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Unveiling the germination requirements for *Cereus hildmannianus* (Cactaceae), a potential new crop from southern and southeastern Brazil

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ABSTRACT

Cereus hildmannianus K. Schum is a columnar cactus native to South and Southeast Brazil. The cultivation of this species seems justifiable for several reasons: its fruits are spineless and edible; it is not threatened with extinction; it naturally occurs in Pampa and Atlantic Forest under non-xeric conditions that may be unsuitable for the cultivation of other tropical cacti; and the plants are pollinator-dependent and so should benefit from native pollinators. This study aimed to test seed germination of *C. hildmannianus* with samples collected at three different localities in southern Brazil, as a necessary step preceding any attempts of management and domestication. Seeds were exposed to temperatures of 20° C, 25° C, 30° C and room temperature. The germinability, average germination time and synchronization index were calculated. All samples showed higher germinability at 20° C and 25° C. Seeds from Caçapava do Sul and Santiago showed significant variation in the synchronization index at 25° C and 30° C, respectively. Seeds from Porto Alegre had maximum germinability, indicating greater vigor. Our results show that the seeds of *C. hildmannianus* germinate well and thrive within a wide range of temperatures and that cultivation of the species from seed-raised plants should not be problematic.

Keywords: cacti, *Cereus hildmannianus*, germinability, germination, synchronicity, tuna

Introduction

For centuries, Native Americans have exploited cacti as food, forage, a source of building materials and for medicinal purposes (Pimienta-Barrios & Nobel 1994). Whereas the cultivation and domestication of native cacti is particularly widespread in Mesoamerica (Casas & Barbera 2002), at least nine cactus species are used for diverse purposes in North-east Brazil (Lucena *et al.* 2013). The usefulness of these cacti has inspired attempts to introduce them into different semi-arid ecozones around the world (Mizrahi 2014). However, the economic potential of several other cacti (either Brazilian or not) has certainly been overlooked.

Cereus hildmannianus K. Schum., popularly known as "tuna", is a species of columnar and arborescent cactus that occurs in Paraguay, South Brazil, Uruguay and the Argentinean Pampa grasslands (Taylor & Zappi 2004). The species is a potential crop, with its fruits being appreciated and used as food (Pesce 2011). In addition, its cladodes are used as a medicinal resource (Chaves & Zanin 2011). Mucilage of tuna has insecticidal properties, and can, for

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example, be used to control the larvae of *Aedes aegypti* (Culicidae) (Kamakshi *et al.* 2015). Nevertheless, tuna is scarcely mentioned in ethnobotanic studies, unlike other species of the same genus, such as *Cereus albicaulis* Britton & Rose (Chaves *et al.* 2015; Silva 2015), *C. jamacaru* DC. (Albuquerque *et al.* 2007; Lucena *et al.* 2013; Lucena *et al.* 2012; Santana *et al.* 2018) and *C. repandus* (L.) Mill. (Pasa *et al.* 2005; Carneiro *et al.* 2014; Mizrahi 2014; as *Cereus peruvianus*), which occur in Northeast Brazil. Many species of Cactaceae show high degrees of parallel evolution in vegetative, fruit and floral traits, which bring a convergence of uses (Barthlott & Hunt 1993). In other words, plants of *C. hildmannianus* could be as useful as the species cited above, and thus an important and useful resource for native human populations.

Tuna occurs throughout the state of Rio Grande do Sul, in its two biomes, the Pampa and Atlantic Forest, and in all its different environments, such as coastline, rainforest and grasslands (Carneiro *et al.* 2016). Two subspecies are recognized: *Cereus hildmannianus* subsp. *hildmannianus*, is restricted to the southern Brazil coastline and around the Lagoa dos Patos region; and *Cereus hildmannianus* subsp. *uruguayanus*, which occurs in western Rio Grande do Sul and Santa Catarina states and throughout the state of Paraná. Morphological differences can be observed in flower length; the flower of *C. hildmannianus* subsp. *hildmannianus* can reach over 20 cm long, while that of *C. hildmannianus* subsp. *uruguayanus* reaches up to 16 cm (Becker, in. prep.). The distinction of the two subspecies is supported by a recent phylogeographic study that evidenced a vicariance process, sorting out the populations of the two subspecies, probably due to environment changes during the Quaternary period (Silva *et al.* 2018). These lineages agree with the currently accepted subspecies (Carneiro *et al.* 2016) and, consequently, match the observed variability in floral tube length (Becker, in. prep.).

