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Review / Revisión

SEED TRAITS AND GERMINATION IN THE CACTACEAE FAMILY: A REVIEW ACROSS THE AMERICAS

RASGOS SEMINALES Y GERMINACIÓN EN LA FAMILIA CACTACEAE: UNA REVISIÓN EN LAS AMÉRICAS

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Abstract

Background: Cactaceae is the fifth taxonomic group with the highest proportion of threatened species. One way to contribute to the preservation of this family is to understand the processes that promote seed germination.

Questions: How common is dormancy and seed banks in Cactaceae*?* Are there general patterns in cacti germination response to temperature, light, water, salinity, phytohormones, hydration/dehydration cycles, mechanical or chemical scarification?

Data description: A total of 333 studies on cactus germination with information on 409 taxa.

Study site and dates: since 1939 to January 2020.

Methods: A search of scientific articles in Google Scholar was performed with the words Cactaceae*,* cacti and cactus, in combination with various matters on germination in English, Spanish and Portuguese.

Results: The main germination studies in cactus deal with photoblasticism (275 taxa), temperature (205 taxa) and seed longevity (142 taxa). Other lines of study in cactus germination (*e.g.,* desiccation tolerance, vivipary, phytohormones, mechanical or chemical scarification, *in vitro* germination, hydration/dehydration cycles, water and saline stress, serotiny, storage in cold, high temperature tolerance and soil seed bank) include between 14 and 65 taxa. Cacti have only physiological dormancy and optimal germination for most species occur between 20 and 30 °C.

Conclusions: Mexico, Brazil and Argentina are the three leading countries in the study of cactus germination.

Keywords: Dormancy, photoblasticism, seed bank, serotiny, temperature, viviparity.

Resumen:

Antecedentes: Cactaceae constituye el quinto grupo taxonómico con mayor proporción de especies amenazadas. Uno de los aspectos que contribuyen a la preservación de estas especies es el entendimiento de los procesos que promueven la germinación de sus semillas.

Preguntas: ¿Qué tan común es la latencia y los bancos de semillas en Cactaceae?¿Existen patrones generales en la respuesta germinativa de los cactus ante la temperatura, luz, agua, salinidad, fitohormonas, ciclos de hidratación/deshidratación o escarificación mecánica o química?

Descripción de datos: Se revisaron 333 estudios sobre germinación de cactus con información de 409 taxa.

Sitio y años de estudio: Estudios de germinación de cactáceas en América, publicados desde 1939 a enero de 2020.

Métodos: Se realizó una búsqueda de artículos científicos en Google Académico con las palabras Cactaceae y cactus, en combinación con varias materias sobre germinación en inglés, español y portugués.

Resultados: Los principales estudios sobre la germinación de cactáceas han versado sobre el fotoblastismo (275 taxones), la temperatura (205 taxones) y la longevidad seminal (142 taxones). Otras líneas de estudio que abordan la germinación de cactus (*e.g.,* tolerancia a la desecación, viviparidad, fitohormonas, escarificación mecánica o química, germinación *in vitro*, ciclos de hidratación/deshidratación, estrés hídrico y salino, serotinia, tolerancia a altas temperaturas y almacenamiento en frío, bancos de semillas) comprenden entre 14 y 65 taxones. Las cactáceas presentan solo latencia fisiológica y una temperatura óptima de germinación entre los 20 y 30 °C.

Conclusiones: México, Brasil y Argentina son los tres países líderes en el estudio de la germinación en cactus.

Palabras claves: Banco de semillas, fotoblastismo, latencia, serotinia, temperatura, viviparidad.

Cactaceae is the family considered to have the largest number of genera within the order Caryophyllales (Hernández-Ledesma *et al.* 2015) and its species occupy a wide range of habitats through the American continent (Anderson 2001, Goettsch *et al.* 2015). For centuries cacti have fascinated humans because of the beauty and the rarity of the majority of their species (Bravo-Hollis 1978, Griffith 2004). Although the most widespread use is ornamental (Goettsch *et al.* 2015), in several countries the fruits, flowers and stems of 154 species are widely consumed (Anderson 2001, Goettsch *et al.* 2015). Plants of the Cactaceae are currently among the most vulnerable to human disturbance because of their slow growth (Godínez-Álvarez *et al.* 2003) and constitute the fifth taxonomic group with the highest proportion of species threatened worldwide (Goettsch *et al.* 2015).

One way to help preserve these species and others with special conservation value is to understand the processes that promote seed germination (Rojas-Aréchiga & Vázquez-Yanes 2000, Anderson 2001, Flores *et al.* 2006). Two remarkable works about cactus seeds have been published. Rojas-Aréchiga & Vázquez-Yanes (2000) published an exhaustive review on cactus seed germination. Barthlott & Hunt (2000) published a book on cactus seed micromorphology, including 213 species and 688 microphotographs from more than 350 taxa. In addition, it contains the compilation of studies with microphotographs of cactus seeds from 1,050 species of 230 genera (Rojas-Aréchiga 2012). Barthlott & Hunt (2000) study describes 26 useful seed traits and attempts to homogenize English terminology. Both Rojas-Aréchiga & Vázquez-Yanes (2000) and Barthlott & Hunt (2000) studies have been referenced for all research in cactus seed germination and seed description during the last two decades.

Since the 2000s, the papers on cactus seed germination almost tripled the available information. This review aims to perform an analysis of the cactus seed literature in the last 80 years. The trends found and gaps in the information are discussed. Specifically, we analyzed the relationship between cactus seed germination and seed traits, as well as between cactus seed germination and phylogeny. We also documented the germination types in cacti, and how common is seed dormancy and how common are seed banks in the cactus family. We also discuss the effect of temperatures, light, water, salt and hydration-dehydration cycles on cactus seed germination.

Materials and methods

A search of scientific articles was performed with the words Cactaceae, cacti or cactus in combination with: germination, photoblasticism, seed bank, vivipary, dormancy, hydration-dehydration cycle, serotiny and *in vitro* germination through the search engine Google Scholar (https://scholar.google.com), in English, Spanish, and Portuguese, the main languages in the American continent. According to Haddaway *et al.* (2015) Google Scholar is a powerful tool for finding specific literature and is adequate for identifying the majority of evidence in a systematic review, the references from each study found were also analyzed. In total 333 studies related to cactus germination from 1939 to January 2020 (Figure 1, Tables 1 and 2) were gathered, with information on 409 taxa. Cactus seed germination has been evaluated in less than 50 % of the genera. The collected information was grouped by subjects and then discussed.

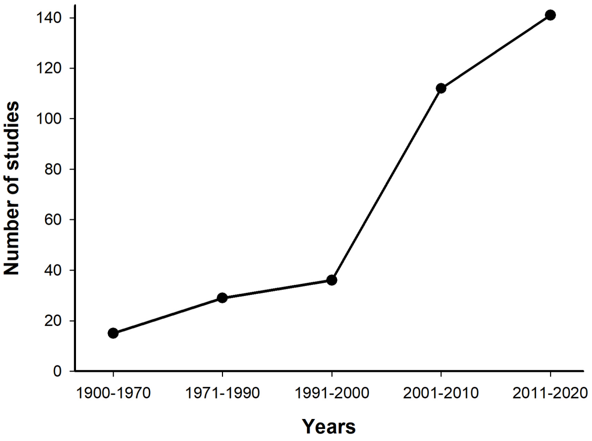

Figure 1. Number of studies of cactus seed germination until January, 2020.

All the information obtained was divided into ten subjects according topics covered in Baskin & Baskin (2014) and that there were also several studies on cacti. In the section on *Cactus seed traits*; shape, color, size, mass, as well as appendices and number of seeds per fruit were considered. The intention of this topic was to introduce readers to the generalities of cactus seeds as a necessary process to discuss the different issues related to germination. Also the section on *Germination types,* that relates the shape of the seed to the mode of germination, was mainly considered as introductory. The information discussed in these two subjects was obtained mainly from classical or compilation studies (*e.g.,* Flores & Engleman 1976, Bregman & Bouman 1983, Barthlott & Hunt 2000, Rojas-Aréchiga & Vázquez-Yanes 2000, Seal *et al.* 2009).

