

# Effects of light and temperature on seed germination of cacti of Brazilian ecosystems

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## Abstract

Environmental factors are used by plants as spatio-temporal indicators of favorable conditions for seed germination. Thus, the objective of this study was to determine the effect of light and temperature on seed germination of 30 taxa of Cactaceae occurring in northeastern Brazil and to evaluate whether fluctuations in temperature are capable of altering light sensitivity. The seeds were tested for germination under two light conditions (12 h photoperiod and continuous darkness) and 10 temperature treatments: eight constant temperatures (10, 15, 20, 25, 30, 35, 40 and 45°C) and two alternating temperatures (30/20°C and 35/25°C). The species studied showed two photoblastic responses. All cacti from the Cactoideae subfamily (22 taxa) were classified as positive photoblastic (i.e., no germination in darkness), regardless of the temperature treatment used. Likewise, temperature fluctuation did not alter the seed sensitivity to light. On the other hand, the species of the Opuntioideae (five taxa) and Pereskioideae (three taxa) subfamilies are indifferent to light (i.e., germinated both in the presence and absence of light). The cacti from the areas of Caatinga and Cerrado showed an optimal germination temperature of 30°C, while the species from Atlantic Forest and Restinga areas showed an optimal germination temperature of 25°C.

*Keywords:* Caatinga, Cactaceae, germinability, photoblastism, semi-arid.

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## Introduction

Establishment success of plant species is often related to the time required for seed germination, which may be affected by several environmental factors (Vázquez-Yanes & Orozco-Segovia 1996). Seeds present in the soil respond to specific combinations of light, humidity, and favorable temperatures for seed germination and seedling establishment, maximizing their reproductive success (Baskin & Baskin 2014). Thus, environmental factors such as light and temperature are simultaneously used by plants as indicators of favorable site and timing for seedling establishment, since after germination, the seed loses its tolerance to desiccation and needs to remain constantly

hydrated, under favorable conditions for its development (Castro *et al.* 2004).

For several years researchers have been trying to understand germinative response patterns of seeds exposed to different intensities and qualities of light. Initially, it was believed that light sensitivity was related only to seed size, since large seeds with many resources would be able to germinate in darkness, simulating the low light intensity observed in deeper soil layers. On the other hand, small seeds with only a few resources stored in their tissue would need to germinate in the presence of light, in more superficial soil layers, establishing themselves and producing leaves rapidly to assume their autotrophic function (Milberg *et al.* 2000; Baskin & Baskin 2014). Recently, several studies have tried to relate light sensitivity to other plant attributes, such as plant growth-form

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(Ortega-Baes *et al.* 2010), plant height (Flores *et al.* 2011), perenniality (De Villiers *et al.* 2002), seed size (Milberg *et al.* 2000; Pearson *et al.* 2003; Rojas-Aréchiga *et al.* 2013), and phylogeny (Moles *et al.* 2005; Wang *et al.* 2009; Rojas-Aréchiga *et al.* 2013). However, as these studies are still in development, the photoblastic response patterns of many plant families are still undetermined.

Some environmental factors such as extreme and/or alternating temperatures may replace the light requirement for seed germination of many species that occur in arid and semi-arid environments, since extreme temperatures and temperature fluctuations interfere with the active production of phytochrome and may induce seed germination in darkness (Pons 2000; Probert 2000). Alterations in the patterns of light response associated with other environmental factors have been determined for several families throughout the years, such as the plants of the Cactaceae family, where the effect of light on seed germination is relatively well known for native species of North America (Flores *et al.* 2011). According to Rojas-Aréchiga *et al.* (1997), the light requirement for seed germination of cacti may be related to the cactus' growth form, due to the maternal effects induced by temperature during seed production. Globose cacti are positive photoblastic and columnar cacti may be positive or neutral photoblastic (Rojas-Aréchiga *et al.* 1997). Several studies with globose cacti (Benítez-Rodríguez *et al.* 2004; Flores *et al.* 2006; Rebouças & Santos 2007; Gurvich *et al.* 2008; Rojas-Aréchiga *et al.* 2008, 2013), as well as with columnar cacti (Rojas-Aréchiga *et al.* 2001; De la Barrera & Nobel 2003; Ortega-Baes & Rojas-Aréchiga 2007; Meiado *et al.* 2008, 2010), corroborate the germination behavior pattern proposed by Rojas-Aréchiga *et al.* (1997). However, some works have demonstrated that columnar cacti showed two types of responses to light and that globose cacti may also germinate when submitted to continuous darkness (Flores-Martínez *et al.* 2002; Jiménez-Aguilar & Flores 2010), though the methodology used to determine the photoblastic response of these globose cacti is not clear. This fact could be related to the geographical distribution of the species or their phylogenetic origin (Flores *et al.* 2011; Rojas-Aréchiga *et al.* 2013).

The Cactaceae family is represented in Brazil by the occurrence of 260 species, grouped into 39 genera within three subfamilies, which are distributed over all phyto-geographic domains in the country (Zappi *et al.* 2014). One of the Brazilian ecosystems that exhibit the higher diversity of cacti is the Caatinga, a semi-arid ecosystem in which 90 cacti species occur (Meiado *et al.* 2012; Zappi *et al.* 2014). Besides Caatinga, other ecoregions are observed in the northeastern region of Brazil, such as "Cerrado" (a tropical and subtropical grassland, savanna, and shrubland ecoregion), "Campo Rupestre" (a montane subtropical forest with rupestrian vegetation on rocky

outcrops that grows at altitudes above 800–900 m), "Floresta Atlântica" (Atlantic Forest, a tropical and subtropical moist forest) and "Restinga" (Restinga Forest, a forest type that grows on stabilized coastal dunes), and several species of Cactaceae are found in all these ecoregions (Meiado *et al.* 2012; Zappi *et al.* 2014). Therefore, the objective of this study was to determine the effect of light and temperature on seed germination of 30 taxa of Cactaceae occurring in different ecosystems of the north-eastern Brazil and to evaluate whether temperature fluctuations are capable of altering the light sensitivity of seeds of these species.

