

Hydropriming changes temperature thresholds for seed germination of tree species from the Caatinga, a Brazilian tropical dry forest

Joana Paula Bispo Nascimento^{1,2} , Bárbara França Dantas³ , Marcos Vinicius Meiado^{1,2*} 

Journal of Seed Science, v.43,
e202143004, 2021

<http://dx.doi.org/10.1590/2317-1545v43238649>

ABSTRACT: This study evaluates the effects of hydration and dehydration cycles (HD cycles) on seed germination of four Caatinga tree species (*Anadenanthera colubrina* var. *cebil*, *Enterolobium contortisiliquum*, *Pityrocarpa moniliformis* and *Pterogyne nitens*) subjected to different temperatures and determine the thermal upper and lower limits of germination. For this, seeds were subjected to 0, 1, 2 and 3 HD cycles and set to germinate at temperatures of 5, 10, 15, 25, 35, 40 and 45 °C. Germinability and t_{50} were calculated and the differences of these parameters were compared by two-way ANOVA. In addition, germination rate ($GR = 1/t_{50}$), as well as ceiling (T_c), optimum (T_o) and base (T_b) temperatures were calculated to estimate the limits below or above which the seeds fail to germinate. We observed that the more HD cycles, the better the seed responds, especially at extreme temperatures. Seeds of all studied species showed T_o between 25 and 35 °C, $T_b < 10$ °C, and $T_c > 40$ °C. The slope of regression curves for germination rate showed that submitting seeds to HD cycles expands its thermal tolerance range, revealing that this seed pre-treatment can be efficient for species as it increases their tolerance to thermal stress.

Index terms: HD cycles, tolerance, thermal stress, modeling.

Hidropriming altera limiares de temperatura para germinação de sementes de espécies arbóreas da Caatinga, uma floresta tropical seca brasileira

RESUMO: Este estudo avaliou os efeitos dos ciclos de hidratação e desidratação (ciclos de HD) na germinação de sementes de quatro espécies arbóreas da Caatinga (*Anadenanthera colubrina* var. *cebil*, *Enterolobium contortisiliquum*, *Pityrocarpa moniliformis* and *Pterogyne nitens*) submetidas a diferentes temperaturas, determinando os limites térmicos para germinação. As sementes foram submetidas a 0, 1, 2 e 3 ciclos de HD e colocadas para germinar nas temperaturas de 5, 10, 15, 25, 35, 35, 40 e 45 °C. Germinabilidade e t_{50} foram calculados e as diferenças foram comparadas pela ANOVA Dois Fatores. Além disso, a taxa de germinação ($GR = 1/t_{50}$), bem como temperaturas teto (T_c), ótima (T_o) e base (T_b) foram calculadas para estimar os limites abaixo ou acima dos quais as sementes não germinam. Foi observado que quanto mais ciclos de HD, melhor é a resposta da semente, principalmente em temperaturas extremas. Sementes de todas as espécies apresentaram T_o entre 25 e 35 °C, $T_b < 10$ °C e $T_c > 40$ °C. A inclinação das curvas de regressão da taxa de germinação mostrou que os ciclos de HD expandem faixa de tolerância térmica das sementes, revelando que esse pré-tratamento pode ser eficiente para as espécies, aumentando sua tolerância ao estresse térmico.

Termos para indexação: ciclos de HD, tolerância, estresse térmico, modelagem.

*Corresponding author
E-mail: meiado@ufs.br

Received: 5/25/2020.
Accepted: 1/12/2021.

¹Laboratório de Fisiologia de Sementes, Departamento de Biociências, Universidade Federal de Sergipe – 49.510-200, Itabaiana, Sergipe, Brazil.

²Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal de Sergipe – 49.100-000, São Cristóvão, Sergipe, Brazil.

³Laboratório de Análise de Sementes, Centro de Pesquisa Agropecuária do Trópico Semiárido, Empresa Brasileira de Pesquisa Agropecuária – 56.302-970, Petrolina, Pernambuco, Brazil.

INTRODUCTION

Knowledge on the environmental conditions that interfere with seed germination is essential for understanding the establishment of plant diversity. Among the environmental conditions that interfere with the germination process, temperature is one of the factors that most affect germinability, germination speed, and specific biochemical and enzymatic reactions that drive the entire germination process (Bewley et al., 2013).

Germination of non-dormant seeds occurs within a temperature range called cardinal temperatures, that is, ceiling (T_c), base (T_b) and optimum (T_o) temperatures at which a seed can germinate. The optimum temperature is considered the ideal temperature for the species to germinate since it results in the largest number of seeds germinated in a shorter period (Bewley et al., 2013). The optimum temperature range can be related to the species' site of occurrence, dispersion period, and plant germination strategies (Meiado et al., 2016). In the Caatinga, a Tropical Dry Forest occurring mainly in the Northeast region of Brazil, many species have optimum germination ranging from 30 to 35 °C, evidencing that these plants have higher tolerance to high temperatures compared to species from more humid ecosystems (Meiado et al., 2012; 2016; Nascimento et al., 2018; Dantas et al., 2020).

Changes in environment temperature can affect the permeability of membranes and sub or supra-optimum temperatures tend to reduce the speed of germination process and expose seeds to adverse factors for longer, reducing reproductive success (Bewley et al., 2013). Future climate scenarios predict, based on greenhouse gases emissions, higher stochasticity and lower volumes of rainfalls and increase in environmental temperatures (IPCC, 2014). These scenarios may compromise seed germination, early seedling development, and the establishment of plants in the nature. Even those species well adapted to hot and dry climates, such as the Caatinga, can be affected by future climate pessimistic scenarios, demanding in such arid environments that species become increasingly tolerant (Chen and Arora, 2013; Alvarado-Lopez et al., 2014).

In view of this scenario, new methods to increase the success of seed germination and seedling establishment have been created and improved, among them hydropriming, priming treatments, or hydration and dehydration cycles (HD cycles). These techniques consist of hydrating seeds just enough to enable initial biochemical processes essential for germination, but not enough to promote the root protrusion (Alvarado-Lopez et al., 2014). Upon passing through such discontinuous hydration cycles, seeds have higher germinability in shorter period, along with the activation of some specific genes related to tolerance to environmental stresses, such as thermal stress, when seeds are allowed to germinate (Dubrovsky, 1996; Alvarado-Lopez et al., 2014).

