ABRATES

Journal of Seed Science
ISSN 2317-1545
www.abrates.org.br/revista

ARTICLE

Journal of Seed Science, v.45, e202345013, 2023

http://dx.doi.org/10.1590/2317-1545v45264166

Climate and seed size of a dry forest species: influence on seed production, physiological quality, and tolerance to abiotic stresses

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ABSTRACT: Seed production, quality and germination are likely to be affected by a drastic climate change in semi-arid areas predicted for the end of the century. We evaluated *Anadenanthera colubrina* var. *cebil* (Griseb.) Altschu (Fabaceae) seeds of different sizes, populations and harvest years for germination and tolerance to environmental stresses aiming to predict impacts of future climate. Seeds were accessed for germination temperature, salinity and osmotic limits and requirements. Germination of large and small seeds harvested in different populations was evaluated in optimum and stressful temperature, salinity and water deficit. A glasshouse pot assay tested weekly irrigation regimes and seedlings emergence and growth. Optimal temperature for seeds germination was 34.8 °C and limits were 5.6 °C and 50.9 °C. Large and small-sized seeds do not differ in germination, however small seeds are more efficient in stressful conditions. Seedlings can emerge and grow under small weekly irrigation for four months. The predicted increase in temperature will not impair germination, however, the time available for seedling establishment will decrease due to lacking rainfall. The increase in the amount of small-sized seeds produced in drought years is a strategy for coping with harsh environments, rather than a decrease in seed quality.

Index terms: climate change, environmental stress, germination, heat sum, irrigation.

RESUMO: A produção, qualidade e germinação das sementes poderão ser afetadas por uma drástica mudança climática das áreas semiáridas previstas para o final do século. Objetivando prever impactos do clima futuro, avaliamos as sementes de angico de diferentes tamanhos, locais/anos de coleta quanto a germinação e tolerância a estresses ambientais. As sementes foram avaliadas quanto aos limites de temperatura, salinidade e potencial osmótico para germinação. A germinação de sementes grandes e pequenas colhidas em diferentes populações foi avaliada em condições ótimas e de estresse térmico, salino ou osmótico. Em casa de vegetação testamos o efeito de regimes/lâminas de irrigação na emergência e crescimento de plântulas. A temperatura ótima para germinação das sementes foi de 34,8 °C e os limites foram 5,6 - 50,9 °C. Sementes grandes e pequenas não diferiram na germinação, mas as pequenas foram mais eficientes em condições de estresse. As mudas emergiram e desenvolveram-se com pouca irrigação semanal durante quatro meses. O aumento previsto da temperatura não prejudicará a germinação, porém, a indisponibilidade hídrica sim. O aumento da quantidade de sementes pequenas produzidas em anos de seca é uma estratégia para lidar com ambientes hostis, não uma diminuição na qualidade das sementes.

Termos para indexação: mudanças climáticas, estresse ambiental, germinação, soma térmica, irrigação.

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Received: 05/19/2022.
Accepted: 12/12/2022.

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INTRODUCTION

Environmental conditions can affect plant growth and metabolism in several ways. Harsh weather conditions can affect seed reserve accumulation and development (size, weight and density) compromising the entire seed production process (Larios et al., 2014). During the seed production and maturation season, there may be variations in seed size and seed physiological quality, since they are characteristics directly influenced by climate, soil fertility, seed maturity and sanity (Marcos-Filho, 2016).

The intensification of deforestation and air pollution has caused significant changes in the climate, due to the accelerated increase in greenhouse gases concentration causing elevation of air temperature, severe droughts and extreme water deficits, due to low precipitation and high evapotranspiration (IPCC, 2014). Regarding a pessimistic future change (increasing temperature and decreasing and stochastic rainfall), the tropical dry forest at northeastern Brazil, named Caatinga can suffer a direct impact on plant distribution, due to increased temperatures, water unavailability and soil salinity (Kelly et al., 2008). However, its native species have physiological adaptations to stressful climatic conditions, such as deciduousness, thorns and decreased leaf size, and highly adapted seeds, which are tolerant to environmental stresses (Dantas et al., 2014; Gomes et al., 2019; Oliveira et al., 2019; Dantas et al., 2020).

For most species, seed size is indicative of physiological quality. Seeds with smaller size, show less germination and vigor in relation to medium and large (Domic et al., 2020). With the decrease and erratic distribution of rainfall observed since 2010 in the Brazilian semiarid and with severe deficits in precipitation as of 2012 (Marengo et al., 2016), the size heterogeneity of seeds of *Anadenanthera colubrina* var. cebil (Griseb.) Altschu (Fabaceae) increased in harvests between 2010 and 2017 (Bispo et al., 2017). The objective of this research was to evaluate the effect of climate on *A. colubrina* seeds (production and germination) and their vulnerability to climate change. Specifically, we aimed to correlate the effect of climate during seed production with the seed size and physiological quality; understand seeds tolerance limits to abiotic stresses and predict the impacts of different future climate scenarios on germination.

MATERIAL AND METHODS

Seeds harvest and climate data

Seeds of *A. colubrina* were harvested in August and September of 2013 and 2017 at Jutaí, Lagoa Grande (40° 12’ 33” W, 8° 34’ 02” S) and of 2014, 2015, 2016 and 2017 at Uruás, Petrolina (40° 28’ 18” W, 9° 06’ 18” S), both at Pernambuco State - Brazil. Brown colored pods at maturation stage were harvested directly from the same 13 randomly selected mother-trees within the same population in each collection site and year. Soon after harvest, processed intact seeds were packed in cloth bags and kept in a cold chamber at 10 °C ± 3 °C and 40% ± 10% relative humidity, for 180 days, until germination tests were performed. Seeds had no change between initial and six months stored seeds in germination percentage and speed was observed in this storage condition (Pinho et al., 2009).

