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Priming effect on seed germination: Is it always positive for cacti species?

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ABSTRACT

In drylands, cacti seeds experience high variability amounts of precipitation throughout a year. Seeds undergo hydration and dehydration cycles (or priming) which can increase the proportion or the speed of germination. However, these advantages differ among cacti. In this study, we test the effect of priming on the germination percentage and the mean germination time of two cacti species. We show that priming does not increase the germination percentage for these cacti species, but does reduce the time to germination. We suggest that the response of cacti seeds could be an adaptation to their habitat and microhabitat conditions.

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1. Introduction

In arid environments, the variability in water availability during the rainy season causes seeds to experience hydration and dehydration cycles (Dubrovsky, 1996). This process known as priming, causes a seed to initiate the germination process without completing it. Priming promotes the synthesis of late embryogenic abundance proteins (LEA), which increases the tolerance to desiccation in seedlings (González-Zertuche et al., 2001), and changes the protein content in primed seeds (López-Urrutia et al., 2013; Santini and Martorell, 2013).

Natural priming has been shown to increase germination synchrony, rate and final percentage in species that form seed banks (either aerial or in the soil); (González-Zertuche et al., 2001; Santini and Martorell, 2013). However, in cacti species, priming effects can be either positive (Contreras-Quiroz et al., 2016a,b; Dubrovsky, 1998, 1996; Sanchez Soto et al., 2005; Santini and Martorell, 2013; López-Urrutia et al., 2013), negative (Contreras-Quiroz et al., 2016a,b; Sanchez Soto et al., 2005; López-Urrutia et al., 2013), or neutral (Sanchez Soto et al., 2005).

In this study, we assessed the germination speed and percentage of *Echinocereus engelmannii* and *Ferocactus hamatacanthus*. Seeds of both cacti species possess characteristics which makes them likely to form a seed bank. These traits are: 1) small or medium sized seeds, 2) rounded form and, 3) positive photoblastism (Rojas-Arechiga and Batis, 2001). Although no seed bank studies are available for either of these species, soil seed bank formation has been reported for the genus *Ferocactus* (Bowers, 2000). Given the variable climate conditions experienced by both species, and that they are likely to form seed banks in which a fraction of seeds can be protected and primed, we predict that seed priming should have a positive effect on the germination percentage and speed in both species.

2. Material and methods

2.1. Seed collection

In 2009, mature fruits were collected from at least 10 plants for each species. Fruits of *E. engelmannii's* were collected from the Sonoran Desert in June, whereas *F. hamatacanthus*' seeds were collected from the Chihuahuan Desert in October. Seeds were

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stored in paper bags at room temperature (20 ± 2 °C) until January 2011, when the experiment began.

2.2. Species description

2.2.1. Echinocereus engelmannii (Parry ex Engelm.) Lem.

Plants can have 3 to 60 green cylindrical stems, with 10–13 ribs. Stems arise near the base and form clumps to nearly 1 m. Plants are 5–60 cm in height, mostly erect and from 3.8 to 7.8 cm in diameter. Central spines (2–7) are angular, and can be straight or twisted. The radial spines (6–14) are up to 8 cm long. Flowers have a short funneliform and varied in colour from purplish red to magenta to lavender. Fruits are 3 cm long, red, juicy and edible with deciduous areoles. Seed weight is 0.87 mg (Royal Botanic Gardens Kew, 2017). Distribution: Baja California, Baja California Sur and Sonora (Anderson, 2001).

2.2.2. Ferocactus hamatacanthus (Muehlenpf.) Britton & Rose

Plants are mostly solitary, with globose or cylindrical stems. Stems can be up to 60 cm in height and 30 cm in diameter. Ribs (12–17) are tuberculated, narrow and rounded. Central spines (4–8) and radial spines (8–20) are brownish red. Funneliform flowers are from 6 to 10 cm in length and 6.5–7.5 cm in diameter. They are either completely yellow or yellow with red throats. Fruits are ovoid or oblong, pinkish red to red, and between 2.5 and 5 cm long (Anderson, 2001). They may remain attached to the stem (MC Mandujano, personal communication). Seeds are medium-sized and weigh 0.58 ± 0.48 mg (Rojas-Aréchiga et al., 2013). Distribution: Mainly in the Chihuahuan Desert (Anderson, 2001).

