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Thermal requirements of seed germination of ten tree species occurring in the western Brazilian Amazon

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Abstract

Regeneration from seed affects species assembly in plant communities, and temperature is the most important environmental factor controlling the germination process. Thermal dependence of seed germination is thus associated with species occurrence in an ecosystem. Hence, we aimed to investigate the role of temperature on seed germination of ten tree species from the western Brazilian Amazon. Seeds were collected in the state of Rondônia, Brazil, and set to germinate under constant temperatures ranging from 10 to 40°C in germination chambers. We calculated germination capacity (G%), germination rate (GR_{50}, reciprocal of germination time), and thermal parameters, such as cardinal temperatures and thermal time requirements. Most species had a large range of temperatures showing G% ≥80%, with optimal temperature varying from 20 to 40°C. Base temperature ranged from 6 to 12°C and ceiling temperatures were mainly >40°C. *Astronium lecointei* and *Parkia nitida* showed high germination capacity under temperatures of 35–40°C, while germination of *Theobroma cacao* dropped from 100% to zero under temperatures between 37 and 40°C. The climax species *Cedrela fissilis* had the slowest germination time (10 days) and highest thermal time requirement, while seeds of *Enterolobium schomburgkii* (a late-successional species) germinated within the first day of the experiment. Rapid recruitment of Amazon species could be favoured with treefall disturbance, which increases temperatures in the understory, but sharp limits might be found in the supra-optimal range of temperatures. Such patterns might indicate different regeneration strategies in the tropical rainforest, providing important information regarding seed germination among Amazon species.

Introduction

Seed germination is a critical part of the regeneration niche, which affects species assembly in plant communities (Grubb, 1977; Poschlod *et al.*, 2013). Temperature is the most important environmental factor governing the capacity and speed of the germination process in the presence of water (Probert, 2000; Bewley *et al.*, 2013). Therefore, thermal niche breadth of germination seems to be related to species occurrence across different ecosystems (e.g. Ranieri *et al.*, 2012; Marques *et al.*, 2014; Rosbakh and Poschlod, 2015; Tudela-Isanta *et al.*, 2018; Picciau *et al.*, 2019). Such 'temperature window' describes seed germination of a given species or population (Labouriau, 1978; Alvarado and Bradford, 2002), thus bounding the limits of the regeneration niche (Thompson *et al.*, 1999; Porceddu *et al.*, 2013).

Temperatures which combine maximal germination capacity (G%) and higher germination rate (GR, reciprocal of germination time) comprise an optimal range, splitting the temperature window into sub- and supra-optimal ranges (Bradford, 2002; Bewley *et al.*, 2013). Hence, the base temperature (T_b) is the sub-optimal limit under which there is no growth, while the ceiling temperature (T_c) marks the supra-optimal limit in which germination ceases because temperatures are too high (Garcia-Huidobro *et al.*, 1982). Within this context, it is mandatory to better understand the thermal limits of germination, especially as seed and germination traits are still under-studied in most plant communities (Jiménez-Alfaro *et al.*, 2016). In Brazil, there is a large knowledge gap regarding seed ecology and germination traits, mainly among Amazon species (Ribeiro *et al.*, 2016).

Thermal limits of seed germination seem to vary between 10 and 40°C in tropical forest species throughout the world (Larcher, 2000; Dürr *et al.*, 2015). Nevertheless, few studies have investigated such limits using controlled temperatures with seeds of Amazon species (Ferraz and Varela, 2003; Bastos *et al.*, 2017; Amoêdo and Ferraz, 2019), although some have addressed this issue under greenhouse uncontrolled conditions (Silva *et al.*, 1988; Moreira and Moreira, 1996). There are many factors limiting seed collection in the region, including the difficult access to native populations and technical restrictions to reach fresh-dispersing propagules in the forest canopy. Moreover, botanical identification can be challenging in such a diverse ecosystem, thus limiting ecophysiological research, including seed germination studies. Despite the generalized difficulties, light requirements have been studied in Amazon seeds (Aud and Ferraz, 2012) as well as morphology of seed and seedlings (Camargo *et al.*, 2008; Ramos and Ferraz, 2008; Ferraz *et al.*, 2012).

Thermal time (θ) requirements for seed germination, which can be defined as the amount of 'thermal energy' a seed population requires to reach a certain percentage of germination (usually 50%; see Trudgill *et al.*, 2005), has never been investigated in Brazilian Amazon species. Theoretically, the environmental temperature is accumulated over time, reaching temperatures above the base temperature threshold (T_b) which is intrinsic to each species. Hence, θ requirements can be used to establish comparisons among species and/or populations (e.g. Covell *et al.*, 1986; Daibes and Cardoso, 2018), as well as modelling seedling emergence and seed dormancy alleviation (Forcella *et al.*, 2000; Bradford, 2005; Orrù *et al.*, 2012).

We aimed to investigate the role of temperature on seed germination of ten tree species occurring in the western Brazilian Amazon. To do so, we carried out germination trials with non-dormant seeds (scarifying them if necessary) under a range of constant temperatures. Specifically, we assessed (1) seed germination (G% and germination rate) under different constant temperatures and (2) parameters of seed germination (cardinal temperatures and thermal time requirement), which allows comparisons among species. We hypothesized that germination would show a high percentage and a rapid rate, favouring seedling recruitment in the moist understory. We also expected that thermal parameters would differ among species, which could further explain their coexistence in the Amazon forest.