## Materials and methods

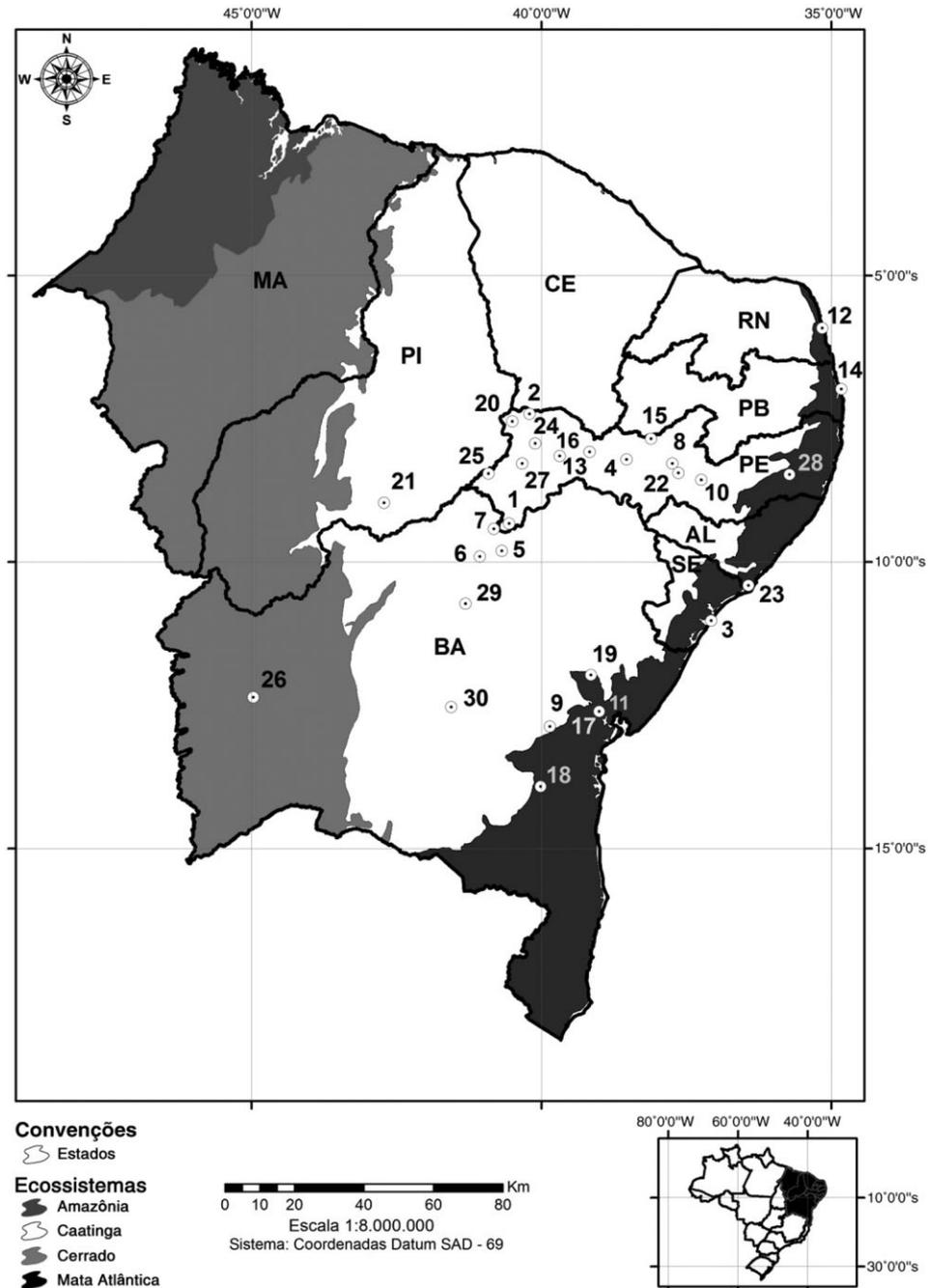
### *Studied taxa and seed collection*

For this study, 30 taxa from the Cactaceae family were selected, grouped into 28 species and 10 genera, representing the three subfamilies with wide distribution that occur over the several ecosystems in the Brazilian north-east. To perform the experiments, the seeds were obtained at the Seed Laboratory of the Reference Centre for the Restoration of Degraded Areas of Caatinga of the Federal University of São Francisco Valley. All seeds used in the experiments were stored in paper bags and cold chambers ( $7 \pm 2^\circ\text{C}$ ), during less than 30 days until the beginning of the experiment. Collections were made in several states of the northeastern region of Brazil (Fig. 1), in the period between April 2007 to September 2011, and the seeds have been used for *ex situ* conservation actions of the Brazilian National Action Plan on Conservation of Cactaceae (Assis *et al.* 2011).

### *Photoblastism and cardinal temperatures*

To determine the photoblastism and to evaluate the effect of temperatures on seed germination of the selected taxa, the seeds were sown in ten temperature treatments: eight treatments of constant temperatures (10, 15, 20, 25, 30, 35, 40, and  $45^\circ\text{C}$ ) and two treatments of alternating temperatures (30/ $20^\circ\text{C}$  and 35/ $25^\circ\text{C}$ ). In each temperature treatment, the seeds were sown under two light treatments: white light (12 h photoperiod with a light intensity of  $200 \mu\text{mol}/\text{m}^2/\text{s}$ ) and continuous darkness (simulated with the use of a black polypropylene plastic). In the alternating temperature treatments, where the seeds were submitted to a photoperiod of 12 h, the highest temperatures corresponded to the period of exposure to light. For each treatment, 100 seeds of each species were used, distributed into four repetitions of 25 seeds.

Seeds were sown in Petri dishes of 9 cm of diameter, containing filter paper moistened with 5 mL of distilled water. Four dishes were used per treatment, which were



**Fig. 1** Distribution of the 30 Cactaceae taxa used in this study occurring in different ecosystems of the northeastern region of Brazil: 1–30, collection locations (see Table 1 for species); MA, Maranhão State; PI, Piauí State; CE, Ceará State; RN, Rio Grande do Norte State; PB, Paraíba State; PE, Pernambuco State; AL, Alagoas State; SE, Sergipe State; BA, Bahia State.

sealed with parafilm plastic, so no more watering was needed during the whole experimentation period. Radicle protrusion was considered to be the criteria for germinated seeds, and was assessed daily over a 60-day period to ensure a longer analysis time of seed germination because the mean germination time was unknown for most species. In the present study, germination is defined

as the time when the radicle tip emerged  $\geq 2$  mm from the seed coat.

#### *Germination parameters and statistical analysis*

For each seed germination treatment, we calculated germinability (%) and mean germination time ( $t = \sum ni.ti / \sum ni$ ,

where  $t_i$  is the period from the start of the experiment to the  $i$ th observation (day) and  $n_i$  is the number of seeds germinated in the time  $i$  [not the accumulated number, but the number corresponding to the  $i$ th observation] according to Ranal and Santana (2006). The temperature treatment that provided the highest final percentage of germination in the shortest time was considered as the optimal temperature of germination of the species. Germinability data were transformed to arcsine  $\sqrt{\%}$  (Ranal & Santana 2006). Data were expressed as mean  $\pm$  standard deviation (SD) values. We tested the normal distribution of the data and homogeneity of the variances using Shapiro–Wilk and Levene tests, respectively (Zar 1999). Differences in germination parameters among treatments were tested for statistical significance using a two-way analysis of variance (light and temperature) followed by a Tukey’s honestly significant difference test (Ranal & Santana 2006).

For each treatment of optimal germination temperature, we determined the relative light germination (RLG, Milberg *et al.* 2000) through the formula  $RLG = G_L / (G_D + G_L)$ , where  $G_L$  is the germination percentage in light and  $G_D$  the germination percentage in darkness. The RLG was considered a response variable and the data were analyzed through three-factor ANCOVA using as explanatory variables the biological attributes of species: the growth form (i.e., arbustive with true leaves, articulated, columnar and globose cacti, according to Anderson (2001)), phylogenetic origin, that is, species grouped into the Cactoideae, Opuntioideae, and Pereskioideae subfamilies (Taylor & Zappi 2004); and the Brazilian ecoregions where the seeds were collected (Caatinga, Cerrado, Atlantic Forest and Restinga). Seed size was determined in a sample of 30 randomly selected seeds, which were measured in length and width in millimeters with an electronic digital vernier caliper (150 mm/ 6-inch micrometer) and used as a co-variable of the model (Flores *et al.* 2011). All statistical analyses were made with the STATISTICA 10.0 program, with a significance index of 0.05 (StatSoft 2012).

