



# Rainfall, not soil temperature, will limit the seed germination of dry forest species with climate change

Barbara F. Dantas<sup>1</sup> · Magna S. B. Moura<sup>1</sup> · Claudinéia R. Pelacani<sup>2</sup> · Francislene Angelotti<sup>1</sup> ·  
Tatiana A. Taura<sup>1</sup> · Gilmara M. Oliveira<sup>2</sup> · Jaciara S. Bispo<sup>3</sup> · Janete R. Matias<sup>4</sup> · Fabricio F. S. Silva<sup>2</sup> ·  
Hugh W. Pritchard<sup>5</sup> · Charlotte E. Seal<sup>5</sup>

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## Abstract

Drylands are predicted to become more arid and saline due to increasing global temperature and drought. Although species from the Caatinga, a Brazilian tropical dry forest, are tolerant to these conditions, the capacity for germination to withstand extreme soil temperature and water deficit associated with climate change remains to be quantified. We aimed to evaluate how germination will be affected under future climate change scenarios of limited water and increased temperature. Seeds of three species were germinated at different temperatures and osmotic potentials. Thermal time and hydrotime model parameters were established and thresholds for germination calculated. Germination performance in 2055 was predicted, by combining temperature and osmotic/salt stress thresholds, considering soil temperature and moisture following rainfall events. The most pessimistic climate scenario predicts an increase of 3.9 °C in soil temperature and 30% decrease in rainfall. Under this scenario, soil temperature is never lower than the minimum and seldomly higher than maximum temperature thresholds for germination. As long as the soil moisture (0.139 cm<sup>3</sup> cm<sup>3</sup>) requirements are met, germination can be achieved in 1 day. According to the base water potential and soil characteristics, the minimum weekly rainfall for germination is estimated to be 17.5 mm. Currently, the required minimum rainfall occurs in 14 weeks of the year but will be reduced to 4 weeks by 2055. This may not be sufficient for seedling recruitment of some species in the natural environment. Thus, in future climate scenarios, rainfall rather than temperature will be extremely limiting for seed germination.

**Keywords** Climate change · Functional trait · Temperature threshold · Drought · Seed germination modelling · Salinity

## Introduction

Drylands cover approximately 40% of the world's land area, and support two billion people, 90% of whom live in developing countries (EMG/UN 2011). Due to climate change, the dryland area is increasing worldwide and the expansion of semi-arid regions accounts for more than half of the drylands. Nowadays, semi-arid regions cover more than 15% of the Earth's land surface (Huang et al. 2016).

The seasonally dry tropical forests occur in regions characterized by pronounced seasonality in rainfall distribution, resulting in several months of drought. These forests have an extremely variable vegetation structure, but with strong floristic links between the different vegetation types, mainly related to variation in climate and soil (Queiroz et al. 2017). These forests are distributed worldwide; however, 67% of their 2700,000 km<sup>2</sup> total area is located in South America, where the Caatinga domain includes an area of around 849,516 km<sup>2</sup>, corresponding to approximately 31% of the New World and 45% of South America (Queiroz et al. 2017).

The ecosystems in such regions, including the Chacos in western Brazil, south-eastern Bolivia, Paraguay and northern Argentina (Portillo-Quintero and Sánchez-Azofeifa 2009), are some of the most threatened across the globe, and highly sensitive to anthropogenic climate change (Janzen 1988; Miles et al. 2006). In northeastern Brazil, the Caatinga dry forest is identified as one of the Brazilian regions

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✉ Barbara F. Dantas  
barbara.dantas@embrapa.br

Extended author information available on the last page of the article

most likely to be affected by climate change (Marengo et al. 2017). Under the most pessimistic climate change scenario, of a temperature increase up to 5.4 °C, this semi-arid region could become arid, with lower rainfall in the rainy season and higher moisture deficiencies in the soil throughout the year, resulting in desertification (Marengo et al. 2009a). As in all semi-arid regions, the main climatic features of this environment are the short and concentrated rainy season (December–March) associated with high incident solar radiation that causes high diurnal temperatures and water deficit (Teixeira 2010), leading to a build-up of salts at the soil surface (Rengasamy 2006).

Whilst the estimates of climate scenarios are based on changes in air temperature, the soil temperature will also change, affecting both seed germination and persistence in the soil seed bank (Ooi et al. 2009). Such effects will depend on soil physical characteristics, vegetation cover and species composition (Harte et al. 1995). Ooi et al. (2009) suggest that the maximum soil temperatures of arid regions could increase by almost 8 °C if air temperatures increase by 5 °C. In contrast, the soils of calcareous fens buffer against extreme air temperatures and may facilitate the resilience of seeds to climate change (Fernández-Pascual et al. 2015a). For the Caatinga dry forest, there are no current estimates of increase in soil temperature and how it might affect seed germination.

In a dry forest, with stochastic rainfall events through the years, such as the Caatinga, recruitment/mortality of tree seedlings is closely related and delimited by the duration of the rainy period (Albuquerque et al. 2012). Moreover, these early stages of the plant life cycle have been identified among the most at risk from climate change (Walck et al. 2011). Thus, modelling germination responses under current and future climate scenarios is critical for understanding of processes that threaten ecosystem resilience (Pavlik 1994).

The response of seed germination to temperature and osmotic potential can be described using thermal time and hydrotime models, respectively (Bierhuizen and Wagenvoort 1974; Gummerson 1986), or combined into a hydrothermal time model (Bradford 1990). These models have been widely used during the past three decades to predict emergence of several crop and weed species (Covell et al. 1986; Gummerson 1986; Bradford 1990) and to consider factors such as dormancy release (Orrù et al. 2012) and environmental regulation and constraints to germination (Gareca et al. 2012). In more recent years, these approaches have been applied to predict the germination of wild or native species under climate change scenarios (Gareca et al. 2012; Stevens et al. 2014; Fernández-Pascual et al. 2015b; Seal et al. 2017).

At the lowest altitude (< 500 m a.s.l.) and in the driest areas of the Caatinga domain, predominating plants are typical of deciduous thorn woodland (or Caatinga sensu stricto), (Rodal and Nascimento 2006). Among the most

representative tree species of the Caatinga sensu stricto dry forest are *Myracrodruon urundeuva* (Allemão) (Anacardiaceae), *Anadenanthera colubrina* var. *cebil* [(Griseb.) Altschul] (Fabaceae) and *Cenostigma pyramidale* [(Tul.) Gagnon & G.P. Lewis] (Fabaceae). These species are economically important for their timber and medicinal properties and of high value for reforestation (Oliveira et al. 2007).