Cereus hildmannianus can reproduce by vegetative means or sexually through seeds produced via pollination. The latter enables genetic enhancement through the mixing of different variants and the selection of individuals with the most appreciated characteristics, such as productivity, fruit shape and climatic adaptations (Rech *et al.* 2014). Besides that, cacti have always been the subject of intensive exploitation due to their great ornamental value and, as a result, their populations have been drastically affected by overcollection and other anthropogenic perturbations such as mining and raising cattle (Rojás-Aréchiga & Vasquez-Yanes 2000). Currently, there are 68 species of cacti known for the state of Rio Grande do Sul (Flora do Brasil 2020 em Construção 2020), which represents about 30 % of Brazilian Cactaceae. Furthermore, 53 of these species are considered endangered according to IUCN guidelines (Carneiro *et al.* 2016). Propagation studies could constitute a contribution to the conservation of this natural resource because it promotes the possibility of obtaining valuable plants through controlled methods that could decrease the demand for illegal wild-collected material (Rojás-Aréchiga & Vasquez-Yanes 2000). Thus, studies involving reproduction and germination are needed in order to understand the best strategies for conservation-wise or economic-wise management, as for *C. repandus*, a fruit-crop marketed in Israel that first needed several studies regarding its ideal germination conditions (Ninio *et al.* 2003; Mizrahi 2014; as *Cereus peruvianus*).

An important factor in germplasm development is temperature, the understanding of which is essential for comprehending the ecophysiological and biochemical features by which species are adapted to the environment (Labouriau 1983; Ferreira & Borghetti 2004). Temperature rules germplasm capacity and breaks or induces dormancy (Bewley & Black 1994), in addition to affecting germination speed and synchronicity (Carvalho & Nakagawa 2000). These parameters are important for comparing germination of different seeds and measuring their respective performances.

The aims of this study, therefore, are to evaluate how temperature affects the germination of *C. hildmannianus* seeds collected from different localities, find the optimum temperature for germination and compare vigor among sampled populations. In our opinion, the cultivation and domestication of *C. hildmannianus* in South and Southeast Brazil could be justified for several reasons: (1) it is a native, widespread plant resource whose spineless fruits are edible and already known as such by nearby human populations; (2) it is not a threatened species (LC - Least Concern, according to Carneiro *et al.* 2016; according to IUCN guidelines); (3) it is widely distributed in two Biomes, the Pampa and Atlantic Forest, which is suggestive of high climatic tolerance; and (4) it is pollinator-dependent and relies on the agency of native insects to set fruit (Becker, in. prep.). Thus, from an environmental point of view, the cultivation of this native cactus could benefit from the services of native pollinators. Indeed, *C. hildmannianus* is native in areas with relatively high rainfall and low temperatures; such localities being probably unsuitable for cacti from the Caatinga (such as *C. jamacaru*) or from other tropical regions. Whereas very ripe fruits of *C. hildmannianus* may split under natural conditions (a fact that could complicate its commercialization), we think that this problem could be solved with appropriated harvesting practices of looking for populations whose fruits lack this feature. In fact, our field observations indicate that not all ripe fruits split (see Results), suggesting that more in-depth research is needed. The questions behind this contribution are: How is the germination of seeds of *C. hildmannianus* from different localities affected by temperature? Do seeds from different localities germinate similarly under the same temperatures or will they perform differently? Our hypothesis is that seeds from some localities may perform differently and, consequently, may be more interesting than others as a source of germplasm.

