



Germination response of palm seeds on a two-way thermogradient plate¹

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ABSTRACT

Palm trees are propagated almost exclusively by seeds and each species germinates under a certain temperature range. In this sense, the two-way thermogradient plate may be used to determine temperature limits for germination and seed response to temperature. The objective was to define the alternating temperature regime promoting higher and faster seed germination of *Carpentaria acuminata* and *Phoenix canariensis* palms using a two-way thermogradient plate. This equipment allowed 64 combinations of alternating and constant temperatures, ranging from 6.97 to 36.42 °C for *C. acuminata*, and 7.96 to 35.94 °C for *P. canariensis*. Seeds were sown in Petri dishes (25 x 9 cm) containing 1% water agar. Linear regressions were estimated to determine cardinal temperatures. After 50 days, non-germinated seeds were transferred from the two-way thermogradient plate to a germination chamber at 30 °C. The temperature regime promoting highest seed germination percentage of *C. acuminata* was 30.45/33.00 °C (day/night), with minimum, optimum, and maximum temperatures of 9.13, 28.53, and 36.33 °C, respectively. For seed germination of *P. canariensis*, the most appropriate temperature regime was 29.77/17.93 °C (day/night), with minimum, optimum, and maximum temperatures of 9.53, 28.03, and 35.43 °C, respectively.

Keywords: Arecaceae; cardinal temperatures; *Carpentaria acuminata*; palm propagation; *Phoenix canariensis*; temperature sensitivity.

INTRODUCTION

Palms belong to the Family Arecaceae that comprises more than 3,500 species from more than 240 genera, spread throughout the world, mainly in the tropical regions of Asia, Indonesia, the Pacific Islands, and the Americas (Lorenzi *et al.*, 2004). According to Uhl & Dransfield (1987), palms are distributed in virtually all tropical and subtropical regions, not occurring in desert or semi-desert areas, except when there is water near the surface, forming oases, with only few species occurring in temperate zones.

The carpentaria palm [*Carpentaria acuminata* (H. Wendl. & Drude) Becc.] originates from banks of rivers and streams in flooded forests of Northern Australia, while the Canary Island date palm (*Phoenix canariensis* Hort. ex Chabaud) comes from coastal areas of open vegetation on stony and dry terrains of the Canary Islands (Lorenzi *et al.*, 2010). Although exotic, both species are widely used in Brazilian landscaping (Batista *et al.*, 2016).

The propagation of palm trees is done, almost exclusive-

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ly, by seeds. However, germination is generally considered slow, uneven, and often low, with great variation along that process which is influenced by several factors, such as seed maturation degree, pericarp presence or absence, period between harvest and sowing, environmental temperature, and substrate (Broschat, 1994; Pivetta *et al.*, 2007; Viana *et al.*, 2016).

Among all, temperature is a critical environmental factor that regulates seed dormancy overcome and induces germination (Baskin & Baskin, 2014; El-Keblawy, 2017). Its effect at germination time affects the rate of water uptake by seeds and may alter, among others, germination percentage, speed, and uniformity (Bewley & Black, 1996; Carvalho & Nakagawa, 2000; Castro & Hilhorst, 2004). Therefore, there is a characteristic thermal range for each species, so values below or above minimum and maximum cardinal temperatures may turn seed germination impossible (Carvalho & Nakagawa, 2000). Moreover, within such range, the temperature also acts on the necessary time to reach maximum germination (Bewley & Black, 1985).

Seeds of certain species show better germinative behavior when submitted to temperature alternation corresponding to natural fluctuations found in the environment, with lower night and higher day temperatures; however, there are also species which seed germination is favored when submitted to constant temperatures (Copeland & McDonald, 1995; Salomão *et al.*, 1995; Lima *et al.*, 1997). Palm seeds usually germinate under a certain temperature range that may be defined by their place of origin, so the ultimate establishment of this amplitude is fundamental to define the possible geographic distribution of each species. Luz *et al.* (2008), for instance, indicate the temperature range of 25 to 30 °C for seed germination of *Dypsis decaryi*, while Wen (2019) recommends 20 to 30 °C for *Archontophoenix alexandrae* germination. Furthermore, Lorenzi *et al.* (2004) and Broschat (1994) suggest the ideal temperatures of 24 to 28 °C and 30 to 35 °C, respectively, for seed germination of several palm species.

In this sense, the two-way thermogradient plate, which is a bi-directional incubator, may generate data to determine the temperature limits for seed germination of many species; furthermore, it may be used for the development of germination temperature threshold models to assess the sensitivity of germination response to temperature (Manger, 1999).

The objective of this work was to define the alternating temperature regime promoting higher and faster seed ger-

mination of *Carpentaria acuminata* and *Phoenix canariensis* palms using a two-way thermogradient plate.