2.2.3. Precipitation

The rainfall distribution in these deserts is highly variable, with some months being extremely dry (<1.6 mm) and despite other being relatively wet (>100 mm; Fig. 1). We calculated the monthly expectation and variability in rainfall in each desert by log +1 transforming the precipitation levels and calculating the mean the confidence intervals for each month over 10 years.

2.3. Hydration-dehydration curves

2.3.1. Hydration process

For each species, we measured the dry weight of five groups of five seeds. After this, each group of seeds was placed into Petri dishes with wet filter paper as a substrate. Each seed group was weighed every 15 min during the first 12 h to register the change in weight using an analytical balance (Sartorius CP225D). Seeds were subsequently weighed every 12 h until there was no change in the total weight.

2.3.2. Dehydration process

The groups of seeds that experienced the hydration phase were placed in Petri dishes with dry filter paper. These groups of seeds were weighed every 15 min to record water loss, until the initial weight was achieved.

2.3.3. Hydration-dehydration cycles

Based on the hydration-dehydration (HD-DH) curves (data not shown), we established one cycle as: 4 days of hydration and 1 day of dehydration. This way seeds get fully hydrated, but do not have enough time to germinate. Seeds were exposed to zero (T0 or control), one (T1), two (T2), and three (T3) HD-DH cycles.

2.4. Seed germination

For each species, 400 seeds were subdivided between the four priming treatments (T0, T1, T2, T3). The 100 seeds were subdivided into five replicates each containing 20 seeds. Seeds were sown on agar 1% and placed in a germination chamber (Lab-Line 844 L) with a photoperiod of 12/12 h and a constant temperature of 25 °C, which is the optimum temperature for germination reported for cacti (Nobel, 1988; Rojas-Aréchiga et al., 1998). Seed germination at each priming treatment was recorded every two days, for 30 days. We assumed that non-germinated seeds after that period were unviable. Petri dishes were randomly moved every third day, in case of any spatial differences in light availability.

2.4.1. Data analysis

A dose response analysis was performed using the "drc" package (Ritz et al., 2015) to estimate three parameters: 1) the time until 50% of the seeds germinate ($t50$), 2) the slope around $t50$ (b), and 3) the maximum proportion of seeds that germinated at each treatment ($Gmax$). The model considers the event as the day on which germination was recorded, and uses a log-logistic distribution. All the statistical analyses were carried out in R Development Core

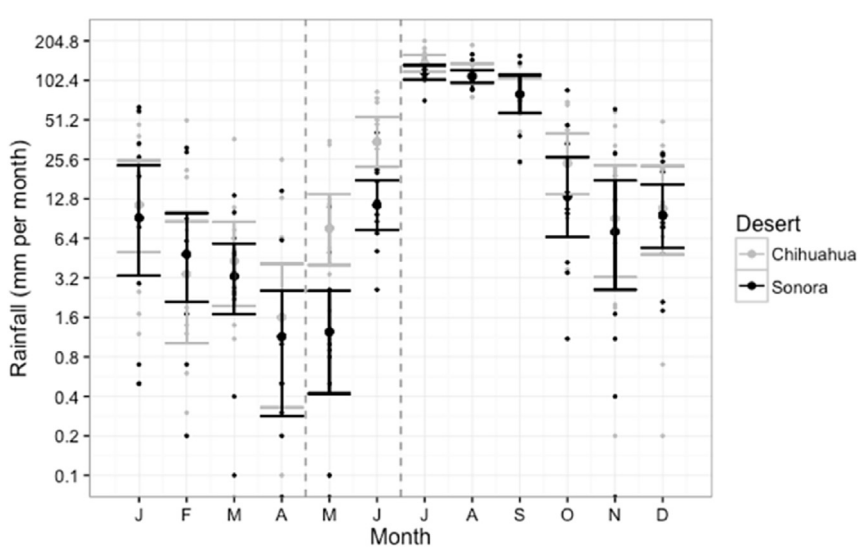

Fig. 1. Rainfall per month at the Chihuahua and Sonora Deserts. We show 10 years of data (2004–2014), where each small point represents the monthly total precipitation for a specific year. Mean (large points) and confidence intervals (error bars) were calculated on the log+1 transformed scale.

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