Materials and methods

We used *Cereus hildmannianus* seeds from fruits collected at the localities of Porto Alegre (30°14'10.3" S; 51°05'57.9" W), Santiago (29°29'57.3" S; 54°43'38.2" W) and Caçapava do Sul (30°39'04.9" S; 53°34'34.9" W), all in Rio Grande do Sul, Brazil) Table 1 summarizes the main climatic features of the collecting localities. Silva *et al*. (2018) showed, through molecular analyses, a vicariance process in the evolutionary history of *C. hildmannianus* populations of South Brazil. This process may have taken place after climate changes in the Quaternary period, originating two main clades. With this information as a framework, the three localities we chose for collecting fruits were also sampled in the study of Silva *et al*. (2018) and represent each haplotype and an intermediate population to guarantee genetic diversity for the germination tests. Thus, Porto Alegre represents the long-flowered lineage (subsp. *hildmannianus*), while Santiago represents the short-flowered lineage (subsp. *uruguayanus*). The phylogeographic study of Silva *et al.* (2018) considered Caçapava do Sul as an intermediate population, yet clearly bearing morphological features of subsp. *hildmannianus*. The use of seeds from different populations encompassing the two currently accepted subspecies allows a systematic comparison of their germination features. Since the present contribution is biased towards the domestication and management of *C. hildmannianus*, testing seeds from different localities or varieties is a powerful tool for discovering valuable germplasm.

Five fruits were collected from each locality in March and April 2019. The fruits were measured and the number of seeds counted. Tests were performed at the Banco de Sementes do Jardim Botânico de Porto AlegreSeeds were washed in tap water and dried on filter paper overnight. The seeds were then stored in polyethylene bags for seven days at room temperature, after which they were kept in plastic boxes (Gerbox) with blotting paper moistened with 10 mL of deionized water. Each box received 25 seeds with four replicates for each locality for a total of 100 seeds per locality/treatment. Seeds were subjected to one of three treatments, constant temperature of 20° C, 25° C or 30° C, in a germinator (Tecnal TE-4020 LED) with photoperiod of 12 h. A control test was made at room temperature (between 20.2 and 30.3 °C; average = 26.6 °C), with natural photoperiod. Germinated seeds were counted daily using a stereomicroscope. Seeds that emitted a visible hypocotyl-root axis were considered germinated.

Indexes calculated after the final count were: germinability as $G=(N_g \cdot 100)/N_t$, where N_g is the number of germinated seeds and N_t is the total number of seeds; average germination time as $\bar{t} = \sum n_i \cdot t_i / \sum n_i$, where t_i is average incubation time and n_i is the number of seeds germinated daily (Edmond & Drapalla 1958); and synchronization as $\bar{E} = -\sum f_i \cdot \log_2 f_i$, where f_i is relative germination frequency (Labouriau & Valadares 1976). Final index values were compared by two-way ANOVA followed by Tukey's significant difference test at 5 %. All statistical analyses were carried out using the software RStudio 1.2.1 (Allaire 2012).

Results

Ripe fruits are of the acrosarcum type with an average diameter of 6.5 ± 0.73 cm, an average length of 8.1 ± 1.5 cm (*n* = 15) and a globular to elliptical shape. The epicarp is spineless, smooth, slightly shiny and yellowish or reddish (Fig. 1A). The endocarp is white, fleshy and edible, with hundreds of very small seeds (Fig. 1B). Some very ripe fruits in the wild were observed to split and open, exposing the pulp and seeds, yet other fruits were consumed by birds without prior splitting (Becker, in. prep.). Fruits can hold between 500 and 1000 seeds (mean 787.7 ± 238.3; *n* = 15), which are darkish, campylotropous, kidney-shaped and bitegumented. The testa is ornate and the hilum possesses a micropylar depression (Fig. 2A). Germination begins between days 4 and 8 after seeding and proceeds for about a week. Seeds were considered germinated when the hypocotyl-root axis protruded from the hilum break (Fig. 2B).

Seedlings are initially white and two short, conical cotyledons are visible on day 10, when the hypocotyl is completely straight. Later, seedlings turn greenish and are typically columnar-shaped and about 2 cm tall (Fig. 2C). Trichome and areole emission takes place around day 20, when the cotyledons disappear and the epicotyl becomes very developed (Fig. 2D).

All three calculated indexes differed significantly among temperatures as well as for the interaction between temperature and locality. Conversely, none of the indexes differed significantly among localities (Tab. 2).

Germinability was considered high for all tests, since samples from all localities reached over 90 % germination at 20° C and 25° C. However, at 30° C seeds from Santiago and Caçapava do Sul had lower germination percentages, although significantly so only for Caçapava do Sul. Seeds from Porto Alegre had excellent germinability in all

Table 1. Main climatic features of the sampled localities (BDMEP 2020).