Seeking to predict the germinative behavior of some species, researchers have resorted to experiments by using controlled conditions and models based on population parameters, such as degree-days (thermal time), which allows estimating the time required for seed germination in a given thermal regime based on germinative parameters (Cardoso, 2011; Nakao and Cardoso, 2015). Such models allow quantifying the germinative response amid temperature changes in the environment. *Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altschul, *Enterolobium contortisiliquum* (Vell.) Morong, *Pityrocarpa moniliformis* (Benth.) Luckow and RW Jobson, and *Pterogyne nitens* Tul. are Caatinga tree species, considered early pioneer or secondary, fast growing and thus used in reforestation programs in degraded areas of the Caatinga (Queiroz, 2009). Thus, this study evaluates the effects of hydropriming, due to discontinuous hydration, on germinative behavior of these four species subjected to different temperatures. We also estimate thermal thresholds for germination by testing the hypothesis according to which a discontinuous hydration can increase the thermal range for germination by reducing T_b and increasing T_c .

MATERIAL AND METHODS

Four tree species of the *Fabaceae* family with wide distribution in the Caatinga were selected: *Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altschul, *Enterolobium contortisiliquum* (Vell.) Morong, *Pityrocarpa*

moniliformis (Benth.) Luckow and RW Jobson, and *Pterogyne nitens* Tul. Seeds were collected in Caatinga areas in the Northeast region of Brazil in 2014 and packed in cloth bags in a cold chamber (5 ± 2 °C), for no longer than six months, until experiments were performed. According to Köppen-Geiger climate classification system, the collection site is characterized by hot semi-arid climate (BSh), with maximum temperatures reaching more than 36 °C in dry seasons (Climate Data, 2020).

HD cycles and temperature treatments

Initially, seeds of *E. contortisiliquum*, *P. moniliformis* and *P. nitens* overcame their physical dormancy by immersing them in concentrated sulfuric acid (H_2SO_4) for sixty, forty and five minutes, respectively. To promote HD cycles in seeds, hydration times were set based on previous studies on hydration curves, which corresponded to two hours for *A. colubrina*, seven hours for *E. contortisiliquum*, five hours for *P. moniliformis*, and eight hours for *P. nitens*. Thus, seeds were placed in trays containing two layers of germitest substrate paper and 200 mL of distilled water and incubated 25 °C during the mentioned hydration times.

The dehydration period of seeds of each species was set according to the time required by the seed to return to its initial biomass in an oven with forced air circulation at 40 °C. For *P. moniliformis* seeds, four hours of drying were necessary. The seeds of *P. nitens* dehydrated after six hours. Seeds of *A. colubrina* and *E. contortisiliquum* were dehydrated after eight hours of drying. Therefore, one HD cycle was the hydration followed by dehydration during specific times for each species. Seeds were subjected to 0, 1, 2 or 3 HD cycles, with similar dehydration periods for all cycles (Lima et al., 2018).

After undergoing the HD cycles, seeds were subjected to thermal stress treatments during germination. For each treatment, 100 seeds of each species were used, distributed in four replications of 25 seeds sown in 15-cm diameter Petri dishes containing filter paper moistened with 15 mL of distilled water. These were placed to germinate in B.O.D. (biological oxygen demand) germination chambers, in a 12-hour photoperiod (light intensity: $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and in seven constant temperature treatments (5, 10, 15, 25, 35, 40 and 45 °C). Germination was evaluated daily for 30 days, and the criterion for considering germinated seeds was primary root protrusion.

Germination parameters, modeling and statistical analysis

At the end of observations, the following were calculated: germinability (%) (arc-sin $\sqrt{\%}$ transformed, Marques et al., 2015) and time to obtain the germination of half the sample of germinated seeds (t_{50} - days) according to the equation:

$$t_{50} = ti + [(N/2 - ni) (tj - ti)] / (nj - ni),$$

where N is the final number of germinated seeds and nj is the cumulative number of germinated seeds by adjacent counts in times tj and ti , respectively, when $ni < N/2 < nj$ (Farooq et al., 2005).

Germination percentages for each temperature were plotted in function of time, creating accumulated germination curves adjusted for Boltzmann sigmoidal curves. The t_{50} was estimated from each curve and the germination rate (GR) was calculated as the reciprocal of t_{50} . The GR values were calculated separately for optimum sub and supra-temperatures (Covell et al., 1986). A linear regression analysis was performed to calculate the interception on the x-axis of both sub and supra-optimum temperatures, providing estimates of base and ceiling temperatures (T_b and T_c) for germination, respectively, below and above which seeds fail to germinate (Covell et al., 1986). The interception of linear regression lines was used to estimate optimum temperature (T_o ; Hardegree, 2006; Oliveira et al., 2019; Dantas et al., 2020).

The thermal time of the species that germinated at sub-optimum temperatures (θ_{sub}) and supra-optimum temperatures (θ_{supra}) were the reciprocal of the slope angle of each linear regression and were calculated according to the equations:

$$\theta_{sub} = (T - T_b) t; (\text{°C days})$$

$$\theta_{supra} = (T_c - T) t; (\text{°C days})$$

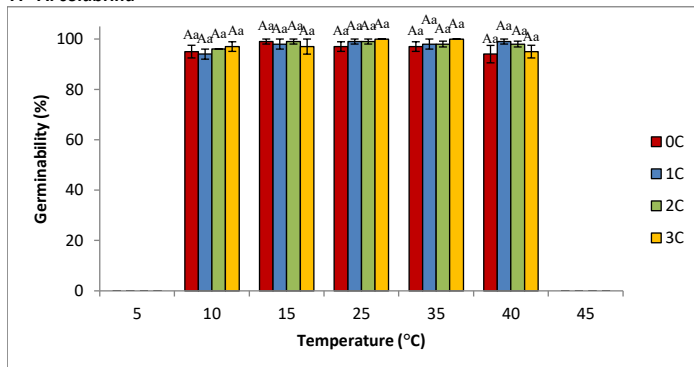
where T is the germination temperature, T_b is the base temperature, T_c is the ceiling temperature, and t is the time since the imbibition started (Covell et al., 1986).

The results of germinability and t_{50} were submitted to two-way ANOVA (HD cycles and temperature), and the means were compared by Tukey test. The normality of data residual and the homogeneity of variances were assessed using the Shapiro-Wilk and Levene tests, respectively, and all statistical analyses were performed using the software STATISTICA 13.0 at 0.05 significance (StatSoft, 2020).