*Myracrodruon urundeuva* is a widely distributed specialist to the seasonally tropical dry forests, and is an abundant seeding, although slow growing, species. It is also one of the most exploited species in the Caatinga due to its hard and long lasting wood, its tannin rich (17%) bark and the pharmaceutical properties of barks, leaves and roots (Leite 2002). Its diaspores, which are dispersed at the end of the dry season, are dry and winged drupes, containing single non-dormant seeds that germinate within a few days when conditions are favourable (Oliveira et al. 2019).

*Anadenanthera colubrina* var. *cebil* is also a species with multiple uses (wood, coal, popular medicine and industry) and widely distributed across all Brazilian territory. Its height ranges from 3 to 15 m in the Caatinga, although in other ecosystems, such as the Atlantic Forest it can reach 30 m. The dehiscent legumes and seeds mature by September (the end of the dry season) and have a barochoric dispersal syndrome. Seeds are very thin, black, coin-shaped, non-dormant and can germinate very quickly (Torres and Repke 2006; Dantas et al. 2014).

*Cenostigma pyramidale* (syn. *Caesalpinia pyramidalis*, *Poincianella pyramidalis*) is an endemic native species to Caatinga dry forest, with high tolerance to drought (Falcão et al. 2015). It is a medium-sized tree with height ranging from 4 to 12 m, with an open and irregular crown. The dehiscent legumes and seeds are mature by the end of dry season and require harvest before autochoric (explosive) seed dispersion. Seeds are light brown, flattened and ovate, with no dormancy. Germination occurs in less than 48 h once given optimum conditions (Dantas et al. 2008).

Although seeds of these specialist trees are known to be well adapted to the harsh environmental conditions in which they germinate and develop, the thermal time and hydrotime parameters for germination are yet to be quantified. Moreover, hydrotime models have not been used to compare osmotic stress [created using polyethylene glycol (PEG) solutions] with salt stress (created using NaCl solutions) to which these seeds show different responses (Dantas et al. 2014). Thus, in this study, we evaluated how germination will be affected under future climate change scenarios of limited water and increased temperature. First, we tested the hypothesis that soil temperatures will be significantly higher than air temperature and derived values for this. Then, we quantified the role of temperature and osmotic potential (created using PEG and NaCl) in limiting the germination of *M. urundeuva*, *A. colubrina* var. *cebil* and *C. pyramidale*, to test

the hypothesis that seeds of these species respond differently to these three stresses. We also parameterized a model to simulate germination in field conditions under current and future climate scenarios. Finally, we aimed to comprehend how the increase of drought, temperature or both might limit the seed germination of these species under projected climate scenarios for the semi-arid Caatinga.

## Materials and methods

### Diaspore collection at study area

Seeds of *M. urundeuva*, *A. colubrina* var. *cebil* and *C. pyramidale* were collected from 10 mother plants located in different sites of Caatinga vegetation with some anthropogenic disturbance at Lagoa Grande (8°38'45.23"S, 40°14'07.32"W) and Custódia (37°44'05"W, 08°13'53"S), Pernambuco State, and Juazeiro, Bahia State (9°43'51.12"S, 40°21'02.52"W), respectively (Online Resource Fig. S1).

The diaspores were harvested between August and September 2013, sun dried and manually processed by removing all impurities, such as fruit remains and wings. After processing, they were packed in cloth bags and placed in cold storage (60% relative humidity and 10 °C air temperature), for no more than 6 months. No change in germination percentage and speed was recorded for seeds stored in this way (Leite 2002; Pinho et al. 2009; Antunes et al. 2010).

### Present and future climate data of the study area

Based on IPCC/AR4 scenarios for high (A2) and low (B1) CO<sub>2</sub> emissions (IPCC 2007), climate information for the year 2055 was generated by INPE (National Institute for Spatial Research) using two regionalized models: PRECIS (Providing Regional Climate for Impacts Studies) and ETA-CPTEC (Centre for Weather Forecasting and Climate Research) (Marengo et al. 2009b; Mesinger et al. 2012). These data, obtained in a 50 km × 50 km resolution, were spatially adjusted and compared to annual baseline climate data (1961–1990) from several meteorological stations supplied by INMET (National Institute of Meteorology) and extracted for an area comprising the study site (Online Resource Fig. S1). According to Chou et al. (2012), these data closely relate to the present climate in the field and, thus, to predicted climate change.

To measure soil temperature and calculate its relationship to air temperature, thermistors (107, Campbell Scientific INC., USA) were installed in the soil at 0.02 m and 0.06 m depths and an air temperature and humidity probe (HMP45C, Vaisala, Finland) was fixed approximately 10 m above the vegetation. Measurements were made every 30 s and an average stored every 30 min, for the years 2011–2015.

Data were correlated and the determination coefficient multiplied to air temperature to estimate soil temperature in the future climate. Measured and the estimated soil temperatures at both depths were compared by paired samples *t* test.

During 1 year (January–December 2015), one tipping bucket rain gage (CS700, Campbell Scientific INC., USA) and two Frequency Domain Reflectometry (FDR) probes (CS615, Campbell Scientific INC., USA) were installed to measure daily rainfall and soil moisture at 0.05 and 0.10 m depths, respectively. Soil moisture was measured at greater depths than soil temperature (0.02 and 0.06 m) due to equipment characteristics and physical properties of soil in study area.

Soil samples were collected to analyse soil physical properties, such as percentage of soil, silt, and clay; total porosity; soil density and particles density (Embrapa 1997).

### Germination experiments

Prior to germination tests, the diaspores of *A. colubrina* var. *cebil* and *C. pyramidale*, containing approximately 10% water content, were macerated in a detergent solution for 5 min to prevent fungal infection during germination, without resulting damage to the seedlings. For *M. urundeuva*, macerated seeds were extracted from fruits using aluminium sieves under running tap water, surface sterilized in sodium hypochlorite (2.5%) for three minutes and rinsed thoroughly with tap water, before treating with captan® fungicide (3 mL fungicide L<sup>-1</sup> seeds).

