoran Desert from the south, following summer low-pressure centres along the Pacific coasts of Mexico, and may bring brief, but intense, showers to the desert (Caso, González-Abraham & Ezcurra 2007). For topographic and latitudinal reasons, in two of our study sites summer rains rarely, if ever, occur; but in the four sites exposed to the arrival of monsoons the false cue of a summer rainstorm could trigger the release of seeds into the environment at a time when high temperatures would not allow *C. rigida*, a strict winter annual, to establish successfully. When winter rains arrive the following year, the involucres in the winter-rain deserts undergo wetting for the first time, while the ones in bi-seasonal deserts have already undergone one or more wetting events.

THE WINTER RAINS: SEED SIZE VARIABILITY AS AN ADAPTATION TO WITHIN-SEASON UNPREDICTABILITY

In some sites, seed size was extremely variable while in others it was more uniform. We found a strong correlation between variation in winter effective precipitation, a measure of environmental unpredictability, and within-individual variance in seed size (Fig. 4), that is the more unpredictable the site, the higher the variation in seed size. Because larger seeds have higher survival rates during unfavourable years (Leishman & Westoby 1994; Lloret, Casanovas & Peñuelas 1999; Leishman *et al.* 2000; Imbert 2002; Moles & Westoby 2004; Larios *et al.* 2014) but more abundant, smaller seeds will yield more seedlings in good years, it has been shown that producing many small seeds and some large seeds within the same individual can increase the chances of long-term survival in highly unpredictable environments (Simons & Johnston 2006; Olofsson, Ripa & Jonzén 2009 and a critical rebuttal by Rees *et al.* 2010; Volis & Bohrer 2012). However, whole life cycle survival experiments beyond germination trials are still needed in order to ascertain the effect of seed size variation on overall plant fitness in *C. rigida*.

THE EFFECT OF SITE AND PROPAGULE SIZE ON GERMINATION

After adding 20 mm of simulated monthly rainfall (equivalent to an effective precipitation value of 0.45), the germination of propagules coming from extremely arid sites was significantly higher than that observed in propagules collected in relatively moister deserts. In agreement with Clauss & Venable (2000), this shows that, at the population scale, the threshold for a favourable winter season is site-dependent. For example, in the Mojave, 20 mm of winter rain in a month is below average and represents a dry year while in Las Tinajas it would represent an extraordinarily wet month.

Our germination experiment showed significant differences in germination percentages between different propagule sizes: germination in small propagules was significantly higher than in larger ones. We also found that, once the achenes were separated from their involucre, there was no significant effect of seed size on germination, suggesting that the differences in whole-propagule germination are regulated by the involucre enclosing the seed. Variability in propagule size implies increased variability in germination within an individual plant, which could have an effect on the plant's fitness (Imbert 2002; and references therein). Our results suggest that smaller spineflower propagules are more risk-prone in their rapid germination response while larger propagules demand a higher water threshold for germination. At the first rain pulse, smaller propagules attached by weak pedicels will fall and germinate while the larger propagules, with larger base areas, will remain attached to the mother plant (Martínez-Berdeja *et al.* 2014) or, if they become detached, will not germinate as readily.

CONCLUSIONS: THE ECOLOGICAL SIGNIFICANCE OF SEROTINY IN *CHORIZANTHE RIGIDA*

Only a few studies (Halkett *et al.* 2004; Wong & Ackerly 2005) have addressed the evolution of traits that allow plants to simultaneously deal with different levels of environmental variability. Our study provides empirical evidence that different scales of rainfall variation influence and shape the propagule morphology of the serotinous *C. rigida*, allowing it to display an integrated strategy to cope with both systematic and random drivers of rainfall. In summary, our results suggest that, while changes in mean environmental conditions from one site to another are met by systematic changes in the mean values of the plant's morphology and germination response, the largely unpredictable variation in winter precipitation from site to site is met by an increased within-individual variance in propagule size and germination.

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Data accessibility

Morphometric data, germination data and seed size data are deposited in the Dryad Digital Repository (doi: 10.5061/dryad.qj5ck) (Martínez-Berdeja, Ezcurra & Torres 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Mass (mean \pm SE) of propagules and achenes used for the germination experiment, and mass (mean \pm SE) of achenes measured from a subsample of propagules.

Table S2. ANCOVA table showing the effect of different factors on involucre base areas.