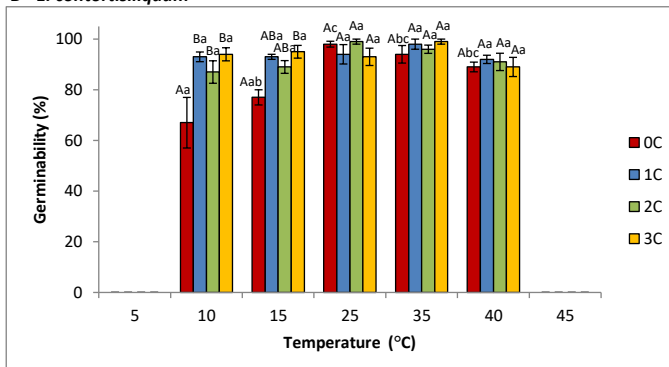
RESULTS AND DISCUSSION

The period of germination is considered the most critical stage for survival and establishment of new plants, with this in mind researchers seek to understand the germinative behavior of species using models to quantify the seed response to some biological phenomena to better control this process (Cardoso, 2011). Figure 1 and Table 1 show, respectively, a temperature response germination model and its parameters for seeds (hydroprimed or not) of the four studied species. According to the model, seeds of all species managed to germinate in a wide temperature range (10–40 °C) and failed to do so at the temperatures 5 °C and 45 °C (Table 1, Figure 1). The optimum temperature (T_o) for germination was around 35 °C for seeds of *E. contortisiliquum* (Table 1, Figure 2B,) and around 25 °C for the other species (Table 1, Figures 2A, C, D).

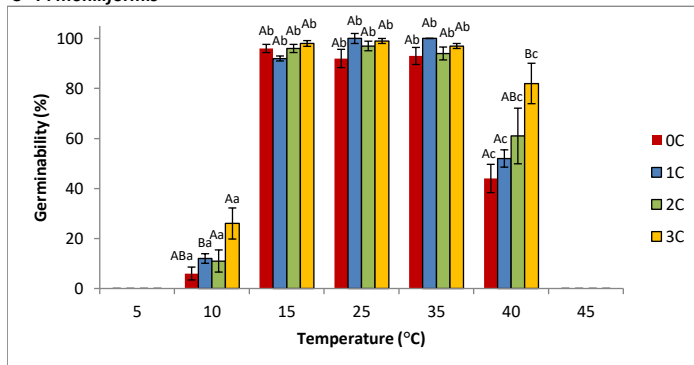
A - *A. colubrina*



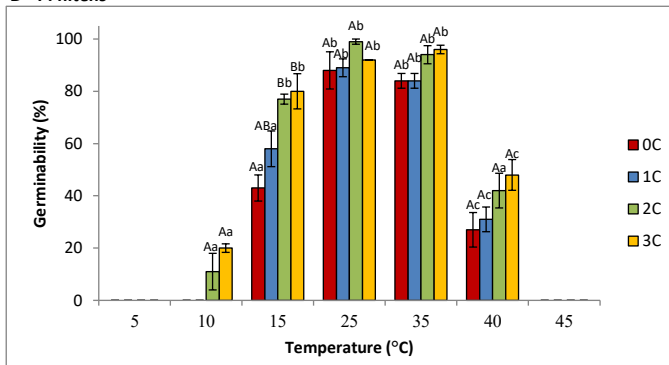
B - *E. contortisiliquum*



C - *P. moniliformis*



D - *P. nitens*



Data expressed as mean \pm standard error. Uppercase letters compare germinability among HD cycles and lowercase letters compare germinability among temperatures.

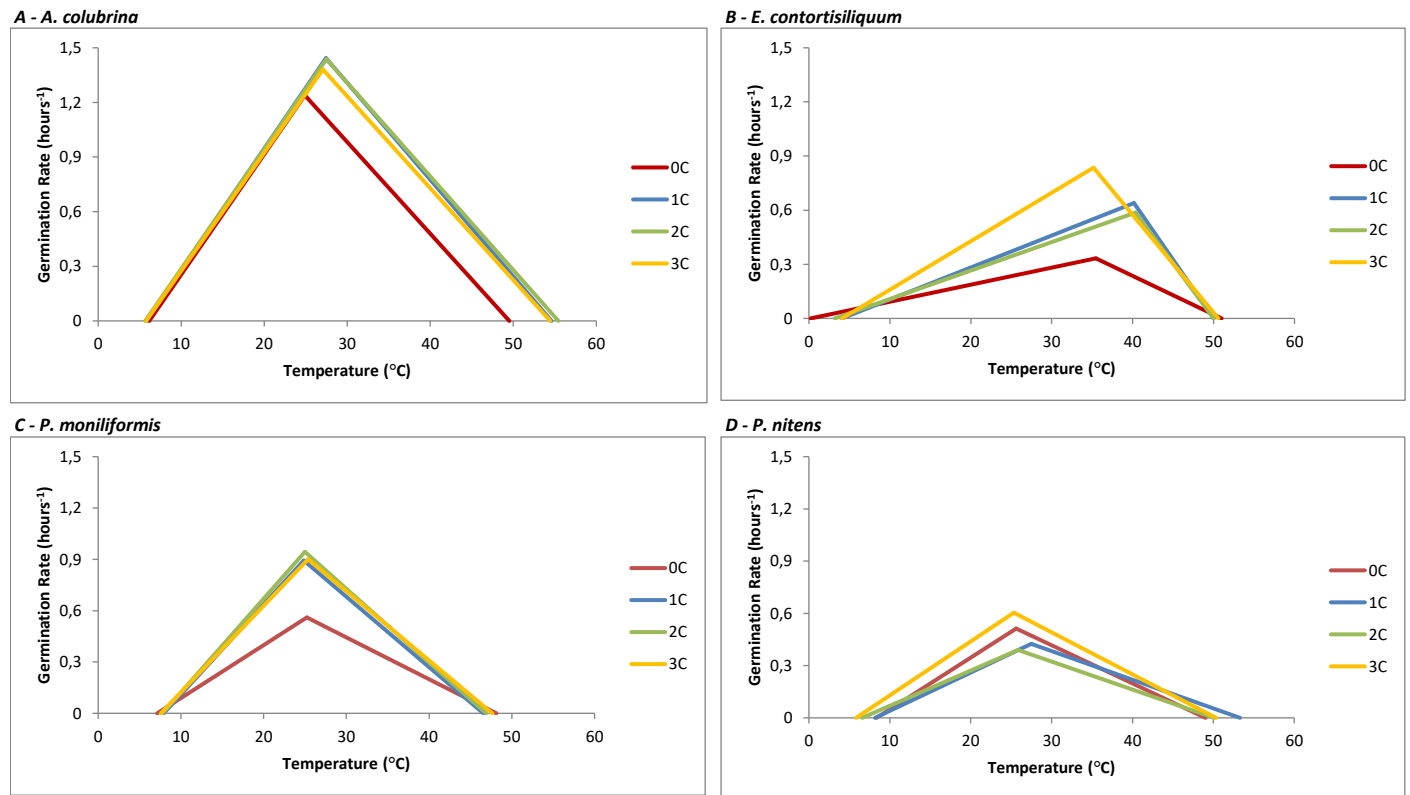
Figure 1. Germinability (%) of (A) *Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altschul, (B) *Enterolobium contortisiliquum* (Vell.) Morong, (C) *Pityrocarpa moniliformis* (Benth.) Luckow and R.W. Jobson e (D) *Pterogyne nitens* Tul. (*Fabaceae*) seeds that were subjected to thermal stress after passing through discontinuous hydration.