All germination tests were performed in a totally randomized design. Four replicates of 25 seeds were sown in transparent germination boxes onto two layers of blotting paper moistened either with distilled water, polyethylene glycol 6000 (PEG) or sodium chloride (NaCl) solutions in a volume corresponding to 2.5 times the weight of the paper.

To create data for a thermal time model, seeds were incubated on blotting paper moistened with water at 10 constant temperatures from 5 to 50 °C (with intervals of 5 °C), with a 12 h photoperiod. To create data for a hydrotime model, seeds were incubated at 25 °C, with a 12 h photoperiod, on blotting paper moistened with seven PEG or NaCl solutions from 0 MPa (pure distilled water) to –1.1 MPa (equivalent to 444 mmol L<sup>-1</sup> NaCl or 30 dS m<sup>-1</sup>) in 0.1 or 0.2 MPa intervals (Villela et al. 1991). Seed germination was evaluated twice a day until no further germination was observed for at least 5 days. Seeds were considered germinated when the length of the emerged radicle was ≥ 1 mm.

### Thermal time and hydrotime modelling

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. The reciprocal of these times (germination rate,  $1/t_{50}$ ) was plotted against temperature and the sub- and supra-optimal germination temperature ranges 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 analyses (Covell et al. 1986).

For each seed lot, the thermal time ( $\theta_T$  °Ch) to germination at sub- and at supra-optimal temperatures was calculated (Covell et al. 1986). A repeated probit analysis was performed in Genstat (v. 14.2.6967; VSN International) on germination values and their corresponding log-thermal time for sub- and supra-optimal temperature ranges, varying the values of  $T_b$  and  $T_c$ , respectively, until the best fit was obtained (Bradford 1990; Online Resource equations S1–S4).

To establish the hydrotime model, cumulative germination was plotted as a function of osmotic potential and a Boltzman sigmoidal fitted to estimate  $t_{50}$  of the population. Estimated  $1/t_{50}$  was plotted against osmotic potential to estimate the x-intercept and slope of each linear regression. The x-intercept resulted in base osmotic potential ( $\psi_b$ ), below which seeds are predicted to not germinate. For each seed lot, the hydrotime ( $\theta_H$  MPa h) to germination was calculated (Gummerson 1986) and a repeated probit analysis (Bradford 1990) was performed in Genstat (v. 14.2.6967; VSN International) by varying  $\psi_b$  until the best fit was obtained (Online Resource equations S5–S6).

## Modelling germination under current and future climate scenarios

### Rainfall requirement

To predict base volumetric moisture content ( $\Theta_b$ ), the soil moisture was related to the  $\psi_b$  obtained from the hydrotime model for both PEG and NaCl using the equation of van Genuchten (1980). Specifically, we used the soil water retention curves at a 0–0.2 m depth for a Quartzarenic Neosol soil, determined near to the study site (Nascimento et al. 2010) (Online Resource, equation S7). Using data relating rainfall and soil moisture measured inside Caatinga vegetation during 2015 (described above), base rainfall (Rb, the minimum amount of rainfall necessary for seed germination) was estimated.

### Soil heat sum

Available historical climate data and the correlation of air and soil temperature enabled the calculation of the heat sum (°Cd) required for germination (Orrù et al. 2012); (Online Resource, equation S8). Differences in mean air temperatures and percentage increase or decrease of rainfall for each scenario (ETA and PRECIS models for low and high CO<sub>2</sub> emissions scenarios) were applied to weekly local climatological data (1970–2014) collected at the Embrapa agrometeorological station (Online Resource Fig. S1). Heat sum was estimated only when the weekly rainfall was higher than the minimum amount of rainfall necessary for seed germination (Rb) during 1 week in a dry Caatinga soil.

## Results

### Climate of the Caatinga dry forest

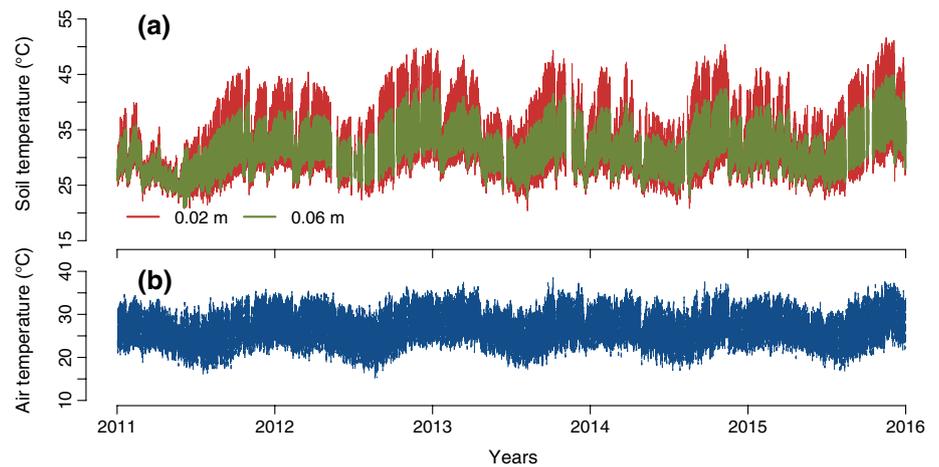
The average temperatures of air and soil at 0.02 and 0.06 m depths were, respectively, 26.62, 31.02 and 30.85 °C, while the daily amplitude varied between 9.41–18.69, 9.96–26.19 and 6.44–19.22 °C (Fig. 1). During the rainy season (September–December), temperatures above 45 °C were recorded every studied year (2011–2015) and the lowest values were higher than 20 °C. Air and soil temperatures of up to 50 °C were recorded, although these high temperatures were infrequent. From 2011 to 2015, the minimum temperature observed at the Caatinga was 15.05 °C (air), 20.4 (soil at 0.02 m) and 20.9 °C (soil at 0.06 m) (Fig. 1).

Air temperature showed a linear relationship to soil temperature both at 0.02 m (soil =  $1.1618 \times \text{air}$ ;  $R^2 = 0.8484$ ,  $P < 2 \times 10^{-16}$ ) and 0.06 m (soil =  $1.1475 \times \text{air}$ ,  $R^2 = 0.7904$ ,  $P < 2 \times 10^{-16}$ ) depths. Using data averaged for 0.02 and 0.06 m depths, for every 1 °C increase in air temperature, soil temperature increased by approximately 1.16 °C (soil =  $1.155 \text{ air}$ ,  $R^2 = 0.8435$ ,  $P < 0 \times 10^{-16}***$ ) (Online Resource Fig. S2).