MATERIAL AND METHODS

The work was carried out at the Seed Conservation Department of the Millennium Seed Bank, Wakehurst, belonging to the Royal Botanic Gardens, Kew, and located in Ardingly, Sussex, UK. Seeds were taken from pulped fruits of carpentaria palm and Canary Island date palm obtained from a commercial company located in London, UK. Water content of the seed lots and embryos were $18.13 \pm 1.7\%$ and $19.12 \pm 2.1\%$, respectively, for carpentaria palm, and $10.32 \pm 1.3\%$ and $18.24 \pm 2.9\%$, respectively, for Canary Island date palm, determined by the oven method at 103 °C for 17 hours (ISTA, 2017).

The germination test was conducted according to the Millennium Seed Bank methodology. Therefore, seeds were washed in a 2% sodium hypochlorite solution for 10 minutes in gentle manual shaking, then washed three times in distilled water, and sown in Petri dishes (25 x 9 cm) containing 1% water agar. There were 20 seeds per Petri dish for each temperature on the two-way thermogradient plate, and 64 temperature combinations for each species.

The Petri dishes were placed on the two-way thermogradient plate in an 8 x 8 factorial scheme. The two-way thermogradient plate was set with two temperature gradients that could vary from 4 to 40 °C. The equipment then ranged from 6.97 to 36.42 °C for Carpentaria palm, and from 7.96 to 35.94 °C for Canary Island date palm, with a 12-hour photoperiod (50-100 W m⁻² light photon flow) in one direction during the day and over the same temperature range in the perpendicular direction at night. Alternating temperatures (day/night) promoted a constant temperature line from the lower left (always cold) to the upper right corner (always hot) (Figure 1).

The equipment then allowed for seed germination testing under a wide range of constant and alternating temperature regimes over time, resulting in 64 temperature combinations (regimes), with eight constant temperatures and 76 alternating temperatures; each combination represented a temperature regime (alternating and/or constant) with no replication. However, for statistical analysis, the germination results of both palm species were grouped into some temperature combinations to obtain the replicates. Eight groups of eight replicates were used for the analysis, considering temperature extreme and central conditions, with up to 5 °C difference among replications.