Climate data (2014 to 2017) were collected at the Bebedouro Automatic Agrometeorological Station of Embrapa Semi-arid (W 40 ° 22 ‘S 09 ° 09’), which is no more than 50 km from seed harvest sites. Temperature data obtained were average (Tav), minimum (Tmin) and maximum temperatures (Tmax); number of days with Tav > 30 °C; number of days with Tav > 35 °C; number of days Tmin > 20 °C; number of days Tmin > 24 °C; number of days Tmax > 35 °C and number of days Tmax > 40 °C. Also, annual rainfall (AR); harvest precipitation (PH); precipitation of the rainy season (PErs), precipitation of the dry season (PEds) and number of days with precipitation greater than 17.5 and 20 mm (p > 17.5 and 20 mm) were acessed.

Climate influence on seed quality and size

Seeds harvested at Uruás, Petrolina-PE from 2014 to 2017, showed visual variation in seeds size along the years, thus, data were collected on the physiological quality of the seeds of this population, such as germination percentage, average seed weight of each lot and weight of 100 seeds (W100) (Brasil, 2009).

From 100 g of each seed lot that presented a variation in size, seeds were separated in subsamples regarding their diameter (Ø) as small (Ø ≤ 1.10 cm) and large (Ø > 1.10 cm), with the aid of a millimeter rule. The percentage of small seeds (PSS) was obtained by dividing the weight of the small seeds subsample by the total weight of the main sample (100 g).

Physiological quality of the seeds was evaluated by the final percentage of germinated seeds after 10 days (Brasil, 2013). The seeds physical and physiological characteristics were correlated with the climate data. Linear correlation and principal component analysis were analyzed using the PAST program version 3.07 (Hammer et al., 2001).

Seed germination at different environmental conditions

The experimental design for each germination experiment was completely randomized with four replications of 25 seeds for each of the three assays performed. Before the germination experiments, processed seeds were immersed in 100ml of water with three drops of neutral detergent for five minutes. Then, seeds were treated with 4 $g.kg^{-1}$ of fungicide thiram. *S*eeds were sowed on two paper towels (Germitest®) moistened with distilled water or solutions (NaCl or PEG 6000), in a proportion of 2.5 times the dry paper weight. The paper rolls containing the seeds were maintained during 10 days in a Biochemical Oxygen Demand germination chamber (BOD), with a photoperiod of 12 hours (Brasil, 2013) and at different conditions according to experiments described below. Seeds were considered germinated when the length of the emerged radicle was ≥ 1 mm.

Seed germination at different temperatures: To evaluate the effect of temperature on *A. colubrina* seed germination, germitest paper moistened with distilled water was used as substrate. The paper rolls containing the seeds were maintained in a BOD at constant temperatures of 5 to 50 °C, with 5 °C increases.

Seed germination in different osmotic potentials: To assess water stress, germitest paper was moistened with pure distilled water (0 MPa) and polyethylene glycol 6000 (PEG 6000) solutions at osmotic potentials (Ψ) corresponding to -0.2; -0.4; -0.6; -0.7; -0.8; -1.1 and - 1.2 MPa (Villela et al., 1991). The paper rolls containing the seeds were incubated in a BOD at 25 °C, previously defined as the optimum temperature for the germination of the species (Brasil, 2013).

Seed germination in different salinity levels: To evaluate salinity effects on seeds, NaCl aqueous solutions with Ψ -0.16; -0.40; -0.56; -0.72; -0.84; -1.08; -1.2; -1.28; -1.36 MPa (Dantas et al., 2014) moistened the paper substrate. The paper rolls containing the seeds were incubated in a BOD germination chamber at 25 °C.

Obtaining thermal and osmotic water limits and requirements

The three assays described previously provided the data used to obtain the thermal and water limits and requirements of *A. colubrina* seeds were harvested in 2013 at Jutaí, Lagora Grande -PE. The limits found were used as parameters to evaluate the effect of combined stresses in seeds of different sizes and populations harvested in 2017.

For each temperature, cumulative germination was plotted as a function of time and a Boltzman sigmoidal curve fitted, from which the time to achieve 50% germination (t_{50}) of the seed population was estimated (Farias and Dantas, 2022). The reciprocal of these t_{50} (germination rate, GR= $1/t_{50}$) were plotted against temperature and the sub- and supra-optimal germination temperature ranges were identified (Covell et al., 1986). Linear regressions of both sets of data in each germination fraction were used to estimate the x-intercept and slope of each regression line. Base temperature (T_b) for germination was estimated as the x-intercept from the dependency of germination rate on temperature in the sub-optimal range. It is assumed that seed germination does not progress below T_b. A similar thermal-germination rate analysis in the supra-optimal range identified the ceiling temperature (T_c), above which there is no germination. Optimum temperature (T_o) was calculated as the intercept of sub- and supra-optimal temperature range curves (Covell et al., 1986). The thermal time of the population that germinated at sub-optimal temperatures (θTsub) and that of the population that germinated at supra-optimal temperatures (θTsupra) were calculated according to Covell et al. (1986). Hydrotime (using data obtained in assay for seed germination in different osmotic potentials) and halotime (using data obtained in assay for seed germination in different salinity levels) models were obtained in the same manner (Seal et al., 2018; Dantas et al., 2020).