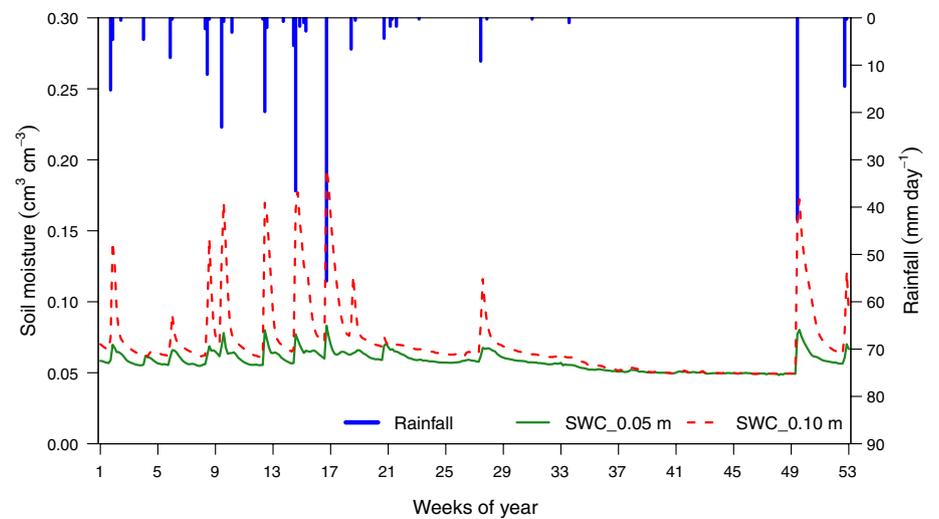
Due to the sandy texture of the soil (> 77%, Online Resource Table S2), evaporation and the presence of plant roots, soil moisture variation at 0.05 m (Fig. 2) was negligible during and after any rainfall event throughout the wet season. Small rainfall events (< 5 mm) did not alter the soil moisture at 0.10 m depth from a dry state (Fig. 2). However, 2 days after rainfall event of 23.11 mm, soil moisture at 0.10 m depth increased from 0.07 to 0.17 m<sup>3</sup> m<sup>-3</sup> and returned to a dry state (0.07 m<sup>3</sup> m<sup>-3</sup>) after 7 days of negligible rain. This cycle is often repeated during the wet season because of the high potential evapotranspiration and sporadic rain events.

Air temperature is predicted to increase under all estimated climate scenarios (Table 1). As the least pessimistic

**Fig. 1** Temperatures of (a) soil at 0.02 m (gray lines) and 0.06 m depths (green lines), and air (b) measured every 30 min from 01/01/2011 to 31/12/2016 in a Caatinga area, Petrolina, Pernambuco Sate, Brazil. This figure is available in colour in the online version of the manuscript



**Fig. 2** Rainfall (blue bars) and soil moisture at 0.05 m (green lines) and 0.10 m (red lines) observed from an agrometeorological tower and FDR probes, during a year in a Caatinga area, Petrolina, Pernambuco Sate, Brazil. This figure is available in colour in the online version of the manuscript



**Table 1** Annual mean air temperatures and rainfall at Petrolina, Pernambuco Sate, Brazil in 1961–1990 (baseline) and 2055 according to the scenarios of low (B1) and high (A2) carbon dioxide emissions, generated by PRECIS and ETA regionalized models

Model	2055 scenario		Baseline (1961–1990)
	B1	A2	
Annual mean average temperature (°C)			
ETA	28.76	29.54	26.86
PRECIS	29.41	30.25	
Annual mean maximum temperature (°C)			
ETA	33.70	34.63	31.88
PRECIS	35.16	36.00	
Annual mean minimum temperature (°C)			
ETA	23.53	24.22	21.62
PRECIS	23.67	24.51	
Annual rainfall (mm)			
ETA	648.14	393.98	557.04
PRECIS	362.16	400.16	

model, ETA estimated an increase of around 2 °C in the B2 scenario and around 3 °C in the A2 scenario. The PRECIS model estimated more drastic increases, up to 3 °C in the B1 scenario and 4 °C in the A2 scenario. The study region could reach an annual mean maximum temperature of 36 °C in 2055 in an A2 scenario of high emissions of CO<sub>2</sub> compared to the baseline of 31.9 °C (Table 1).

Due to the stochasticity of rainfall events in this region, each regionalized model made divergent predictions. According to the ETA model, the B1 scenario predicts an increase in rainfall by 16% in 2055; however, the PRECIS model predicts a 35% decrease in the same scenario, showing a lack of consensus between the two models. The A2 scenario predicts, for both models, approximately 30% decrease in rainfall by 2055 (Table 1).

## Thermal and osmotic requirements for seed germination

Germination percentages (Fig. 3) and time courses (Online Resource Figs. S3–S5) varied with temperature and osmotic potential, and differed among the species. Germination of *M. urundeuva* was higher than 70% at 20–35 °C (Fig. 3a), or at 25 °C in osmotic potentials > –0.2 MPa in NaCl solutions and > –0.5 MPa in PEG solutions (Fig. 3b). Radicle emergence required 26 h for *M. urundeuva* at 25–35 °C in distilled water (Online Resource Fig. S2a). Seeds of *M. urundeuva* failed to germinate at 45 °C, < –0.4 MPa in NaCl solutions and < –0.7 MPa in PEG solutions (Fig. 3b).

*Anadenanthera colubrina* var. *cebil* germinated > 90% at 10–40 °C, indicating tolerance to high temperatures, 20% of seeds even germinated at 47 °C and germination only failed at 50 °C (Fig. 3c). From 20–47 °C, germination was observed after only 8 h imbibition. High germination (> 90%) was also observed in *A. colubrina* var. *cebil* in NaCl solutions with osmotic potentials down to –0.75 MPa (Fig. 3d).

The first germination event for seeds of *C. pyramidale* was after 16 h incubation at 30 and 35 °C (Online Resource Fig. S5a). From 15 to 35 °C, more than 90% of seeds germinated. At 10 and 40 °C, germination was around 50% and germination was not observed at 5 and 45 °C (Fig. 3e).