Table 1. Temperature requirements and limits, represented by base temperature (T_b), ceiling temperature (T_c), optimum temperature (T_o), thermal time of seed germination at sub-optimum (θ_{sub}) and supra-optimum (θ_{supra}) temperatures, of *Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altschul, *Enterolobium contortisiliquum* (Vell.) Morong, *Pityrocarpa moniliformis* (Benth.) Luckow and R.W. Jobson and *Pterogyne nitens* Tul. (*Fabaceae*) seeds that were subjected to thermal stress after passing through discontinuous hydration.

Temperature requirements and limits	Discontinuous hydration cycles			
	0 cycle	1 cycle	2 cycles	3 cycles
<i>Anadenanthera colubrina</i> (Vell.) Brenan var. <i>cebil</i> (Griseb.) Altschul				
T_b (°C)	6.1	5.8	5.7	5.8
T_c (°C)	49.5	54.6	55.4	54.4
T_o (°C)	24.9	27.4	27.5	27.1
θ_{sub} (°C days ⁻¹)	15.1	15.0	15.2	15.4
θ_{supra} (°C days ⁻¹)	19.9	18.8	19.4	19.8
<i>Enterolobium contortisiliquum</i> (Vell.) Morong				
T_b (°C)	2.0	4.1	3.2	4.1
T_c (°C)	51.0	50.0	50.0	50.6
T_o (°C)	35.5	40.2	40.4	35.2
θ_{sub} (°C days ⁻¹)	105.8	56.4	63.4	37.2
θ_{supra} (°C days ⁻¹)	46.7	15.4	16.4	18.5
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow and R.W. Jobson				
T_b (°C)	7.1	7.9	7.8	7.6
T_c (°C)	48.1	46.6	46.9	47.6
T_o (°C)	25.2	24.9	25.0	25.4
θ_{sub} (°C days ⁻¹)	32.3	19.0	18.2	19.8
θ_{supra} (°C days ⁻¹)	40.9	24.3	23.2	24.7
<i>Pterogyne nitens</i> Tul.				
T_b (°C)	8.4	8.2	6.6	5.8
T_c (°C)	49.0	53.3	50.1	50.3
T_o (°C)	25.6	27.5	25.9	25.3
θ_{sub} (°C days ⁻¹)	33.7	45.5	49.4	32.3
θ_{supra} (°C days ⁻¹)	45.6	60.8	62.2	41.4

Regarding hydropriming, the more cycles resulted in better seed response, especially at extreme temperatures, both sub and supra-optimum, not having much effect when the seeds germinated at temperatures close to T_o . Furthermore, the species showed different germination response pattern when subjected to extreme temperatures and to the HD cycles (Tables 1, 2; Figures 1, 2).

The temperature thresholds for seed germination were calculated from the GR plotted against temperature. The seeds of all species showed wide a thermal threshold, with an optimum temperature (T_o) between 25 °C and 35 °C, a base temperature (T_b) below 10 °C, and a ceiling temperature (T_c) above 40 °C (Figure 2). The slope of regression curves for germination rates showed seeds that undergone HD cycles, were even more tolerant to thermal stress and had increased thermal range.



Parameters of curves are in Table 1: when $y = 0$, $x = T_b$ and T_c (for sub and supra-optimal temperature curves, respectively). Angular coefficients of curves are θ_{sub} and θ_{supra} (for sub and supra-optimal temperature curves, respectively).

Figure 2. Germination rate (days^{-1}) (A) *Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altschul, (B) *Enterolobium contortisiliquum* (Vell.) Morong, (C) *Pityrocarpa moniliformis* (Benth.) Luckow and R.W. Jobson e (D) *Pterogyne nitens* Tul. (*Fabaceae*) seeds that were subjected to thermal stress after passing through discontinuous hydration.

Seeds of *A. colubrina* showed germinability higher than 90% at all temperatures evaluated ($F = 2.39$, $df = 4$, $p = 0.0610$, Figure 1A) and discontinuous hydration did not confer greater higher germinability in any temperature for seeds of this species ($F = 0.80$, $df = 3$, $p = 0.4970$). However, supra-optimal temperature threshold for germination was increased with 1 to 3 cycles of HD, and T_c increased from 49.5 to 55 °C (Figure 2A).

Seeds of *E. contortisiliquum* subjected to HD cycles showed higher tolerance to sub-optimum temperatures (10 and 15 °C), with an increase of about 20% in seed germination ($F = 8.18$, $df = 4$, $p < 0.0001$, Figure 1B). Although HD cycles increased GR and altered the GR curves slope, decreasing thermal time (θ_{sub} , θ_{supra}) these pre-treatments did not alter temperature limits for germination (Figure 2B, Table 1).

Discontinuous hydration provided greater tolerance to seeds of *P. moniliformis* and *P. nitens* at all extreme temperatures evaluated, mainly after undergoing three HD cycles ($F = 315.751$, $df = 4$, $p < 0.0001$, Figure 1C; and $F = 254.303$, $df = 4$, $p < 0.0001$, Figure 1D, respectively). *P. moniliformis* seeds showed about 20 and 40% increase in germination at 10 and 40 °C, respectively (Figure 1C). For *P. nitens* seeds, such increase corresponded to approximately 20% at the same temperatures (Figure 1D). These two species also responded to HD cycles by increasing GR, altering the GR curves slope and, decreasing thermal time (θ_{sub} , θ_{supra}), rather than altering temperature thresholds for germination (Figures 2C, D; Table 1).

