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How do young cacti (seeds and seedlings) from tropical xeric environments cope with extended drought periods?

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ABSTRACT

Tropical dry forest is one of the most threatened ecosystems in the Neotropics and climatic projections suggest that frequency and duration of drought episodes could increase and threaten them even more. The aim of this study was to: 1) evaluate germination success under different water soil conditions, 2) analyze seedling survival and transpiration rate under prolonged water shortage and 3) measure gas exchange to determine the photosynthetic metabolism (CAM vs. C3) at seedling stage on three common cactus species, *Acanthocereus tetragonus, Melocactus curvispinus* and *Stenocereus griseus,* at Tatacoa, a tropical dry forest remnant in Colombia. Seed germination decreased as soil water potential decreased for all species. At seedling stage, all species have a strict water regulation strategy, showing low transpiration rate even when well-watered. This water saving strategy could explain the 100% seedling survival observed in all species during 6 months of water deprivation. All species had nocturnal CO_2 fixation, consistent with them being CAM, but *S. griseus* presented also C_3 behavior as it was growing up. Our findings indicate that all species can withstand water deprivation for eight months, and only under prolonged drought scenarios, recruitment may be reduced because of a decrease in germination and seedling survival.

1. Introduction

Tropical dry forest is one of the most threatened ecosystems in the neotropics (Janzen, 1988; Miles et al., 2006; Wright, 2005) and has one of the highest rate of forests loss worldwide, 12% was lost between 1980 and 2000 (Hansen et al., 2013; Lerdau et al., 1991; Miles et al., 2006; Trejo, 2000). Deforestation, forest fragmentation, fire, ranching and farming activities, and climate change are the most important threats that tropical dry forests are facing (Miles et al., 2006). Climatic projections of the Intergovernmental Panel on Climate Change (IPCC) suggest that the frequency and duration of drought episodes could increase in tropical xeric environments (IPCC, 2014) and 37% of the South American dry forest are considered at high risk (Miles et al., 2006). Although xeric species are well adapted to endure drought, it is possible that not all are equally equipped to withstand longer or more intense drought episodes, especially as seedlings. Understanding how xeric plant species will respond to these changes in dry episodes' duration and intensity will help us determine the future of tropical xeric environments composition and diversity (Dale et al., 2000; Engelbrecht et al., 2005; McDowell et al., 2008; Venturas et al., 2016). One group that may be particularly vulnerable to climate change is the Cactaceae family, because their low individual and population growth rates, and low recruitment rates (Hernández and Barcenas, 1996; Hernández and Godínez-Álvarez, 1994). In fact, all cacti species are included in appendix 2 of the CITES book of endangered species (Hunt et al., 1999).

Cactaceae is a family of slow-growing species comprising more than 2000 species, and are an iconic group of plants found on xeric habitats in the Americas (Bravo-Hollis and Sánchez-Mejorada, 2018). They have developed extraordinary adaptations to deal with the stressful conditions of their habitat: low water availability, intense solar radiation, high temperatures, low nutrient availability and high herbivory (Godínez-Álvarez and Valverde, 2003; Martínez-Berdeja and Valverde, 2008). Even though the adult cacti withstands quite well these conditions, and are well known for their high longevity, many demographic studies suggest that early life stages of germination and seedling recruitment are the most vulnerable and often a limitation of population growth (Arroyo-Cosultchi et al., 2016; Contreras and Valverde, 2002; Gurvich et al., 2017; Martínez-Berdeja and Valverde, 2008).

Seed germination and seedling recruitment are already infrequent events and represent the main bottlenecks in the population dynamics of various cacti species (Contreras and Valverde, 2002; Gurvich et al., 2017). How will young stages of cacti be affected by longer drought

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periods, and whether species will differ in their response is still unknown. Seedling survival will depend on seeds germinating in the proper season and/or water conditions, and on the ability to germinate fast and produce longer roots on time before the next drought episode arrives (Cordero and Di Stéfano, 1991; Evans and Etherington, 1990). Once seeds germinate, seedling survival also depends upon how long they have to endure drought because their shallow roots limit access to water and its small size restricts their capacity to store carbohydrates and water (Engelbrecht et al., 2005; Lüttge, 2004). We know that cacti species differ in their water requirements for seed germination (Rojas and Vázquez, 2000), and might differ in other traits that are likely to facilitate survival of seedlings under drought such as; fast root growth to access water sources quickly, high water storage capacity and regulation of gas exchange and transpiration to avoid water loss and carbon starvation (i.e. CAM vs. C3 metabolism).

Under the possibility of longer periods of drought in the future, it is crucial to understand if species differ in their germination rates and establishment success of seedlings under longer dry periods, since those differences may determine competition success and maintenance of populations over time (Flores and Briones, 2001) and therefore species composition under future climate change scenarios. To be able to predict vegetation responses to future global changes we have to start evaluating how species will differ in their response to these incoming scenarios, and in this study we do so by studying, under controlled laboratory conditions: 1) germination success under different water soil potentials, 2) seedling survival and transpiration rate under various prolonged water shortage scenarios and 3) gas exchange at the seedling stage on three of the most common cactus species found in la Tatacoa, one of the few patches of tropical dry forest that remains in Colombia, *Acanthocereus tetragonus, Melocactus curvispinus* and *Stenocereus griseus*.