## Results

The Cactaceae species studied that occur in the northeastern Brazilian ecosystems showed a wide variation in seed size and two distinct behaviors with respect to their response to light (Table 1). All species of the Cactoideae subfamily were classified as positive photoblastic, since we did not observe seed germination in continuous darkness, regardless of the constant temperature treatment the seeds were submitted to (Tables 2,3). Besides, temperature fluctuation did not alter the seeds’ sensitivity to light, since we did not observe seed germination in the absence of light in either of the alternating temperature treatments

(Tables 2,3). All species of this subfamily showed high germination percentages ( $\geq 70\%$ ), indicating the absence of dormancy. *Pilosocereus gounellei* subsp. *gounellei* showed maximal germination percentage (100%) and the shortest mean germination time ( $4.2 \pm 0.2$  days) among all species studied, when their seeds were submitted to a temperature of 30°C and a photoperiod of 12 h (Tables 2,3). On the other hand, seed germination of all the species of the Opuntioideae and Pereskioideae subfamilies was not affected by the absence of light, and a similar germinative behavior was observed when the seeds were submitted to both treatments (12 h photoperiod and continuous darkness) (Table 2). In addition, the mean germination time of the species was similarly not affected by absence of light, confirming the seed insensitivity of this factor (Table 3).

Regardless of the ecosystem where the seeds were collected the three species of *Pereskia* Mill. genus showed a high final germination percentage ( $\geq 90\%$ ) in both light treatments, being classified as neutral photoblastic or aphotoblastic (Table 2). However, the seeds of the species of Opuntioideae subfamily, which were also insensitive to light and classified as aphotoblastic, presented low germinability ( $\leq 40\%$ ), regardless of the temperature treatments the seeds were submitted to (Table 2), suggesting some kind of dormancy unrelated to light.

The results of the covariance analysis indicated that the combined global effect of the seed size and the explanatory variables growth form, phylogenetic origin and collection ecosystem on the RLG was not significant ( $r^2 = 0.1116$ ;  $F = 3.1568$ ;  $P = 0.6511$ ). Analyzed separately, among all the biological attributes evaluated, only the phylogenetic origin affected the RLG ( $P = 0.0021$ ). Together, these results suggest that growth form and collection site did not influence the type of photoblastic response of seeds submitted to different light treatments; however, the phylogenetic origin did.

No alternating temperature treatment was more favorable to seed germination than the constant temperature treatments (Tables 2,3) and the optimal germination temperatures of the seeds of the studied cacti were between 20 and 35°C (Table 4). Besides, we did not observe seed germination in any of the species studied in the extreme temperatures of 10 and 45°C and although we have observed high germinability ( $> 80\%$ ) in both light treatments in the temperatures between 15 and 35°C, the three studied *Pereskia* species did not germinate at 40°C.

Also regarding the temperature effect, the seeds of the studied species also presented two distinct germinative behaviors. A group of species germinated in a higher thermal amplitude (germinability  $\geq 50\%$ ) and their optimal germination temperature was between 30 and 35°C. This group was represented by cacti of the three subfamilies evaluated, that are endemic of Caatinga and/or that presented wide distribution in the ecosystem,

**Table 1** Seed size (length × width), ecosystem, and coordinates of the collection locations of seeds of 30 Cactaceae taxa occurring in the northeastern region of Brazil

Collection location	Subfamily	Species	Seed size (mm)	Ecosystem	Coordinates
01	Cactoideae	<i>Arrojadoa rhodantha</i> (Gürke) Britton & Rose	1.2 × 0.7	Caatinga	09°19'44,20"S, 040°33'30,10"W
02		<i>Cereus albicaulis</i> (Britton & Rose) Luetzelb.	2.0 × 1.4	Caatinga	07°23'97,20"S, 040°12'31,40"W
03		<i>Cereus fernambucensis</i> Lem. subsp. <i>fernambucensis</i>	2.0 × 1.5	Restinga	11°01'30,80"S, 037°04'37,80"W
04		<i>Cereus jamacaru</i> DC. subsp. <i>jamacaru</i>	3.2 × 1.8	Caatinga	08°12'37,70"S, 038°32'06,60"W
05		<i>Discocactus bahiensis</i> Britton & Rose	1.8 × 1.5	Caatinga	09°48'26,20"S, 040°41'19,30"W
06		<i>Discocactus zehntneri</i> Britton & Rose subsp. <i>zehntneri</i>	1.7 × 1.5	Caatinga	09°54'05,48"S, 041°03'49,26"W
07		<i>Facheiroa squamosa</i> (Gürke) P.J.Braun & E.Esteves Pereira	1.2 × 0.6	Caatinga	09°24'70,60"S, 040°48'90,70"W
08		<i>Harrisia ascendens</i> (Gürke) Britton & Rose	3.8 × 1.8	Caatinga	08°16'37,10"S, 037°44'50,10"W
09		<i>Melocactus bahiensis</i> (Britton & Rose) Luetzelb. subsp. <i>bahiensis</i>	1.2 × 0.8	Caatinga	12°52'12,00"S, 039°51'32,00"W
10		<i>Melocactus ernestii</i> Vaupel subsp. <i>ernestii</i>	1.3 × 0.8	Caatinga	08°33'55,10"S, 037°14'37,90"W
11		<i>Melocactus oreas</i> Miq. subsp. <i>cremnophilus</i> (Buining & Brederoo) P.J.Braun	1.2 × 1.0	Caatinga	12°35'92,30"S, 038°59'91,50"W
12		<i>Melocactus violaceus</i> Pfeiff. subsp. <i>violaceus</i>	1.5 × 1.2	Restinga	05°54'57,00"S, 035°09'35,80"W
13		<i>Melocactus zehntneri</i> (Britton & Rose) Luetzelb.	1.4 × 1.2	Caatinga	08°04'38,80"S, 039°10'22,00"W
14		<i>Pilosocereus catiingicola</i> (Gürke) Byles & G.D.Rowley subsp. <i>salvadorensis</i> (Werderm.) Zappi	2.0 × 1.4	Restinga	06°58'51,00"S, 034°50'02,00"W
15	<i>Pilosocereus chrysostele</i> (Vaupel) Byles & G.D.Rowley	1.7 × 1.2	Caatinga	07°50'42,10"S, 038°06'42,70"W	
16	<i>Pilosocereus gounellei</i> (F.A.C.Weber) Byles & G.D.Rowley subsp. <i>gounellei</i>	1.8 × 1.4	Caatinga	08°08'44,00"S, 039°40'80,80"W	
17	<i>Pilosocereus pentaedrophorus</i> (J.F.Cels) Byles & G.D.Rowley subsp. <i>pentaedrophorus</i>	1.7 × 1.1	Atlantic Forest	12°35'92,30"S, 038°59'91,50"W	
18	<i>Pilosocereus pentaedrophorus</i> (J.F.Cels) Byles & G.D.Rowley subsp. <i>robustus</i> Zappi	1.8 × 1.3	Atlantic Forest	13°55'15,00"S, 040°00'54,20"W	
19	<i>Pilosocereus pachycladus</i> F.Ritter subsp. <i>pachycladus</i>	2.0 × 1.2	Caatinga	11°57'86,10"S, 039°08'66,00"W	
20	<i>Pilosocereus pachycladus</i> F.Ritter subsp. <i>pernambucoensis</i> (F.Ritter) Zappi	1.6 × 1.0	Caatinga	07°31'90,20"S, 040°29'79,00"W	
21	<i>Pilosocereus piauhyensis</i> (Gürke) Byles & G.D.Rowley	1.5 × 1.0	Caatinga	08°57'59,40"S, 042°42'56,20"W	
22	<i>Pilosocereus tuberculatus</i> (Werderm.) Byles & G.D.Rowley	1.4 × 0.8	Caatinga	08°26'30,60"S, 037°38'20,70"W	
23	Opuntioideae	<i>Brasiliopuntia brasiliensis</i> (Willd.) A.Berger	6.0 × 4.8	Atlantic Forest	10°24'21,10"S, 036°26'05,20"W
24		<i>Tacinga inamoena</i> (K. Schum.) N.P. Taylor & Stuppy	4.0 × 3.5	Caatinga	07°55'46,60"S, 040°06'37,30"W
25		<i>Tacinga funalis</i> Britton & Rose	4.2 × 3.8	Caatinga	08°27'09,40"S, 040°55'09,40"W
26		<i>Tacinga palmadora</i> (Britton & Rose) N.P. Taylor & Stuppy	5.5 × 4.5	Caatinga	12°21'46,10"S, 044°58'22,80"W
27	<i>Tacinga saxatilis</i> (F. Ritter) N.P. Taylor & Stuppy subsp. <i>saxatilis</i>	4.5 × 3.5	Caatinga	08°16'47,50"S, 040°20'13,00"W	
28	Pereskioideae	<i>Pereskia grandifolia</i> Haw. subsp. <i>grandifolia</i>	7.0 × 5.0	Atlantic Forest	08°28'12,10"S, 035°43'44,00"W
29		<i>Pereskia bahiensis</i> Gürke	5.5 × 3.8	Caatinga	10°43'40,80"S, 041°18'41,00"W
30		<i>Pereskia aculeata</i> Mill.	4.5 × 3.2	Caatinga	12°31'44,10"S, 041°33'32,30"W