Localities	Coordinates	Altitude (masl.)	Mean Annual temperature (min-max) (° C)	Mean monthly precipitation (mm)	Subspecies
Santiago	29°29'57.3" S 54°43'38.2" W	190	19.5 (14.7–25.7)	142.6	*uruguayanus*
Caçapava do Sul	30°39'04.9" S 53°34'34.9" W	374	17.4 (13.5–23.1)	126.5	*hildmannianus*
Porto Alegre	30°14'10.3" S 51°05'57.9" W	4	19.7 (15.7–25.2)	113.2	*hildmannianus*

treatments.The average germination time index did not differ significantly among temperature treatments. Under the control treatment, however, seeds from Caçapava do Sul had a longer average germination time than did seeds from Santiago. The synchronization index differed significantly between seeds from Porto Alegre and seeds from Caçapava do Sul at 25° C and 30° C, and between seeds from Porto Alegre and seeds from Santiago at 30° C (Tab. 3).

Discussion

Morphological characterization of seeds is very important for the taxonomy of Cactaceae. For instance, testa ornamentation patterns have been proven to be taxonomically informative among species of *Stenocereus* (Arroyo-Cosultchi *et al.* 2006). However, details about the seeds of native Brazilian cacti, and their potentially

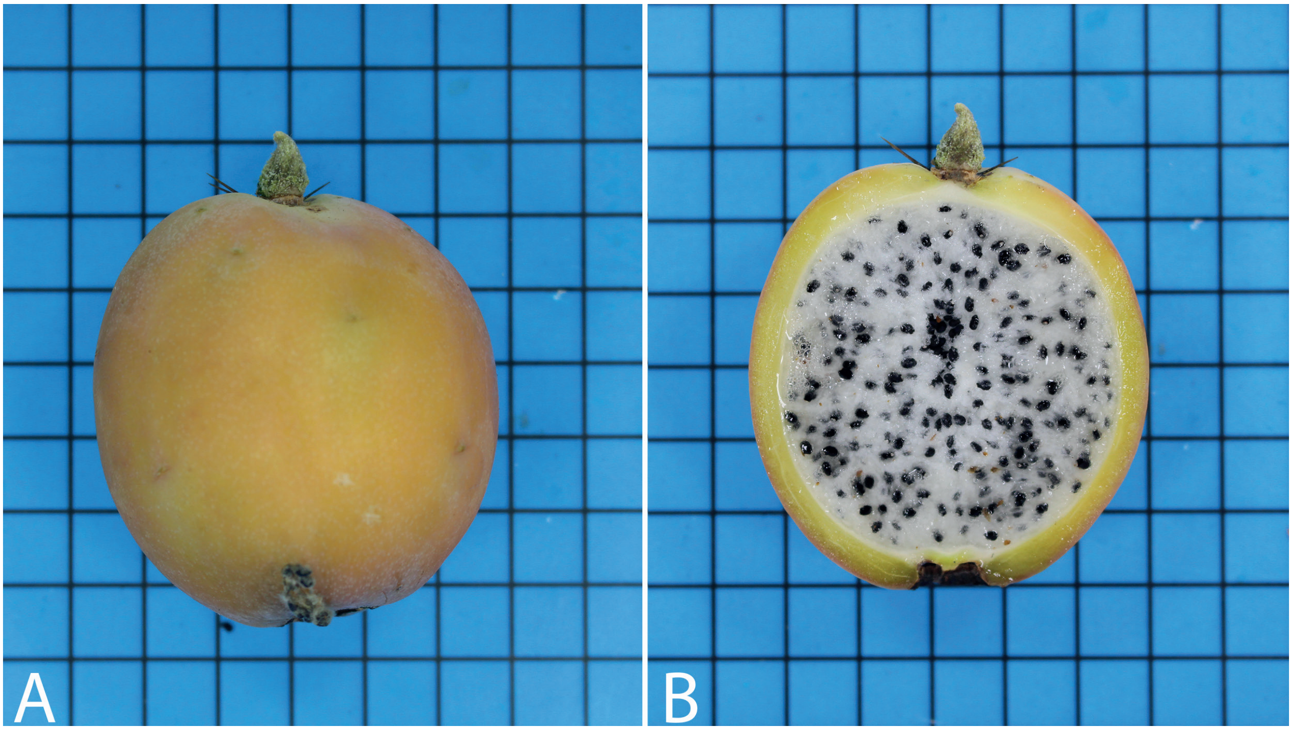

Figure 1. Ripe fruit of *Cereus hildmannianus* **(A)**; transversal section of ripe fruit of *C. hildmannianus* showing the edible endocarp and countless seeds **(B)**. Scale: 1 cm.

