Potential impact of global warming on seed bank, dormancy and germination of three succulent species from the Chihuahuan Desert

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Abstract

We assessed inter-seasonal dynamics of seed banks, dormancy and seed germination in three endemic Chihuahuan Desert succulent species, under simulated soil warming conditions. Hexagonal open top-chambers (OTCs) were used to increase soil temperature. Seeds of *Echinocactus platyacanthus* (Cactaceae), *Yucca filifera* and *Agave striata* (Asparagaceae) were collected and buried within and outside OTCs. During the course of one year, at the end of each season, seed batches were exhumed to test viability and germination. Soil temperature in OTCs was higher than in control plots. *Yucca filifera* seeds always had high germination independently of warming treatment and season. *Agave striata* seeds from OTCs had higher germination than those from control plots. *Agave striata* exhibited low germination in fresh seeds, but high germination in spring. Seeds from this species lost viability throughout the experimental timeframe, and had no viable seeds remaining in the soil. *Echinocactus platyacanthus* showed high germination in fresh seeds and displayed dormancy cycling, leading to high germination in spring, low germination in summer and autumn, and high germination in winter. Germination of this species was also higher in seeds from OTCs than those from control plots. *Echinocactus platyacanthus* formed soil seed banks and its cycle of inter-seasonal dormancy/germination could be an efficient physiological mechanism in a climate change scenario. Under global warming projections, our results suggest that future temperatures may still fall within the three studied species' thermal germination range. However, higher germination for *A. striata* and *E. platyacanthus* at warmer temperatures may reduce the number of seeds retained in the seed bank, and this could be interpreted as limiting their ability to spread risk over time. This is the first experimental study projecting an increase in soil temperature to assess population traits of succulent plants under a climate change scenario for American deserts.

Introduction

Soil seed banks play a crucial role in the population dynamics of many plant communities (Baskin and Baskin, 1998). They guarantee natural regeneration and persistence of ecosystems because soil seed banks provide a stock of viable seeds either on the surface or buried in the soil (Cheib and Garcia, 2012), mainly in habitats with variable disturbance regimes and unpredictable environmental conditions (Fenner and Thompson, 2005), such as arid environments (Montiel and Montaña, 2003; Jurado and Flores, 2005; Cheib and Garcia, 2012; Álvarez-Espino *et al.*, 2014). Global climate models forecast that arid environments might experience both increased temperatures and a decline in frequency and magnitude of rainfall events (IPCC, 2013, 2014). To understand the long-term effects of climate change in plant species, it is necessary to link future environmental changes to mechanisms that control plant regeneration such as seed germination, dormancy (Ooi *et al.*, 2009, 2012; Cochrane, 2016, 2017) and soil seed banks.

Succulent species are common in arid and semi-arid American environments (Reyes-Agüero *et al.*, 2000; Ortega-Baes and Godínez-Alvarez, 2006); population studies for these plants are common (Bowers, 2000, 2005; Montiel and Montaña, 2003; Cheib and Garcia, 2012; Álvarez-Espino *et al.*, 2014). Álvarez-Espino *et al.* (2014) found high germination after dormant seeds of *Stenocereus stellatus* (Cactaceae) were buried for 6 months. However, the potential impact of small temperature increases, as projected by global warming, on seed germination and soil seed banks has been poorly assessed (Pérez-Sánchez *et al.*, 2011).

A key factor in the demographic patterns of plants is seed dormancy (Rojas-Aréchiga and Vázquez-Yanes, 2000). It is a process where germination is prevented, to help maximize the probability to seedling establishment and spread the risk of recruitment failure (bet-hedging strategy) across time (Baskin and Baskin, 1998; Jurado and Flores, 2005) until conditions for seedling establishment are suitable (e.g. adequate moisture, light and temperature during early growth stages). Thus, dormancy is closely linked with the formation of soil seed banks (Baker, 1989).

Recent studies on the potential effects of global warming in succulent species have considered physiological (Aragón-Gastélum *et al.*, 2014), ecological (Aragón-Gastélum *et al.*, 2017), biochemical (Musil *et al.*, 2005, 2009) and human (Martorell *et al.*, 2015) aspects. Some functional traits in population and community dynamics such as the role that future temperature increases could play on seed viability, germination, dormancy and soil seed banks have been neglected.