such as *Arrojadoa rhodantha*, *Cereus jamacaru* subsp. *jamacaru*, *Discocactus zehntneri* subsp. *zehntneri*, *Melocactus zehntneri*, *Pereskia bahiensis*, *Pilosocereus gounellei* subsp. *gounellei*, and *Tacinga inamoena* (Table 4). On the other hand, some species collected in tropical moist forests (i.e., Atlantic Forest and Restinga), such as *Cereus fernambucensis* subsp. *fernambucensis*, *Melocactus violaceus* subsp. *violaceus*, *Pilosocereus catiingicola* subsp. *salvadorensis*, *Pilosocereus pentaedrophorus* subsp. *pentaedrophorus*, *Pilosocereus pentaedrophorus* subsp. *robustus*, and *Pereskia grandifolia* subsp. *grandifolia* were more sensitive to extreme temperatures, as well as to the variation of temperature, and the seed germination of these species occurred in a narrower range of temperature. In this second group of species, the optimal germination temperature was between 20 and 25°C (Table 4).

## Discussion

The results obtained in this study indicate the occurrence of two very distinct behaviors in relation to the response to light during seed germination: seeds that germinated only in the presence of light and were considered positive photoblastic (all species of the Cactoideae subfamily) and seeds that were also capable of germinating in continuous darkness, being classified as neutral photoblastic or aphotoblastic (all species of the Opuntioideae and Pereskioideae subfamilies). Germinative responses of other species of native cacti of Brazil can be found in Meiado (2012) and corroborate the results found in this study.

Sensitivity to light during seed germination is an important strategy to prevent the occurrence of germinative events in unfavorable place and time to seedling

**Table 2** Germination percentage of seeds of 30 Cactaceae taxa from the northeastern region of Brazil under different constant and alternating temperatures, and under 12-h light (L) and continuous darkness (D) treatments. Different letters indicate significant differences ( $p \leq 0.05$ )