The number of taxa studied by genera, subfamilies and country or region of origin of the taxon was compiled for the rest of the subjects. *Seed dormancy,* was not included in the summary table because we used the number of cactus species having seed dormancy from Willis *et al.* (2014). The species where vivipary has been studied were also included in the summary table.

Table 1. Abstract of the cactus studies on different research lines related with seed germination in 80 years and 333 papers with information on 409 taxa. Taxa: Number of taxa studied; Cact: *Cactoideae*; Opt: *Opuntioideae*; Per: *Pereskioideae*; Mah: *Maihuenioideae*. Countries or regions, MX: Mexico; BR: Brazil; AR: Argentina; CH: Chile; PE: Peru; BO: Bolivia; PA: Paraguay; CO: Colombia; USA: Unites States of America; CA: Caribbean region; SOU: South America; MX-U: Mexico - USA; CU: Cuba. It is possible to find a higher number of species per country when in a same taxon several studies in natural populations from different countries were done. In parenthesis the percentage of genera with at least one species studied.

Matter	**Genus**	**Taxa**	**Subfamilies**				**Countries or regions**												
			Cact	**Opt**	**Per**	**Mah**	**MX**	**BR**	**AR**	**CH**	**PE**	**BO**	**PA**	**CO**	**USA**	**CA**	**SOU***	**MX-U***	**CU***
Photoblasticism	62 (50.0)	275	251	20	3	1	129	46	41	37	9	0	0	0	7	4	0	0	16
Temperatures	62 (50.0)	205	184	17	3	1	64	43	30	14	12	4	1	0	14	10	13	0	17
Longevity [1]	43 (34.7)	142	128	12	1	1	70	25	10	19	2	1	0	0	11	2	7	0	9
Desecation tolerance	30 (24.2)	65	53	2	0	0	19	0	6	13	6	1	0	0	1	2	10	7	0
Vivipary	21 (16.9)	58	58	0	0	0	12	5	27	0	0	1	0	0	1	6	6	0	13
Phytohormones (AG_3)	29 (23.4)	59	50	9	0	0	36	4	4	4	0	0	1	0	6	2	4	0	10
Mechanical or chemical scarification [2]	23 (18.5)	52	41	11	0	0	40	2	2	0	0	0	0	0	7	0	1	0	12
In vitro germination	18 (14.5)	42	38	4	0	0	26	14	0	0	0	0	0	0	0	3	0	0	0
Water stress	23 (18.5)	39	37	1	1	0	15	10	9	2	0	0	0	3	0	0	0	0	9
Serotiny	9 (7.2)	24	22	2	0	0	20	0	0	0	0	0	0	0	3	1	0	0	1
Hydration/dehydration cycles	11 (8.8)	20	20	0	0	0	11	2	7	0	0	0	0	0	0	0	0	0	1
Storage in cold [3]	7 (5.6)	20	20	0	0	0	2	16	0	0	0	0	0	0	2	0	0	0	0
Soil seed bank	10 (8.1)	19	17	2	0	0	7	3	6	0	0	0	0	0	3	0	0	0	9
High temperature tolerance	9 (7.2)	17	13	4	0	0	14	1	0	0	0	0	0	0	3	0	0	0	0
Saline stress	8 (6.4)	14	12	2	0	0	7	7	0	0	0	0	0	0	0	0	0	0	8

[1] It includes studies where the viability of seeds of at least three months stored at room temperature was tested.

[2] It includes studies where the germination response was tested after subjecting the seeds to various scarification methods that include sand, sandpaper, cuts (mechanical scarification) or with H_2SO_4, HCl, NaClO and H_2O_2 (chemical scarification).

[3] Only studies where the seeds were kept at temperatures equal to or below 0 °C were included.

* The species referred for SOUD and MX-U comprise species where the seed collection site was not declared and the distribution covers two or more countries. The references for Cuba were not added to the total species, because they include studies that have not yet been published, the germination studies of Cuban cacti that have already been published were included in the Caribbean list.

In the subject *Temperature and seed germination*, the mean and the confidence intervals of the germination percentage at 30 °C were plotted between cacti from temperate and warm climates. The type of weather was obtained from the information of each article reviewed; the comparison was based on 43 data from temperate and 34 from warm climate. Similarly, in the subject *Water and saline stress and germination,* the mean and standard deviation of the germination response of cactus seeds were plotted against different water potentials induced with polyethylene glycol (PEG).

On the subject *Light and seed germination*, we consider the photoblastic response of the seeds according to the Relative Light Germination index (RLG) (Milberg *et al.* 2000) and the proportions proposed by Funes *et al.* (2009). Values with RLG > 0.75 were considered positive photoblastic, < 0.25 negative photoblastic, species with RLG values between 0.25 and 0.75 were considered indifferent photoblastic (Funes *et al.* 2009). We calculate the RLG, to define the photoblastic response of the seeds in the studies where they had not calculated it.

Results and Discussion

Cactus seed traits. Both the works of Flores & Engleman (1976) and Bregman & Bouman (1983), as well as of Barthlott & Hunt (2000), present the structure and general anatomy of cacti seeds. In such studies, it was shown that in cacti the embryo is covered by two layers of tissue: the external (known as the testa) is generally thick, while the

Table 2. Taxa of the *Cactaceae* having at least nine species with seed germination studies. Taxonomy was based in Hunt *et al.* (2006). Spp = Species number per genus. Review based in 333 papers published in the last 80 years.

Subfamily/genus	spp	With information	Subfamily/Genus	spp	With information
Cactoideae			***Cactoideae***		
Armatocereus	9	1	*Melocactus*	50	18
Browningia	9	0	*Micranthocereus*	10	2
Cereus	29	6	*Pachycereus*	13	6
Cleistocactus	48	5	*Parodia*	66	8
Coleocephalocereus	10	1	*Pediocactus*	10	0
Copiapoa	30	6	*Peniocereus*	20	2
Corryocactus	12	1	*Pfeiffera*	10	0
Coryphantha	53	9	*Pilosocereus*	49	18
Discocactus	12	3	*Pseudorhipsalis*	9	0
Disocactus	16	1	*Rebutia*	40	1
Echinocereus	106	4	*Rhipsalis*	48	9
Echinopsis	101	28	*Sclerocactus*	28	2
Epiphyllum	18	4	*Selenicereus*	27	1
Eriosyce	51	17	*Stenocereus*	25	9
Escobaria	23	5	*Thelocactus*	20	3
Espostoa	12	2	*Turbinicarpus*	36	22
Ferocactus	42	13	*Weberocereus*	10	1
Frailea	18	1	***Opuntioideae***		
Gymnocalycium	63	9	*Austrocylindropuntia*	9	0
Haageocereus	14	5	*Corynopuntia*	14	0
Harrisia	9	7	*Cylindropuntia*	33	5
Hylocereus	14	7	*Opuntia*	75	17
Leptocereus	11	1	*Pterocactus*	9	1
Mammillaria	232	43	***Pereskioideae***		
Matucana	21	0	*Pereskia*	18	3

internal one only forms a fine membrane around the embryo (Bregman & Bouman 1983) that completely collapses during seed maturation in most species (Barthlott & Hunt 2000) (Figure 2). A distinctive trait in Cactaceae seeds, but not exclusive of the family, is a small area called the hilum-micropylar region, which is caused by the presence of campylotropous ovules (Bregman & Bouman 1983, Barthlott & Hunt 1993), although Flores & Engleman (1976) considered the amphitropous ovules dominant. This characteristic is considered a variant of campylotropous ovules according to Font Quer (1973). For descriptive purposes Barthlott & Hunt (2000) divided cactus seeds in four regions: ventral, dorsal, apical and the edge of the hilum-micropylar region.