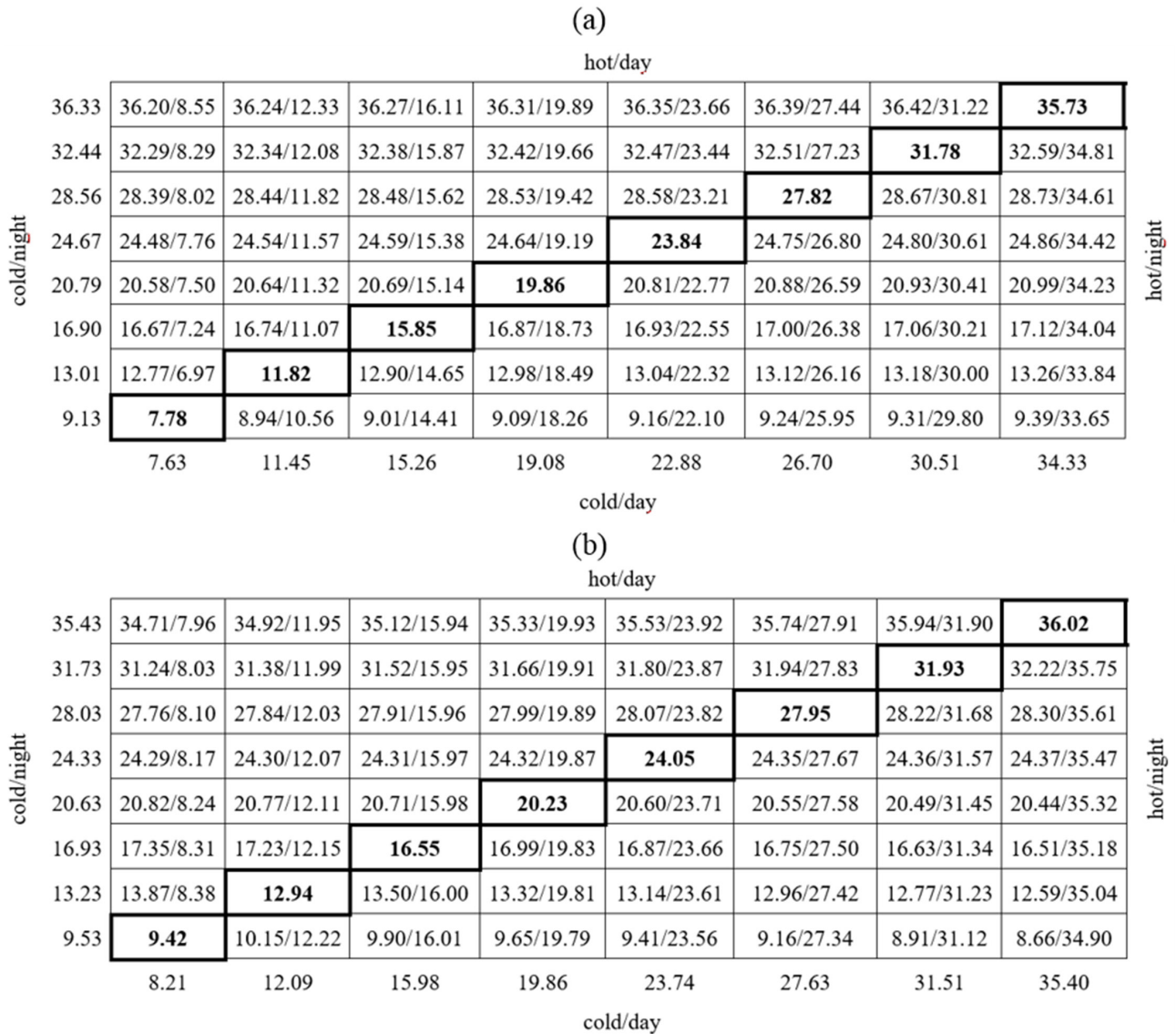


Figure 1: Temperature distribution on the two-way thermogradient plate used to evaluate seed germination response of Carpentaria palm (*Carpentaria acuminata*) (a) and Canary Island date palm (*Phoenix canariensis*) (b) along 50 days.

Seed germination was evaluated based on the emission of the germinative bud, every two days, for 50 days. Germination proportion was then plotted to produce a contour map of the 'landscape' germination to highlight optimal conditions for germination. Mean germination percentage was also calculated for the constant temperatures, i.e., from the lower left corner of the plate (always cold) to the upper right corner of the plate (always hot). Germination rate was also evaluated, expressed as $1/T_{50}$, which is the time, in days, to reach 50% of the final germination percentage. Linear regressions were estimated using the germination rate values to determine base and maximum temperatures (T_b and T_m , respectively) (Covell *et al.*, 1986). The optimal

temperature (T_o) was estimated by the intersection between these two regression lines (Hardegree, 2006).

In addition, at the end of the experiment, seeds that did not germinate on the two-way thermogradient plate were transferred to a germination chamber type BOD, at 30 °C with a 12-hour photoperiod, to verify whether the extreme temperatures (either low or high) caused any harm in the seeds.

Germination percentage data were transformed into arcsine and submitted to the variance analysis, and means were compared by the Tukey test ($P \leq 0.05$). The Sigma Plot 9.0 (Sigma Plot, 2004) software was used to plot the combination of the germination data with temperature regimes.

RESULTS

Both species germinated under a great temperature range on the two-way thermogradient plate. However, seeds under low temperature regimes did not germinate, i.e., those placed near the lower left corner (always cold), with temperatures close to 7.78 °C for *Carpentaria* palm (Figure 2) and 9.42 °C for Canary Island date palm (Figure 3).

The main germination range of *Carpentaria* palm at the alternating temperatures was concentrated between 24 and 34 °C during the day and 10 and 36 °C overnight. At constant temperatures, it occurred mainly between 20 and 36 °C (Figure 2a). Seeds germinated faster under warmer temperatures, especially when it was always warm (on the upper right corner) (Figure 2b).