Germination of seeds of different sizes and populations in environmental stresses

After obtaining the data of thermal and water limits and requirements, seed of different sizes were submitted to three germination experiments in optimum conditions, conditions around thermal (Tb and Tc) or osmotic (ψb) limits and also in conditions that reduced GR in 50%. The experimental design for each experiment was completely randomized with four replications of 25 seeds.

The seeds used in these assays were harvested in 2017, from two harvest sites (Jutaí and Uruás) and classified regarding their diameter (Ø) as small (Ø ≤ 1.10 cm) and large (Ø > 1.10 cm).

Three different assays were performed with a 2 x 2 x 3 factorial scheme , with seed harvested from two sites/ populations (Uruás and Jutaí), two sizes (small and large) and three constant temperatures (15, 30 and 40 ° C) in temperature assay; or three osmotic potentials (0, -0.4, -0.8 MPa), using solutions of PEG 6000 in osmotic potential assay; or three osmotic potentials 0, -0.648, -0.972 MPa (corresponding to EC 18 $dS.m^{-1}$ and 27 $dS.m^{-1}$, respectively) in salinity assay.

Emergence and development of seedlings in irrigation regimes

In order to validate previous results, this experiment was conducted in a greenhouse with average temperature of 35.4 ± 3 °C and an average relative humidity of 32.7 ± 6%. Seeds were sown in 18.5 cm diameter plastic pots filled with 5 liters of sand + native loamy soil (1: 1). Ten seeds were sown at 3 cm depth in each pot and then thinned to 5 seedlings after germination. The experimental design was completely randomized, and the double factorial scheme was 3 x 2, with three water volumes equivalent to the weekly precipitation of 10; 17.5 and 25 mm, applied once a week or divided into three weekly irrigations.

Emerged seedlings were evaluated daily, for 10 days the final percentage of emergence (E%) was calculated. At the end of 98 days (14 weeks) five plants of each replication were evaluated for shoot and root length (SL and RL, cm, respectively), shoot and dry biomass (SDB and RDB, g).

The data obtained in all assays were verified for normality and homogeneity by the Shapiro-Wilk and Levene tests, respectively. If the non-transformed data or transformed into arcosene data were normal and homogeneous, they were interpreted by means of an analysis of variance (ANOVA) and the means compared by the Tukey test at a significance level of 5% by the SISVAR program. If not, the data were analyzed using the Kruskal-Wallis non-parametric test, with a probability level of 0.05.

Seed germination prediction for current and future climate

In order to predict germination events of *A. colubrina* seeds during the year and in different scenarios climate change, available historical climate data (1970 a 2018) and the future climate scenarios (IPCC, 2014) were used to calculate the environmental heat sum (Heat sum = (Tm-Tb)⁄t °Cd) required by the species (Orrù et al., 2012) and to predict seed germination, based on the limits and requirements for germination (Tb, Tc, To, θT, ψb, θH) . By 2100, in a RCP 2.6 future climate scenario, average temperature is expected to increase up to 1°C and in a RCP 8.5 scenario, it is predicted a temperature increase of 3.5 ° C and precipitation decrease of 40% (PBMC, 2013).

RESULTS AND DISCUSSION

During seed production, environment affects the dynamics of seed filling and desiccation. When in limited environmental resources or at high competition, maturation can occur prematurely, thus producing large seeds has a high cost for plants (Larios et al., 2014).

Based on the 12 evaluated variables, the PCA revealed some clear trends. The first two principal components (PCs), which represent linear combinations of variables that are often highly correlated (Figure 1) with each other accounted for 94.9% of the variation in the dataset (Figure 2). At PC1 (first principal component), the main variables that explained the formation of the seed lots with positive auto-vector were G%, seed size, most temperature variables (Tmax, Tmin, Tmin > 20 °C) and P> 17.5 mm. In this same axis with negative auto-vector was Tmax > 40 °C and PErs. For PC2 the main variables were seed weight W100 and most precipitation variables (PH, PErs, P > 20 mm) (Figure 2). According to PCA, the 2014 harvest was affected mostly by number of days with Tmax > 40 °C. Precipitation contributed most to the formation of the seeds of the 2015 and 2016 harvests, which also affected the weight of seeds (W100) and germination. The high percentage of small seeds of the 2017 harvest (Table 1) was mainly affected by high Tmax and Tmin (Figures 1 and 2).

Drought can result in faster seed development, including faster decline in seed moisture content, an earlier end to seed filling, reduced number of seeds per fruit, and reduced seed size and weight (Rahman and Ellis, 2019). Combining drought with high temperature usually results in greater reduction in seed dry weight than each stress alone (Rahman and Ellis, 2019). The variations in rainfall and the high temperatures observed in the Brazilian semiarid since 2012 have caused serious water deficits (Marengo et al., 2016), and this affected the production of seeds of *A. colubrina.* Seeds harvested in August 2017 showed a large number of small seeds, as this year there was an increase in maximum and minimum temperatures, a greater number of days with rains below 17.5 mm, on the other hand seeds harvested 2014 were large, but showed low germination due to a high number of days with high temperatures (Table 1 and Figure 2).