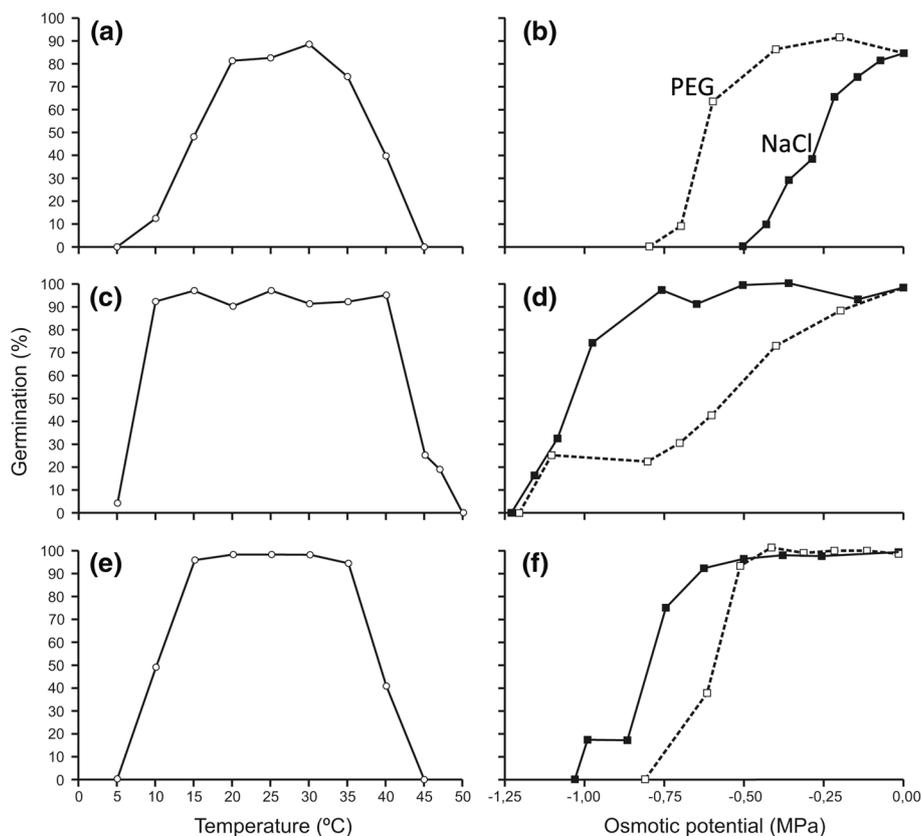
Seeds of *C. pyramidale* were more tolerant to NaCl than PEG at < –0.5 MPa, with germination recorded down to –1 MPa in NaCl (Fig. 3f).

For all three species, the estimated values of  $T_b$  were below 10 °C and the values of  $T_c$  were above 40 °C (Table 2). *C. pyramidale* showed the widest thermal germination range (i.e.  $T_c - T_b$ ), spanning 43 °C, in comparison to *M. urundeuva* (32 °C range) and *A. colubrina* var. *cebil* (38 °C range).  $T_0$  estimates were 34.5, 38.4 and 35.5 °C for *M. urundeuva*, *A. colubrina* var. *cebil* and *C. pyramidale*, respectively (Table 2).

We observed little variation in  $\psi_b$  among the studied species when osmotic potentials were generated using PEG, which ranged from –0.72 to –0.8 MPa. However, when NaCl was used to create different osmotic potentials, the germination responses varied significantly: *C. pyramidale* and *A. colubrina* var. *cebil* had values of  $\psi_b$  around –1 MPa; and for *M. urundeuva*,  $\psi_b$  was –0.28 MPa (Table 2).

According to the physical properties and water retention curve of a typical Caatinga soil (dos Nascimento et al. 2010), all the estimated values of  $\psi_b$  (–1 to –0.28 MPa) are equivalent to 0.139 m<sup>3</sup> m<sup>–3</sup> soil moisture. This soil moisture can be achieved 1 day after a 17.5 mm rainfall event in the dry soil at 0.10 m depth. After a 27.5 mm rainfall event, if no further rain occurs, sufficient soil moisture to guarantee seed germination

**Fig. 3** Seed germination of *Myracrodruon urundeuva* (a, b), *Anadenanthera colubrina* var. *cebil* (c, d) and *Cenostigma pyramidale* (e, f) at different temperatures (a, c, e) and osmotic potentials (b, d, f) produced from NaCl (filled squares) or polyethylene glycol (PEG; open squares) solutions. Mean standard errors were < 1% and, therefore, are not shown



**Table 2** Germination thresholds for temperature and osmotic potential, thermal time and hydrotime of seeds of *Myracrodruon urundeuva* (Allemão), *Anadenanthera colubrina* var. *cebil* [(Griseb.) Altschul] and *Cenostigma pyramidale* [(Tul.) Gagnon & G.P. Lewis]

Species	Sub-optimal temperature				$T_o$ (°C)	Supra-optimal temperature			
	$T_b$ (°C)	$\sigma$	$R^2$	$\theta_{Tsub}$ (°Cd)		$T_c$ (°C)	$\sigma$	$R^2$	$\theta_{Tsupra}$ (°Cd)
<i>M. urundeuva</i>	9.5	2.501	0.6974*	44.9	34.5	41.5	<0.001	0.7734**	12.5
<i>A. colubrina</i> var. <i>cebil</i>	5.0	3.913	0.9587**	20.7	38.4	48.0	<0.001	0.8573**	23.3
<i>C. pyramidale</i>	7.0	5.183	0.7007*	27.7	35.5	45.0 <sup>a</sup>			9.1
	Osmotic potential (PEG solutions)				Osmotic potential (NaCl solutions)				
	$\psi_{bPEG}$ (MPa)	$\sigma$	$R^2$	$\theta_{HPEG}$ (MPa d <sup>-1</sup> )	$\psi_{bNaCl}$ (MPa)	$\sigma$	$R^2$	$\theta_{HNaCl}$ (MPa d <sup>-1</sup> )	
<i>M. urundeuva</i>	-0.72	2.968	0.8400**	1.41	-0.28	5.400	0.8822**	0.55	
<i>A. colubrina</i> var. <i>cebil</i>	-0.73	2.456	0.6984**	0.96	-1.09	2.421	0.7767**	0.83	
<i>C. pyramidale</i>	-0.80	5.119	0.7067**	1.67	-1.06	4.432	0.7688**	1.46	