One of the main effects of HD cycles was to reduce the germination thermal requirements (thermal time) at sub and supra-optimum temperatures, which was observed in seeds of *E. contortisiliquum* and *P. moniliformis* (Table 1). The untreated seeds of *E. contortisiliquum*, germinated after 105 °C.day⁻¹ and, after HD cycles, this was reduced to 37.2

$^{\circ}\text{C}\cdot\text{day}^{-1}$. At supra-optimum temperatures, this change would be from $46.7^{\circ}\text{C}\cdot\text{day}^{-1}$ to $18.5^{\circ}\text{C}\cdot\text{day}^{-1}$. The untreated seeds of *P. moniliformis* showed θ_{sub} and θ_{supra} , respectively, 32.3 and $40.9^{\circ}\text{C}\cdot\text{day}^{-1}$ and after 2 HD cycles required only 18.2 and $23.2^{\circ}\text{C}\cdot\text{day}^{-1}$. Seeds of *A. colubrina* however, did not show alterations in thermal requirements after undergoing HD cycles and *P. nitens* showed increase in thermal requirements after undergoing 1 and 2 HD cycles (Table 1).

The temperature changes also influenced the t_{50} of the seeds. All species germinated faster as of 25°C and milder temperatures provided a higher t_{50} . Thus, seeds took longer to germinate at lower temperatures compared to higher ones (*A. colubrina*: $F = 30.9846$, $df = 4$, $p < 0.0001$; *E. contortisiliquum*: $F = 19.8560$, $df = 4$, $p < 0.0001$; *P. moniliformis*: $F = 14.6808$, $df = 4$, $p < 0.0001$; *P. nitens*: $F = 143.035$, $df = 4$, $p < 0.0001$; Table 2).

Undergoing HD cycles reduced t_{50} for seeds of *P. nitens* at lower temperatures, but not for seeds of the other studied species (*A. colubrina*: $F = 14.92$, $df = 12$, $p = 0.9999$. *E. contortisiliquum*: $F = 0.8417$, $df = 12$, $p = 0.6081$. *P. moniliformis*: $F = 0.8701$, $df = 12$, $p = 0.5806$; Table 2).

Seeds of all studied species were able to germinate over a wide temperature range, with optimum temperatures for seed germination at 25°C (*A. colubrina*, *P. moniliformis*, *P. nitens*) and 35°C (*E. contortisiliquum*), since, at these temperatures' germination was higher and/or faster. Previous studies have pointed out that the optimum temperature

Table 2. Number of days for germination of 50% of the seed population (T_{50} , days) of *Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altschul, *Enterolobium contortisiliquum* (Vell.) Morong, *Pityrocarpa moniliformis* (Benth.) Luckow and R.W. Jobson e *Pterogyne nitens* Tul. (*Fabaceae*) subjected to thermal stress after passing through discontinuous hydration.

Number of HD cycles	Temperatures ($^{\circ}\text{C}$)				
	10	15	25	35	40
<i>Anadenanthera colubrina</i> (Vell.) Brenan var. <i>cebil</i> (Griseb.) Altschul					
0	$5.74 \pm 1.67\text{Aa}$	$2.53 \pm 0.77\text{Aab}$	$1.53 \pm 0.01\text{Ab}$	$1.63 \pm 0.08\text{Ab}$	$1.66 \pm 0.14\text{Ab}$
1	$4.11 \pm 3.58\text{Aa}$	$1.35 \pm 0.90\text{Aab}$	$0.53 \pm 0.01\text{Ab}$	$0.62 \pm 0.04\text{Ab}$	$0.70 \pm 0.13\text{Ab}$
2	$4.50 \pm 3.31\text{Aa}$	$1.82 \pm 0.12\text{Aab}$	$0.52 \pm 0.02\text{Ab}$	$0.70 \pm 0.06\text{Ab}$	$0.82 \pm 0.09\text{Ab}$
3	$5.39 \pm 1.42\text{Aa}$	$2.35 \pm 0.96\text{Aab}$	$0.53 \pm 0.03\text{Ab}$	$0.85 \pm 0.11\text{Ab}$	$1.00 \pm 0.34\text{Ab}$
<i>Enterolobium contortisiliquum</i> (Vell.) Morong					
0	$11.43 \pm 4.41\text{Aa}$	$7.41 \pm 1.83\text{Aab}$	$5.23 \pm 0.59\text{Ab}$	$4.46 \pm 0.69\text{Ab}$	$4.17 \pm 0.03\text{Ab}$
1	$9.98 \pm 0.83\text{Aa}$	$6.86 \pm 0.83\text{Aab}$	$3.64 \pm 1.18\text{Ab}$	$2.87 \pm 1.63\text{Ab}$	$1.68 \pm 0.05\text{Ab}$
2	$7.29 \pm 4.96\text{Aa}$	$6.84 \pm 1.43\text{Aa}$	$3.91 \pm 1.40\text{Aa}$	$3.25 \pm 0.80\text{Aa}$	$1.77 \pm 0.16\text{Aa}$
3	$6.20 \pm 1.77\text{Aa}$	$6.30 \pm 1.24\text{Aa}$	$3.52 \pm 1.77\text{Aa}$	$4.22 \pm 5.90\text{Aa}$	$2.79 \pm 1.14\text{Aa}$
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow and R.W. Jobson					
0	$10.88 \pm 9.95\text{Aa}$	$8.30 \pm 0.43\text{Aa}$	$1.90 \pm 0.11\text{Aa}$	$5.22 \pm 1.16\text{Aa}$	$7.58 \pm 1.07\text{Aa}$
1	$5.13 \pm 3.42\text{Aa}$	$7.75 \pm 5.19\text{Aa}$	$0.65 \pm 0.06\text{Aa}$	$3.75 \pm 0.20\text{Aa}$	$9.31 \pm 2.97\text{Aa}$
2	$9.21 \pm 6.19\text{Aa}$	$9.33 \pm 0.72\text{Aa}$	$1.94 \pm 2.71\text{Aa}$	$3.11 \pm 0.29\text{Aa}$	$7.86 \pm 1.31\text{Aa}$
3	$13.08 \pm 7.20\text{Aa}$	$7.97 \pm 0.68\text{Aa}$	$1.84 \pm 0.02\text{Aa}$	$3.27 \pm 1.23\text{Aa}$	$11.50 \pm 4.99\text{Aa}$
<i>Pterogyne nitens</i> Tul.					
0	–	$17.96 \pm 3.23\text{Aa}$	$1.75 \pm 0.11\text{Ab}$	$7.20 \pm 1.34\text{Ac}$	$5.13 \pm 1.45\text{Abc}$
1	–	$20.56 \pm 2.16\text{Aa}$	$2.44 \pm 0.43\text{Ab}$	$4.24 \pm 1.82\text{Abc}$	$5.21 \pm 2.99\text{Ac}$
2	$11.88 \pm 0.10\text{Aa}$	$16.75 \pm 3.85\text{Ab}$	$2.71 \pm 0.57\text{Ac}$	$7.20 \pm 1.34\text{Ac}$	$7.17 \pm 0.35\text{Ac}$
3	$6.58 \pm 2.14\text{Ba}$	$7.34 \pm 2.10\text{Ba}$	$1.57 \pm 0.01\text{Ab}$	$5.99 \pm 0.82\text{Ab}$	$4.49 \pm 0.64\text{Aab}$