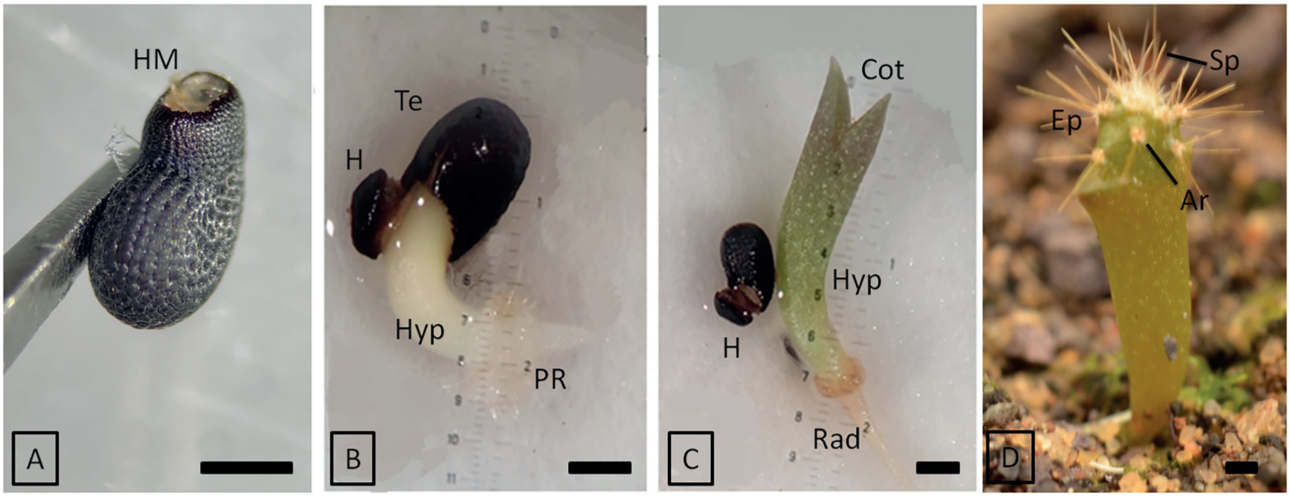

Figure 2. Seed germination stages for *Cereus hildmannianus*. **(A)** general appearance of seed with hilum micropilar and ornate testa; **(B)** day 4 – emission of hypocotyl-root axis; **(C)** day 10 – chlorophyllous seedling with visible cotyledon; **(D)** day 20 – established seedling with areole and spines. Abbreviations: hm (micropilar hilum); hil (hilum); teg (testa); hyp (hypocotyl); pr (primordial root); cot (cotyledon); ep (epicotyl); r (rootlet); ar (areole); sp (spine). Scale: 1mm.

Table 2. Two-way ANOVA of germinability (G), average germination time (t) and synchronization index (E). Statistically significant values are marked with (*).

		Temperature	Localities	Interaction
G	Levels of freedom	3	2	6
	F statistic	13.159*	1.200	6.030*
	p-Value	5.901	0.312	< 0.001
t	Levels of freedom	3	2	6
	F statistic	8.076*	3.246	2.415*
	p-Value	< 0.001	0.052	0.045
E	Levels of freedom	3	2	6
	F statistic	8.200*	0.420	4.873*
	p-Value	< 0.001	0.660	< 0.001

Table 3. Values of mean germinability (G), average germination time (t) and mean synchronization index (E) for seeds collected in Porto Alegre, Santiago and Caçapava do Sul at control, 20° C, 25° C and 30° C. Values with the same letter in a column do not differ significantly according to Tukey's test at 5 %.