$T_b$ ,  $T_o$  and  $T_c$  are base, optimum and ceiling temperatures for germination, respectively;  $\psi_b$  is the base osmotic potential;  $\sigma$  is the standard deviations and  $R^2$  is the square of the correlation coefficients for germination and different thermal or hydrotimes ( $\theta_T$  and  $\theta_H$ , respectively)

\*\* $P < 0.01$ ; \* $P < 0.05$

<sup>a</sup>Repeated probit analysis failed to provide ceiling temperature ( $T_c$ ) and this was obtained by linear regression, and the thermal time for supra-optimum temperature was estimated by the reciprocal of the slope

(i.e.  $> 0.139 \text{ m}^3 \text{ m}^{-3}$ ) is maintained for 4 days, gradually decreasing to  $0.071 \text{ m}^3 \text{ m}^{-3}$  in 1 week (Fig. 2), very close to the plant wilting point moisture level for this soil of  $0.05 \text{ m}^3 \text{ m}^{-3}$  (Nascimento et al. 2010). Thus, germination predictions for future climate scenarios were related to the total amount of rainfall in a week, assuming a base rainfall (Rb) of 17.5 mm.

Combining climate data with temperature and rainfall volume thresholds for seed germination, the results show, for all species evaluated, that air or soil temperature is rarely limiting to seed germination in the current climate or under future climate scenarios modelled by two different regionalized models (PRECIS and ETA), since average weekly temperatures are never lower than  $T_b$  and maximum soil temperatures only briefly exceed  $T_c$  (Fig. 1, Table 1). Because of the heat capacity of the soil at 0.02–0.06 m depth, the average temperature is usually close to  $T_o$  for seed germination all year round (Fig. 4). Seeds of *M. urundeuva* required 30°Cd of heat sum to reach 50% germination under current and all future scenarios. In contrast, seeds of *A. colubrina* var. *cebil* and *C. pyramidale* germinated faster, requiring 17°Cd and 20°Cd, respectively (Fig. 4). These cumulative germination times are all achieved during only 5 days in the Caatinga region when the Rb of 17.5 mm is met. Under current climatic conditions, there are 14 weeks of the year when rainfall is higher than the Rb of 17.5 mm. The PRECIS model, in all climate scenarios, predicted that by 2055 this hydration window will reduce to only 4 weeks. This was also observed for the A2 scenario of the ETA model (Fig. 4).

## Discussion

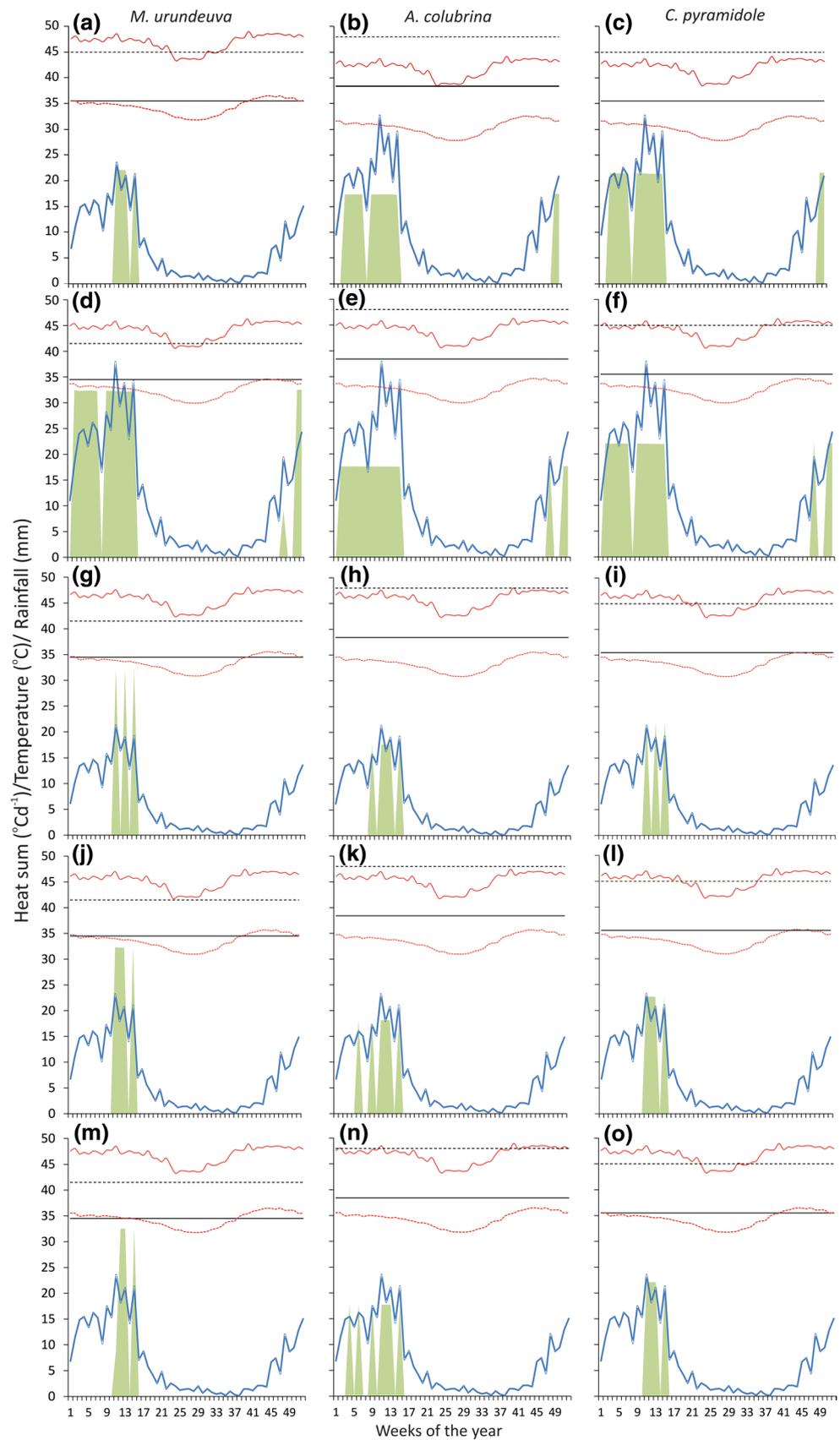
### Current germination niche requirements

There are hardly any data describing how seeds from dry forests, especially from the Caatinga, will germinate under cyclic drought years and/or climate change. However, this study presents new data on germination modelling in the current and future climate of three tree species native to the Caatinga.