Cactaceae seeds vary in shape. Bregman & Bouman (1983) in their review presented 12 seed variants, while Barthlott & Hunt (2000) in accordance with the treatment of Voit (1979) considered eight types of seeds, which they themselves reduced to four, according to the length/width relationship. In general, cactus seeds have been described as reniform, pyriform, globular, oval, hat-shaped, lenticular or mussel-shaped (Rojas-Aréchiga & Vázquez-Yanes 2000, Barthlott & Hunt 2000) (Figure 3). In spite of the great variability of terminologies, the majority of the previous studies have followed Barthlott & Hunt (2000) (see: Arias & Terrazas 2004, Arroyo-Consultchi *et al.* 2006, 2007, Arias *et al.* 2012, and Franco-Estrada *et al.* 2014). Although it is possible that some relationship between the shape of the cactus seeds and their germination exists, this aspect has been little studied. Bregman & Bouman (1983) associated the seed shape with differences in the formation of germination cracks. Hat-shaped seeds occur in North American genera such as *Astrophytum* and *Epithelanta*, as well in species of several South American genera, such as *Frailea*, *Matucana*, *Discocactus*, *Notocactus* (*Parodia*), and *Thrixanthocereus* (*Espostoa*) (Barthlott & Hunt 2000).

Experimental evidence of floating capabilities (hat shape, a funicular envelope covering a prominent hilum, and air chambers throughout the tegument) and potential water dispersal of hat-shaped seeds in Cactaceae have been found in *Astrophytum capricorne* and *Astrophytum ornatum* (Sánchez-Salas *et al.* 2012), as well as in *Astrophytum myriostigma* (Romero-Méndez *et al.* 2018). Seeds of *Selenicereus wittii* from the Amazonia, in Brasil, are mussel-shaped, and also have an air chamber and are adapted to inundation hydrochory (Barthlott *et al.* 1997).

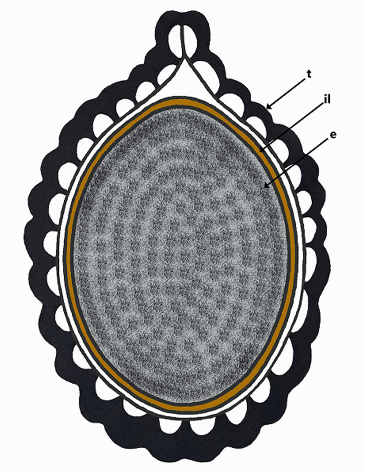

Figure 2. Transversal section of a cactus seed. t: testa; il: internal layer and e: embryo. Drawing by Alfredo Ruiz Fleitas

Unlike the high variability in terms of shape, seed color in the family is mainly between black and brown (Leuenberger 1986, Barthlott & Hunt 2000, Arias & Terrazas 2004, Arroyo-Consultchi *et al.* 2006, Seal *et al.* 2009, Arias *et al.* 2012, Loza-Cornejo *et al.* 2012, Franco-Estrada *et al.* 2014). In some cases; however, they can be reddish-brown, yellow, green or off-white (Rojas-Aréchiga & Vázquez-Yanes 2000, Barthlott & Hunt 2000, Arias *et al.* 2012). A potential relationship between seed color and seed germination in cactus remains to be tested.

Consistent with seed shape, the embryo of the cactus is generally curved (Barthlott & Hunt 2000) and peripheral (Finch-Savage & Leubner-Metzger 2006), with great variation in the region that occupies the storage structure. In *Leuenbergeria*, *Opuntia* and *Pereskiopsis* species, a greater development of the cotyledons is observed with respect to the hypocotyl. Nevertheless, the tendency in the family is a greater development of the hypocotyl with respect to the cotyledons. Cactus genera like *Mammillaria* and *Parodia* show upright embryos with 90 % of the volume occupied by the hypocotyl (Barthlott & Hunt 2000).

In terms of the average number of seeds produced per fruit, an enormous variation exists in cacti. Some authors report cactus fruits (e.g. *Epiphyllum anguliger*, *Ferocactus histrix*, *Pachycereus pringlei*, *P. weberi*, *Pilosocereus chrysacanthus, Echinopsis atacamensis* subsp. *pasacana*, *Gymnocalycium monvillei*), with ranges between 1,000 and 8,000 seeds (Zimmer 1966, Del Castillo 1988, Fleming *et al.* 1994, Valiente-Banuet *et al.* 1997, de Viana 1999, Gurvich *et al.* 2008), although it is possible to find species with fewer than 20 seeds per fruit in genera such as *Mammillaria* (Valverde & Zavala-Hurtado 2006, Valverde *et al.* 2015), *Pereskia* and *Leuenbergeria* (Leuenberger 1986).

Cactus seeds are generally smaller than one centimeter (Barthlott & Hunt 2000, Seal *et al.* 2009, Rojas-Aréchiga *et al.* 2013) and vary from 0.2 mm in *Blossfeldia liliputana* (Barthlott & Porembski 1996) to 7.5 mm in *Pereskia bleo* (Leuenberger 1986), and their weight varies from 0.016 mg in *Mammillaria bocasana* (Flores *et al.* 2006) to 56.04 mg in *Opuntia basilaris* (Royal Botanic Gardens Kew 2019).

Differences in seed mass among cactus species and localities have been found, *e.g.*, Romo-Campos *et al.* (2010) found that *Opuntia* spp. seeds collected in moist areas were heavier than those collected in dry sites. These authors also found a correlation between seed mass and seed germination for *Opuntia jaliscana* in which larger seeds germinated more than smaller seeds. Sosa-Pivatto *et al.* (2014) found no correlation between seed mass and germination characteristics in central Argentinian cacti; however, they found that species with heavier seeds produced bigger and more cylindrical seedlings.

Other traits associated with cactus seeds are appendages or structures, such as funicula, arils, strophioles and mucilage. In the subfamily Opuntioideae, the ovule is surrounded by the funiculus that is lignified during development (Bregman & Bouman 1983, Strittmatter *et al.* 2002) and forms a structure considered as an aril by Barthlott & Hunt (2000) but as a covering by Bravo-Hollis (1978). Orozco-Segovia *et al.* (2007) found that lignified funiculus in *Opuntia tomentosa* acts as a partial barrier to water diffusion into the seed and that in this species, water uptake occurs mainly through the water channel mediated by a valve, both formed in the hilum-micropyle region during seed dehydration and ageing. Various genera like *Mammillaria*, *Aztekium* (Bravo-Hollis 1978) and *Blossfeldia* (Barthlott & Hunt 2000) show strophioles that can be considered arils, but to differentiate them from the structure of Opuntioideae, this term has continued to be used (Barthlott & Hunt 2000). A mucilage sheath is present in more than 40 species of cactus belonging to 22 genera and is formed by pectins (Barrios *et al.* 2015, Mascot-Gómez *et al.* 2020). Bregman & Graven (1997) and Mascot-Gómez *et al.* (2020) suggested that the layer of mucilage in cactus seeds improves the germination through the effect of the intake and distribution of water. Barrios *et al.* (2015) suggested that maybe the presence of mucilage in