	Localities	Control (sd)	20 °C (sd)	25 °C (sd)	30 °C (sd)
G	Porto Alegre	84 aA (± 16.451)	99 aA (± 2.000)	100 aA (0)	98 aA (± 6.928)
	Santiago	87 aA (± 10.519)	99 aA (± 2.000)	100 aA (0)	82 aA (± 14.966)
	Caçapava do Sul	84 aA (± 5.163)	93 aA (± 8.869)	99 aA (± 2.000)	63 bB (± 13.216)
t	Porto Alegre	10.582 abA (± 1.150)	9.860 aA (± 0.708)	8.078 aA (± 0.762)	9.820 aA (± 0.684)
	Santiago	8.211 aA (± 0.989)	8.330 aA (± 0.475)	7.851 aA (± 0.804)	8.789 aA (± 1.222)
	Caçapava do Sul	12.130 bA (± 3.768)	9.583 aAB (± 1.350)	6.555 aB (± 0.643)	9.006 aAB (± 1.181)
E	Porto Alegre	1.416 aA (± 0.320)	1.996 aB (± 0.312)	1.878 aB (± 0.118)	1.255 aA (± 0.105)
	Santiago	1.042 aA (± 0.457)	2.222 aB (± 0.152)	1.787 aB (± 0.275)	1.953 bB (± 0.451)
	Caçapava do Sul	1.678 aA (± 0.193)	2.223 aB (± 0.427)	0.928 bC (± 0.391)	2.170 bB (± 0.422)

informative characters, are scarce in the literature. As a whole, fruit size and shape and seed features of *C. hildmannianus* are similar to those of *C. jamacaru* (Abud *et al*. 2013) and those of *C. repandus* (Mizrahi 2014; Ninio *et al*. 2003; as *C. peruvianus*). Yet, to date, seed features, germination, seedling features and early development have been studied in depth for only *C. jamacaru* (Abud *et al*. 2013). Abud *et al*. (2013) described the fruits of *C. jamacaru* with very similar dimensions as those found here for *C. hildmannianus*, yet with a higher number of seeds (mean 1439 ± 189.78; *vs*. 787.7 ± 238.3 in *C. hildmannianus*). The seeds of *C. jamacaru* were morphologically characterized as being darkish, kidney-shaped and bitegumented (Abud *et al* 2013), which is in agreement with the characters observed here for *C. hildmannianus*. The embryo of *C. jamacaru*, as in *C. hildmannianus,* occupies almost the entire space inside the seed, a common characteristic for Cactaceae (Carneiro *et al*. 2016). An ornate testa was also observed for *C. jamacaru* (Abud *et al*. 2013), and the two species probably have specific patterns, but we are unaware of such studies for species of *Cereus*. All in all, seedling features (overall shape and morphology), as well as early plant development, of *C. hildmannianus* are quite similar to those reported for *C. jamacaru* (Abud *et al*. 2013).

All samples of *C. hildmannianus* treated at 20° C and 25° C had high germinability rates (over 90 %), which is in agreement with data already reported for *C. jamacaru* with 89 % germinability at 25° C (Abud *et al*. 2013). All samples had shorter average germination times at 25° C. In practical terms, this means that germination is faster and more efficient at higher temperatures, but until a certain limit (Bewley & Black 1994). In fact, the best results in the present study were obtained at 25° C, while a decrease in germination time was observed at 30° C. Average germination time is an important variable because seeds that take a long time to germinate are usually more susceptible to diseases (Scremin-Dias *et al*. 2006) or may miss the climatic opportunity to grow. Thus, germination time can be used as an indicator of vigor.

As with average germination time, the synchronization index had lower values at 25° C. These results are similar to those found for *Cereus fernambucensis* (Socolowski *et al*. 2010), *Pereskia aculeata* and *Pereskia grandifolia* (Souza *et al*. 2016). These authors reported the same decrease in synchronization from 25° C to 30° C. Lower synchronization values for this temperature range should indicate an influence of external environmental factors, which is also reflected in higher germinability and germination speed (Labouriau & Osborn 1984). According to Souza *et al*. (2016), synchronization values increase above and below this temperature range (25° C to 30° C), and synchronization implies the establishment of a great number of seedlings with a better chance of survival. However, low synchronization could allow the species to germinate all seeds over a long period of time, thus avoiding a potential loss of all offspring in the case of an extreme weather event.

The synchronization index for seeds from Caçapava do Sul exposed to 25° C and 30° C and for seeds from Santiago at 30° C differed significantly from that for seeds from Porto Alegre under the same conditions. Whereas seeds from Porto Alegre maintained their germinative behavior in all treatments, those from Caçapava do Sul and Santiago exhibited variation in synchronization when exposed to the aforementioned temperatures.