After dispersal, seeds are buried in the soil or reside at its surface. Thus, soil temperature, which was registered to be higher than air temperature (Fig. 1), is more realistic for modelling seed germination. The species studied in this work are dispersed at the end of the Caatinga dry season (August to November; Griz and Machado 2001) and are not persistent in the soil seed bank (Santos et al. 2016). Requiring at least 17.5 mm of rainfall during 1 week to germinate, additional rainfall is necessary to form seedling/juvenile banks (Oliveira et al. 2007). In the hot and semi-arid Caatinga dry forest, low temperature is not a restriction to germination as the minimum air temperature is never lower than 12 °C (Teixeira 2010), which is higher than the  $T_b$  of all species (Table 2).

*Cenostigma pyramidale* is endemic to the Caatinga dry forest. On the other hand, *A. colubrina* var. *cebil* is known to be well adapted to different gradients of average temperature, relative humidity and precipitation in the several ecosystems (Caatinga, Cerrado and Chacos) in which it

**Fig. 4** Heat sum for germination events of seeds of *Myracrodruon urundeuva* (a, d, g, j, m); *Anadenanthera colubrina* var. *cebil* (b, e, h, k, n) and *Cenostigma pyramidale* (c, f, i, l, o) under current (a–c) and future (d–o) climate scenarios. Heat sum for germination events (green histogram) estimated when rainfall was > 17.5; accumulated weekly rainfall (blue line); maximum (continuous red line) and average (interrupted red lines) soil temperature; optimum (continuous black line) and ceiling temperature for seed germination (interrupted black line). Future climate scenarios (IPCC 2007) according to estimation models are: (d–f) B1/ETA model; (g–i) B1/Precis model; (j–l) A1/ETA model; (m–o) A1/Precis model. This figure is available in colour in the online version of the manuscript



occurs (Mogni et al. 2015), and to have a wider distribution than other Fabaceae species (Torres and Repke 2006). Both species demonstrated the capability to germinate over a wider range of temperatures, with lower values of  $T_b$  and higher values of  $T_c$  than the broadly distributed *M. urundeuva*. Consequently, the distributional range of these species was not apparently related to their thermal germination niche.

All three species were able to germinate to some extent above 40 °C (Table 2). Contrary to laboratory experiments utilising constant temperatures, seeds in the field will be exposed to such high temperatures only briefly each day (Online Resource Table S1), and periods of short exposure to very high temperatures might not have the same deleterious effect on germination as exposure to constant high temperatures (Reino et al. 2011). Thus, the increase in soil temperature might not be a limiting factor for these seeds both for current and future climates, because the average soil temperature is seldom higher than  $T_c$  (Fig. 4) and if the temperature exceeds  $T_c$ , this occurs only very briefly (Fig. 1). However, germination may still be affected since germination begins to slow when the soil temperature exceeds  $T_o$ , most likely due to thermal stress (Seal et al. 2017).

Drought is a frequent phenomenon triggered by the persistent lack of significant rainfall (Teixeira 2010) and salinized soil or brackish groundwater, which are characteristics of the Caatinga dry forest (Pessoa et al. 2016). Many native species from this dry forest are known to be tolerant to drought and salinity, including trees (Reis et al. 2012), shrubs (Marin et al. 2004) and herbs (Fernandes-Júnior et al. 2015). Although these species are acknowledged to be tolerant to drought, their seeds showed very little or no germination at and below  $-0.8$  MPa in PEG solutions, consistent with the responses observed here where  $\psi_b$  ranged from  $-0.72$  to  $-0.8$  MPa. Furthermore, this threshold is higher than some other Caatinga native species of the Caatinga which germinate at much lower osmotic potentials, such as *Mimosa tenuiflora* that achieved 53% germination at  $-1.2$  MPa (Bakke et al. 2006).

Salinization can occur naturally in arid and semi-arid environments due to the physical, chemical and geological nature of soils (Pessoa et al. 2016). The salinized soils and brackish groundwater from the Caatinga domain originate from the weathering of Precambrian crystalline rocks, which geologically form 30% of the Caatinga, during soil genesis. Due to water deficiency and a high rate of evaporation, these salts surface (Moro et al. 2016). The excess of salt in the soil solution can induce, along with osmotic stress, toxicity in seed tissues (Parvaiz and Satyawati 2008). Such ionic stress might have affected *M. urundeuva* since  $\psi_b$  in solutions of NaCl was much higher than in PEG solutions. Conversely, the Caatinga legume seeds studied here showed much higher tolerance to salt. Seeds of salt-tolerant species accumulate

reducing sugars when germinating in brackish water (Dantas et al. 2014; Ribeiro et al. 2014), which maintain the stability of certain macromolecules and thereby reduces the loss of enzymatic activity or membrane integrity that occurs with saline, or drought, stress (O'Brien et al. 2015).

To simulate germination under field conditions,  $\psi$  was converted to soil moisture and consequently to the amount of rainfall. The physical characteristics of a Caatinga soil collected close to the seed collection site and its water retention curve (Nascimento et al. 2010) made it possible to estimate the water infiltration and storage in the soil after a rainfall event (Santos et al. 2011). The high sand content of this soil, typical of several soils that occur in the Caatinga dry forest (Pacchioni et al. 2014; Schulz et al. 2016), leads to rapid water infiltration at the soil surface and low water storage at the superficial layer. This meant that water potentials ranging from  $-1$  MPa up to  $-0.09$  MPa were translated to a soil moisture of  $0.139 \text{ m}^3 \text{ m}^{-3}$ . For the three study species, with  $\psi_b$  of  $-0.28$  to  $-1$  MPa, the volume of soil moisture required is  $0.139 \text{ m}^3 \text{ m}^{-3}$ . Moreover, for a dry soil at wilting point, a total of 17.5 mm rainfall (in 1 week) will raise soil moisture at 0.10 m depth to this value (Fig. 2). Small rainfall events have a major ecological role in semi-arid regions, in which events of 17.5 mm or less account for 90% of total annual rainfall events and have very large effects on ecosystem dynamics (Sala and Lauenroth 1982). This is also the case in the Caatinga, as rainfall events are stochastic, even during the rainy season (Moura et al. 2015; Silva et al. 2017).