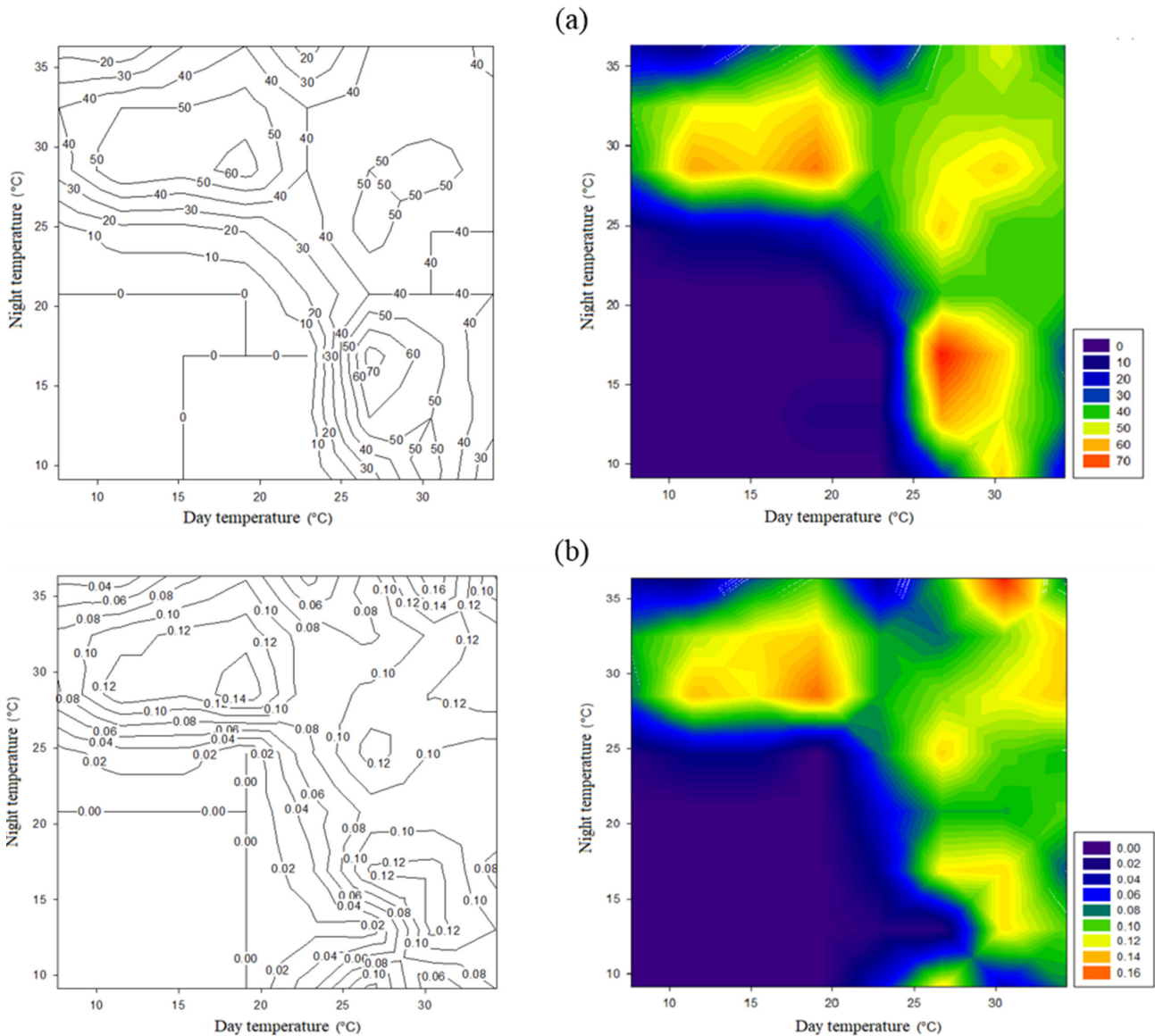


Figure 2: Germination percentage (%) (a) and germination rate ($1/T_{50}$) (days^{-1}) (b) of *Carpentaria* palm (*Carpentaria acuminata*) seeds on the two-way thermogradient plate with a 12-hour photoperiod along 50 days [numbers and colors indicate germination percentage (a) and germination rate (b); curves show limits among results obtained in the contour maps].

The main germination range of Canary Island date palm seeds at the alternating temperatures was concentrated from 22 to 35 °C during the day and from 10 to 35 °C overnight. At constant temperatures, it occurred mostly between 18 and 35 °C. There was 100% germination at the alternating

temperatures varying from 24 to 32 °C during the day and at 22 °C overnight (Figure 3a). Seeds also germinated faster under warmer temperatures, especially at the alternating temperatures of 24 to 32 °C during the day and 27 to 32 °C at night (Figure 3b).