Species	15°C		20°C		25°C		30°C		35°C		40°C		30 / 20°C		35 / 25°C	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
01	10.5 ± 5.5 c	-	60.0 ± 5.0 b	-	95.0 ± 3.5 a	-	100.0 ± 0.0 a	-	90.5 ± 2.5 a	-	15.5 ± 3.5 c	-	90.0 ± 8.5 a	-	98.0 ± 2.0	-
02	40.0 ± 5.0 c	-	84.0 ± 4.5 b	-	95.5 ± 1.5 a	-	98.0 ± 2.5 a	-	95.0 ± 2.5 a	-	22.5 ± 1.5 d	-	95.0 ± 3.5 a	-	94.0 ± 2.0 a	-
03	45.0 ± 3.5 c	-	84.0 ± 2.5 b	-	98.5 ± 2.5 a	-	97.5 ± 1.5 a	-	43.0 ± 4.5 c	-	10.0 ± 2.0 d	-	96.5 ± 2.0 a	-	48.0 ± 2.0 c	-
04	20.5 ± 2.6 c	-	78.5 ± 5.2 b	-	94.0 ± 1.6 a	-	95.8 ± 2.7 a	-	85.8 ± 2.6 ab	-	1.8 ± 0.8 d	-	90.0 ± 3.5 a	-	98.2 ± 2.5	-
05	25.5 ± 2.5 c	-	80.0 ± 5.0 b	-	93.0 ± 1.0 a	-	95.5 ± 1.5 a	-	93.5 ± 1.5 a	-	15.0 ± 3.5 d	-	85.5 ± 5.0 b	-	90.0 ± 2.0 ab	-
06	10.0 ± 5.0 e	-	65.0 ± 2.0 c	-	90.0 ± 3.5 b	-	98.0 ± 1.0 a	-	99.5 ± 0.5 a	-	55.5 ± 5.0 d	-	85.5 ± 5.0 b	-	90.0 ± 2.0 b	-
07	38.0 ± 2.0 c	-	80.0 ± 5.0 b	-	86.0 ± 4.0 ab	-	93.0 ± 3.0 a	-	88.0 ± 2.0 ab	-	25.5 ± 2.5 d	-	87.0 ± 0.2 ab	-	88.0 ± 2.0 ab	-
08	35.0 ± 5.0 c	-	75.0 ± 5.0 b	-	87.0 ± 2.0 a	-	90.0 ± 5.0 a	-	84.0 ± 2.0 a	-	15.0 ± 5.0 d	-	83.0 ± 5.0 ab	-	85.0 ± 5.0 ab	-
09	28.5 ± 2.5 c	-	85.0 ± 4.0 b	-	95.0 ± 1.0 a	-	95.5 ± 1.5 a	-	93.5 ± 1.5 a	-	20.0 ± 3.5 d	-	85.5 ± 4.0 b	-	90.0 ± 2.0 ab	-
10	15.0 ± 5.5 c	-	65.0 ± 5.0 b	-	95.0 ± 3.5 a	-	98.0 ± 2.0 a	-	95.0 ± 2.5 a	-	30.0 ± 3.5 c	-	90.0 ± 3.5 a	-	95.0 ± 3.5 a	-
11	25.0 ± 5.5 c	-	53.0 ± 2.0 b	-	82.0 ± 2.5 a	-	85.0 ± 2.0 a	-	83.0 ± 2.5 a	-	40.0 ± 5.0 c	-	80.0 ± 3.5 a	-	82.0 ± 2.5 a	-
12	45.5 ± 5.0 c	-	92.0 ± 2.0 a	-	90.0 ± 5.0 a	-	70.0 ± 5.0 b	-	40.0 ± 5.0 c	-	5.0 ± 2.0 d	-	80.0 ± 5.0 ab	-	40.0 ± 5.0 c	-
13	10.5 ± 5.5 c	-	65.0 ± 5.0 b	-	95.0 ± 3.5 a	-	100.0 ± 0.0 a	-	90.5 ± 2.5 a	-	35.5 ± 3.5 c	-	90.0 ± 8.5 a	-	98.0 ± 2.0	-
14	40.0 ± 2.0 c	-	85.0 ± 5.0 ab	-	92.0 ± 2.0 a	-	80.0 ± 5.0 b	-	45.0 ± 5.0 c	-	10.0 ± 5.0 d	-	85.0 ± 5.0 ab	-	45.0 ± 5.0 c	-
15	20.0 ± 5.0 c	-	84.0 ± 4.5 b	-	96.0 ± 2.0 a	-	98.0 ± 2.0 a	-	90.0 ± 5.0 ab	-	40.0 ± 1.5 d	-	95.0 ± 3.5 a	-	94.0 ± 2.0 a	-
16	40.0 ± 5.0 e	-	83.0 ± 3.0 c	-	92.0 ± 2.0 b	-	100.0 ± 0.0 a	-	98.0 ± 2.0 a	-	55.0 ± 5.0 d	-	95.0 ± 5.0 ab	-	97.0 ± 2.0 a	-
17	65.0 ± 5.0 b	-	85.5 ± 2.5 a	-	83.5 ± 3.5 a	-	45.0 ± 2.0 c	-	35.5 ± 3.5 d	-	5.0 ± 2.0 e	-	60.0 ± 5.0 b	-	42.0 ± 2.0 c	-
18	62.0 ± 2.0 b	-	81.5 ± 1.5 a	-	80.0 ± 2.0 c	-	65.0 ± 2.0 c	-	40.0 ± 3.0 d	-	15.0 ± 8.0 e	-	70.0 ± 5.0 b	-	72.0 ± 2.0 b	-
19	48.0 ± 3.0 d	-	90.0 ± 2.0 b	-	100.0 ± 0.0 a	-	98.0 ± 2.0 a	-	82.0 ± 4.0 c	-	25.0 ± 5.0 e	-	94.0 ± 3.0 b	-	90.0 ± 2.0 b	-
20	20.0 ± 5.0 e	-	80.0 ± 5.0 c	-	93.0 ± 1.0 b	-	98.0 ± 2.0 a	-	96.0 ± 4.0 ab	-	52.0 ± 2.0 d	-	88.0 ± 4.0 b	-	90.0 ± 2.0 b	-
21	38.0 ± 2.0 e	-	90.0 ± 4.0 b	-	90.0 ± 4.0 c	-	99.0 ± 1.0 a	-	90.0 ± 2.0 c	-	45.0 ± 1.0 d	-	95.0 ± 2.0 b	-	90.0 ± 2.0 c	-
22	25.0 ± 5.0 c	-	85.0 ± 4.0 b	-	96.0 ± 4.0 a	-	96.0 ± 2.0 a	-	90.0 ± 2.0 ab	-	40.0 ± 1.5 d	-	95.0 ± 3.5 a	-	94.0 ± 2.0 a	-
23	8.0 ± 2.0 Ab	10.0 ± 5.0 Ab	20.0 ± 2.0 Aa	20.0 ± 5.0 Aa	20.0 ± 5.0 Aa	18.0 ± 2.0 Aa	13.0 ± 2.0 A ab	15.0 ± 5.0 Aa	8.0 ± 2.0 Ab	8.0 ± 2.0 Ab	5.0 ± 2.0 Ab	6.0 ± 2.0 Ab	18.0 ± 2.0 Aa	15.0 ± 5.0 A ab	15.0 ± 5.0 A ab	15.0 ± 5.0 A ab
24	10.0 ± 2.0 Ac	8.0 ± 4.0 Ac	15.0 ± 2.0 Ab	12.0 ± 2.0 Ac	20.0 ± 3.0 A ab	22.0 ± 2.0 A ab	28.5 ± 2.5 Aa	25.0 ± 3.0 Aa	25.0 ± 3.0 Aa	25.0 ± 5.0 Aa	5.0 ± 1.5 Ad	8.0 ± 2.0 Ab	15.0 ± 3.0 Ab	18.0 ± 2.0 Ab	20.0 ± 5.0 A ab	20.0 ± 5.0 A ab
25	12.0 ± 2.0 Ac	10.0 ± 4.0 Ac	17.0 ± 2.0 Ab	15.0 ± 2.0 Ac	22.0 ± 3.0 A ab	24.0 ± 2.0 A ab	29.0 ± 2.0 Aa	27.0 ± 3.0 Aa	27.0 ± 3.0 Aa	25.0 ± 5.0 Aa	10.0 ± 1.5 Ad	10.0 ± 2.0 Ab	15.0 ± 3.0 Ab	18.0 ± 2.0 Ab	22.0 ± 5.0 A ab	20.0 ± 5.0 A ab
26	10.0 ± 5.0 Ac	8.0 ± 4.0 Ac	15.0 ± 5.0 Ab	12.0 ± 2.0 Ac	20.0 ± 3.0 A ab	22.0 ± 2.0 A ab	28.5 ± 2.5 Aa	25.0 ± 3.0 Aa	25.0 ± 3.0 Aa	25.0 ± 5.0 Aa	5.0 ± 1.5 Ad	8.0 ± 2.0 Ab	15.0 ± 3.0 Ab	18.0 ± 2.0 Ab	20.0 ± 5.0 A ab	20.0 ± 5.0 A ab
27	12.0 ± 2.0 Ac	10.0 ± 3.0 Ac	17.0 ± 2.0 Ab	15.0 ± 2.0 Ac	20.0 ± 3.0 A ab	20.0 ± 2.0 A ab	25.5 ± 2.5 Aa	25.0 ± 3.0 Aa	20.0 ± 3.0 Aa	20.0 ± 5.0 Aa	10.0 ± 2.0 Ad	8.0 ± 2.0 Ab	20.0 ± 4.0 Ab	18.0 ± 2.0 Ab	22.0 ± 4.0 A ab	22.0 ± 4.0 A ab
28	95.0 ± 2.5 Aa	98.2 ± 2.3 Aa	96.5 ± 2.0 Aa	96.0 ± 2.0 Aa	97.0 ± 1.5 Aa	95.2 ± 1.5 Aa	99.0 ± 0.5 Aa	98.5 ± 2.0 Aa	95.0 ± 2.5 Aa	95.0 ± 2.0 Aa	-	-	94.0 ± 2.0 Aa	95.0 ± 2.0 Aa	98.0 ± 2.0 Aa	96.5 ± 2.5 Aa
29	85.0 ± 3.5 Aa	87.0 ± 2.5 Aa	84.5 ± 5.0 Aa	86.0 ± 5.0 Aa	88.0 ± 2.5 Aa	85.2 ± 5.5 Aa	88.0 ± 4.5 Aa	90.5 ± 2.0 Aa	90.0 ± 2.0 Aa	90.0 ± 3.5 Aa	-	-	84.0 ± 5.0 Aa	85.0 ± 3.0 Aa	88.5 ± 2.0 Aa	86.5 ± 3.5 Aa
30	90.5 ± 2.5 Aa	91.2 ± 2.2 Aa	91.5 ± 2.0 Aa	90.0 ± 2.0 Aa	88.0 ± 5.5 Aa	90.2 ± 4.5 Aa	90.0 ± 1.5 Aa	90.5 ± 2.5 Aa	92.0 ± 2.0 Aa	90.0 ± 2.5 Aa	-	-	90.0 ± 2.0 Aa	95.0 ± 3.0 Aa	94.5 ± 2.5 Aa	92.5 ± 3.5 Aa

**Table 3** Mean germination time (days) of seeds of 30 Cactaceae taxa from the Northeastern region of Brazil under different constant and alternating temperatures and under 12-h light (L) and continuous darkness (D) treatments. Different letters indicate significant differences ( $p \leq 0.05$ )