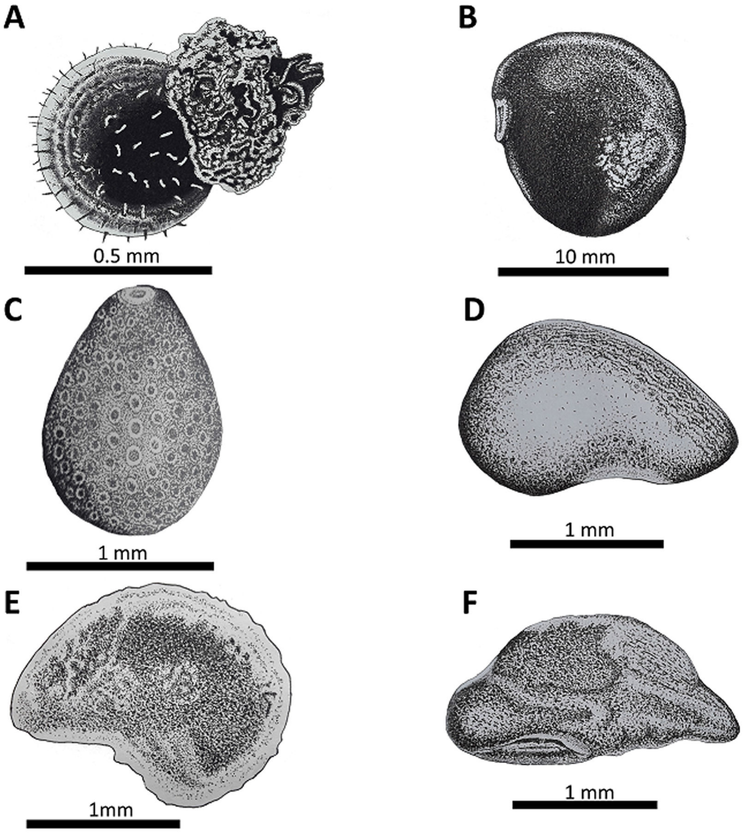

Figure 3. Shape of cactus seeds. A: globular (*Blossfeldia liliputana*); B: lenticular (*Leuenbergeria bleo*); C: pyriform (*Escobaria cubensis*); D: mussel-shaped (*Selenicereus grandiflorus*); E: reniform (*Neobuxbaumia multiareolata*); F: hat-shaped (*Frailea phaeodisca*). According Barthlott & Hunt (2000) A and B: circular; C and D: oval; E and F: broadly oval. Drawings by Alfredo Ruiz Fleitas

Leptocereus scopulophilus seeds serves other purposes such as the adhesion of seeds to the soil or camouflage from seed eaters.

Germination types. Seed germination is a series of events that begin with imbibition and end with the emergence of the radicle from the seed coat. There are few studies that consider germination types in Cactaceae (Almeida *et al.* 2009, Secorun & Souza 2011), since the classic study by Bregman & Bouman (1983). The aforementioned authors described 11 variants of germination where the radicle is the first organ of the seedling to break the testa and hypothesized the phylogenetic relationships between variants. In addition, they considered that the mode of germination in a cactus is correlated to the seed shape, and they defined the *Cereus* variant as the most numerous in the family. Curiously, although for the genus *Leptocereus* Areces-Mallea (2003) only recognized the *Cereus* variant in two species (*L. quadricostatus* and *L. sylvestris*), García-Beltrán *et al.* (2017) found four variants in only one species (*L. scopulophilus*). In addition to the *Cereus* variant in *L. scopulophilus*, García-Beltrán *et al.* (2017) recognized the *Pereskia* variant and another two where the cotyledons are the first organ to break the testa. The aforementioned variants were considered exceptions by Bregman & Bouman (1983). Nevertheless, in one of the seed morphs of *L. scopulophilus*, these "alternative variants" account for over 20 % (García-Beltrán *et al.* 2017).

Seed dormancy. Rojas-Aréchiga & Vázquez-Yanes (2000) only found reports of seeds with innate and forced dormancy. The forced dormancy of seeds is considered by Baskin & Baskin (2014) as non-dormant. The classification proposed by those authors establishes that seeds that germinate within the first four weeks after dispersion are non-dormant and that the seeds that do not germinate because of inadequate conditions (forced dormancy) must be considered as latent or quiescent. Previous cactus studies have reported viviparous seeds (without innate dormancy) in 58 species (Table 1) (Cota-Sánchez 2004, Cota-Sánchez *et al.* 2007, 2011, Rojas-Aréchiga & Mandujano-Sánchez 2009, Barrios *et al.* 2012, Aragón-Gastélum *et al.* 2013, 2017). Viviparous are also considered as non-dormant in the system of Baskin & Baskin (2014). The studies about cactus seed dormancy are few (Potter *et al.* 1984, Côrtes *et al.* 1994, Olvera-Carrillo *et al.* 2003, Mandujano *et al.* 2005, Flores *et al.* 2005, 2008, Orozco-Segovia *et al.* 2007, Delgado-Sánchez *et al.* 2010, 2011, 2013), may be because of the rapid germination that the majority of the studied species possess. In addition, few works about germination mention how many un-germinated seeds are dormant (Flores *et al.* 2005, 2006, Ortega-Baes *et al.* 2010, Aragón & Lasso 2018).

The most used methods for interrupting dormancy in cactus seeds have been through chemical scarification (by immersion in H_2SO_4, HCl, NaClO and H_2O_2 at various concentrations and times) and mechanical scarification, which together encompass some 52 species studied (Table 1). In addition, gibberellic acid has been used as a promoter of germination, but its role is discussed later in reference to light. Few studies have used thermal shock but without obtaining good results with this type of treatment (Sánchez-Venegas 1997, Rosas-López & Collazo-Ortega2004, Carbajal *et al.* 2010, Villanueva *et al.* 2016, Podda *et al.* 2017, Gonzalez-Cortés *et al.* 2018). Other studies have used fungal inoculation in some species of *Opuntia* (Delgado-Sánchez *et al.* 2010, 2011, 2013) or hydration/dehydration cycles (Dubrovsky 1996, 1998, Santini & Martorell 2013, Contreras-Quiroz *et al.* 2016a, 2016b) with good results. Research in the last decade that has addressed treatments to break dormancy in cactus seeds are however, not common (Rojas-Aréchiga *et al.* 2011, Amador-Alférez *et al.* 2013, Delgado-Sánchez *et al.* 2010, 2011, 2013, Podda *et al.* 2017, Gonzalez-Cortés *et al.* 2018).

In cacti, a rapid and high percentage of germination is associated with a thin testa (Maiti *et al.* 1994). However, although testa functions as regulator in imbibition (Souza & Marcos-Filho 2001), physical dormancy has not been found in cactus seeds. Although works about germination in *Opuntia* and *Harrisia* have suggested the presence of physical, morphological or morphophysical dormancy (Potter *et al.* 1984, Olvera-Carrillo *et al.* 2003, Podda *et al.* 2017), morphological (Mandujano *et al.* 1997) or morphophysiological (Dehan & Pérez 2005). None of these studies demonstrated a lack of seed imbibition, or an undifferentiated or underdeveloped embryo, which are traits used to show the existence of these types of dormancy (Baskin & Baskin 2014). Previous studies of *Opuntia* (including the species erroneously classified with physical and morphological dormancy) have demonstrated that only physiological dormancy can be attributed to them (Mandujano *et al.* 2005, Orozco-Segovia *et al.* 2007). In addition, cactus seeds having physiological dormancy can show dormancy cycling, Aragón-Gastélum *et al.* (2018) found that buried seeds of *Echinocactus 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.

Finch-Savage & Leubner-Metzger (2006), Willis *et al.* (2014) and Baskin & Baskin (2014) currently only recognize non-dormant seeds (including viviparous) and seeds with physiological dormancy for Cactaceae. According to Willis *et al.* (2014), in 153 cactus species studied 65 % showed physiological dormancy and 35 % non-dormant seeds. Most cacti inhabit arid and semiarid environments, so it is expected that future studies will find new species with physiological dormancy and probably species with physical dormancy as an adaptation to delay of germination, as has been proposed for species that occupy extreme or seasonal habitats (Jurado & Flores 2005, Baskin & Baskin 2014). In addition, a greater presence of heteromorphism in Cactaceae seeds with different degrees of physiological dormancy could be expected, as it occurs in *Leptocereus scopulophilus* (García-Beltrán *et al.* 2017) and *Leptocereus arboreus* seeds (unpublished data). Seed heteromorphism is considered a "*bet hedging*" strategy that favors the reproductive success of the offspring in unpredictable and heterogeneous environments (Venable 2007).

Seed banks. A seed bank is formed through the presence of viable seeds that remain in the habitat without germinating during a given period (Thompson & Grime 1979). Two types of banks have been defined in terms of the longevity of the seeds: a transient seed bank, when the seeds do not stay viable for more than a year (Thompson & Grime 1979) or until the next germination season (Walck *et al.* 2005) and a persistent seed bank when the seeds achieve permanence for more than a year.