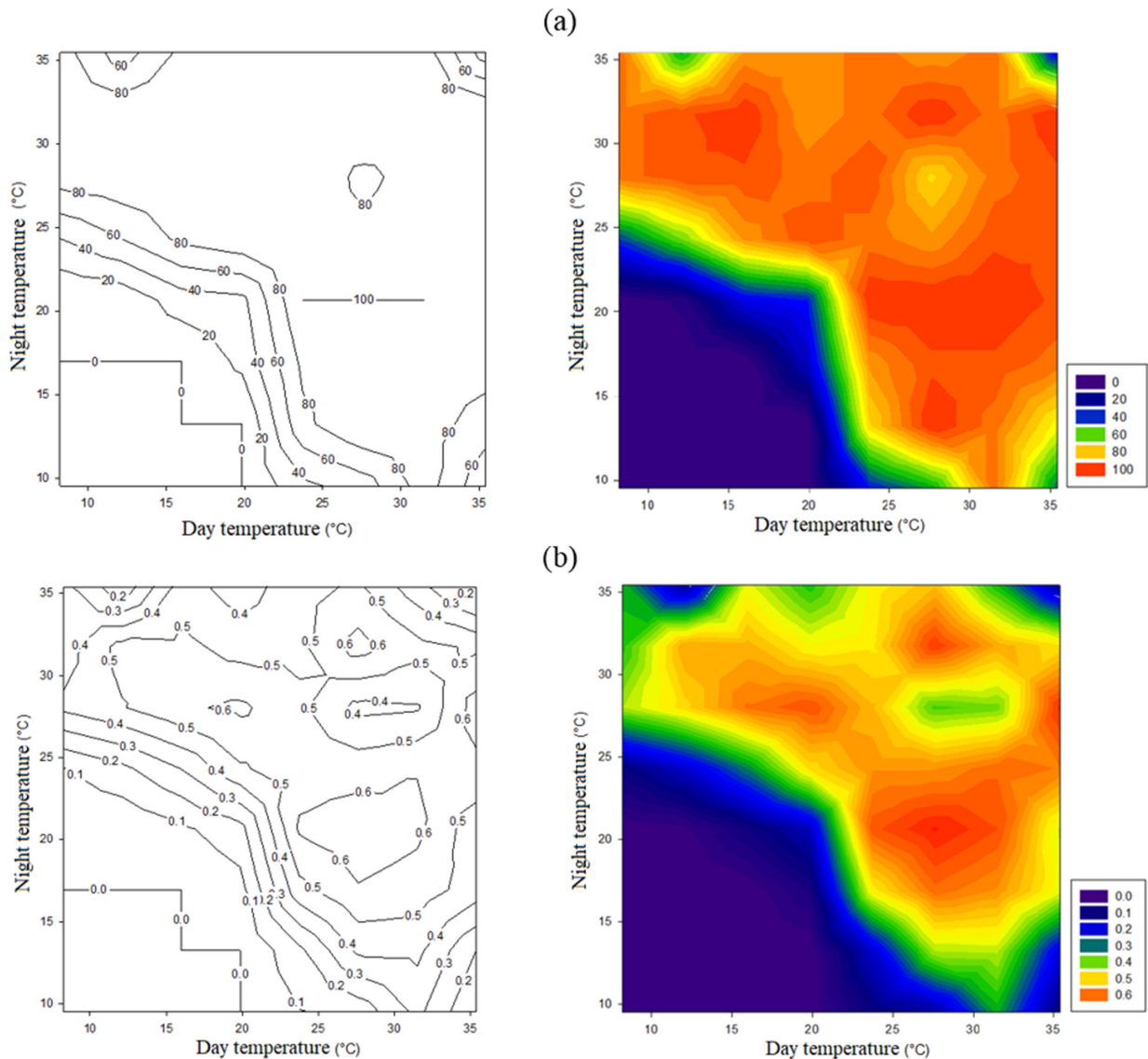


Figure 3: Germination percentage (%) (a) and germination rate ($1/T_{50}$) (days^{-1}) (b) of Canary Island date palm (*Phoenix canariensis*) seeds on the two-way thermogradient plate with a 12-hour photoperiod along 50 days [numbers and colors indicate germination percentage (a) and germination rate (b); curves show limits among results obtained in the contour maps].

There was a significant difference among the temperature amplitudes for germination percentage of Carpentaria palm seeds (Figure 4). The highest value ($41.75 \pm 2.63\%$) was observed at the alternating temperature of 30.45°C during the day and 33°C at night, which did not differ from the alternating temperatures of $31.20/9.83$, $30.45/17.64$, $30.39/25.43$, $15.02/24.35$, and $15.15/32.02^\circ\text{C}$ (day/night). There was no germination under the alternating temperatures of $14.49/9.28$ and $14.65/16.92^\circ\text{C}$ (day/night) (Figure 4a). Seeds also germinated faster at the alternating temperature of 30.45°C during the day and 33°C at night, which did not differ from the alternating temperatures of $30.45/17.64$, $30.39/25.43$, and $15.15/32.02^\circ\text{C}$ (day/night) (Figure 4b).

Similarly, a significant difference was observed among

temperature ranges for both germination percentage and germination rate of Canary Island date palm seeds (Figure 5). The highest germination percentage ($73.07 \pm 6.23\%$) was observed at the alternating temperature of 29.77°C during the day and 17.93°C at night, which did not differ from the alternating temperatures of $29.55/10.04$, $29.93/25.88$, $30.17/33.74$, $14.77/29.37$, and $14.62/33.20^\circ\text{C}$ (day/night) (Figure 5a). No germination was observed at the alternating temperatures of $15.32/10.47$ and $15.11/18.02^\circ\text{C}$ (day/night). The highest germination rate occurred at the alternating temperature of 29.93°C during the day and 25.88°C at night, which did not differ from the alternating temperatures of $29.55/10.04$, $29.77/17.93$, $30.17/33.74$, $14.77/29.37$, and $14.62/33.20^\circ\text{C}$ (day/night) (Figure 5b).