2. Methods and materials

2.1. Study site and species

Tatacoa is the second largest xeric zone of Colombia with an extension of 355 km^2 located at 440 m.a.s.l. at the eastern bank of the Magdalena River (3° 11.3’ – 3° 20.4′ N and 75° 7.4’ – 75° 13.7’ W; (Figueroa and Galeano, 2007; Olaya et al., 2000). Tatacoa climate is characterized by an average temperature of 28 °C (but can reach 40 °C in the driest months), a mean annual precipitation of 1000 mm and a bimodal rainfall pattern with one rainy period from March to May and the other from October to November (Figueroa and Galeano, 2007; Ruiz et al., 2000). Under current conditions plants are rarely exposed to periods of drought longer that 5 months and in this study, we simulated two possible drastic scenarios, 8 and 11 months of drought.

Based on the annual precipitation and Holdridge life zones system, Tatacoa should be classified as a tropical dry forest. However, its vegetation has been altered by savannah and desertification processes due to anthropogenic activities (farming and livestock) and the geologic history of the region and the vegetation nowadays is mainly composed of low-lying bushes, pastures, stubble and cactus (Figueroa and Galeano, 2007; Lasso and Barrientos, 2015; Ruiz et al., 2000, Fig. 5 in suplementary material). However, along rivers some typical dry forest trees are found. Figueroa and Galeano (2007) identified 223 species of plants in the area belonging to 70 genera and 60 families. One of the most common families is the Cactaceae with eight species: *Stenocereus griseus*, *Melocactus curvispinus* subsp. *obtusipetalus*, *Cereus hexagonus*, *Opuntia pubescens*, *O. elatior, Praecereus euchlorus* subsp. *smithianus*, *Hylocereus undatus* and *Acanthocereus tetragonus.*

Here we studied three of the most common species in the area; *Acanthocereus tetragonus, Melocactus curvispinus,* and *Stenocereus griseus. A. tetragonus* is a columnar cactus with one of the most widespread distributions, found from southern United States (Florida and Texas) to northern South America in lowlands up to 1700 m.a.s.l. *M. curvispinus* is a small globose cactus found in lowlands up to 1250 m.a.s.l., and *S. griseus* is an arborescent cactus that reaches heights of 6–9 m. These two-last species have a similar geographical distribution from Mexico to northern South America.

2.2. Water potential and germination

To evaluate if longer drought periods could reduce seed germination we exposed seeds of all studied species to four osmotic water potentials 0, -1.0, −1.5 and −2.0 MPa. We used osmotic water potential to simulate soil matric potential given that matric and osmotic potentials have equivalent effects on the germination performance of seeds (McWilliam and Phillips, 1971). The four treatments were chosen to represent soil water potential values found in dry environments that typically range from −0.5 to −1.6 MPa (Dürr et al., 2015; Oliveira et al., 2010). Additionally, we chose an extreme value of −2.0 MPa to represent extreme water shortage conditions. The saturation soil point and permanent wilting point are 0 and -1.5 MPa respectively (Arnold et al., 2014; McWilliam and Phillips, 1971). To simulate these four osmotic water potentials we used different solutions of polyethylene glycol 6000 (PEG 6000) prepared using the equation derived by Michel and Kaufmann (1973) and reviewed by Wood et al. (1993) with Ψ in kPa:

$$\Psi_O = (6.3 \times 10^{-5} T - 0.02196)\ O^{2.2357} \tag{1}$$

Where Ψ_O is the osmotic potential in KPa, T is the temperature in Kelvin (K = 298.15) and O the osmolality in grams 1000 g^{-1} of water. Using this formula, we prepared a series of solutions from 0 to 2000 KPa and from now on we refer to these solutions in MPa (0–2.0 MPa).

Seeds were collected in Tatacoa and taken to the lab for germination trials. Prior germination, seeds were surface sterilized with a 10% Clorox solution. Four petri dishes with thirty seeds each per specie were allocated to one of the four treatments (0.0, −1.0, −1.5, −2.0 MPa) for a total of 480 seeds per specie. Each petri dish had a layer of filter paper as substrate and received 15 ml of the PEG 6000 solution of interest, except for the control treatment that received 15 ml of water. All dishes were wrapped with Parafilm® to reduce evaporation of the solution and were left to germinate for 40 days under constant temperature (28 °C) and humidity conditions (60%) in a 12 h/12 h photoperiod.

To quantify germination success we measured the percentage of seeds that germinated (G) during the observation period and the mean time required for maximum germination of a seed lot $\bar{t}$ (days) (Ranal and Santana, 2006). Germination is expressed as the number of germinated seeds (g) relative to the total number of seed per replicate (n = 30):

$$G = (g/n) * 100 \tag{2}$$

The time required for maximum germination $\bar{t}$ (days) was calculated as the number of days required by germinated seeds to germinate where t_i is the time elapsed between the initiation of the experiment and the time in which the last seed germinated:

$$\bar{t} = \sum_{i=1}^{k} g_i t_i / \sum_{i=1}^{k} g_i \tag{3}$$

2.3. Seedlings drought tolerance and transpiration rate

To determine how long seedlings can withstand drought for before wilting and dying, we exposed one-year-old seedlings to five different water deprivation treatments. Thirty-five seedlings per species were transplanted into 40 mL pots, 7 of those seedlings were randomly allocated to one of the following treatments: 0 (control), 6, 7, 8 and 11 months without water. All seedlings during the experiment were subjected to constant temperature (28 °C), humidity conditions (60%) and a photoperiod of 12 h/12 h.