When the place where the seeds are stored is referred to, two types of banks have been described: aerial and terrestrial (Baskin & Baskin 2014). Seeds are typically stored in the soil (the soil or terrestrial seed bank) but, in some species, seeds may be retained in plant canopy (the aerial seed bank) until seed release is triggered (Günster 1992). The formation of seed banks requires from the species an orthodox storage behavior that allows them to remain viable for long periods, as well as to escape from predators (Baskin & Baskin 2014).

The first studies about cactus seed banks concluded their existence whether through the collection of viable seeds in the soil (de Viana 1999), by examining seeds viability after different burial periods (Bowers 2000, 2005) or the dormancy present in some species (Potter *et al.* 1984, Mandujano *et al.* 1997). Silvius (1995) observed that *Stenocereus griseus* seeds obtained from bird feces took between two and five months to germinate, so at least a transient seed bank was possible for the species.

Most of the cactus seeds studied show small size, positive photoblasticism or skotodormancy (seed dormancy after darkness incubation) that allow them to persist in seed banks (Rojas-Aréchiga & Vázquez-Yanes 2000, Rojas-Aréchiga & Batis 2001, Flores *et al.* 2006, 2011, Ruiz-González *et al.* 2011, Rojas-Aréchiga *et al.* 2013, Sosa-Pivatto *et al.* 2014, Bauk *et al.* 2017, García-Beltrán *et al.* 2017, Rojas-Aréchiga & Mandujano-Sánchez 2017). Corresponding to the expected behavior for such seed traits, Seal *et al.* (2009) published a database with 83 species with seeds that remained viable for more than a year after collection and 65 species with desiccation tolerance. We found one hundred and forty-two cacti species contain seeds capable of remaining viable for at least three months after collection (Table 1). Even some works where the cactus seeds were stored under controlled conditions have demonstrated that these can germinate after various years (Flores *et al.* 2005, Sánchez-Salas *et al.* 2006) up to a maximum of 10 years (Alcorn & Martin 1974, Fearn 1977, Trujillo *et al.* 2014). Few studies have directed their efforts toward evaluating the viability of cactus seeds under natural conditions and their permanence in seed banks (Álvarez-Espino *et al.* 2014, Aragón-Gastélum *et al.* 2018).

Some recent work suggests the possibility of seed banks because of germination trials for various months or years (Flores *et al.* 2005, Faife-Cabrera & Toledo-Reina 2007, De la Rosa-Manzano & Briones 2010, Salazar *et al.* 2013, Jiménez-Sierra & Matías-Palafox 2015) or through the collection and measurement of seed viability (Cano-Salgado *et al.* 2012), although in this case it is impossible to determine the age of the collected seeds. Only in 19 species has the existence of a seed bank in the soil been clearly established (Table 1).

There are few studies that have submitted the seeds to environmental conditions and have examined their viability after different burial periods (Bowers 2000, 2005, Matías-Palafox 2007 Olvera-Carrillo *et al.* 2009, Cheib & Souza 2012, Goodman *et al.* 2012, Álvarez-Espino *et al.* 2014, Ordoñez-Salanueva *et al.* 2017, Lindow-López *et al.* 2018a, Aragón-Gastélum *et al.* 2018) or have assessed the effective seed bank, extracting the seeds from the soil in different times of the year (Montiel & Montaña 2003). Only the studies of Bowers (2005) and Ordoñez-Salanueva *et al.* (2017) shows two species (*Mammillaria grahamii* and *Polaskia chende*) capable of possessing a long-term, continuous seed bank (up to at least five years) according to the classification of Bakker *et al.* (1996).

Serotiny represents an alternative to the traditional seed bank and in many cases is known as an aerial form of seed bank, with the advantage of protecting the seeds in structures that are inaccessible to predators (Rodríguez-Ortega *et* al. 2006). Serotiny is known as a delayed dispersion mechanism because of the retention of mature seeds in structures of the mother plant for more than a year (Peters *et al.* 2009). In the Cactaceae family, serotiny probably is a common phenomenon in species that inhabit several North American deserts like the Mojave and the Sonora (Martínez-Berdeja *et al.* 2015). So far 24 species of cacti with a retention of mature seeds have been listed (Table 1), although around 25 species showed some degree of retention in the work of Bravo-Hollis & Sánchez-Mejorada (1991) according to Peters *et al.* (2009) but the role that serotiny plays in the population dynamic of the species where it occurs has not been extensively studied.

Seed retention in cacti has been observed in the axils of tubers (Rodríguez-Ortega *et al.* 2006, Peters *et al.* 2009), in chained fruits (Martínez-Berdeja *et al.* 2015), in the apex of the stems and in the cephalia (Bravo-Hollis & Sanchez-Mejorana 1991). The duration of the seeds in the stems has mainly been studied in the *Mammillaria* genus, where it has been demonstrated that the seeds can be retained from one (Santini & Martorell 2013) to eight years, forming an aerial seed bank (Boke 1960, Peters *et al.* 2009, Rodríguez-Ortega *et al.* 2006).

Temperature and seed germination. The current knowledge about the germination response of cactus seeds concerning different temperatures includes approximately 205 taxa (Table 1); the majority possesses an optimal germination between 20 - 30 °C (Zimmer 1968, 1982, 1998, Rojas-Aréchiga & Vázquez-Yanes 2000, Meiado *et al.* 2016, Seal *et al.* 2017). In a few species, greater germination was obtained at 15 °C, including those found in *Parodia aureicentra*, *Pereskia grandifolia* subsp. *grandifolia*, *Pereskia bahiensis, Pereskia aculeata, Echinopsis schickendantzii, Acanthocalycium spiniflorum, Ferocactus glaucescens*, *Mammillaria polythele*, *Browningia hertlingiana*, *Cephalocereus senilis*, *Rebutia minuscula*, *Rhipsalis pilocarpa*, *Rhipsalis teres* and *Copiapoa cinerea* var. *haseltoniana* (Zimmer 1968, 1982, 1998, Ortega-Baes *et al.* 2011, Lone *et al.* 2016, Meiado *et al.* 2016, Seal *et al.* 2017, Lindow-López *et al.* 2018b). Most of the species mentioned above inhabit temperate climates with annual average temperatures between 10.1 and 19.4 °C (https://es.climate-data.org), except *Pereskia* spp. and *Rhipsalis* spp. that inhabit warm climates with annual averages between 23.2 and 26.4 °C (Da Silva 2004, https://es.climate-data.org).

There are species with different growth forms with seeds that can germinate more than 50 % at temperatures as high as 40 °C. The majority have been reported in columnar species such as: *Pilosocereus gounellei* subsp. *gounellei*, *Pilosocereus pachycladus* subsp. *pernambucoensis* (Meiado *et al.* 2016), *Stenocereus thurberi*, *Pachycereus pringlei*, *Pachycereus pecten-aboriginum*, *Ferocactus peninsulae* (Yang *et al.* 2003) and *Stenocereus griseus* (Arias & Williams 1978), as well as the globular species *Melocactus curvispinus* subsp. *caesius* (Arias & Lemus 1984) and the epiphyte *Selenicereus setaceus* (Simão *et al.* 2007). The general tendency however, in cacti is that temperatures equal or higher than 35 °C and lower than 15 °C do not promote germination (Zimmer 1968, 1982, 1998, Rojas-Aréchiga & Vázquez-Yanes 2000, Meiado *et al.* 2016, Seal *et al.* 2017).

Because temperatures continually vary in nature, various studies have compared the germination response of the cactus seeds between constant and alternating temperatures. In such studies, the alternation of temperature can produce three types of responses: (1) lower percentage of germination (Rojas-Aréchiga *et al.* 1997, 1998, 2001, Matías-Palafox 2007, Ortega-Baes & Rojas-Aréchiga 2007, Lindow-López *et al.* 2018b), (2) similar percentage of germination (Godínez-Álvarez & Valiente-Banuet 1998, Ruedas *et al.* 2000, De la Barrera & Nobel 2003, Yang *et al.* 2003, Ramírez-Padilla & Valverde 2005, Matías-Palafox 2007, Sánchez-Soto *et al.* 2010, Ortega-Baes *et al.* 2011, Mazzola *et al.* 2013, Jiménez-Sierra & Matías-Palafox 2015, Kin *et al.* 2015, Lindow-López *et al.* 2018b) or (3) higher percentage of germination (Godínez-Álvarez & Valiente-Banuet 1998).