(a)

Night temperature (°C)	36.33	29.79 ± 11.79% 31.20/9.83 °C (a)	39.53 ± 9.00% 30.45/17.64 °C (a)	38.97 ± 4.72% 30.39/25.43 °C (a)	41.75 ± 2.63% 30.45/33.00 °C (a)					
	32.44									
	28.56									
	24.67									
	20.79	0% 14.49/9.28 °C (b)	0% 14.65/16.92 °C (b)	27.44 ± 17.56% 15.02/24.35 °C (a)	36.97 ± 8.00% 15.15/32.02 °C (a)					
	16.90									
	13.01									
	9.13									
		7.63	11.45	15.26	19.08	22.88	26.70	30.51	34.33	
Day temperature (°C)										

(b)

Night temperature (°C)	36.33	0.064 ± 0.039 31.20/9.83 °C (b)	0.093 ± 0.043 30.45/17.64 °C (a)	0.085 ± 0.018 30.39/25.43 °C (a)	0.117 ± 0.024 30.45/33.00 °C (a)					
	32.44									
	28.56									
	24.67									
	20.79	0 14.49/9.28 °C (c)	0 14.65/16.92 °C (c)	0.062 ± 0.039 15.02/24.35 °C (b)	0.092 ± 0.021 15.15/32.02 °C (a)					
	16.90									
	13.01									
	9.13									
		7.63	11.45	15.26	19.08	22.88	26.70	30.51	34.33	
Day temperature (°C)										

Figure 4: Germination percentage (a) and germination rate ($1/T_{50}$) (days⁻¹) (b) of *Carpentaria palm* (*Carpentaria acuminata*) seeds on the two-way thermogradient plate with a 12-hour photoperiod along 50 days – each cell represents the mean of eight alternating and constant temperatures (Different letters indicate statistical difference among temperatures by the Tukey test at 1% significance).

(a)

Night temperature (°C)	35.43	62.98 ± 13.49% 29.55/10.04 °C (a)	73.07 ± 6.23% 29.77/17.93 °C (a)	72.02 ± 5.76% 29.93/25.88 °C (a)	71.14 ± 9.48% 30.17/33.74 °C (a)					
	31.73									
	28.03									
	24.33									
	20.63	0% 15.32/10.47 °C (b)	0% 15.11/18.02 °C (b)	69.44 ± 17.32% 14.77/29.37 °C (a)	69.72 ± 10.13% 14.62/33.20 °C (a)					
	16.93									
	13.23									
	9.53									
		8.21	12.09	15.98	19.86	23.74	27.63	31.51	35.40	
Day temperature (°C)										

(b)

Night temperature (°C)	35.43	0.316 ± 0.137 29.55/10.04 °C (a)	0.472 ± 0.083 29.77/17.93 °C (a)	0.513 ± 0.057 29.93/25.88 °C (a)	0.462 ± 0.132 30.17/33.74 °C (a)					
	31.73									
	28.03									
	24.33									
	20.63	0 15.32/10.47 °C (b)	0 15.11/18.02 °C (b)	0.394 ± 0.194 14.77/29.37 °C (a)	0.389 ± 0.135 14.62/33.20 °C (a)					
	16.93									
	13.23									
	9.53									
		8.21	12.09	15.98	19.86	23.74	27.63	31.51	35.40	
Day temperature (°C)										

Figure 5: Germination percentage (a) and germination rate ($1/T_{50}$) (days⁻¹) (b) of *Canary Island date palm* (*Phoenix canariensis*) seeds on the two-way thermogradient plate with a 12-hour photoperiod along 50 days – each cell represents the mean of eight alternating and constant temperatures (Different letters indicate statistical difference among temperatures by the Tukey test at 1% significance).

According to the models obtained, the optimal temperature for seed germination of *Carpentaria* palm is 28.53 °C, with minimum temperature of 9.13 °C and maximum of 36.33 °C. For Canary Island date palm, the optimum temperature for seed germination is 28.03 °C, with minimum of 9.53 °C and maximum of 35.43 °C.

Seeds of *Carpentaria* palm that did not germinate under cold temperatures [alternating temperatures of 14.49/9.28 and 14.65/16.92 °C (day/night) – lower right corner of the two-way thermogradient plate] did achieve germination

when transferred to the constant temperature of 30 °C, considered close to the ideal, which is 28.53 °C; there was then 10 to 40% germination (Figure 6).

Similar effect was observed for Canary Island date palm seeds, which did not germinate under colder temperatures [alternating temperatures of 15.32/10.47 and 15.11/18.02 °C (day/night) – lower right corner of the two-way thermogradient plate]; when transferred to the constant temperature of 30 °C, which is close to the ideal (28.03 °C), presented 80% germination (Figure 7).