The largest warm desert of North America is the Chihuahuan Desert (Archer and Predick, 2008) ranging from the southwestern United States to the Central Mexican Highlands. Models of global change for this region indicate an increase in summer temperatures (June–September) of 1–2°C by 2030 (Tejeda-Martínez *et al.*, 2008). This raises concerns because the desert harbours a high richness of succulent plants (Rzedowski, 1991), many of them protected by Mexican environmental laws (SEMARNAT, 2010).

Ooi (2012) highlighted that increased soil temperatures could accelerate the decline of seed viability and compromise bet-hedging strategies of species in dryland regions. Because of the crucial role that soil seed banks and dormancy might have in population dynamics in arid and semi-arid environments, our aim in this study was to explore how warmer soils could affect the seasonal dynamics and persistence of soil seed banks in three succulent species of two common plant families from the Chihuahuan Desert: *Echinocactus platyacanthus* Link and Otto form *visnaga* (Cactaceae), *Yucca filifera* Chabaud (Asparagaceae), and *Agave striata* Zuccarini (Asparagaceae). Under current climatic conditions, emergence of succulent species in the Chihuahuan Desert coincides with summer rainfall (Mandujano *et al.*, 1998).

Physiological seed dormancy is expected in these species, because it is common in their families (Baskin and Baskin, 1998). Cactus seeds can enter secondary dormancy with cues from specific conditions such as darkness (Flores *et al.*, 2006; Rojas-Aréchiga and Mandujano-Sánchez, 2017), and at specific times, according to variation of environmental factors (Álvarez-Espino *et al.*, 2014; Ordóñez-Salanueva *et al.*, 2017). Thus, some seeds of succulent species germinate in summer, the rainy season, but others can enter dormancy. Seed dormancy is considered a very common adaptive plant strategy in unpredictable and harsh environments, such as arid and semi-arid landscapes (Jurado and Flores, 2005). Improving our understanding of both the mechanistic response and the adaptive capacity of seed banks to climate change will provide a solid basis for improved predictions of future distribution of species and risk of extinction (Ooi, 2012).

Materials and methods

Studied species and plant material

The three target-species are endemic to México and widely distributed, and have been previously studied for germination traits (Jiménez-Aguilar and Flores, 2010; Pérez-Sánchez *et al.*, 2011). *Echinocactus platyacanthus* f. *visnaga* is a barrel-like cactus that can reach 2 m in height and 80 cm in diameter (Jiménez-Sierra *et al.*, 2007). This species is specially protected by the environmental laws of México (SEMARNAT, 2010) and considered as near threatened in the Red List of the International Union for Conservation of Nature (IUCN, 2014) due to over-exploitation. *Yucca filifera* is one of the largest and most common *Yucca* species; it is 9 m tall (Irish and Irish, 2000). *Agave striata* is a short rosette plant that can reach 100 cm in height and 119 cm in diameter (Irish and Irish, 2000). This species forms dense and extensive colonies even in very dry environments (Irish and Irish, 2000). *Yucca filifera* and *A. striata* are not included under any protection status (SEMARNAT, 2010), although they are widely distributed, and the impact of global change in their population dynamics is still unknown.

Seeds from *E. platyacanthus* have positive photoblasticism and small seeds (1.8 mg) (Flores *et al.*, 2011) compared with the other two species in our study. High temperatures promote seed germination for this species, as germination after exposure to 70°C for 14 days was higher than for seeds with no exposure to heat (Pérez-Sánchez *et al.*, 2011). Seeds from *Y. filifera* have neutral photoblasticism and are large (70 mg) (Flores *et al.*, 2016). *Agave striata* seeds are also neutrally photoblastic (Jiménez-Aguilar and Flores, 2010) and small (2.3 mg) (Ramírez-Tobías *et al.*, 2012).