### Germination niche under projected climate change

The projected increase in soil temperature as well as the decrease in rainfall by 2055, according to climate change scenarios predicted by PRECIS and ETA models, was estimated weekly and plotted against germination thermal and water requirements (Fig. 4). Although seed germination of the studied species is not inhibited by the predicted increase in temperature under any scenario, the predicted decrease in rainfall will largely influence the germination timing. Information in the literature about the conditions or timing of Caatinga species seed germination and seedling recruitment is limited. In this study, *A. colubrina* var. *cebil* had very fast germinating seeds requiring a thermal time of less than 21 °Cd in the sub-optimal temperature range. Seeds of this species, as well as for *C. pyramidale* ( $\theta_{Tsub} = 27.7$  °Cd), can germinate in less than 1 day during the rainy season in the Caatinga, when the soil temperature is around 28 °C. Although *M. urundeuva* seeds have a longer thermal requirement for germination ( $\theta_{Tsub} = 44.9$  °Cd), these are also considered fast germinating seeds for tree species (Dürr et al. 2015). If rainfall is sufficient to raise soil moisture to at least  $0.139 \text{ m}^3 \text{ m}^{-3}$ , seeds of the three study species will easily

germinate and emerge from the soil as vigorous seedlings in 2–5 days (Ribeiro et al. 2014; Oliveira et al. 2019) before the soil dries again (Santos et al. 2011; Moura et al. 2015).

Except for the ETA model prediction for low greenhouse gas emission, weekly rainfall will decrease and the period of water availability (weekly rainfall  $\geq 17.5$  mm) for seed germination, seedling recruitment and establishment, will decrease from 14 weeks to 3 or 4 weeks (Fig. 4). This significantly reduces the window of opportunity for germination to occur and is also likely to reduce the probability of successful seedling establishment. The divergent projections of the PRECIS and ETA models for rainfall under B1 scenario demonstrate a level of uncertainty for predicting the future climate (Moura et al. 2015; Silveira et al. 2016). However, models that identify different possible scenarios are an important contribution to the awareness of the potential seriousness and uncertainty surrounding climate impacts, provide reference cases for future analyses, and support risk assessments and policy decision making (Groves and Lempert 2007).

Studies on seedling production for reforestation indicate that *C. pyramidale* has very fast growing seedlings that can be transplanted in the field after about 40 days in the nursery (Dantas et al. 2011). In contrast, *M. urundeuva* and *A. colubrina* var. *cebil* have very fragile and slow growing seedlings that require about 3–4 months in the nursery before field transplantation (Gonçalves et al. 2012; Tsukamoto Filho et al. 2013). For these latter two species, the shortened hydration window predicted by future climate scenarios may not be enough for seedling recruitment in the natural environment. However, further studies may be required on evaluating the accuracy of the proposed model on seedling emergence and growth in pot experiments or field trials, as well as evaluating combined environmental constraints (e.g. high temperatures x saline substrates).

Among the species studied in this work, *M. urundeuva* is most vulnerable to climate change, due to its lower  $T_0$  and  $T_c$ , as well as its slow seedling growth. In the soil seed bank, only 0.5% of *M. urundeuva* seeds germinated, while seeds of *C. pyramidale* achieved 15% germination, during a 6-month trial in which the total rainfall was 83 mm, distributed in small rainfall events (Silva et al. 2017). These findings confirm the criticality of weekly rainfall below 17.5 mm as a barrier to the progress of germination. Although hotter and drier conditions will likely modify juvenile and adult tree physiology, shifting utilization of water resources (Grossiord et al. 2016), such adaptation may be insufficient for plants to tolerate the most pessimistic predicted climate scenarios for the Caatinga. Under these scenarios, some specialist species such as *A. colubrina* var. *cebil* and *M. urundeuva* might shift their distribution uniquely to areas currently occupied by savannas and rainforest (Rodrigues et al. 2015). These findings highlight the importance of understanding plant

regeneration niche through seed germination in response to the environment.

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**Author contribution statement** BFD, CRP, FA and CES conceived and designed the experiments. GMO, JBS, JRM performed the experiments. MSBM provided climate data and interpretation. TAT and FFSS geo-referenced and mapped mother plants. BFD, FA, CES, MSBM and HWP interpreted the data, wrote and reviewed the paper. BFD and CES share equal authorship in this work.

## Compliance with ethical standards

**Conflict of interest** The authors have no conflict of interest.

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## Affiliations

Barbara F. Dantas<sup>1</sup>  · Magna S. B. Moura<sup>1</sup>  · Claudinéia R. Pelacani<sup>2</sup>  · Francislene Angelotti<sup>1</sup>  · Tatiana A. Taura<sup>1</sup>  · Gilmar M. Oliveira<sup>2</sup>  · Jaciara S. Bispo<sup>3</sup>  · Janete R. Matias<sup>4</sup>  · Fabricio F. S. Silva<sup>2</sup>  · Hugh W. Pritchard<sup>5</sup>  · Charlotte E. Seal<sup>5</sup> 

Magna S. B. Moura  
magna.moura@embrapa.br

Claudinéia R. Pelacani  
claudineiapelacani@gmail.com

Francislene Angelotti  
francislene.angelotti@embrapa.br

Tatiana A. Taura  
tatiana.taura@embrapa.br

Gilmar M. Oliveira  
gilmar\_5@hotmail.com

Jaciara S. Bispo  
jaciabispo@ymail.com

Janete R. Matias  
janete07@hotmail.com

Fabricio F. S. Silva  
fabriciofrancisco2006@gmail.com

Hugh W. Pritchard  
h.pritchard@kew.org

Charlotte E. Seal  
c.seal@kew.org

<sup>1</sup> Embrapa Semiárido, Caixa Postal 23, Rodovia BR-428, Km 152, Zona Rural, Petrolina 56302-970, PE, Brazil

<sup>2</sup> Universidade Estadual de Feira de Santana- UEFS, Feira de Santana, BA, Brazil

<sup>3</sup> Universidade do Estado da Bahia- UNEB, Juazeiro, BA, Brazil

<sup>4</sup> Universidade Federal Rural do Semiárido- UFERSA, Mossoró, RN, Brazil

<sup>5</sup> Department of Comparative Plant and Fungal Biology, Royal Botanic Gardens, Kew, Wakehurst Place, Ardingly, UK