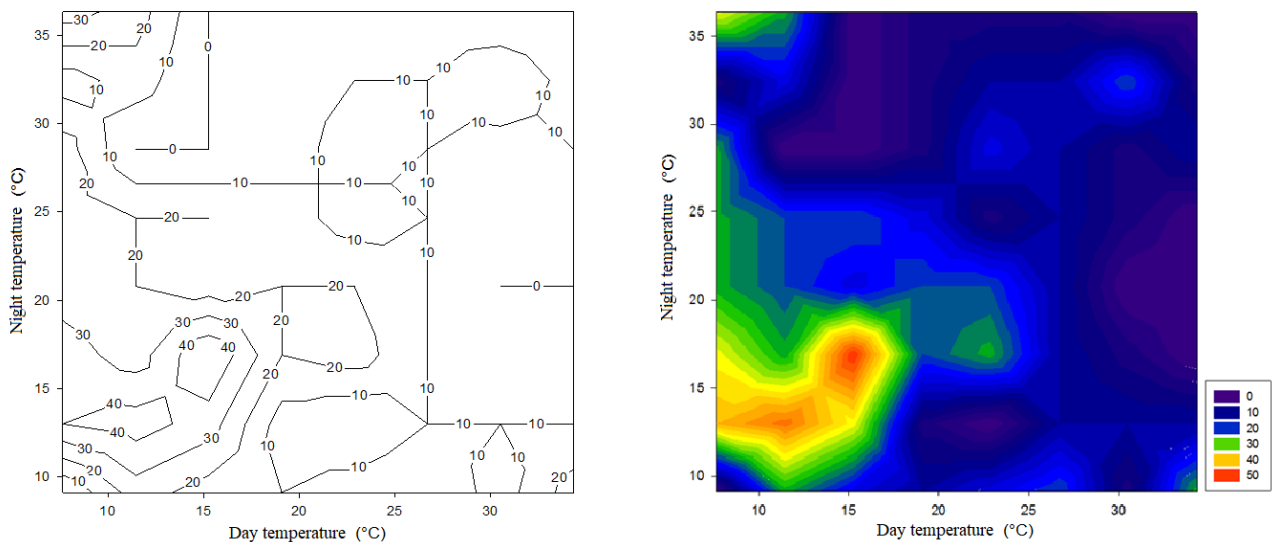


Figure 6: Germination percentage (%) of *Carpentaria* palm (*Carpentaria acuminata*) seeds in the BOD incubator at 30 °C with a 12-hour photoperiod [numbers and colors indicate germination percentage; curves show limits among results obtained in the contour maps].

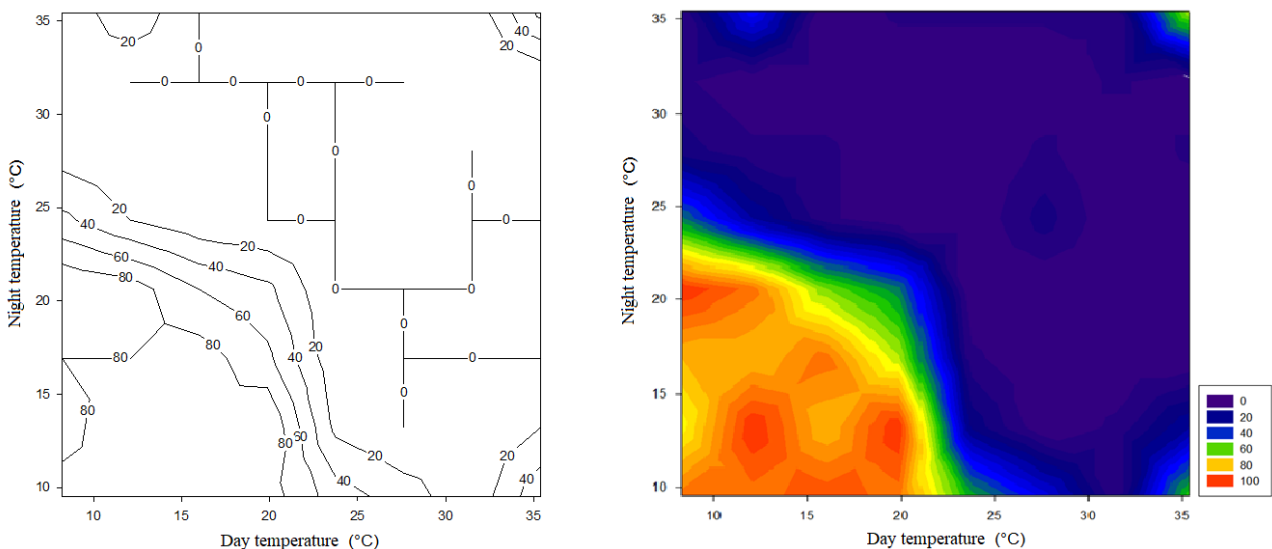


Figure 7: Germination percentage (%) of Canary Island date palm (*Phoenix canariensis*) seeds in the BOD incubator at 30 °C with a 12-hour photoperiod [numbers and colors indicate germination percentage; curves show limits among results obtained in the contour maps].