Seeds from Porto Alegre had the best performance among the localities. In addition to the very similar synchronization indexes for Porto Alegre seeds, these seeds had the highest germination rate for each treatment (over 98 % germinated seeds), indicating that this population has the best vigor among the tested samples. The decrease in the synchronization index at 25° C for all populations is interesting for a species whose germination occurs over a long period of time, revealing its capacity to adapt to different environmental conditions that may vary during the course of a year. Seasons are highly marked in South Brazil, with a hot summer and a cold winter, in addition to well-distributed rainfall throughout the year (Pessoa 2017), and a wide range of temperatures can be favorable to germination for species adapted to such conditions. Although locality did not show any influence in the tests, the interaction between locality and temperature may be acting in the recovered results. This possible synergy may explain the good and stable behavior for seeds from Porto Alegre, and the significant variation in germination synchronicity for seeds from the other localities between 25° C and 30° C, besides the decrease in germinability for seeds from Caçapava do Sul at 30° C.

The effect of temperature in this experiment is evidenced by the decrease of the synchronization index in seeds from Caçapava do Sul and Santiago, at 25° C and 30° C respectively, and the decrease in germinability for the same populations at 30° C. In general, the results found herein for these populations were similar to what has been found for other columnar cacti, such as *Pachycereus hollianus*, *Cephalocereus chrysacanthus*, *Neobuxbaumia tetetzo* (Rojas-Aréchiga *et al*. 1998), *Stenocereus queretaroensis* (Barrera & Nobel 2003) *Trichocereus terscheckii* (Ortega-Baes & Rojas-Aréchiga 2007), *Cereus fernambucensis* (Socolowski *et al*. 2010), *Pilosocereus pachycladus* (Abud *et al*. 2010), *C. jamacaru* (Meiado *et al*. 2010; Abud *et al*. 2013), *Pilosocereus aurisetus* (Reis *et al*. 2012), and *Melocactus sergipensis* (Filho *et al*. 2019). The species in all of these studies had high germinability and low average germination time within a wide range of temperatures, with better performances around 25° C. As a rule, indexes normally decrease at temperatures near 30° C, except for *Pilosocereus gounellei* (Abud *et al*. 2012), which showed optimum germinability at this temperature. According to Meiado *et al*. (2010), decreased germinability at extreme temperatures may be of ecological importance, since seedling survival in these conditions is low. Even when tuna had peak germinability and germination speed at 25° C, the values found at 20° C and 30° C were also high, indicating that this species has a wide range of temperatures favorable for germination.

It is important to point out that, in spite of occurring in the same biome, plants from Porto Alegre and Santiago belong to a different subspecies than those from the other localities. Remarkably, all the indexes calculated for the two populations were statistically similar, except for the synchronization index at 30° C. The most different germinative behavior was for the Caçapava do Sul seeds, a population identified as *C. hildmannianus* subsp. *hildmannianus* on morphological grounds (Becker in. prep.), which likely presents haplotypes more similar to those of the Porto Alegre populations (Silva *et al*. 2018). This intermediate population showed more instability with germinability and synchronization at high temperatures.

Most seeds of Cactaceae have a good germination response over large temperature gradients, with optimal temperatures usually around 25° C (Rojas-Aréchiga & Vázquez-Yanes 2000). This broad gradient is characteristic of species adapted to semi-arid environments, as rapid germination indicates an ease of forming seedlings at different temperatures, thus increasing the chance of survival compared to species with closer cardinal temperatures (Souza *et al*. 2016).

Conclusion

Seeds of *Cereus hildmannianus* have an optimum germination temperature of 25° C, with higher germinability and lower average germination times at this temperature. Remarkably, the synchronization index decreased at 25° C as well, a fact that can be interpreted as an adaption to germination over long periods of time. In addition, seeds collected at Porto Alegre were close to maximum germinability and showed more stability for all indexes in all treatments, which means that this population had higher vigor than seeds collected at Santiago and Caçapava do Sul. Species with large geographic distributions are also related to large temperature ranges due to adaptions to different climates in which such species may occur (Larcher, 2000). *Cereus hildmannianus* occurs in South and Southeast Brazil, Uruguay and the Argentinean Pampa, a fact that indicates an ability to develop under different conditions. In agreement, the data recovered herein for germination rates under different conditions support that *C. hildmannianus* is highly adaptable, a finding that not only explains its broad distribution, but also indicates that this cactus should not be problematic for cultivation and domestication purposes.

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