Seed collection and storage

Ripe fruits from the three species studied were collected in the Southern Chihuahuan Desert in San Luis Potosi, Mexico in October 2012, from at least 10 mother plants for each species. This area is dominated by desert shrublands and has an annual rainfall of 300–450 mm and a mean temperature of 18–25°C (INEGI, 2002).

The harvested fruits from each species were transferred to the ecology laboratory, where seeds were removed. Seeds were left to dry and kept in paper bags for 3 months at room temperature in normal day/night conditions before sowing in the field.

Viability test

Seed viability was evaluated using a tetrazolium test (Grabe, 1970) with a solution of 2,3,5-triphenyltetrazolium at 1%. In order to evaluate initial viability, 30 seeds for each species were placed in three groups of 10 seeds. These seeds were soaked for 24 h in distilled water before being placed in the tetrazolium solution. In order to facilitate the entry of the solution into the seed, an incision was made with a scalpel, parallel to the hypocotyl axis.

Each experimental unit was a group of 10 seeds, and three groups were prepared. Seeds from each group were placed in a

beaker with 50 ml of tetrazolium solution. Each beaker was covered and wrapped with aluminum foil to maintain the seeds in darkness. Seeds were kept at 25°C for 48 h. Seeds were transversely cut with a scalpel and embryos were observed under a stereo-microscope (Motic model MAIN). The seeds showing whole red embryos without apparent damage were considered viable (Baskin and Baskin, 1998). Viability percentage was estimated for each species.

Germination test

In a second seed lot, 100 seeds of each species were selected and their initial germination assessed in a completely randomized experiment. This consisted of 10 replicates of 10 seeds placed on moistened cotton wool in Petri dishes. Petri dishes were then placed in a growth chamber set to a relative humidity of 80%, a 12 h/12 h photoperiod, and a constant temperature of 25°C. Germination was determined when radicle protrusion was at least 2 mm and recorded daily for 30 days. Germination was calculated based on initial viable seeds.

Seed burial

The potential for soil seed bank formation was evaluated by burying the seeds and subsequently examining their germination percentage at regular intervals (Cheib and Garcia, 2012) following the design used by Ordóñez-Salanueva et al. (2017). Forty-eight batches containing 55 seeds (2640 seeds) per species were made. Each batch was placed inside translucent cloth bags of 10 cm by 10 cm sewn with thread to prevent seed loss.

Twenty-four bags per species were allocated for burial across six replicate hexagonal open top chambers (OTCs) which induced warming. The other 24 bags per species were buried in ambient conditions outside the OTCs (also across six replicate areas).

Experimental design of germination with warming treatments across seasons

This experiment was conducted in an abandoned agricultural field located in the southernmost section of the Chihuahuan Desert (22°14′11′′N, 100°51′46′′W, 1844 m), in central México. Annual rainfall in the study area is 341 mm and is concentrated in the summer months. The rainy season occurs between June and October; mean annual temperature is 17.8°C, but it can be higher than 35°C in summer (Medina-García et al., 2005). Vegetation is dominated by sclerophyllous shrubs, with some cacti and succulent monocots scattered among woody species. In our study area, vegetation was cleared from the surface in a 25 m × 25 m enclosure fenced with wire (2 m height) to prevent access from cattle and people. Within this enclosure, twelve experimental plots of 5 m × 5 m were outlined following a rectangular arrangement (3 plots wide × 4 plots long). Six of these plots were randomly assigned to the induced warming treatment, while the other six plots were used as a control under ambient environmental conditions (Aragón-Gastélum et al., 2014, 2017). Warming was implemented using hexagonal OTCs. Warming from the OTCs allowed passive heating and are a simple approach for assessing the responses of plants to warming in the field (Musil et al., 2005, 2009; Aragón-Gastélum et al., 2014, 2017). OTCs were built with UV-resistant transparent acrylic (3 mm thick; wavelength transmission 110 < 280 nm) following the

design proposed by Marion (1996). The resulting structures were 0.50 m tall, 1.5 m wide at the open top, and 2.08 m wide at the base attached to the ground. This OTC design increases air temperature during the day by between 1.9 and 5.0°C compared with external ambient conditions (Musil et al., 2005, 2009; Aragón-Gastélum et al., 2014, 2017).