(–) no seed germination. Uppercase letters compare averages among HD cycles and lowercase letters compare averages among temperatures.

for germination of tropical species occurs within a range of 20 to 35 °C and that the appropriate temperature for germination varies according to the region of occurrence of the species and the favorable time for the germination of its seeds, growth and plant development (Azerêdo et al., 2011; Oliveira et al., 2014; Ramos et al., 2018).

The results presented here suggest that the species can germinate and withstand high environmental temperatures, expanding their establishment and distribution to different habitats in the Caatinga. Regarding hydropriming treatment, the results showed that the responses of the seeds to the temperature treatments were affected by discontinuous hydration. HD cycles improved germination, mainly at extreme temperatures, both sub and supra-optimum (10 and 40 °C), not having much effects when the seeds were put to germinate at temperatures close to optimum (25 and 35 °C). These results corroborate those reported by Mendonça et al. (2005) with the species *Triplaris americana* L. (Polygonaceae), whose germination percentage at sub-optimum temperature (20 °C) was favored by osmotic conditioning. In addition to these authors, Jeller and Perez (2003) also found in seeds of *Senna spectabilis* (DC.) HS Irwin and Barneby var. *excelsa* (Schrad.) HS Irwin and Barneby (*Fabaceae*) that osmotic conditioning, in general, provided increases in seed performance under conditions of thermal stress both at a sub-optimum temperature (12 °C) and supra-optimum temperature (39 °C), revealing that this is also an efficient treatment (Jeller and Perez, 2003). Similar results showed that *Urochloa* sp. (Poaceae) primed seeds had their optimum temperature changed to higher temperatures and that effect of priming was more intense at non-optimum temperatures, widening its germination temperature range (Nakao and Cardoso, 2015). In addition, the authors observed that there is generally a higher increase in T_c than decrease in T_b which may explain the increase in optimal and ceiling temperatures of the species in this study occurring in the Caatinga ecosystem, naturally characterized by high temperatures.

The number of cycles also affected the response of seeds, and the passage through three cycles of HD provided higher germinability and shorter germination time compared to untreated seeds. This can be explained by the longer time of exposure to water, suggesting that the greater the number of cycles, the greater the progress of the initial physiological processes related to seed germination (Lima and Meiado, 2017). Hydropriming can be limited by the amount and time of exposure of seeds to water or conditioning agents. In natural conditions, seeds can undergo several short cycles of hydration and dehydration, which would lead to a greater tolerance to high temperatures at which seeds are exposed to germinate in this semiarid ecosystem (Lima and Meiado, 2017; 2018a; 2018b; Lima et al., 2018). Cycles of hydration and dehydration of seeds provide biochemical changes, such as mobilization of protein storage, mainly globulins and prolamins (Aragão et al., 2002), synthesis of stress proteins and late embryogenesis proteins (LEA) (Bray, 2004), and accumulation of organic solutes (Matias et al., 2015) allowing seeds to cope better with drought periods, such as the predicted by future climate scenarios (IPCC, 2014).

Seeds GR has been studied on different species subjected to several factors, such as storage time, water deficit and different temperatures, in order to obtain the germination thresholds (Oliveira et al., 2019; Gomes et al., 2019; Daibes and Cardoso, 2020). In this study, the temperature thresholds, as well as the sub and supra-optimum thermal times of the species, showed that they can germinate in a wider temperature range after undergoing HD cycles, obtaining with T_b below 10 °C and T_c above 40 °C. Agreeing to our results, studies on seeds native to the Caatinga reported that different species and all seed lots (from different harvests and provenances) germinated in a wide thermal range, with T_b below 10 °C and/or T_c above 40 °C (Gomes et al., 2019; Oliveira et al., 2019; Dantas et al., 2020).

According to Bewley et al. (2013), higher temperatures increase the water absorption and the enzymatic activities of the seeds, making them germinate more quickly, however extremely high environmental temperatures (above 40 °C) affect germination by denaturation enzymes and/or inducing water loss.

Other studies have already demonstrated the benefits of hydropriming in relation to the time required for seeds to germinate (Contreras-Quiroz et al., 2016; Lima and Meiado, 2017; 2018a; 2018b; Lima et al., 2018). In these works, carried out on species that also occur in the Caatinga seeds that undergone HD cycles significantly decreased the germination time. This acceleration of germination speed can be beneficial for seeds to germinate and for seedlings to establish themselves in more favorable times and not be exposed to other environmental adversities, such as water

scarcity, contamination by pathogens, predation, among others.

According to IPCC, global warming is human based, and its activities will determine optimistic or pessimistic scenarios, with temperature increase up to 1.5 and 4.8 °C, respectively (IPCC, 2014). The Caatinga dry forest is identified as one of the Brazilian regions most likely to be affected by climate change (Marengo et al., 2017). Under the most pessimistic climate change scenario, a temperature increase up to 4.8 °C is predicted, building up to average temperatures over 30 °C and maximum temperatures over 40 °C (Marengo, 2014). However, as we observe in this and other studies, several Caatinga tree species are tolerant to high temperatures, and will be able to germinate, during the rainy season, even in pessimistic scenarios of temperature increase (Oliveira et al., 2019; Gomes et al., 2019; Dantas et al., 2020). Seeds hydration memory and their hydropriming by undergoing HD cycles, may allow seeds to cope better with extreme temperature in future climate and other environmental stresses that arises from temperature increase, such as drought and soil salinization (Lima and Meiado, 2017; Lima et al., 2018).