Brazilian topical dry forest species have a wide temperature range for germination. These are shown to be adapted to temperature fluctuations, with an optimum range of 20 to 35 °C, and the ceiling temperature above 40 °C (Gomes et al., 2019; Oliveira et al., 2019; Dantas et al., 2020). *Anadenanthera colubrina* seeds germinated in a wide range of temperatures (5 to 45 °C), with a high percentage of germination (70-80%) at temperatures of 20 to 35 °C, while at 10, 15 and 40 °C germination remained between 70% and 30% (Table 2 and Figure 3). These demonstrated a germinative capacity to occur at any time of the year, in milder temperatures or in hotter seasons and enabled a wide distribution of the species in South American drylands (Mogni et al., 2015).

The temperature usually indicated for evaluating the germination of *A. colubrina* seeds is 25 °C (Brasil, 2013), based on work carried out on seeds from regions with milder temperatures than the temperatures occurring in the Brazilian semiarid region. However, the optimum temperature (To) for germination of the lots of seeds of *A. colubrina*

Table 1. Seed traits and climate data (rainfall and temperature) collected from Bebedouro Automatic Agrometeorological Station of Embrapa Semi-arid.

Harvest (year)	W100 (g)	PSS (%)	G (%)	------------------ Rainfall (mm) ----------------			
				AR	PH	PErs	PEds
2014	13.85	0	22	347.8	261	239	16.5
2015	14.08	22.72	86	216.3	373	276	56
2016	14.74	15.31	95.5	270	338	326	9
2017	11.23	46.98	88.5	391	209	168.5	7.5
	P> 17.5 mm	P> 20 mm	Tav (°C)	Tmax (°C)	Tmin (°C)	Tav > 30 °C	Tmax > 40 °C	Tmin > 20 °C
2014	1	2	24.9	30.5	19.8	2	29	0
2015	4	4	25.5	31.2	20.6	3	0	230
2016	4	4	27.1	33.3	21.2	35	0	227
2017	3	1	27.4	33.7	21.6	27	0	266

Variables are weight of 100 seeds (W100), percentage of small seeds (PSS), percentage of germinated seeds (G%), temperature minimum (Tmin) and maximum (Tmax), number of days with Tmin> 20 °C and Tmax > 40 °C. Harvest precipitation (PH); precipitation of the rainy season (PErs), precipitation of the dry season (PEds) and number of days with precipitation greater than 17.5 and 20 mm (p > 17.5 and 20 mm).

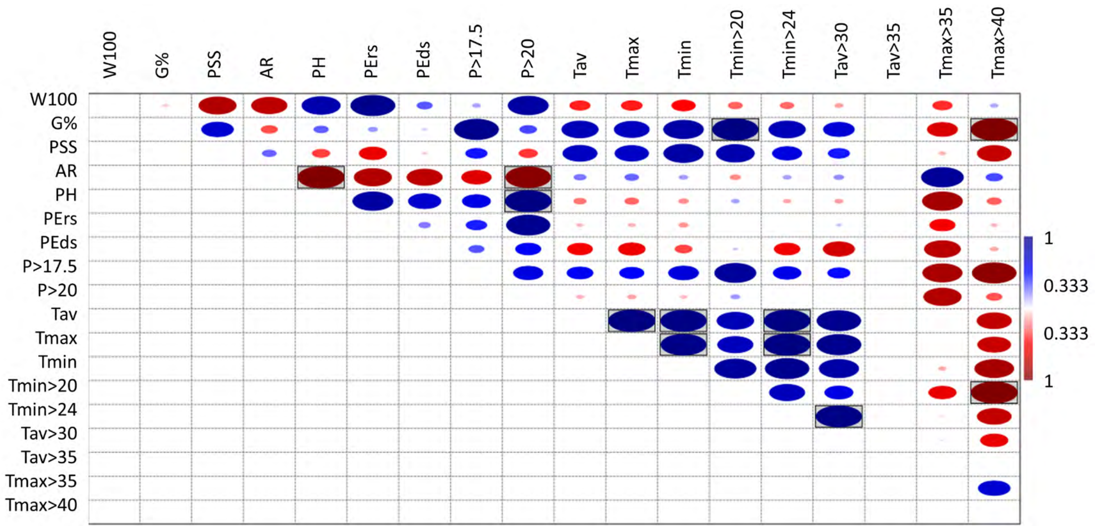

Figure 1. Linear correlation between seed traits and rainfall and temperature data. Variables were weight of 100 seeds (W100); percentage of germinated seeds (G%); percentage of small seeds (SS); annual rainfall (AR); precipitation harvest to harvest (PH); precipitation of the rainy season (PR), precipitation of the dry season (PD); number of days with precipitation greater than 17.5 and 20 mm (D17 and D20); average temperature (Tav); maximum temperature (Tmax); minimum temperature (Tmin); number of days with Tav> 30 and 35 °C (AV30 and AV35); days with Tmin> 20 and 24 °C (MIN20 and MIN24) and days with Tmax > 35 and 40 °C (MAX35 and MAX40). Blue ellipses mean positive correlation; red ellipses mean negative correlation; size of the ellipses means correlation intensity; rectangles mean significant correlation at the 5% probability level.