To assess the magnitude with which OTCs modified microclimate, air and soil temperature as well as relative humidity were continuously monitored within and outside these structures during the entire experiment. For this, data-loggers were used (HOBO Pro v2 and HOBO Pendant, Onset Computer Corporation, MA, USA). One data logger was fixed 10 cm above the ground at the centre, while the second one was buried so the sensor would be at <0.5 cm under the soil surface in each OTC and control plot. Readings were programmed to be recorded every hour and averaged daily. These measures were conducted from 1 March 2013 to 28 February 2014, and recorded data were used to calculate the daily mean air and soil temperatures, as well as average daily mean air relative humidity in both treatments (OTCs and control). Data of daily rainfall (mm) were obtained from the National Institute of Forestry, Agriculture and Livestock (INIFAP San Luis Potosí, México), at 2 km from our study site.

Four lots of seed for each species were buried <0.5 cm under the soil surface, at the centre of each experimental plot. In plots with OTCs, the seed lots were located directly under the opening to avoid both overwarming and reduced rainfall interception by the acrylic walls. One bag per replicate for each species and treatment (six replicates per species in OTCs and six in controls) was exhumed at the end of each season (spring, summer, autumn and winter) during one year. Seeds from each bag were distributed in five Petri dishes used in the germination experiment per season for each environment; there were six replicates from OTC and six controls.

Seed viability was evaluated using a tetrazolium test, using three replicates of 10 seeds per species. Seed germination was assessed in a completely randomized experiment considering six replicates for warming and six for control. Seeds were sown in Petri dishes with moist cotton wool (five Petri dishes for each treatment) with 10 seeds in each one. Petri dishes were placed in conditions similar to those of our initial germination trial described above. Germination records were made daily for 30 days. The remaining five seeds per replicate and treatment (60 seeds for each species) were transversely cut to assess viability across seasons by exposing the embryos in the stereoscope, to see if an embryo was present and looked healthy. Mouldy and pulverized seeds were considered unviable.

Statistical analyses

Abiotic variables were summarized for each data-logger ($n = 6$ per treatment) and compared between OTCs and control plots with repeated measures ANOVA. Initial viability and germination were analysed by one-way ANOVA for each species. Viability and seed germination data were arcsine transformed to fulfil the normality assumption.

Germination across seasons was analysed by two-way ANOVA using each removed bag as a single replicate at the OTC level for each species, with seed exhumation season and warming (OTCs and control plots) as predictor factors, having OTC as a random factor and season as a fixed factor. Tukey's tests were used to test for significant differences between means.

Results

Abiotic variables

Total rainfall during the study period was 296.2 mm and was distributed as follows: spring, 21.7 ± 0.12 mm; summer, 103 ± 0.30 mm; autumn, 87.9 ± 0.31 mm; winter, 83.6 ± 0.43 mm.

Between 1 March 2013 and 28 February 2014, mean daily air temperature was 19.8 ± 0.16°C inside OTCs and 18.1 ± 0.02°C in control plots. This variable significantly differed between warming treatments ($F_{(1,6)}$ = 23.94, $P < 0.0001$) and season ($F_{(3,2184)}$ = 156.61, $P < 0.0001$), and the interaction was also significant ($F_{(3,2184)}$ = 92.17, $P < 0.0001$), in that mean daily air temperature was higher in the OTC plots in spring and summer than in the other treatments combined (Fig. 1a).

Air average daily relative humidity in the control plots was 65.8 ± 0.33% and 63.3 ± 1.12% within OTCs. We found no significant effects of warming ($F_{(3,2184)}$ = 4.36, $P > 0.05$), but season ($F_{(3,2184)}$ = 86.92, $P < 0.0001$), and the interaction between both factors were significant ($F_{(3,2184)}$ = 99.29, $P < 0.0001$), in that relative humidity was higher in the control plots in autumn than in the other combined treatments (Fig. 1b).

