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Short communication

Is seed hydration memory dependent on climate? Testing this hypothesis with Mexican and Argentinian cacti species

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ABSTRACT

Seed hydration memory has been observed in some cacti species, but it remains unclear how general this process is. Our hypothesis is that hydration memory of cacti seeds depends on the environmental conditions where the species occur. To test this we used seven species from the Argentinian Córdoba Mountains (mesic environment): *Gymnocalycium capillense*, *Parodia mammulosa*, *Echinopsis candicans*, *Gymnocalycium bruchii*, *Gymnocalycium mostii*, *Gymnocalycium quehlianum* and *Gymnocalycium monvillei*, and two species from the Mexican Chihuahuan Desert (dry environment): *Echinocactus platyacanthus* and *Ferocactus pilosus*. Four hydration (hours)/dehydration (days) treatments were applied: T1 = 24 h/5 days, T2 = 3 consecutive cycles of 24 h/5 days, T3 = 72 h/5 days and T4 = untreated seeds. The response variables were final seed germination (%) and mean germination time (t_{50}). The two Mexican species responded to at least one treatment by increasing their germination and decreasing their mean germination time. For the Argentinian species, only *G. mostii* increased its germination in T1 and T2 while t_{50} was reduced in three species after hydration-dehydration treatments. For *G. monvillei* the shortest germination time occurred in T2 and T3, and for *G. capillense* and *G. quehlianum* t_{50} was shortest in T3. Hydration memory seems more common in arid environments, but it is also present in more mesic ones.

Cactus seeds on the soil surface experience hydration-dehydration (HD) cycles as a result of the precipitation patterns typical of desert environments. Dubrovsky (1996), in a study on seeds of three cactus species from the Sonora Desert in Mexico, reported reduced germination times after treating the seeds with HD cycles. The results suggest the presence of a "hydration memory," defined as the ability of seeds to maintain physiological changes produced during hydration, such as differential protein expression (López–Urrutia et al., 2014), through discontinuous dehydration periods. The hydration memory phenomenon is not unique to cacti, as it is also common in non-succulent and non-desert species (Dubrovsky, 1996). Although this process was characterized in cacti almost 20 years ago, so far there is little evidence about how general this trait is, since the few existing studies address only a small number of species (Dubrovsky, 1996, 1998; McDonough, 1964; Rito et al., 2009; Sánchez–Soto et al., 2005; Santini and Martorell, 2013, Contreras et al., 2016), mostly from arid areas.

Intermittent hydration processes stimulate changes in the embryo that the seed "memorizes" during periods of drought, and when moist conditions occur, faster germination is promoted (Dubrovsky, 1996). Germination speed has been shown by several authors in the form of mean germination time (t_{50}) when studying the germination dynamics of the species, as it reflects the behavior of a significant percentage of seeds (Pérez-Sánchez et al., 2011).

In desert environments, availability of water in the soil plays an important role as rainfall is usually unpredictable both in quantity and the time of the year it occurs (Mazzola et al., 2013). Therefore, seeds should take advantage of the rare moments when moisture is adequate to germinate rapidly (Gutterman, 1993). Although cacti live mostly in the arid environments of North and South America, many species occur in moist environments (Saraiva and Souza, 2012; Gurvich et al., 2014). In these environments, hydration

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memory would probably not be an important process in seed germination. However, so far no study has analyzed this process in cactus species from humid or sub-humid areas such as the Córdoba Mountains in Central Argentina.

The aim of this study was to determine whether hydration memory is a condition always present in cactus seeds. To do this, imbibition and dehydration times were determined to identify the different phases of water absorption kinetics, as well as the germination percentage and mean germination time (t_{50}). It was hypothesized that hydration memory of cacti seeds depends on the environmental conditions where the species occur.

Nine cactus species were analyzed: one globular and one columnar from a semi-desert area in northeastern Mexico, and seven globular species from a sub-humid area of central Argentina. Seeds of the nine species were collected in the field from at least three mother plants. The seeds were cleaned and stored at room temperature in sealed plastic bottles forming lots of approximately 2000 seeds.

The seeds of *Echinocactus platyacanthus* (Link & Otto) and *Ferocactus pilosus* (Galeotti) Werderm were collected in September 2012 in the south of the Chihuahuan Desert in Mexico, where the annual rainfall regime is less than 500 mm (Espinosa et al., 2008). In Argentina, the seeds were collected in January 2014 in the Córdoba Mountains where the climate is temperate humid to subtropical (Capitanelli, 1979), with mean annual rainfall of around 800 mm, most of which occurs from October to April (de Fina, 1992). The analyzed species were *Gymnocalycium capillense* (Schick) Hosseu, *Parodia mammulosa* (Lemaire) Taylor, *Echinopsis candicans* (Salm–Dyck) Hunt, *Gymnocalycium bruchii* (Spegazzini) Hosseus, *Gymnocalycium mostii* (Gürke) Britton & Rose, *Gymnocalycium quehlianum* (F. Haag ex Quelch) Vaupel ex Hosseus and *Gymnocalycium monvillei* (Lem.) Britton & Rose.

A sample of 20 seeds was randomly chosen, weighed and placed in a Petri dish with distilled water to hydrate (Phase I). Seed weight was measured every hour until it stabilized, reaching maximum imbibition (Phase II). Seeds were then dehydrated at room temperature on filter paper and the weight was recorded every hour. Maximum imbibition and drying times of seeds were used to define HD cycles in order to prevent seeds germinating during treatments.