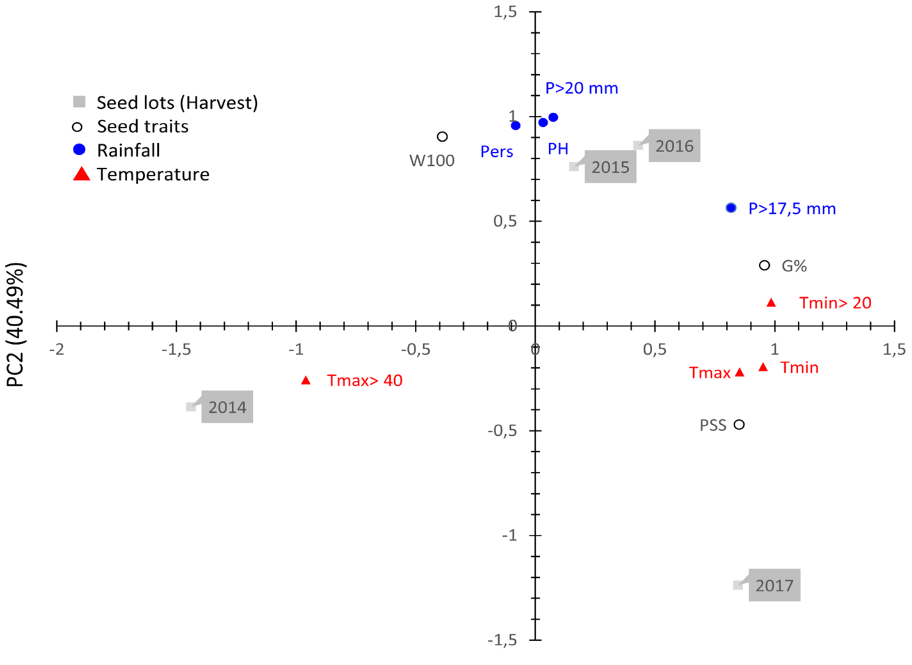

Figure 2. Biplot showing the projection of the variables of the first two principal components with distinction in seed traits, rainfall and temperature data in the four harvests (2014-2017) evaluated. Variables were weight of 100 seeds (W100), percentage of small seeds (PSS), percentage of germinated seeds (G%), temperature minimum (Tmin) and maximum (Tmax), number of days with Tmin> 20 ºC and Tmax > 40 ºC. Harvest precipitation (PH); precipitation of the rainy season (PErs) and number of days with precipitation greater than 17.5 and 20 mm (P> 17.5 and 20 mm).

Table 2. Germination (%), germination speed (GS) of small and large *Anadenanthera colubrina* seeds from different harvest sites, submitted to different temperatures and osmotic potentials prepared with polyethylene glycol (PEG) 6000 and sodium chloride (NaCl).

		Harvest Sites			
Size	Temperature (°C)	Jutaí		Uruás	
		Germination (%)			
S	15	94 aA		93 aA*	
	30	94 aA		97 aA	
	40	94 aA		82 bB	
L	15	99 aA		74 bB*	
	30	97 aA		94 aA	
	40	86 bA		86 aA	
		CV(%) = 6.77; W = 0.129^{ns} ; F = 5.067^{*}			
		Harvest Sites		Harvest Sites	
Size	ΨPEG (MPa)	Jutaí	Uruás	Jutaí	Uruás
		Germination (%)		Germination speed ($days^{-1}$)	
S	0	98 a	92 a	0.44 a	0.88 a
	-0.4	39 ab	48 b	0.24 ab	0.37 ab
L	0	97 a	92 a	0.40 ab	0.62 ab
	-0.4	5 b	55 ab	0.13 b	0.29 b
		CV(%) = 25.52; W = 0.0^{*}; F= 5.494^{*}		CV(%) = 25.97; W = 0.003^{*}; F = 5.399^{*}	
		Harvest Sites		Harvest Sites	
Size	ΨNaCl (MPa)	Jutaí		Uruás	
		Germination (%)			
S	0	94 a		97 a	
	-0.65	75 ab		80 ab	
	-0.97	60 ab		49 b	
L	0	97 a		94 ab	
	-0.65	66 ab		71 ab	
	-0.97	12 b		55 b	
		CV(%) = 25.52; W = 0.001^{*}; F = 3.520^{*}			

Averages followed by the same lower letter case in columns and upper case in rows do not differ by Tukey's test at 5%. *Comparing the different seed sizes, only the averages followed by an asterisk differ from each other by the Tukey test at 5%. Averages followed by the same letter, lower case in the columns, do not differ by the Kruskal-Wallis test at 5%. CV(%): coefficient of variation;W; F: statistics of Shapiro-Wilk and Levene's test respectively indicate residue with normal distribution and variance. * = significant at 5%, ^{ns}= not significant.

harvested at the Caatinga areas for this work was 34.8 °C. The base temperature (Tb), below which germination does not occur, was 5.6 °C and the ceiling temperature (Tc), above which seeds fail to germinate, was 50.9 °C. The thermal time obtained for supra-optimal temperatures (θsupra = 154.1 hours) was less than that obtained for sub-optimal temperatures (θsub = 280.1 hours) (Figure 3). In this work, seed size influenced germination only at 15 °C where small seeds from Uruás had higher germination than the large ones. Provenance of seeds influenced germination at extreme temperatures, in which at 15 °C for large seeds and at 40 °C for small seeds from Jutaí obtained the higher percentages (Table 2).

Seed vigor and seedling development and establishment are positively correlated to larger seeds (Domic et al., 2020), in many cases germination at optimum temperature range is not affected by seeds size (Bispo et al., 2017; Leão-Araújo et al., 2020). On the other hand, since stress may have transgenerational effects on seeds and seedlings, resulting in stress-induced improvement of seed endurance due to inter-generational stress memory, formed by stress-induced changes in the epigenome of the seedling (Hatzig et al., 2018).