Species	15°C		20°C		25°C		30°C		35°C		40°C		30 / 20°C		35 / 25°C	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
01	8.9 ± 0.3 a	-	7.7 ± 0.5 b	-	7.2 ± 0.2 b	-	6.5 ± 0.2 c	-	7.5 ± 0.5 b	-	8.5 ± 0.4 ab	-	7.4 ± 0.2 b	-	7.5 ± 0.5 b	-
02	9.2 ± 0.4 a	-	8.2 ± 0.4 b	-	7.5 ± 0.2 b	-	6.8 ± 0.3 c	-	7.8 ± 0.5 b	-	8.8 ± 0.4 ab	-	7.7 ± 0.3 b	-	7.7 ± 0.3 b	-
03	8.3 ± 0.3 a	-	7.3 ± 0.4 b	-	6.4 ± 0.4 c	-	7.2 ± 0.3 b	-	7.5 ± 0.4 b	-	8.2 ± 0.4 ab	-	7.5 ± 0.3 b	-	7.6 ± 0.4 b	-
04	18.2 ± 0.6 a	-	10.0 ± 0.4 b	-	6.6 ± 0.6 c	-	5.5 ± 0.1 d	-	6.4 ± 0.2 c	-	9.4 ± 2.1 b	-	5.4 ± 0.2 d	-	6.5 ± 0.2 c	-
05	9.5 ± 0.5 a	-	7.5 ± 0.3 b	-	5.8 ± 0.2 c	-	5.2 ± 0.3 d	-	6.0 ± 0.3 c	-	7.8 ± 0.5 b	-	7.7 ± 0.3 b	-	7.3 ± 0.3 b	-
06	6.7 ± 0.3 a	-	6.5 ± 0.5 a	-	5.5 ± 0.3 b	-	5.2 ± 0.3 bc	-	4.9 ± 0.2 c	-	5.6 ± 0.2 b	-	6.8 ± 0.3 a	-	5.8 ± 0.5 ab	-
07	8.5 ± 0.2 a	-	8.2 ± 0.2 ab	-	7.8 ± 0.3 b	-	7.1 ± 0.2 c	-	7.7 ± 0.2 b	-	8.4 ± 0.2 a	-	8.2 ± 0.2 ab	-	7.8 ± 0.2 b	-
08	9.6 ± 0.2 a	-	9.3 ± 0.2 ab	-	8.9 ± 0.3 b	-	8.2 ± 0.2 c	-	8.8 ± 0.2 b	-	9.5 ± 0.2 a	-	9.3 ± 0.2 ab	-	8.9 ± 0.2 b	-
09	9.4 ± 0.5 a	-	7.4 ± 0.3 b	-	5.7 ± 0.2 c	-	5.1 ± 0.3 d	-	6.0 ± 0.3 c	-	7.7 ± 0.5 b	-	7.6 ± 0.3 b	-	7.3 ± 0.3 b	-
10	8.4 ± 0.3 a	-	7.2 ± 0.5 b	-	6.7 ± 0.2 b	-	6.0 ± 0.2 c	-	7.0 ± 0.5 b	-	8.0 ± 0.4 a	-	6.9 ± 0.2 b	-	7.0 ± 0.5 b	-
11	8.0 ± 0.3 a	-	6.8 ± 0.5 b	-	6.3 ± 0.2 b	-	5.3 ± 0.2 c	-	6.6 ± 0.5 b	-	7.6 ± 0.4 a	-	6.5 ± 0.2 b	-	6.6 ± 0.5 b	-
12	12.5 ± 0.5 a	-	9.0 ± 0.5 bc	-	8.8 ± 0.2 c	-	9.7 ± 0.3 b	-	12.0 ± 0.2 a	-	11.8 ± 0.5 a	-	9.5 ± 0.5 b	-	10.2 ± 0.2 b	-
13	8.7 ± 0.3 a	-	7.5 ± 0.5 b	-	7.0 ± 0.2 b	-	6.3 ± 0.2 c	-	7.3 ± 0.5 b	-	8.3 ± 0.4 a	-	7.2 ± 0.2 b	-	7.5 ± 0.5 b	-
14	9.5 ± 0.8 ab	-	8.5 ± 0.5 b	-	7.5 ± 0.2 c	-	10.8 ± 1.2 a	-	10.5 ± 1.0 a	-	11.5 ± 1.5 a	-	9.5 ± 1.0 ab	-	9.0 ± 0.2 ab	-
15	9.0 ± 0.4 a	-	8.0 ± 0.4 b	-	7.3 ± 0.2 b	-	6.6 ± 0.3 c	-	7.6 ± 0.5 b	-	8.6 ± 0.4 ab	-	7.5 ± 0.3 b	-	7.5 ± 0.3 b	-
16	7.0 ± 0.5 a	-	6.5 ± 0.8 a	-	5.5 ± 0.5 ab	-	4.2 ± 0.2 c	-	4.5 ± 0.3 c	-	6.8 ± 0.5 a	-	5.1 ± 0.2 b	-	5.0 ± 0.2 b	-
17	9.5 ± 0.5 bc	-	8.8 ± 0.2 c	-	9.5 ± 0.5 bc	-	10.0 ± 0.5 b	-	12.5 ± 1.5 a	-	13.5 ± 2.5 a	-	9.4 ± 0.4 bc	-	9.5 ± 0.5 bc	-
18	11.2 ± 0.2 b	-	9.0 ± 0.2 c	-	9.1 ± 0.2 c	-	11.5 ± 0.5 b	-	13.5 ± 0.5 a	-	15.0 ± 1.0 a	-	10.0 ± 1.0 bc	-	11.5 ± 0.5 b	-
19	9.4 ± 0.2 a	-	9.6 ± 0.4 a	-	7.2 ± 0.2 c	-	7.0 ± 2.0 c	-	8.5 ± 0.2 b	-	9.5 ± 0.5 a	-	9.0 ± 0.2 a	-	8.8 ± 0.4 ab	-
20	9.5 ± 0.5 a	-	8.5 ± 0.6 a	-	7.0 ± 0.5 ab	-	5.7 ± 0.2 c	-	6.0 ± 0.3 c	-	8.2 ± 0.5 a	-	6.6 ± 0.2 b	-	6.5 ± 0.2 b	-
21	9.5 ± 0.5 bc	-	8.8 ± 0.2 c	-	9.5 ± 0.5 bc	-	10.0 ± 0.5 b	-	12.5 ± 1.5 a	-	13.5 ± 2.5 a	-	9.4 ± 0.4 bc	-	9.5 ± 0.5 bc	-
22	9.5 ± 0.5 bc	-	8.8 ± 0.2 c	-	9.5 ± 0.5 bc	-	10.0 ± 0.5 b	-	12.5 ± 1.5 a	-	13.5 ± 2.5 a	-	9.4 ± 0.4 bc	-	9.5 ± 0.5 bc	-
23	35.0 ± 3.0 Aa	34.0 ± 2.0 Aa	32.0 ± 2.0 Aa	33.5 ± 3.5 Aa	30.0 ± 2.0 Aa	30.0 ± 5.0 Aa	22.0 ± 5.0 Ab	20.0 ± 5.0 Ab	23.5 ± 3.5 Ab	24.0 ± 4.0 Aab	36.0 ± 2.0 Aa	36.0 ± 3.0 Aa	25.0 ± 3.0 Aab	25.0 ± 2.0 Aab	26.5 ± 2.5 Aab	28.0 ± 5.0 Aa
24	35.0 ± 3.0 Aa	34.0 ± 2.0 Aa	32.0 ± 2.0 Aa	33.5 ± 3.5 Aa	30.0 ± 2.0 Aa	30.0 ± 5.0 Aa	22.0 ± 5.0 Ab	20.0 ± 5.0 Ab	23.5 ± 3.5 Ab	24.0 ± 4.0 Aab	36.0 ± 2.0 Aa	36.0 ± 3.0 Aa	25.0 ± 3.0 Aab	25.0 ± 2.0 Aab	26.5 ± 2.5 Aab	28.0 ± 5.0 Aa
25	35.0 ± 3.0 Aa	34.0 ± 2.0 Aa	32.0 ± 2.0 Aa	33.5 ± 3.5 Aa	30.0 ± 2.0 Aa	30.0 ± 5.0 Aa	22.0 ± 5.0 Ab	20.0 ± 5.0 Ab	23.5 ± 3.5 Ab	24.0 ± 4.0 Aab	36.0 ± 2.0 Aa	36.0 ± 3.0 Aa	25.0 ± 3.0 Aab	25.0 ± 2.0 Aab	26.5 ± 2.5 Aab	28.0 ± 5.0 Aa
26	35.0 ± 3.0 Aa	34.0 ± 2.0 Aa	32.0 ± 2.0 Aa	33.5 ± 3.5 Aa	30.0 ± 2.0 Aa	30.0 ± 5.0 Aa	22.0 ± 5.0 Ab	20.0 ± 5.0 Ab	23.5 ± 3.5 Ab	24.0 ± 4.0 Aab	36.0 ± 2.0 Aa	36.0 ± 3.0 Aa	25.0 ± 3.0 Aab	25.0 ± 2.0 Aab	26.5 ± 2.5 Aab	28.0 ± 5.0 Aa
27	35.0 ± 3.0 Aa	34.0 ± 2.0 Aa	32.0 ± 2.0 Aa	33.5 ± 3.5 Aa	30.0 ± 2.0 Aa	30.0 ± 5.0 Aa	22.0 ± 5.0 Ab	20.0 ± 5.0 Ab	23.5 ± 3.5 Ab	24.0 ± 4.0 Aab	36.0 ± 2.0 Aa	36.0 ± 3.0 Aa	25.0 ± 3.0 Aab	25.0 ± 2.0 Aab	26.5 ± 2.5 Aab	28.0 ± 5.0 Aa
28	20.0 ± 5.0 Aa	22.0 ± 2.0 Aa	7.2 ± 1.5 Ab	5.5 ± 2.5 Ab	6.0 ± 2.5 Ab	6.0 ± 2.5 Ab	5.0 ± 2.5 Ab	5.0 ± 2.5 Ab	5.5 ± 2.5 Ab	5.5 ± 2.5 Ab	6.0 ± 2.5 Ab	6.0 ± 2.5 Ab	6.0 ± 2.5 Ab	6.0 ± 2.5 Ab	5.5 ± 2.0 Ab	5.5 ± 2.5 Ab
29	25.5 ± 3.0 Aa	28.0 ± 4.0 Aa	10.2 ± 3.5 Ab	9.0 ± 3.5 Ab	8.5 ± 2.5 Ab	8.5 ± 2.0 Ab	7.0 ± 4.5 Ab	7.5 ± 2.5 Ab	8.5 ± 2.0 Ab	8.0 ± 2.5 Ab	8.5 ± 2.0 Ab	8.5 ± 2.0 Ab	9.0 ± 2.5 Ab	9.5 ± 2.0 Ab	9.5 ± 2.0 Ab	9.0 ± 2.0 Ab
30	18.0 ± 2.5 Aa	17.0 ± 2.5 Aa	8.2 ± 2.5 Ab	8.0 ± 2.5 Ab	8.5 ± 2.5 Ab	8.0 ± 2.5 Ab	9.0 ± 2.5 Ab	9.0 ± 2.5 Ab	8.5 ± 2.5 Ab	9.0 ± 3.5 Ab	8.5 ± 2.5 Ab	8.5 ± 2.5 Ab	8.0 ± 2.5 Ab	8.0 ± 2.0 Ab	8.5 ± 2.5 Ab	8.5 ± 3.0 Ab