CONCLUSIONS

Seeds of the Caatinga harvested studied species germinated over an already wide temperature range, however undergoind HD cycles increased germinability and decreased germination time at extreme temperatures, as well as widened the temperature range for germination. Since HD cycles occurs in nature after rainfall (mainly small rainfall) events, this is an indication that in hotter future climate scenarios, even the pessimistic ones, seeds of the studied species will still be able to germinate in their original environments of occurrence.

REFERENCES

- ALVARADO-LÓPEZ, S.; SORIANO, D.; VELÁZQUEZ, N.; OROZCO-SEGOVIA, A.; GAMBOA-DEBUEN, A. Priming effects on seed germination in *Tecoma stans* (Bignoniaceae) and *Cordia megalantha* (Boraginaceae), two tropical deciduous tree species. *Acta Oecologica*, v.61, n.1, p.65-70, 2014. <https://doi.org/10.1016/j.actao.2014.10.007>
- ARAGÃO, C.A.; DANTAS, B.F.; ALVES, E.; CORRÊA, M.R. Sementes de feijão submetidas a ciclos e períodos de hidratação-secagem. *Scientia Agrícola*, v.59, n.1, p.87-92, 2002. <https://doi.org/10.1590/S0103-90162002000100013>
- AZERÊDO, G.A.; PAULA, R.C.; VALERI, S.V. Temperatura e substrato para a germinação de sementes de *Piptadenia moniliformis* Benth. *Scientia Forestalis*, v.39, n.92, p.479-488, 2011. <https://www.ipef.br/publicacoes/scientia/nr92/cap11.pdf>
- BEWLEY, J.D.; BRADFORD, K.J.; HILHORST, H.W.M.; NONOGAKI, H. *Seeds: physiology of development, germination and dormancy*. 3rd ed. New York: Springer, 2013. 392p.
- BRAY, E.A. Genes commonly regulated by water-deficit stress in *Arabidopsis thaliana*. *Journal of Experimental Botany*, v.55, n.407, p.2331-2341, 2004. <https://europepmc.org/article/med/15448178>
- CARDOSO, V.J.M. Metodologia para análise da dependência térmica da germinação pelo modelo de graus-dia. *Oecologia Australis*, v.15, n.2, p.236-248, 2011. <https://revistas.ufrj.br/index.php/oa/article/view/8126/6583>
- CHEN, K.; ARORA, R. Priming memory invokes seed stress-tolerance. *Environmental and Experimental Botany*, v.94, n.1, p.33-45, 2013. <https://doi.org/10.1016/j.envexpbot.2012.03.005>
- CLIMATE DATA. *Dados climáticos para cidades mundiais*. Available on: <https://pt.climate-data.org/>. Accessed on April 28th, 2020.
- CONTRERAS-QUIROZ, M.; PANDO-MORENO, M.; JURADO, E.; FLORES, J.; BAUK, K.; GURVICH, D.E. Is seed hydration memory dependent on climate? Testing this hypothesis with Mexican and Argentinian cacti species. *Journal of Arid Environments*, v.130, n.1, p.94-97, 2016. <https://doi.org/10.1016/j.jaridenv.2016.03.001>
- COVELL, S.; ELLIS, R.H.; ROBERTS, E.H.; SUMMERFIELD, R.J. The influence of temperature on seed germination rate in grain legumes: I. A comparison of chickpea, lentil, soyabean and cowpea at constant temperatures. *Journal of Experimental Botany*, v.37, n.5, p.705-715, 1986. <https://doi.org/10.1093/jxb/37.5.705>