Mean soil temperature was affected by warming ($F_{(1,6)}$ = 4.78, $P = 0.0290$), season ($F_{(3,2184)}$ = 16.09, $P < 0.0001$), and by the warming × season interaction ($F_{(3,2184)}$ = 115.70, $P < 0.0001$). The daily mean soil temperature was 23.1 ± 0.21°C in OTCs and 22.1 ± 0.15°C in control plots. In spring, we found warmer daily mean soil temperature inside OTCs (29.0 ± 0.21°C) than in control plots (27.0 ± 0.10°C; $F_{(3,552)}$ = 31.01, $P < 0.0001$; Fig. 2). There were no differences between treatments in the other seasons: summer ($F_{(3,558)}$ = 3.45, $P = 0.0647$; Fig. 2), autumn ($F_{(3,528)}$ = 0.099, $P = 0.7529$; Fig. 2) and winter ($F_{(3,528)}$ = 2.209, $P = 0.1390$; Fig. 2); and they showed a decreasing pattern over time.

Seed viability and initial seed germination

Initial viability of fresh seeds was similar for the three studied species, which was 100% for *Y. filifera* and *E. platyacanthus* and 90 ± 10% for *A. striata* ($F = 1.00$, $P = 0.4218$; Fig. 3a). There were no changes in seed viability across seasons except for *A. striata*, which had more unviable seeds (appearing pulverized) in autumn (30%) and winter (15%). Germination differed between species ($F = 16.20$, $P = 0.0002$): *Y. filifera* initial germination reached 83 ± 9.4%; in *A. striata* it reached 30 ± 6.1%; and for *E. platyacanthus* it reached 49 ± 4.4% (Fig. 3b).

Germination under warming treatments across seasons

We found variation in germination for the three species studied; *Y. filifera* had similar germination between warming treatments and seasons ($P > 0.05$). Germination was high in the spring (77.2 ± 5.0%) and summer (81.9 ± 2.5%). After that, 90% of seeds germinated inside the bags buried in the soil, thus there were no remaining bags for the rest of the experimental timeframe.

In contrast, germination of *A. striata* significantly differed between warming treatments ($F_{(1,47)}$ = 9.278, $P = 0.005$) and seasons ($F_{(3,47)}$ = 31.262, $P < 0.0001$), but the interaction between warming and season was not significant ($F_{(3,4)}$ = 1.549, $P = 0.21$). Germination of seeds from OTCs (49.89 ± 4.57%) was higher than those from control plots (37 ± 5.7%). Germination was higher in spring (76.8 ± 3.1%) than in summer (42.8 ± 4.3%), which in turn was higher than in both autumn (30 ± 5.1%) and winter (24 ± 3.3%).
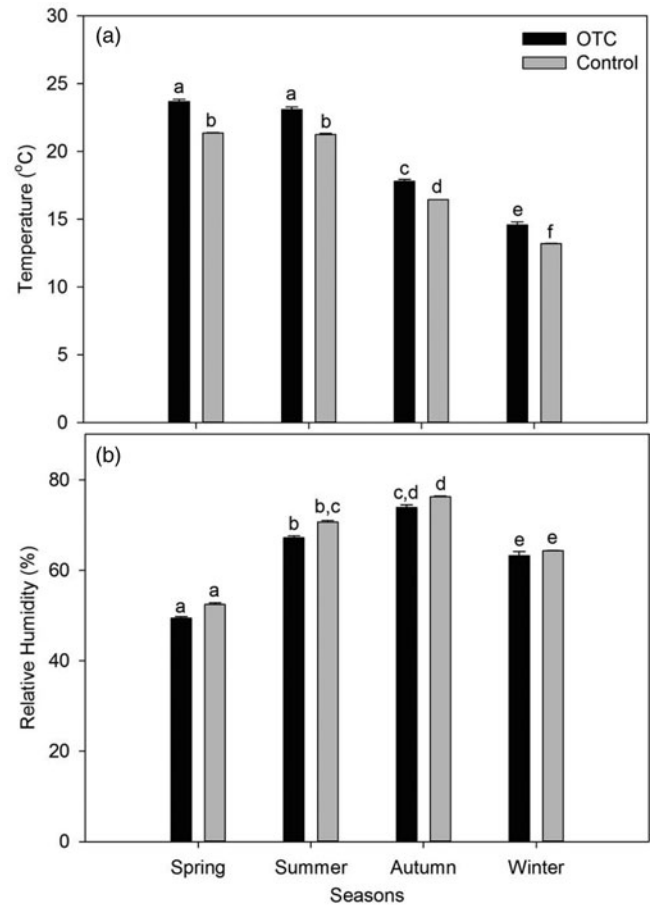

Figure 1. Daily air mean temperature and relative humidity (mean ± standard error) across of the seasons measured in control plots (grey bars) and within OTCs (black bars) used in the field experiment (± 95% CI).