There is a critical osmotic potential (Ψ) threshold below which germination does not occur for each species (Tribouillois et al., 2016). Germination was ≥ 40% at the osmotic potentials from 0 to -0.4 MPa and ≤ 40% at -0.6 to -1.2 MPa. Hydrotime (θH), the time that the seed needs to germinate under water deficit conditions, was 28 hours. The base water potential reached (ψb) in PEG 6000 was -1.2 MPa, thus showing good tolerance to water restriction (Figure 4A). This result may differ in seeds produced in different habitats or climate conditions. Studies with other species native to the Caatinga, such as *Cenostigma pyramidale* (Tul.) E. Gagnon & G.P. Lewis (syn. *Caesalpinia pyramidalis, Poincianella pyramidalis)*, Astronium *urundeuva* (M.Allemão) Engl. (syn. *Myracrodruon urundeuva*) and *A. colubrina* presented similar results in relation to water restriction (Santos et al., 2016; Gomes et al., 2019; Oliveira et al., 2019; Dantas et al., 2020). In different sized-seeds germination percentage in distilled water was higher than 90%, regardless of the size and provenance of the seeds. The percentage and speed of seed germination were reduced with the decrease of the osmotic potential (of PEG 6000 and NaCl solutions) for all sizes and provenances (Table 2). Small seeds showed higher germinated percentage and speed than large seeds when submitted to -0.4 MPa of PEG 6000 solutions.

Maternal environmental effects can alter seed fitness, size, mass and even tolerance to environmental stresses occurring in subsequent generation (Jacobs and Lesmeister, 2012). Thus, the large seeds collected at Uruás showed

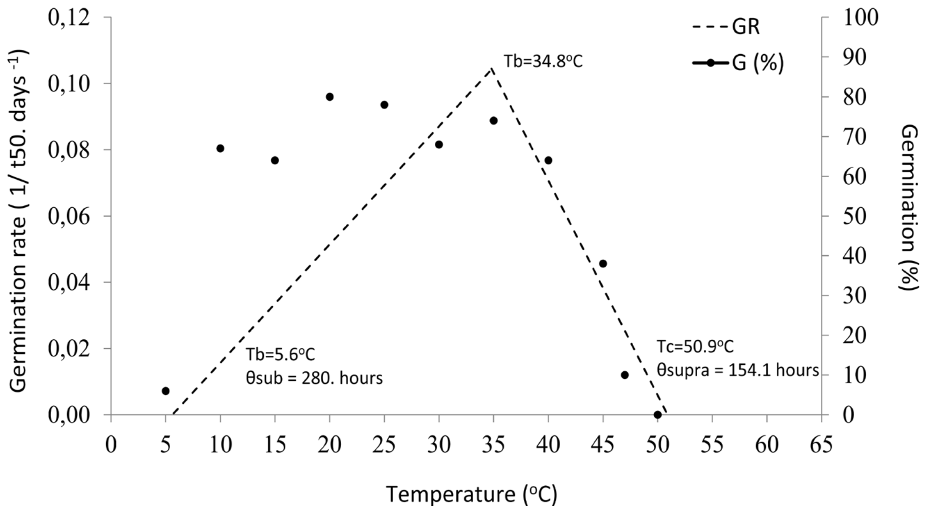

Figure 3. Germination rate (GR), thermal limits and requirements of *Anadenanthera colubrina* harvested in 2013 and subjected to different temperatures. Tb and Tc correspond to base and ceiling temperatures for germination, respectively (the point on which the regression curves intercept the x-axis); To is the optimum temperature; Θsub and Θsupra correspond respectively to the thermal time of the sub- and supra-optimum temperature ranges, obtained by the reciprocal function of the regression curve angle.

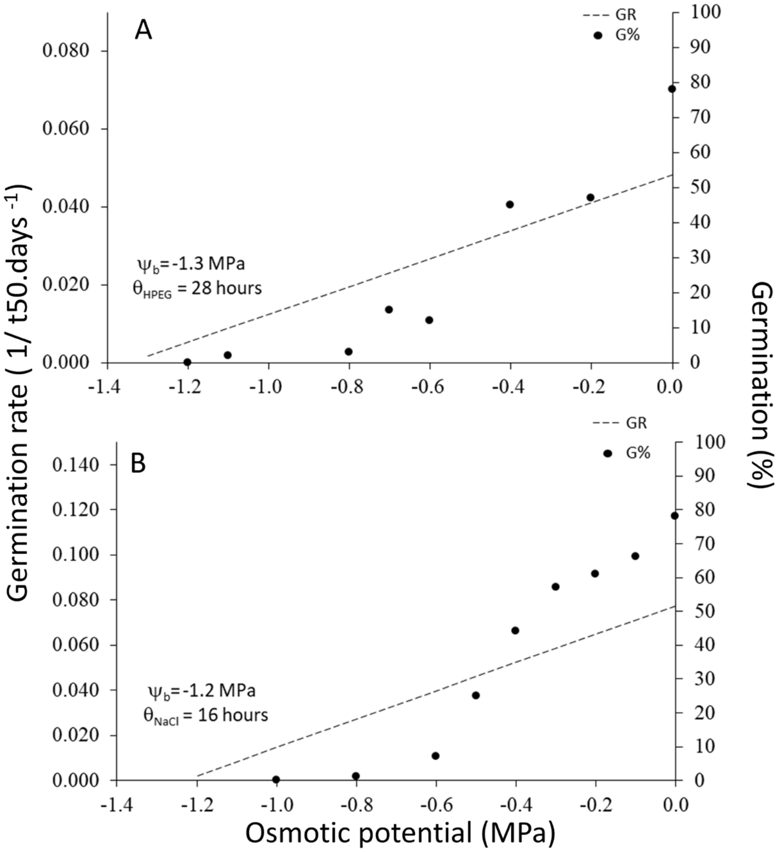

Figure 4. Germination rate (GR), osmotic limits and requirements of *Anadenanthera colubrina* harvested in 2013 and subjected to different osmotic potentials produced from PEG 6000 (A) or NaCl (B) solutions. Ψb corresponds to the osmotic base potential for germination (the point on which the regression curves intercept the x-axis); ΘHPEG corresponds to the hydrotime and θHalo corresponds to the halotime, both obtained by the reciprocal function of the regression curve angle.