In some studies, the three types of responses have been observed (Ortega-Baes *et al.* 2010, Meiado *et al.* 2016). From these results, it can be inferred that the germination response concerning the constancy or variation of the temperature becomes species-specific (Ortega-Baes *et al.* 2010) so that a general tendency does not exist in the Cactaceae family such as in other families (Baskin & Baskin 2014).

Some studies of the 1990s (Cancino *et al.* 1993, Nolasco *et al.* 1996, Vega-Villasante *et al.* 1996) demonstrated that exposing *Pachycereus pringlei* and *P. pecten-aboriginum* seeds to temperatures from 55 to 70 °C for various hours, days or even weeks prior to sowing; left some seeds viable. Studies performed on 17 species (Table 1), with seeds that have been exposed to temperatures between 60 - 90 °C (Ruedas *et al.* 2000, Olvera-Carrillo *et al.* 2003, Mandujano *et al.* 2005, Ramírez-Padilla & Valverde 2005, Sánchez-Soto *et al.* 2010, Pérez-Sánchez *et al.* 2011), found four types of response: a) For *Isolatocereus dumortieri* at 70 °C the final germination percentage decreased (Pérez-Sánchez *et al.* 2011); b) For *Mammillaria magnimama*, decreasing only occurred in lots of old seeds (Ruedas *et al.* 2000); c) For several species, the most common response was to show similar germination than in the controls (Ruedas *et al.* 2000, Olvera-Carrillo *et al.* 2003, Ramírez-Padilla & Valverde 2005, Sánchez-Soto *et al.* 2010); d) For several species the exposure to high temperatures exceeded the final germination of the control (Olvera-Carrillo *et al.* 2003, Sánchez-Soto *et al.* 2010, Pérez-Sánchez *et al.* 2011), demonstrating cactus seed tolerance to high temperatures, at least for short periods. The seed tolerance to extreme temperatures may have evolved as a mechanism to enable persistence in the soil in predominantly desert species with high temperatures on the soil surface (Daws *et al.* 2007).

In recent years, various studies of cactus have directed their efforts to evaluating the possible impact of global warming on the germination of the seeds (Ordoñez-Salanueva *et al.* 2015, Flores *et al.* 2017, Gurvich *et al.* 2017, Seal *et al.* 2017, and Aragón-Gastélum *et al.* 2018), through the assessment of the germination response faced with different temperatures. Other studies, although not directly mentioning global warming, show useful results to evaluate the response of cactus seeds faced with temperatures higher than 30 °C (Kin *et al.* 2015, Meiado *et al.* 2016). However, conclusions are ambiguous.

The results shown by Seal *et al.* (2017) showed a possible explanation for the ambiguity of the response of cacti seeds to high temperatures. That study showed the tendency of species that inhabit temperate environments (extratropical or tropical cactus species that inhabit altitudes > 1,000 m asl) possess optimal germination temperatures generally, between 5 and 10 °C of difference above the average of the period when germination occurs. This study revealed the capability of thermal buffering for the germination that these species possess. Although Seal *et al.* (2017) only included a few species that inhabit warm environment (tropical species that grow between 0 - 1,000 m asl.) the aforementioned species were shown to possess near optimal germination temperatures, generally between 1 and 3 °C of difference or slightly lower than the current average in the rainy period (Seal *et al.* 2017). For these species, the models predict an impact through the increase of the temperatures for the RCP 8.5 scenario (of greater warming) and in some cases until the RCP 2.6 scenario (of lower warming) (Seal *et al.* 2017).

Most germination studies performed on cacti, where different temperatures are compared, generally include species that inhabit temperate environments (Seal *et al.* 2009, 2017). Seal *et al.* (2009) gathered information about germination from approximately a hundred cacti with values between 30 and 41 °C, but only 12.6 % were species from warm climates. From this compilation, it can be deduced that both the cactus species that inhabit temperate climates and those of warm climates generally possess a similar response to this temperature range.

The germination study that included the greatest quantity of tropical cacti species was performed by Meiado *et al.* (2016) with 30 species, mostly endemic of the Caatinga in Brazil. These authors found a germination response higher than 50 % to temperatures of 35 °C and an optimal temperature around 30 °C, which is a temperature near or slightly higher than the average temperatures reported for that region according to Da Silva (2004). Although it could be expected that the cactus species that inhabit temperate environments have a lower optimal germination temperature than species that inhabit warmer environments, the information available shows that both cacti groups generally possess a similar germination response to 30 °C (Figure 4).

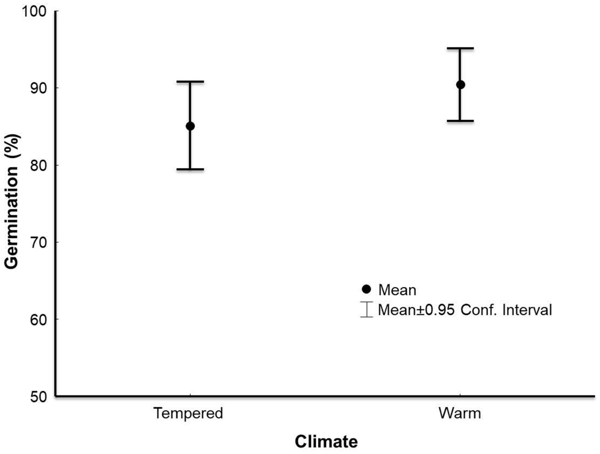

Figure 4. Seed germination responses at 30 °C between cacti from temperate and warm climates, based on 43 data from temperate and 34 from warm climate.

This similar response implies that the cactus species of temperate climates possess the greatest capacity for thermal buffering of germination, as the results of Seal *et al.* (2017) suggest. The warm climate species, being within the limit or very close to the optimal germination temperature will possess a lower capacity for buffering and in consequence it will possibly be these cacti that are the most vulnerable to the effects of the expected climatic change.

Light and seed germination. The germination response considering conditions of light and darkness has been assessed in 275 cactus species (Table 1). So far no negative photoblastic seeds have been found in cacti and 80.9 % have presented positively photoblastic seeds (Matías-Palafox & Jiménez-Sierra 2006, Flores *et al.* 2006, 2011, Cheib & Souza 2012, Delgado-Sánchez *et al.* 2013, Rojas-Aréchiga *et al.* 2013, Meiado *et al.* 2016). Among the cacti with indifferent or neutral photoblastic seeds, 34 taxa have been reported in the Cactoideae subfamily that represent only 13.8 % of its species, however, 75 % of the 24 taxa studied of the subfamilies Opuntioideae, Pereskioideae and Maihuenioideae, have indifferent photoblastic seeds, which suggests that this character is ancestral in Cactaceae.

Several studies indicate a strong influence from phylogeny in the photoblastic response within the family (Flores *et al.* 2011, Rojas-Aréchiga *et al.* 2013, Meiado *et al.* 2016). Rojas-Aréchiga *et al.* (2013) found a phylogenetic influence between various species of the Cacteae tribe, while Flores *et al.* (2011) found that the Cacteae, Pachycereeae and Trichocereeae tribes include species with greater germination response to light than in Notocacteeae. On the other hand, Meiado *et al.* (2016) found that the phylogenetic origin was the only variable influencing the germination response to light in 30 cactus species of Brazil, and only the species of Pereskioideae and Opuntioideae showed an indifferent photoblastic response, while all the Cactoideae species were positively photoblastic.