Subfamily										
Species	10	15	20	25	30	35	40	45	30/20	35/25
<b>Cactoideae</b>										
<i>Arrojadoa rhodantha</i>	■	■	■	■	■	■	■	■	■	■
<i>Cereus albicaulis</i>	■	■	■	■	■	■	■	■	■	■
<i>Cereus fernambucensis</i> subsp. <i>fernambucensis</i>	■	■	■	■	■	■	■	■	■	■
<i>Cereus jamacaru</i> subsp. <i>jamacaru</i>	■	■	■	■	■	■	■	■	■	■
<i>Discocactus bahiensis</i>	■	■	■	■	■	■	■	■	■	■
<i>Discocactus zehntneri</i> subsp. <i>zehntneri</i>	■	■	■	■	■	■	■	■	■	■
<i>Facheiroa squamosa</i>	■	■	■	■	■	■	■	■	■	■
<i>Harrisia adscendens</i>	■	■	■	■	■	■	■	■	■	■
<i>Melocactus bahiensis</i> subsp. <i>bahiensis</i>	■	■	■	■	■	■	■	■	■	■
<i>Melocactus ernestii</i> subsp. <i>ernestii</i>	■	■	■	■	■	■	■	■	■	■
<i>Melocactus oreas</i> subsp. <i>cremnophilus</i>	■	■	■	■	■	■	■	■	■	■
<i>Melocactus violaceus</i> subsp. <i>violaceus</i>	■	■	■	■	■	■	■	■	■	■
<i>Melocactus zehntneri</i>	■	■	■	■	■	■	■	■	■	■
<i>Pilosocereus catiingicola</i> subsp. <i>salvadorensis</i>	■	■	■	■	■	■	■	■	■	■
<i>Pilosocereus chrysostele</i>	■	■	■	■	■	■	■	■	■	■
<i>Pilosocereus gounellei</i> subsp. <i>gounellei</i>	■	■	■	■	■	■	■	■	■	■
<i>Pilosocereus pentaedrophorus</i> subsp. <i>pentaedrophorus</i>	■	■	■	■	■	■	■	■	■	■
<i>Pilosocereus pentaedrophorus</i> subsp. <i>robustus</i>	■	■	■	■	■	■	■	■	■	■
<i>Pilosocereus pachycladus</i> subsp. <i>pachycladus</i>	■	■	■	■	■	■	■	■	■	■
<i>Pilosocereus pachycladus</i> subsp. <i>pernambucoensis</i>	■	■	■	■	■	■	■	■	■	■
<i>Pilosocereus piauhyensis</i>	■	■	■	■	■	■	■	■	■	■
<i>Pilosocereus tuberculatus</i>	■	■	■	■	■	■	■	■	■	■
<b>Opuntioideae</b>										
<i>Brasiliopuntia brasiliensis</i>	■	■	■	■	■	■	■	■	■	■
<i>Tacinga inamoena</i>	■	■	■	■	■	■	■	■	■	■
<i>Tacinga funalis</i>	■	■	■	■	■	■	■	■	■	■
<i>Tacinga palmadora</i>	■	■	■	■	■	■	■	■	■	■
<i>Tacinga saxatilis</i> subsp. <i>saxatilis</i>	■	■	■	■	■	■	■	■	■	■
<b>Pereskioideae</b>										
<i>Pereskia aculeata</i>	■	■	■	■	■	■	■	■	■	■
<i>Pereskia bahiensis</i>	■	■	■	■	■	■	■	■	■	■
<i>Pereskia grandifolia</i> subsp. <i>grandifolia</i>	■	■	■	■	■	■	■	■	■	■

□, null germinability; ◻, germinability  $\geq 1$  and  $< 50\%$ ; ◼, germinability  $\geq 50\%$ ; ■, optimal germination temperature.