higher germination (55%) at -0.4 MPa than those from Jutaí (5%). The germination speed was higher in the seeds from Jutaí than those from Uruás in all osmotic potentials and sizes (Table 2). Although the base osmotic potential (ψb) of 2013 harvested *A. colubrina* seeds was found to be -1.3 MPa (Figure 4A), there was no germination of 2017 harvested seeds at -0.8 MPa, for any provenance nor size (Table 2).

The germinative response to the saline soils, with EC > 4 $dS.m^{-1}$, is specific and this is associated with environmental factors such as temperature and water availability (Gomes et al., 2019). The dryland specialist *A. colubrina* is adapted to the Caatinga soils, which are salinized both by the weathering of rocks and by the rise of brackish groundwater through evaporation (Pedrotti et al., 2015). Under salinity conditions, the base osmotic potential (ψb) was -1.2 MPa, below which seeds failed to germinate (Figure 4B). The germination percentage was above 50% at the potentials from 0 to -0.3 MPa and below 50% from -0.4 to -0.6 MPa and failed to germinate in lower potentials. The halotime (θHalo) that the seed needs to germinate in saline conditions was 16 hours (Figure 4B). Small seeds harvested at Jutaí showed higher germination percentage (60%) than large seeds (12%) at -0.97 MPa or 27 $dS.m^{-1}$ (Table 2). The *A. colubrina* seeds presented high germination, even with the increase of the concentration of NaCl up to 27 $dS.m^{-1}$ (-0.97 MPa) (Table 2), demonstrating high tolerance of these seed to the salinized environment of the Caatinga. Also, in this work, germination of *A. colubrina* was more affected by drought than by salinity, showing higher percentages at the same osmotic potential of NaCl solutions than PEG solutions (Table 2).

The size of the seeds is usually considered an indicator of their quality, and smaller seeds generally have less germination and vigor than larger seeds, due to a higher amount of reserves available (Marcos-Filho, 2016). However, the results found in this study did not confirm this hypothesis, small seeds showed same or higher germination under both favorable and stressful conditions (Table 2). This might indicate adaptative functional trait in response to harsh environmental conditions, instead of a loss in seed quality.

Germination and seedling establishment are important steps for the survival of forest species, especially when these species cope with limited water availability (Al-Shamsi et al., 2018). *Anadenanthera colubrina* seeds were hardly affected by the tested weekly irrigation volume or by its distribution (Table 3) The seedlings emergence in pots decreased when irrigated with 10 mm per week fractioned in three times, however it was faster (Table 3). The ability of seeds to germinate quickly, such as *A. colubrina*, and to develop seedlings under favorable (or not) environmental conditions is an important measure of vigor for forest species (Marcos-Filho, 2016). Also, high speed germination can be considered as a strategy for survival in the environment, by which with little water available, as soon as the seed is dispersed, it germinates quickly, guaranteeing its survival (Dorneles et al., 2013). Our results (Table 3) mean that small rainfall events (10mm.week^{-1} or 3.33mm individual events) which occur at any time of the year, can be ecologically significant in a semi-arid region such as the Caatinga, favoring the germination of seeds in soil banks, as well as its seedlings development (Sala and Lauenroth, 1982).

An early physiological consequence of water deficit is the reduction of cellular elongation that alters the growth process (Fahad et al., 2017), compromising subsequent events that develop gradually, such as reduction in accumulation fresh mass, and other morphological characters of the seedlings (Mickky and Aldesuquy, 2017). Plants submitted to irrigation of 10 mm/week, had lower growth than those with more water available (Table 3). Thus, *A. colubrina* seeds

Table 3. Emergence and development of *Anadenanthera colubrina* seedlings in different irrigation regimes. Evaluated variables were percentage of emergence (E%); shoot and root length (SL and RL, cm, respectively), shoot and root dry biomass (SDB and RDB, g)

Irrigation volume (mm/week)	Irrigation frequency			
	1x	3x	1x	3x
	Emergence (%)		Emergence time (days)	
10	40 aA	32.5 bA	3.10 aA	1.95 bA
17.5	65 aA	62.5 aA	2.87 aA	3.87 aA
25	52.5 aA	72.5 aA	2.20 aB	4.21 aA
	CV(%) = 26.94; W = 0.096^{ns}; F = 1.017^{ns}		CV(%) = 31.43; W = 0.297^{ns}; F = 1.343^{ns}	
	SL (cm)		RL (cm)	
10	4.9 aA	2.61 bB	16.5 aA	11.4 bA
17.5	6.23 aA	5.01 aA	20.9 aA	19.6 abA
25	5.73 aA	5.80 aA	22.3 aA	24.4 aA
	CV(%) = 22.5; W = 0.538^{ns}; F = 6.096*		CV(%) = 24.4; W = 0.189^{ns}; F = 3.145^{ns}	
	SDB (g)		RDB (g)	
10	0.30 a	0.70 a	0.05 b	
17.5	1.05 a	2.27 a	1.17 ab	
25	0.60 a	1.18 a	2.37 a	
	CV(%) = 53.85; W = 0.000*; F = 4.182*		CV(%) = 65.0; W = 0.000*; F = 5.999*	

Averages followed by the same lower-case letter in columns and upper case in rows do not differ by Tukey's test at 5%. CV(%): coefficient of variation; W and F: statistics of Shapiro-Wilk and Levene's test respectively indicate residue with normal distribution and variance homogeneity. * = significant at 5%, ^{ns}= not significant.