- DAIBES, L.F.; CARDOSO, V.J.M. Effect of reduced water potential on seed germination of a forest tree: a hydrotime approach. *Journal of Seed Science*, v.42, e202042003, 2020. <https://doi.org/10.1590/2317-1545v42224519>
- DANTAS, B.F.; MOURA, M.S.B.; PELACANI, C.R.; ANGELOTTI, F.; TAURA, T.A.; OLIVEIRA, G.M.; BISPO, J.S.; MATIAS, J.R.; SILVA, F.F.S.; PRITCHARD, H.W.; SEAL, C.E. Rainfall, not soil temperature, will limit the seed germination of dry forest species with climate change. *Oecologia*, v.192, n.1, p.529-541, 2020. <https://doi.org/10.1007/s00442-019-04575-x>
- DUBROVSKY, J.G. Seed hydration memory in Sonoran Desert cacti and its ecological implication. *American Journal of Botany*, v.83, n.5, p.624-632, 1996. <https://doi.org/10.1002/j.1537-2197.1996.tb12748.x>
- FAROOQ, M.; BASRA, S.M.A.; AHMAD, N.; HAFEEZ, K. Thermal hardening: a new seed vigor enhancement tool in rice. *Journal of Integrative Plant Biology*, v.47, n.2, p.187-193, 2005. <https://doi.org/10.1111/j.1744-7909.2005.00031.x>
- GOMES, S.E.V.; OLIVEIRA, G.M.; ARAÚJO, M.N.; SEAL, C.E.; DANTAS, B.F. Influence of current and future climate on the seed germination of *Cenostigma microphyllum* (Mart. ex G. Don) E. Gagnon and G.P. Lewis. *Folia Geobotanica*, v.54, n.1, p.19-28, 2019. <https://doi.org/10.1007/s12224-019-09353-4>
- HARDEGREE, S.P. Predicting germination response to temperature. I. Cardinal temperature models and subpopulation-specific regression. *Annals of Botany*, v.97, n.6, p.1115-1125, 2006. <https://doi.org/10.1093/aob/mcl071>
- IPCC. *Climate Change 2014: synthesis report*. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change (ed. Core Writing Team, R.K. Pachauri, L.A. Meyer). Geneva: IPCC, 2014. 151p. https://www.ipcc.ch/site/assets/uploads/2018/05/SYR_AR5_FINAL_full_wcover.pdf
- JELLER, H.; PEREZ, S.C.J.G.A. Condicionamento osmótico na germinação de sementes de cássia-do-nordeste sob estresse hídrico, térmico e salino. *Pesquisa Agropecuária Brasileira*, v.38, n.9, p.1025-1034, 2003. <https://doi.org/10.1590/S0100-204X2003000900002>
- LIMA, A.T.; CUNHA, P.H.J.; DANTAS, B.F.; MEIADO, M.V. Does discontinuous hydration of *Senna spectabilis* (DC.) H.S. Irwin and Barneby var. *excelsa* (Schrad.) H.S. Irwin and Barneby (*Fabaceae*) seeds confer tolerance to water stress during seed germination? *Journal of Seed Science*, v.40, n.1, p.36-43, 2018. <http://dx.doi.org/10.1590/2317-1545v40n1182838>
- LIMA, A.T.; MEIADO, M.V. Discontinuous hydration alters seed germination under stress of two populations of cactus that occur in different ecosystems in Northeast Brazil. *Seed Science Research*, v.27, n.4, p.292-302, 2017. <https://doi.org/10.1017/S0960258517000241>
- LIMA, A.T.; MEIADO, M.V. Effect of hydration and dehydration cycles on *Mimosa tenuiflora* seeds during germination and initial development. *South African Journal of Botany*, v.116, n.5, p.164-167, 2018a. <https://doi.org/10.1016/j.sajb.2018.03.017>
- LIMA, A.T.; MEIADO, M.V. Effects of seed hydration memory on initial growth under water deficit of cactus from two populations that occur in different ecosystems in Northeast Brazil. *Plant Species Biology*, v.33, n.4, p.268-275, 2018b. <https://doi.org/10.1111/1442-1984.12219>
- MARENGO, J.A. O futuro clima do Brasil. *Revista USP*, v.103, n.1, p.25-32, 2014. <https://doi.org/10.11606/issn.2316-9036.v0i103p25-32>
- MARENGO, J.A.; TORRES, R.R.; ALVES, L.M. Drought in Northeast Brazil – past, present, and future. *Theoretical and Applied Climatology*, v.129, n.1, p.1189-1200, 2017. <https://doi.org/10.1007/s00704-016-1840-8>
- MARQUES, F.R.F.; MEIADO, M.V.; CASTRO, N.M.C.R.; CAMPOS, M.L.O.; MENDES, K.R.; SANTOS, O.O.; POMPELLI, M.F. GerminaQuant: a new tool for germination measurements. *Journal of Seed Science*, v.37, n.3, p.248-255, 2015. <http://dx.doi.org/10.1590/2317-1545v37n3145605>
- MATIAS, J.R.; RIBEIRO, R.C.; ARAGÃO, C.A.; ARAÚJO, G.G.L.; DANTAS, B.F. Physiological changes in osmo and hydroprimed cucumber seeds germinated in biosaline water. *Journal of Seed Science*, v.37, n.1, p.7-15, 2015. <https://doi.org/10.1590/2317-1545v37n1135472>
- MEIADO, M.V.; ROJAS-ARÉCHIGA, M.; SIQUEIRA-FILHO, J.A.; LEAL, I.R. Effects of light and temperature on seed germination of cacti of Brazilian ecosystems. *Plant Species Biology*, v.31, n.2, p.87-97, 2016. <http://dx.doi.org/10.1111/1442-1984.12087>

MEIADO, M.V.; SILVA, F.F.S.; BARBOSA, D.C.A.; SIQUEIRA-FILHO, J.A. Diaspore of the Caatinga: a review. In: SIQUEIRA-FILHO, J.A. (org.). Flora of the Caatingas of the São Francisco River: natural history and conservation. Rio de Janeiro: *Andrea Jakobsson Estúdio Editorial*, 2012. p.306-365.

MENDONÇA, A.V.R.; COELHO, E.A.; SOUZA, N.A.; BALBINO, E.; SILVA, R.F.; BARROSO, D.G. Efeito da hidratação e do condicionamento osmótico em sementes de pau-formiga. *Revista Brasileira de Sementes*, v.27, n.2, p.111-116, 2005. <https://doi.org/10.1590/S0101-31222005000200016>

NAKAO, E.A.; CARDOSO, V.J.M. Priming e temperaturas limites de germinação de unidades de dispersão de *Urochloa brizantha* (Stapf) Webster cv. *basilisco*. *Brazilian Journal of Biology*, v.75, n.1, p. 234-241, 2015. <http://dx.doi.org/10.1590/1519-6984.13812>

NASCIMENTO, J.P.B.; SIQUEIRA-FILHO, J.A.; MEIADO, M.V. Seed germination of three endangered subspecies of *Discocactus* Pfeiff. (Cactaceae) in response to environmental factors. *Journal of Seed Science*, v.40, n.3, p.253-262, 2018. <http://dx.doi.org/10.1590/2317-1545v40n3183036>

OLIVEIRA, G.M.; MATIAS, J.R.; DANTAS, B.F. Temperatura ótima para germinação de sementes nativas da Caatinga. *Informativo ABRATES*, v.24, n.3, p.44-47, 2014. https://www.abrates.org.br/img/informations/d199fc2d-1279-4f13-98e2-77622f4163b3_IA_v24_n3.pdf

OLIVEIRA, G.M.; SILVA, F.F.S.; ARAUJO, M.N.; COSTA, D.C.C.; GOMES, S.E.V.; MATIAS, J.R.; ANGELOTTI, F.; CRUZ, C.R.P.; SEAL, C.E.; DANTAS, B.F. Environmental stress, future climate, and germination of *Myracrodruon urundeuva* seeds. *Journal of Seed Science*, v.41, n.1, p.32-43, 2019. <http://dx.doi.org/10.1590/2317-1545v41n1191945>

QUEIROZ, L.P. Leguminosas da Caatinga. Feira de Santana: *Universidade Estadual de Feira de Santana*, 2009. 443p.

RAMOS, M.G.C.; CRISOSTOMO, N.M.S.; SILVA, C.L.; BERTO, T.S.; COSTA, E.A.; MELO-JUNIOR, J.L.A.; MELO, L.D.F.A. Efeito da luz e temperatura na germinação de sementes de *Enterolobium contortisiliquum* (Vell.). *Ciência Agrícola*, v.16, p.59-63, 2018. <https://pdfs.semanticscholar.org/b94d/883cef2bc426af36ce74aa1a9215c07ef812.pdf>

STATSOFT. *Statistica 13.0*. StatSoft South America, 2020. Available on: <http://www.statsoft.com.br>. Accessed on April, 28th, 2020.