Cold temperatures were not lethal to seeds of both *Carpentaria* palm and Canary Island date palm, even when exposed to low temperatures for 50 days, as they did germinate when submitted to the warmer, possibly ideal, temperature.

DISCUSSION

Seeds of *Carpentaria* palm and Canary Island date palm germinated at different temperature regimes following their, respectively, tropical and subtropical origin that determines the ideal temperatures for germination. Seeds of both species did not germinate under cold temperatures (lower left corner of the two-way thermogradient plate) but did germinate under hot temperatures (upper right corner of the two-way thermogradient plate) or when seeds were placed under 30 °C after such cold period. However, Orozco-Segovia *et al.* (2003) report that some subtropical species do not require high temperatures for germination and, also, some even needs a period of cool temperature to reach highest germination. Nevertheless, He *et al.* (2021) mention that, for Canary Island date palm, seed germination happens when dormancy is released by a cold stratification in the soil over winter.

Sandoval (2011), when studying temperature regimes from 5.8 to 36.3 °C for seed germination of *Browningia candellaris* on the two-way thermogradient plate, also observed that there was either no germination under extreme temperatures or it was very low. Similarly, Asomaning *et al.* (2010) reported that seeds of *Khaya anthotheca*, when submitted to temperature ranges from 5 to 40 °C on the two-way thermogradient plate, did not germinate under extreme temperatures.

Seeds of both species presented an optimum temperature for germination of approximately 28 °C, either constant or alternating, although constant high temperatures may not be always appropriate for palm seed germination (Orozco-Segovia *et al.*, 2003). Nevertheless, it has been proven by several authors that temperatures close to this are favorable for seed germination of many palm species, such as 25 °C for *Syagrus coronata* (Porto *et al.*, 2018) and *Copernicia prunifera* (Reis *et al.*, 2010), 30 °C for *Oenocarpus minor* (Silva *et al.*, 2006) and *Elaeis guineensis* (Norsazwan *et al.*, 2016), or 25-30 °C for *Dypsis decaryi* (Luz *et al.*, 2008). Furthermore, close temperatures may even be applied before germination to overcome dormancy, as reported by Ferreira & Gentil (2017) for *Phytelephas macrocarpa* seeds maintained under 25 °C for nine months

without losing viability. Therefore, high temperatures may be necessary to overcome seed dormancy of many species (Orozco-Segovia *et al.*, 2003).

Lorenzi *et al.* (2004), for example, mention that temperatures between 24 and 28 °C are considered favorable for seed germination of several palm species, while Broshat (1994) observed that many palm seeds germinate better at 30 to 35 °C. Constant temperatures of about 30 °C also promoted seed germination of eight tropical palm species of *Phoenix* and *Syagrus* genera (Pritchard *et al.*, 2004). Similarly, seeds of four species of *Ravenea* germinated rapidly at 30 °C (Rakotondranony *et al.*, 2004).

As seeds of palm species are considered recalcitrant, Roberts (1973) and Sarasan *et al.* (2002) report that seeds shall not be exposed to low temperatures because of viability losses would occur from only few weeks to few months. This is due to high humidity present in the seeds, so cell freezing may occur and, consequently, cell disintegration, hindering germination. However, this effect may also be related to the characteristic seed dormancy of each palm species but, as reported by Orozco-Segovia *et al.* (2003), mechanisms of both seed germination and dormancy are yet poorly understood for many palms. For both *Carpentaria* palm and Canary Island date palm, cold temperatures were not lethal.

The low water content found in seeds of both *Carpentaria* palm and Canary Island date palm ($18.13 \pm 1.7\%$ and $10.32 \pm 1.3\%$, respectively) probably prevented seed degradation. However, for many palm species, such low water content is considered critical, but these seeds have been reported to be tolerant to desiccation, that is, the low seed water content does not affect germination (Batista *et al.*, 2016).

CONCLUSIONS

The temperature regime promoting highest seed germination percentage of *Carpentaria* palm (*Carpentaria acuminata*) was 30.45/33.00 °C (day/night), with minimum, optimum, and maximum temperatures of 9.13, 28.53, and 36.33 °C, respectively. For practical purposes, the alternating temperature of 31/33 °C (day/night) may be recommended.

For seed germination of Canary Island date palm (*Phoenix canariensis*), the most appropriate temperature regime was 29.77/17.93 °C (day/night), with minimum, optimum, and maximum temperatures of 9.53, 28.03, and 35.43 °C, respectively. For practical purposes, the alternating

temperature of 30/18 °C (day/night) may be recommended.

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