Echinocactus platyacanthus germination was affected by warming ($F_{(1,47)}$ = 13.223, $P < 0.001$), and by season ($F_{(3,47)}$ = 52.750, $P < 0.0001$), but it was not affected by the warming × season interaction ($F_{(3,47)}$ = 2.245, $P = 0.09$). Germination of seeds from OTCs (50.75 ± 3.6%) was higher than those from control plots (40.28 ± 4.9%). Higher germination was found in spring (62.36 ± 2.6%) and winter (62.61 ± 4.2%) than in summer (37.5 ± 4.3%), which was higher than in autumn (19.59 ± 1.5%).

Discussion

This is the first study to explore soil temperature increase under climate change scenarios in American deserts and their impact on seeds; our approach using OTCs appears to have provided realistic temperature scenarios. We found a 1.7°C increase in mean daily air temperature in our warming treatments (OTC *vs* control plots) between 1 March 2013 and 28 February 2014. This was within the 1–3°C increment projected for global change by the late 21st century (IPCC, 2013, 2014) in arid ecosystems worldwide. In addition, we found a small but significant decrease in mean relative humidity (2.5%) within OTCs compared with control plots. Low relative humidity decreases the atmospheric water vapour and consequently the water condensation in the soil (Matimati *et al.*, 2012), which has a negative impact on water availability and thus, potentially limiting adequate water uptake
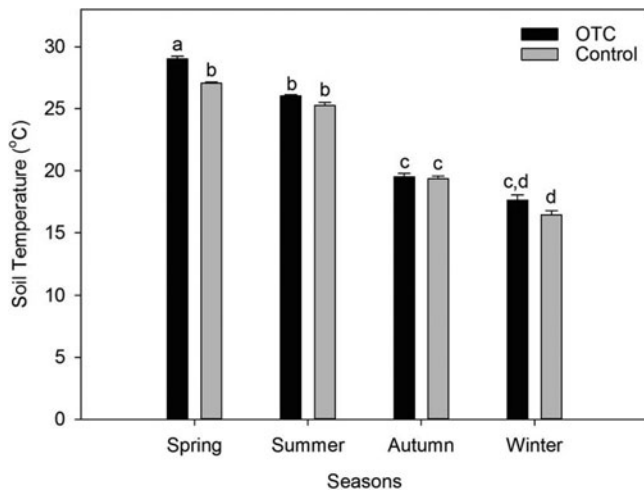
Figure 2. Daily soil mean temperature (mean ± standard error) across of the seasons measured in control plots (grey bars) and within OTCs (black bars) used in the field experiment (± 95% CI).

of some succulent species. This could have a detrimental effect in the perpetuation mechanisms and persistence for these species, although reduced relative humidity may be caused by OTCs deflecting rainfall away from the studied plot. Both air temperature increments and mean relative humidity decrements coincide with those found by Aragón-Gastélum *et al.* (2014, 2017) in short-term experiments in the same area.

Under global warming models, a 1°C increase in air temperature could result in an associated mean soil temperature increase of 1.5°C in some environments (Ooi *et al.*, 2012). This coincides with our results because we found a 1°C increase in mean soil temperature. These results agree with those of Cochrane *et al.* (2015) who found an analogous daily soil temperature rise in a Mediterranean ecosystem from South West Australia using similar OTCs.

In the Southern Chihuahuan Desert, soil temperature can, for short periods reach ~45°C at the hottest time of the day (Pérez-Sánchez *et al.*, 2015). During the study period, we found a higher maximum temperature in OTCs in mid-spring of 47°C. We found an increase of 2°C in the warming treatment, which falls within projection from models of global change for this region (Tejeda-Martínez *et al.*, 2008).