The seed response to light in Cactaceae has traditionally been evaluated in association with the form of life (Rojas-Aréchiga *et al.* 1997, Ortega-Baes *et al.* 2010, Flores *et al.* 2011), size and seed mass (Flores *et al.* 2006, Ortega-Baes *et al.* 2010, Rojas-Aréchiga *et al.* 2013), as well as to different wavelengths or solar irradiation (Alcorn & Kurtz 1959, McDonough 1964, Zimmer 1969a, 1973, Rojas-Aréchiga *et al.* 1997, Nolasco *et al.* 1997, Benítez-Rodríguez *et al.* 2004, Olvera-Carrillo *et al.* 2009, Meiado *et al.* 2010, Zerpa-Catanho *et al.* 2019) and concentrations of gibberellins (Alcorn & Kurtz 1959, McDonough 1964, Rojas-Aréchiga *et al.* 2001, Ortega-Baes & Rojas-Aréchiga 2007, Rojas-Aréchiga *et al.* 2011, Mascot-Gómez *et al.* 2020). Some preliminary studies suggested that an association between the life-form and the photoblasticism could exist (Rojas-Aréchiga *et al.* 1997, Rojas-Aréchiga & Vázquez-Yanes 2000). Other research has subsequently opposed that hypothesis (Ortega-Baes *et al.* 2010, Flores *et al.* 2011, Meiado *et al.* 2016). Moreover, Flores *et al.* (2011) found a negative relationship between the germination response to light and the height of the plant, probably because tall cacti produce larger seedlings than short cacti (Flores *et al.* 2011). Similar readings can be obtained from the data of Rojas-Aréchiga *et al.* (1997).

Several cactus studies have shown a relationship between seed size and the requirement of light to germinate (Maiti *et al.* 2003, Sánchez *et al.* 2015). Both Flores *et al.* (2006) and Ortega-Baes *et al.* (2010) considered that positive photoblastism in the 37 cactus species they studied could be related to the small size of their seeds and their potential for building soil seed banks. Similarly, Flores *et al.* (2011) obtained a negative relationship between seed mass and the dependence on light to germinate; nevertheless, in species without dormancy this relationship was marginal or non-significant, which the authors attributed to the differences that were presented between dormant and non-dormant seeds or to the size of the sample.

Some previous studies of around 80 species of cacti (Rojas-Aréchiga *et al.* 2013, Meiado *et al.* 2016) found no relationship between the requirement of light for germinating and seed size. Probably these results with a certain ambiguity could be explained by the small size and mass that cacti show in general and because the role of the phylogenetic relationships (as already referred to) can distort the interpretation of the data.

The influence of gibberellic acid (AG_3) as a light substitute has been studied in cacti since Alcorn & Kurtz (1959) found that a fraction of positively photoblastic seeds of *Carnegiea gigantea* were stimulated in darkness with the addition of AG_3. Subsequently, McDonough (1964) confirmed the aforementioned results and also included *Stenocereus thurberi* with similar results. Similar findings have been found in several cactus genera by Brencher *et al.* (1978), Arias & Williams (1978), Zimmer & Büttner (1982) and López-Gómez & Sánchez-Romero (1989). Nevertheless, even though the role of AG_3 has not been subsequently studied (Ortega-Baes & Rojas-Aréchiga 2007, Rojas-Aréchiga *et al.* 2011), the works that refer to it in cacti have not found a stimulation of germination under darkness (Williams & Arias 1978, Arias & Lemus 1984, Rojas-Aréchiga *et al.* 2001, 2011, Olvera-Carrillo *et al.* 2003, Ortega-Baes & Rojas-Aréchiga 2007, Rojas-Aréchiga 2008, Mascot-Gómez *et al.* 2020). Even when the AG_3 effect as a promoter of germination under white light has been evaluated, in the majority of the studies an enhancer effect on different concentrations in intact seeds has not been found (Mandujano *et al.* 2007, Ortega-Baes & Rojas-Aréchiga 2007, Rojas-Aréchiga 2008, Olvera-Carrillo *et al.* 2009, Amador-Alférez *et al.* 2013, Loustalot *et al.* 2014, Rodríguez-Ruíz *et al.* 2018, Gonzalez-Cortés *et al.* 2018). The difficulty in clearly establishing the role of AG_3 as a germination promoter for Cactaceae could be related to the fact that in the studies homogeneity has not been maintained in the following parameters: light conditions, age of the seeds, types of dormancy, time and mode of application of the AG_3 concentrations, among others. These differences among parameters can include changes in the behavior of seeds' germination in the species and thus hinder the comparisons among the performed studies (Rojas-Aréchiga 2008). Nevertheless, possibly AG_3 does not possess such an important role as a germination promoter in cacti seeds, such as Rojas-Aréchiga (2008) and Rojas-Aréchiga *et al.* (2011) refer to.

Water and saline stress and germination. In general, seeds of most plants studied stop germinating at water potentials between -0.5 and -2.0 MPa (Dürr *et al.* 2015, Tribouillois *et al.* 2016). These potentials are experimentally achieved with the use of different concentrations of three main substances: mannitol (Maldonado *et al.* 2002, Guerrero *et al.* 2016), polyethylene glycol (PEG) (Yang *et al.* 2010, Luna & Chamorro 2016, Pantané *et al.* 2016) and NaCl (Zhang *et al.* 2010, Gorai *et al.* 2014, El-Keblawy *et al.* 2016).

In cacti, only four studies have assessed the germination at water potentials lower than -1.0 MPa (Martins *et al.* 2012, Guerrero *et al.* 2016, Aragón & Lasso 2018, Zerpa-Catanho *et al.* 2019), maybe because in most cases the species do not achieve germination at such potentials (Flores & Briones 2001, Ramírez-Padilla & Valverde 2005, De La Rosa-Manzano & Briones 2010, Guillén *et al.* 2011, 2015, Rodríguez-Morales *et al.* 2013, Flores *et al.* 2017, Bispo *et al.* 2018). The studies in cacti reveal that germination mainly occurs at water potentials between 0 and -0.6 MPa (Figure 5) and at temperatures of 25 to 30 °C (Vega-Villasante *et al.* 1996, Kin *et al.* 2015, Gurvich *et al.* 2017, Flores *et al.* 2017, Bispo *et al.* 2018).

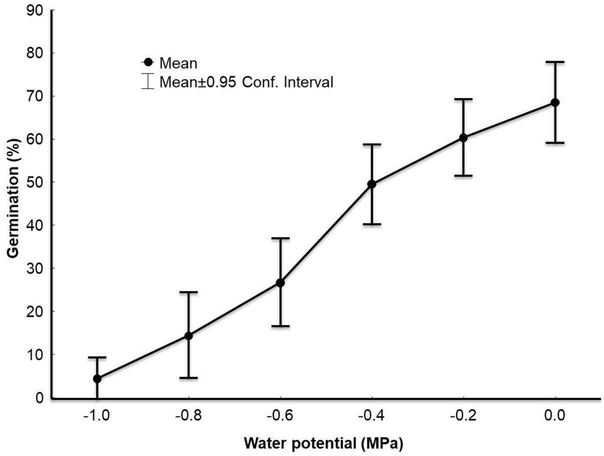

Figure 5. Seed germination response under water stress. Data are based on 28 cactus species studied.

In some species, it has been observed that the water potentials of -0.2 MPa (Guillén *et al.* 2009, 2015, Gurvich *et al.* 2017, Flores *et al.* 2017) or even -0.4 MPa (Flores & Briones 2001, Guillén *et al.* 2011, 2015, Flores *et al.* 2017) or -0.6 MPa (Flores & Briones 2001) favor germination. Nevertheless, generally water potentials lower than -0.6 MPa notably decrease the percentage of germination (Meiado *et al.* 2010, Guillén *et al.* 2011, 2015, Gurvich *et al.* 2017, Flores *et al.* 2017, Bispo *et al.* 2018). Thus, cactus seeds adapted to germinate at high soil moisture, but not necessarily at the soil field water capacity, would have an advantage germinating in arid environments. However, this may have a trade-off between germination at relatively low soil water potential and seedling establishment because seedlings generally require higher soil water potential to compensate for transpiration (Flores & Briones 2001).