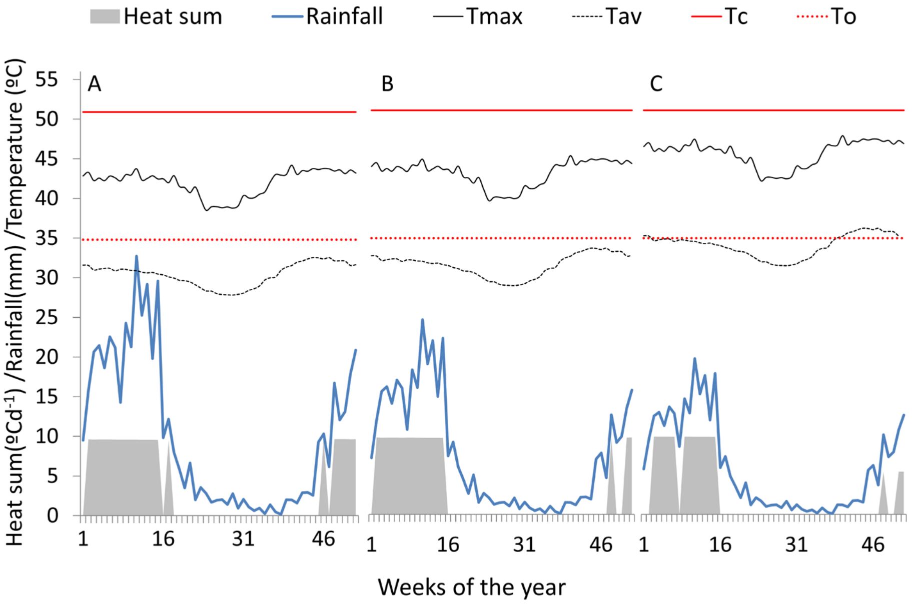

Figure 5. Heat sum available for germination events of *Anadenanthera colubrina* seeds in current climatic scenarios (A) climate change scenarios RCP 2.6 (B) and RCP 8.5 (C) from the Fifth Report of the Intergovernmental Panel on Climate Change - IPCC/AR5 (IPCC, 2014). Heat sum: calculated heat sum ($^{o}C.d^{-1}$) for germination events when rainfall was > 10mm; Rainfall: accumulated weekly rainfall; Tmax soil: maximum soil temperature; Tmax av soil: average soil temperature; Tc: ceiling temperature for seed germination. To: optimum temperature for seed germination.

can emerge and develop plants for up to 14 weeks. However, seedlings growth may be affected by the low water availability in the soil. This result leads to an important characteristic of the species, which requires less moisture in the soil for germination and recruitment in the field than the modeled 17.5 mm (Dantas et al., 2020).

The irregularity of the rains may affect the germination of the seeds if combined with high temperatures and evapotranspiration. In addition, this environmental condition can also increase soil salinity, altering germination time (Al-Shamsi et al., 2018). In a pessimistic climate scenario, it is expected a reduction from 21 to 15 weeks with rainfall > 10 mm (Figure 5), a decrease in total volume of precipitation by up to 40% and an increase in soil salinity (Marengo et al., 2014). However, *A. colubrina* seeds will be able to germinate more quickly, allowing reduced exposure of young seeds and seedlings to the environment (El-Keblawy et al., 2017). Besides that, the species had a ceiling temperature (Tt) or maximum of 50.9 ºC, thus, germination will not be inhibited (Figures 3 and 5) by the temperature increase predicted by climatic changes of up to 3.5 ºC until the end of the century (PBMC, 2013).

Climate change is expected to produce new combinations in patterns of precipitation, temperature and their fluctuations (IPCC, 2014). These changes will affect the plant development, from seed germination to plant growth and establishment (Walck et al., 2011). Changes in temperature and precipitation directly affect seed production, disrupting the maturation and development processes and consequently decreasing the quality, size, quantity and vigor of the seeds (Marcos-Filho, 2016). In a climate change scenario, studies on the correlations of seed production are important in order to elucidate characteristics of the seeds that can allow their germination. In this sense, the results of this work indicate that the increase in the amount of small seeds within the lots of *A. colubrina* collected in the Caatinga can be considered a strategy of the species to cope with the harsh environment, rather than a decrease in seed quality.

CONCLUSIONS

The predicted temperature increase and rainfall reduction will affect seed production, resulting in smaller seeds produced, however, with faster germination and more tolerant to environmental stresses.

A. colubrina seeds germinate in a wide temperature range, thus temperature increases predicted in future scenarios will not inhibit germination. Large and small seeds show similar germination under optimal conditions; however, small seeds are more tolerant than large ones to environmental stresses.

Seed germination and seedling recruitment of *A. colubrina* can be accomplished in low soil moisture and with small rainfall events. In a future climate, the decrease in rainfall predited for the Caatinga ecosystem, may result in less time for the emergence and development of *A. colubrina* seeds.

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