**Table 4** Germinability under a constant temperature range (10 to 45°C) and under alternating temperatures (30/20°C and 35/25°C) for seeds submitted to a photoperiod of 12 h for 30 Cactaceae taxa from the northeastern region of Brazil

establishment (Flores *et al.* 2011). Some studies were developed to characterize the photoblastic responses of other cactus species and the light requirements for the germination of seeds was also related to biological attributes of the species, such as the seed size and the perenniality of plants (see review in Rojas-Aréchiga & Vázquez-Yanes 2000). Rojas-Aréchiga *et al.* (1997) tested the hypothesis that the cacti' photoblastism would be related to the plant growth-form. According to the authors, globose and barrel cacti are always positive photoblastic and columnar cacti may be positive or neutral photoblastic, which could be due to the micro-

climatic conditions that prevail during seed development promoting a different maternal effect (Rojas-Aréchiga *et al.* 1997). Globose and barrel cacti produce fruit closer to the soil, where the temperature is relatively higher. On the other hand, the production of fruit in columnar cacti occurs in the extremities of the cladodes, providing warmer temperatures during seed production (Rojas-Aréchiga *et al.* 1997). Thus, the differences in temperature to which the seeds are submitted during the seed production would determine, according to the authors, the photoblastism of different cactus species.

Although this photoblastic response related to growth form proposed by Rojas-Aréchiga *et al.* (1997) has been observed in Brazilian cacti (all globose and columnar cacti evaluated in the present study were positive photoblastic) and in several studies with cacti that are native to other countries (see Benítez-Rodríguez *et al.* 2004; Flores *et al.* 2006; Rebouças & Santos 2007; Gurvich *et al.* 2008; Rojas-Aréchiga *et al.* 2008 for globose cacti and Rojas-Aréchiga *et al.* 2001; De la Barrera & Nobel 2003; Ramírez-Padilla & Valverde 2005; Ortega-Baes & Rojas-Aréchiga 2007 for columnar species), the results of the covariance analysis of the present study made with the biological attributes selected showed that RLG was influenced only by phylogenetic origin, indicating that the photoblastism of the cacti studied is not related to other biological attributes rather than by phylogeny, since all species of the same subfamily showed the same germinative behavior, which is in accordance with results obtained for tribe Cactaceae (Rojas-Aréchiga *et al.* 2013). So, these results do not support the hypothesis proposed by Rojas-Aréchiga *et al.* (1997) already mentioned above, and suggest that the seed responses to light of cacti occurring in Brazilian ecosystems do not depend on their growth form.

Many species of cactus that occur in the Brazilian northeast ecosystems, such as *Cereus jamacaru* subsp. *jamacaru*, present a similar final germination percentage between 25 and 30°C (Meiado *et al.* 2010). However, the average germination time of the above-mentioned species was favored when submitted to the treatment of 30°C (Meiado *et al.* 2010). This behavior was similar in most of the species evaluated in the present study (faster germination at high temperatures) and may be favorable for the germination of species of Brazilian cacti, since even during the rainy season the soil interface temperature might be high throughout the day in several ecosystems of the northeastern region of Brazil.

Different temperatures also produced different germinative behaviors in the cacti species; however, the positive response to a higher thermal amplitude during seed germination has no relationship with the phylogenetic origin and consequently with the taxonomic group that the cactus belongs to. Regardless of phylogenetic origin, species with germinability higher than 50% and that occurred in higher thermal amplitude were collected in areas of Caatinga and Cerrado, locations where the annual mean temperature is high and can exceed 40°C during the hottest seasons of the year (Marengo 2008). On the other hand, seeds collected in areas of Atlantic Forest and Restinga, whose annual mean temperatures are warmer, were more sensitive to extreme temperatures and to temperature variations. The reduction of the seed germination of the species studied in extreme temperatures may have an ecological significance, since the survival of seedlings

may decrease in these temperatures, hindering the establishment of seedlings in unfavorable periods of the year (Meiado *et al.* 2010).

Another result observed in this study, which also suggests that the germinative behavior of the seeds submitted to different temperatures is not related to the taxonomic group to which the species belongs to, is the differential germinative response among subspecies. Although the same sensitivity to light was observed, the subspecies collected in the same ecosystem (*Pilosocereus pentaedrophorus* subsp. *pentaedrophorus* and *Pilosocereus pentaedrophorus* subsp. *robustos* – Atlantic Forest and *Pilosocereus pachycladus* subsp. *pachycladus* and *Pilosocereus pachycladus* subsp. *pernambucoensis* – Caatinga) presented a differentiated germinative behavior when their seeds were submitted to extreme temperature treatments. This differential behavior of germinative response among species is not an exclusive characteristic of the subspecies of the genus *Pilosocereus*. Similar results were also observed in subspecies of the genus *Arthrocareus* A. Berger (*Arthrocareus melanurus* subsp. *magnus*, *Arthrocareus melanurus* subsp. *melanurus*, *Arthrocareus melanurus* subsp. *odorus*) studied in areas of Campo Rupestre, in Minas Gerais (Cheib & Garcia 2012). According to Cheib and Garcia (2012), although the subspecies of *Arthrocareus melanurus* have shown the same germinative behavior in optimal germination temperatures, the germinability of seeds submitted to extreme temperatures was significantly different among the subspecies evaluated and *Arthrocareus melanurus* subsp. *melanurus* presented the highest germinability and the shortest average germination time in the treatments of 15 and 35°C.

This study shows, besides providing information on the germinative behavior of seeds of new taxa of the Cactaceae family that occur exclusively in Brazil, that the germinative behavior might be determined by biological attributes such as phylogenetic origin and the Brazilian ecoregions where the seeds were collected, which can help in the interpretation of the physiological behavior of native species. According to Wang *et al.* (2009), variation in seed germinability of a semi-arid plant community is largely dependent upon phylogeny and dispersal mode, and some seed traits, for example, seed size or seed mass, can also influence the final germination percentage. This response related to biological attributes can be observed in both types of photoblastic responses, suggesting that these factors may constrain the evolution of seed germination strategies, while environmental pressures act effectively on life-history traits of species that are part of the community (Wang *et al.* 2009). Although, other factors beyond the phylogeny and the dispersal mode should be considered in assessing the photoblastic response, such as seed mass, life form, and adult plant height (Flores *et al.* 2011), because phylogeny may not be the unique

characteristic responsible for variation on photoblastic response during seed germination of all tribes of the family Cactaceae, although it has been demonstrated in members of tribe Cacteae that no evidence exists of a relationship between seed size and photoblastic response and that photoblastism is phylogenetically fixed and coupled with environmental factors that fine tune the germination response (Rojas-Aréchiga *et al.* 2013).

The average RLG of Cacteae, Pachycereeae, and Trichocereae did not differ but was higher than for Notoacteae, indicating the phylogenetic influence on photoblastic response of cacti seeds (Flores *et al.* 2011). Similar results were observed in this study and the differences observed among the subspecies collected in the different ecosystems (Caatinga, Campo Rupestre, and Atlantic Forest) indicate changes in the physiological behavior that may promote the appearance in the future of individuals morphologically distinct, which can inhabit the same environment, which may need different requirements for seed germination and seedling establishment in these ecosystems.

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