The applied treatments were: **T1:** a 24-h hydration cycle and five days of desiccation, **T2:** three 24-h cycles with five days of dehydration between each cycle, **T3:** a 72-h cycle and five days of dehydration and **T4**: the control (untreated seeds). The treatments were carried out in germination chambers at a constant temperature of 25 °C, with 12 h of light and 12 h of darkness, in containers with distilled water. The treatments were applied in 2014 in both countries.

Seeds were placed in Petri dishes, where 16% bacteriological agar was added as a source of constant moisture. The seeds were germinated in February of 2014 in México and in August of 2014 in Argentina. Ten seeds for each species were placed in each Petri dish, with five replicates per species in each treatment. Germination was measured daily for 30 days and was determined after protrusion of the radicle.

Mean germination time (t_{50}) indicates the number of days it took for 50% of the germinated seeds to germinate during the 30 days the experiment lasted. t_{50} was calculated only for species showing more than 20% germination in at least one of the treatments, to avoid unrepresentative results. Under this criterion *P. mammulosa* was excluded. This variable was classified according to Jurado and Westoby (1992) as follows: fast when 50% of germinated seeds was reached by day 3, medium when 50% of germinated seeds was reached between days 4 and 6, and slow when 50% of the germinated seeds was reached after day 6.

Normality of the data was analyzed by the Kolmogorov–Smirnov statistical test. Percentage values were normalized with arcsine and to log 10 for nominal values (t_{50}) (Sokal and Rohlf, 1995). Analysis of variance ($P \leq 0.05$) was performed. Data from each species were analyzed separately. By applying Levene's test, homogeneity of variances was determined and a Tukey (homogeneous variances) or Games-Howell (non-homogeneous variances) test was applied. The analyzed factors were the four HD treatments and the dependent variables were germination percentage and mean germination time (*t50*). The analyses were performed using SPSS STATISTICS 18® software.

The average weight of the seeds of Chihuahuan Desert cactus species was 1.5 ± 0.01 mg, and 0.9 ± 0.01 mg for the seeds from the Córdoba Mountains species.

In three species the germination percentage was higher in treated than in untreated seeds. *F. pilosus* had a higher germination percentage under T2 and T3, *G. mostii* germinated more under T1 and T2, and *E. platyacanthus* had more germinated seeds in T1, T2 and T3 than in the control group (Table 1). Similar results have been found when HD treatments were applied to *Pachycereus pecten-aboriginum* (Dubrovsky, 1996) and *Ferocactus peninsulae* (Dubrovsky, 1996; López–Urrutia et al., 2014) both from Baja California Sur, Mexico, as well as in *Carnegiea gigantea* and *Stenocereus thurberi* from the Sonoran Desert (McDonough, 1964), *Cereus jamacaru* from the Caatinga, Brazil (Rito et al., 2009), and *Mammillaria hernandezii* from the Tehuacán-Cuicatlán Valley, Oaxaca, Mexico (Santini and Martorell, 2013). Conversely, germination percentages in *G. capillense*, *G. monvillei* and *G. bruchii* were higher in untreated seeds compared to those treated with an HD cycle. The remaining three species, *E. candicans*, *P. mammulosa* and *G. quehlianum*, showed no differences between treatments, similar to findings by Sánchez-Soto et al. (2005) for the cacti *Mammillaria mazatlensis*, *Stenocereus alamosensis* and *S. thurberi* from Mazocahui Island in northern Sinaloa, Mexico.

Mean germination time (t_{50}) is an indicator of germination speed (Jurado and Westoby, 1992). Mean germination time was highly variable among species after HD treatments. For *F. pilosus*, t_{50} was 6.0 ± 0.4 days with T2, whereas for *G. monvillei* the shortest germination time was with T2 and T3, and for *G. capillense* t_{50} was shortest with T3. These differences meant that germination occurred six and two days earlier, respectively. For *G. quehlianum* t_{50} was two days earlier with T3, while in *E. platyacanthus* it was six days earlier in T1 and T2 compared to the control (Table 2). Results of t_{50} in these five species were similar to those found in seeds of *P. pecten-aboriginum* and *F. peninsulae* (Dubrovsky, 1996), *S. thurberi* (Sánchez-Soto et al., 2005), as well as *C. jamacaru* subsp. *jamacaru* from the Caatinga, Brazil (Rito et al., 2009) where t_{50} was significantly lower in the seeds treated with HD cycles than in the untreated seeds.

Based on the classification system suggested by Jurado and Westoby (1992), in the four treatments, four species had a moderate germination speed. In at least one of the HD treatments of the four other species, the speed was slow, as was the case in all the treatments for *E. platyacanthus* where it was slow. Only one cactus species from the Córdoba Mountains (*G. mostii*) had a higher germination percentage when treated with HD cycles but treatments did not have any effect in the germination speed of this species. However, the two species tested from the Chihuahuan Desert (*E. platyacanthus* and *F. pilosus*) showed a higher germination percentage and a slower germination speed after HD treatments. According to the germination speed classification system described by Jurado and Westoby (1992) high germination tends to be associated with moderate and slow germination speed, which is consistent with the results obtained in *F. pilosus* and *E. platyacanthus*, which had the highest germination percentages and a slow germination speed in most treatments, whereas in the species from the Córdoba Mountains the speed was moderate and