In addition, in the species where the effect of water potential and temperature has been combined, normally at 25 °C, better results have been obtained than at temperatures of 30 °C or higher (Oliveira *et al.* 2017, Gurvich *et al.* 2017, Flores *et al.* 2017, Bauk *et al.* 2017). For primarily arid and semiarid species with small seeds, as occurs in Cactaceae, the preference for germinating in humid soil can be an advantage that permits to reduce seedling mortality when faced with transient rain followed by prolonged droughts. These conditions could favor germination but could also result in death of seedlings through subsequent drought (Venable & Lawlor 1980).

Approximately a dozen studies (Table 1) have evaluated the germination response of cacti faced with conditions of salinity (Romero-Schmidt *et al.* 1992, Vega-Villasante *et al.* 1996, Nolasco *et al.* 1996, Meiado *et al.* 2010, Martins *et al.* 2012, Ortiz *et al.* 2014, Lima & Meiado 2017, Podda *et al.* 2017, Bispo *et al.* 2018). A germination response in the range of 0 to -0.6 MPa with NaCl is similar to the results obtained with PEG, even though there are species where the germination percentages with NaCl are higher than in a similar osmotic potential of PEG (Meiado *et al.* 2010, Bispo *et al.* 2018). In other cases, the seeds germinate better in PEG (Martins *et al.* 2012). On the other hand, there is very little information about the application of the hydrotime model to evaluate the effects of water or saline stress on germination speed (or germination time) in cactus species (see: Simão *et al.* 2010). Germination time is an important feature of plant life history that determines germination capacity under dry conditions and recruitment time (Sánchez-Soto *et al.* 2005, Donohue *et al.* 2010, Dürr *et al.* 2015).

Hydration-dehydration cycles and germination. Two pioneering studies of Dubrovsky (1996, 1998) demonstrated the utility of the hydration-dehydration cycles in increasing the speed and final percentage of germination in four cactus species. However, still there are a few cactus studies (Table 1) that address these treatments as germination promoters (Sánchez-Soto *et al.* 2005, Rito *et al.* 2009, Santini & Martorell 2013, López-Urrutia *et al.* 2014, Contreras-Quiroz *et al.* 2016a, 2016b, Santini *et al.* 2017, Lima & Meiado 2017, 2018, Sánchez *et al.* 2018), although hydration-dehydration cycles have been and are widely used in innumerable species worldwide (Sánchez & Pernús 2018). The evaluation of this type of pre-germinative treatment in cactus seeds should be tested more in the future, because the seeds are subject to hydration-dehydration cycles in nature, which can influence not only germination but also aspects related to conditional or cyclical dormancy, seed longevity and seedling survival, among others (Baskin & Baskin 2014). Similarly, water treatments (or cycles) could be implemented as ecotechnologies in ecological restoration projects and in conservation programs of germplasm (Sánchez & Pernús 2018).

The ability of seeds to maintain physiological changes produced during hydration, such as differential protein expression, through discontinuous dehydration periods (López-Urrutia *et al.* 2014), has been called "hydration memory" (Dubrovsky 1996). Contreras-Quiroz *et al.* (2016b) evaluated this phenomenon in cacti from a semi-desert area in northeastern Mexico, and from a sub-humid area of central Argentina, and suggested that the presence of hydration memory in the seeds of Cactaceae depends on the climate and the microenvironment where the cacti occur, indicating that environmental conditions imposed on the parental plants influence the germination responses of the cacti seeds when subjected to discontinuous hydration. This hypothesis was corroborated by Lima & Meiado (2017) who found that the seeds of the same species (*Pilosocereus catingicola* subsp. *salvadorensis*) collected from populations located in different ecosystems have different germination responses after passage through discontinuous hydration and HD cycles. This finding gives evidence that "hydration memory" provides greater tolerance to environmental stresses but with different responses among populations.

Cactus seed dispersal. Rojas-Aréchiga & Vázquez-Yanes (2000) reported six studies about cactus seed dispersion through endozoochory. In the last two decades, a few more than a dozen species have been studied regarding this type of interaction and its effect on germination (Godínez-Álvarez & Valiente-Banuet 2000, Montiel & Montaña 2000, Godínez-Álvarez *et al.* 2002, Naranjo *et al.* 2003, Baraza & Valiente-Banuet 2008, Pérez-Villafaña & Valiente-Banuet 2009, Casado & Soriano 2010, Fonseca *et al.* 2012, Gomes *et al.* 2014, Nascimento *et al.* 2015, Lasso & Barrientos 2015, Vázquez-Castillo *et al.* 2018, Santos *et al.* 2019). Other types of cactus seed dispersal referred to by Rojas-Aréchiga & Vázquez-Yanes (2000) as synzoochory (Munguía-Rosas *et al.* 2009, Fonseca *et al.* 2012), epizoochory (Lasso & Barrientos 2015) and hydrochory (Lenzi *et al.* 2012, Sánchez-Salas *et al.* 2012, Sánchez-Salas *et al.* 2013, Romero-Méndez *et al.* 2018) have been reported in a small number of studies.

In vitro propagation. Although in a great number of cactus species high percentages of germination have been found (Zimmer 1969b, 1998, Meiado *et al.* 2016), various studies have explored *in vitro* germination as an alternative of propagation (Salas-Cruz *et al.* 2011, Xavier & Jasmim 2015, López-Escamilla *et al.* 2016, Cortés-Olmos *et al.* 2018, Ramírez-González *et al.* 2019). Studies of this type have been performed on more than 40 cactus species (Table 1), with good results in germination and later seedling growth. The *in vitro* germination with enriched resources could be a necessary and essential method in the propagation of rare species with few seeds or with a low percentage of germination, both for preservation of the species or another purpose.

Seed storage at low temperatures. Although in the present review the seed desiccation tolerance and the longevity of cactus seeds have been commented on, few studies have evaluated the seed preservation in controlled conditions. Only in 20 species has a preservation at - 0 °C been evaluated, up to a maximum of 13 months (Nolasco *et al.* 1996, Vega-Villasante *et al.* 1996, Veiga-Barbosa *et al.* 2010, Goodman *et al.* 2012, Marchi *et al.* 2013, Salazar *et al.* 2013, Bárbara *et al.* 2015, Civatti *et al.* 2015, Dos Santos *et al.* 2018). Studies of this type are necessary when faced with the increasing threats that confront the family (Goettsch *et al.* 2015) and the need to search for secure alternatives for long-term preservation.

Concluding remarks. In the last two decades, the number of studies related to cactus germination has increased exponentially, with Mexico, Brazil and Argentina being the three countries leading this scientific field. Seed germination has been evaluated in less than 50 % of the genera. Only physiological dormancy has been found in the family. Terrestrial and aerial cactus seed banks have been little studied but are perhaps common and play an important role in the population dynamics of the species. The two most studied research topics on cactus seed germination are photoblasticism and the response to temperature. No cactus with a negatively photoblastic response has been found, and most of the species of the subfamily *Cactoideae* have positively photoblastic seeds. The optimal temperature range for cacti is found between 20 and 30 °C. However, there are still genera with more than 20 species that have not been studied such as *Matucana,* and others genera like *Frailea*, *Rebutia*, and *Selenicereus* where only one species has been studied.

There is not enough evidence on seed traits and cactus seed germination, but seed shape has been related with seed dispersal in that the hat-shaped seeds have been associated with hydrochory. The relationships between cactus seed germination and phylogeny depends on the species studied and the tribe. The germination types or variants do not appear to be related with seed germination percentage. Cactus seeds are adapted to germinate at high soil moisture, but not necessarily at the soil field water capacity. Seeds germinate at saline potentials between 0 and -0.6 MPa. Hydration-dehydration cycles or hydration memory increase the speed and the final percentage of germination in some species; the presence of hydration memory in the seeds of Cactaceae depends on the climate and the microenvironment where the cacti occur.

Preserving cactus seeds in banks is an encouraging concept because their longevity in general surpasses six months, and a high percentage of species possess seeds that maintain their viability for periods between one to two years without extreme storage requirements. Similarly, studies about desiccation tolerance and cryopreservation that have been performed demonstrate their feasibility. In the future, it would be useful if more cactus germination studies included measurement of seed traits, such as length, width and compression, total dry mass, mass of the covering of the embryo, moisture content, as well as imbibition rate.

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