Our assessment of the effects of increased mean soil temperature on the formation, dynamics and persistence of soil seed banks uncovered differential responses among the studied species. For *A. striata*, germination was initially high and decreased throughout the year. However, higher germination was maintained in the warmed OTC plots compared with the controls, meaning seeds retained their germination capability for longer in OTCs presumably because of maintenance of higher temperatures. Under current climatic conditions, emergence of succulent species in the Chihuahuan Desert coincides with summer rainfall (Mandujano *et al.*, 1998). In future warmer environmental conditions, however, seeds could germinate when rainfall or temperature would no longer be suitable for seedling establishment.

Our germination results provide evidence of seed dormancy in aged seeds, because the proportion of seeds that are viable is larger than the proportion of the ones that germinate (Jiménez-Aguilar and Flores, 2010; Ramírez-Tobías *et al.*, 2012)
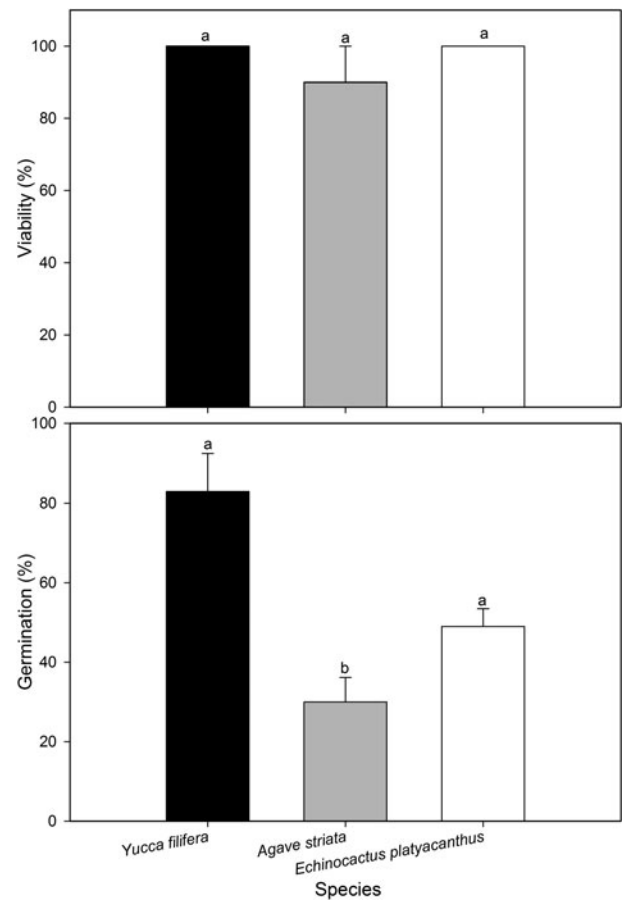

Figure 3. (a) Initial viability and (b) initial seed germination (mean ± standard error) in fresh seeds of three succulent species. Different lower case letters indicate significant differences ($P < 0.005$).

and consequently form soil seed banks. The lower germination recorded in autumn–winter is probably due to the onset of cold temperatures. A temperature drop is often a cue for development of secondary dormancy (Baskin and Baskin, 2014), and soil warming under future conditions could delay this. Delayed onset of secondary dormancy is an important issue for this species, because seeds could germinate under warming but seedlings would perhaps not tolerate the following winter.

The *Agave* species have developed exceptional physiological (e.g. Crassulacean acid metabolism, 'CAM') and ecological adaptations to high temperature and scarce water (Nobel, 2010; García-Moya *et al.*, 2011). In *A. striata*, a high germination over a wide temperature range has been documented (from 15 to 30°C) (Jiménez-Aguilar and Flores, 2010; Ramírez-Tobías *et al.*, 2012), which is consistent with the final germination found in fresh seeds and those exhumed in spring for this species. Furthermore, *A. striata* also displays a high water uptake under different water potentials (Ramírez-Tobías *et al.*, 2014). These authors suggest that for *A. striata* low water availability is required to achieve an adequate hydration to germinate. Thus, loss of viability and poor germination from summer to the end of our study in *A. striata* could be attributed to a low tolerance to moist conditions, which possibly promoted the attack of fungi and pathogens causing seed decay. A loss of viability in *A. striata* could also be the consequence of faster seed ageing. Seeds of *A. striata* had a lower initial viability than the other two species. Although

90% is still relatively high, even a loss of a small percentage could have a significant impact on longevity, particularly if conditions are wet and warm which might promote rapid ageing.

In a global climate change scenario, both temperature increases and atmospheric CO_2 level are expected (IPCC, 2013, 2014). Other studies suggest that *Agave* species may cope well under climate change, but they only consider the adult life-history stage (Nobel, 2010; García-Moya *et al.*, 2011). As our results show, the effects on the potential timing of germination and maintenance of the seed bank could affect the ability of *A. striata* to cope due to changes to these early life-history stages.

Seed germination of *Y. filifera* was high in spring and summer (with no seeds remaining viable to test for germination in the other seasons) at both temperature conditions. Rapid germination could be beneficial for seedling establishment, providing an advantage in a seasonally dry environment (Flores and Briones, 2001). The high germination we found for *Y. filifera* seeds was consistent with other studies (Jiménez-Aguilar and Flores, 2010; Cambrón-Sandoval *et al.*, 2013; Flores *et al.*, 2016) as well as for other *Yucca* species (Flores and Briones, 2001; Pérez-Sánchez *et al.*, 2011; Flores *et al.*, 2017). If *Y. filifera* seeds germinate fast and lose viability quickly, they probably have persistence mechanisms other than germination, such as vegetative propagation (Matuda and Piña-Luján, 1980) to rely on, more than the other species studied.

Echinocactus platyacanthus seeds had higher germination with higher mean soil temperature inside OTCs than in control plots, similar to *A. striata* seeds. Our findings coincide with those of Ordóñez-Salanueva *et al.* (2015), who found that projected future temperature increments would not have detrimental effects on germination in *Polaskia chende* and *P. chichipe*, two Mexican cactus species. Ours results also support the findings of Seal *et al.* (2017), who projected the mean temperature of the wettest quarter of the seed collection sites from 55 cactus species from the Americas, under two climate change scenarios, and predicted under the least conservative scenario (+3.7°C) that 75% of cactus species will have increased germination performance.

We also found dormancy cycling of *E. platyacanthus* seeds, because buried seeds of *E. platyacanthus* acquired secondary dormancy in the rainy seasons (summer and autumn), which was alleviated at the end of the subsequent dry season (winter), possibly because of the high variation registered in mean and minimum soil temperature at the end of winter. Physiological dormancy is the type of dormancy found in the Cactaceae (Rojas-Aréchiga *et al.*, 2000). Seeds with physiological dormancy can cycle through a gradation of dormancy 'states' in response to their environment, during which the range of conditions in which the seeds are able to germinate widens and contracts (Long *et al.*, 2015). Dormancy cycling has also been found in the cactus *Polaskia chende* from the Tehuacan Valley (Ordóñez-Salanueva *et al.*, 2017). Dormancy cycling indicates that the ungerminated seeds are viable seeds in the soil seed bank of *E. platyacanthus*. Reduced germination without loss of viability may contribute to a seed bank that allows population persistence in face of increased environmental fluctuations in the future (Ooi, 2012).

In conclusion, we found air and soil temperature increments and a lower air relative humidity within OTC plots during one year. This average soil temperature increment changed the dynamics and persistence of soil seed banks as well as dormancy in two of the three species studied, which was reflected in differential responses in germination across seasons. Under global warming projections, unchanged or greater germination of our study species might imply that early life-history stages are resilient to climate change, however greater germination of *A. striata* and *E. platyacanthus* could impact their bet-hedging strategies. Unlike *Y. filifera*, which showed loss of viability after summer, *E. platyacanthus* forms a soil seed bank and its cycling inter-seasonal dormancy/germination associated with seasonal changes could be an efficient physiological mechanism to face climate change.

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