Materials and methods

Seed collection

Seeds were collected in non-flooded forest areas in the western Brazilian Amazon, mostly in the *Floresta Nacional (Flona) do Jamari*, state of Rondônia (Table 1). These forest areas are characterized by a closed and tall canopy rich in woody species. The species used in this study are mostly legume trees with a height of 15 to 40 m. Mature fruits of five to ten individuals per species were collected and taken to the laboratory where seeds were removed from fruits and screened in order to discard malformed and/or predated seeds. Seeds were then stored under laboratory conditions for a few months prior to the germination trials, except for *Theobroma cacao*, which produces recalcitrant seeds (Venial *et al.*, 2017) and thus germination trials were set up immediately after these seeds were harvested.

All studied species have a broad distribution across the Amazon basin. One species (*T. cacao*) is cultivated in South and Central America and three species (*Apuleia molaris*, *Cedrela fissilis* and *Senna multijuga*) also occur throughout most of the Brazilian territory. According to the literature, the species used in this study are considered as successional species (Ferraz *et al.*, 2004; Amaral *et al.*, 2009). Seed size was classified from information extracted from the literature and based on the criteria established by Cornejo and Janovec (2010) (Table 1). The forest areas sampled show a tropical rainy climate, similar to most areas across the Amazon basin (see Bastos, 1982), with a mean annual temperature of 25°C, minimum temperature of 18°C, maximum temperature >30°C (Bastos and Diniz, 1982), and a mean annual precipitation that can reach over 2000 mm (INMET, 1961–1990). Rainfall is well distributed throughout the year but may be reduced during drier months, from June to August (Marengo *et al.*, 2001).

Germination trials

For all species, germination trials were conducted under 10 constant temperatures (10, 13, 15, 17, 20, 25, 30, 35, 37 and 40°C) in different germination chambers under constant white light, except for *Enterolobium schomburgkii*, in which experiments at 35 and 37°C were not carried out due to restraints in seed availability. Number of replicates varied between four and five, and number of seeds per replicate varied from 20 to 50 seeds (Table 1). For the germination experiments, seeds were placed in plastic boxes with two layers of filter paper saturated with distilled water. Germination was determined by protrusion of the primary root (Bewley *et al.*, 2013) and experiments were monitored daily for 30 days. By the end of the trials, non-germinated seeds were visually inspected to assure they were unviable and thus counted as dead.

Some of the study species (legumes, see Table 1) had impermeable seed coats (physical dormancy; see Baskin *et al.*, 2000) and physical dormancy was confirmed by preliminary germination tests where seeds showed no signs of imbibition. Thus, seeds of these species were mechanically scarified with sandpaper prior to the germination experiments, except for *A. molaris*, in which seeds were chemically scarified with sulfuric acid for two minutes.

Germination thermal parameters

Germination capacity (G%) was determined as the proportion of germinated seeds in relation to the total number of seeds sown in the plastic boxes. In addition, we calculated the germination time (t_{50}) and the germination rate (GR, i.e. inverse of germination time) for 50% of germinated seeds at each temperature for each species. Germination time and germination rate were also calculated separately only for the replicates in which G% reached 50%, even though the mean of G% might not reach 50% in some exceptional cases. To calculate germination time, we used a linear interpolation between two points of the cumulative germination curve around the desired percentage of germination (G% = 50) from the *y*-axis and used a line equation to calculate the estimated time (t_{50}) from the *x*-axis (Steinmaus *et al.*, 2000; Soltani *et al.*, 2015). We established two optimal temperature ranges: one considering high G% (values over 80%) and one considering the highest GR_{50} (lowest t_{50}) combined with a high G%, which usually delimits a sub- and a supra-optimal range. Thus, best germination times (t_{50}) were assigned as the lowest numerical value of t_{50} (days) within the optimal G% range.

We used regression analysis to examine the association between GR_{50} and temperatures. The base temperature (T_b) was then calculated as the point in which the regression line touches

Table 1. Study species, family, distribution, successional status, population origin (native or cultivated) and number of seeds per replicate

Species	Family	Successional status	Species distribution	Seed size	Population origin	Locality	Collection date	Scarified seeds	*N* seeds/ replicate
Apuleia molaris Spruce ex Benth.	Leguminosae	Early succession	Widespread	S[1]	Native	Flona Jamari	May 2011	Yes	50 × 4
Astronium lecointei Ducke	Anacardiaceae	Late succession	Amazon	L[2,3]	Native	Flona Jamari	June 2010	No	20 × 5
Cedrela fissilis Vell.	Meliaceae	Climax	Widespread	L[4,5]	Native	Flona Jamari	July 2010	No	20 × 5
Enterolobium schomburgkii (Benth.) Benth.	Leguminosae	Late succession	Amazon/ Cerrado	S-M[6,7]	Native	Flona Jamari	June 2010	Yes	50 × 5
Parkia multijuga Benth.	Leguminosae	Late succession	Amazon	L[8,9]	Native	Flona Jamari	Nov 2010	Yes	25 × 4
Parkia nitida Miq.	Leguminosae	Late succession	Amazon	M-L[8–10]	Native	Flona Jamari	Oct 2010	Yes	25 × 4
Schizolobium amazonicum Huber ex Ducke	Leguminosae	Pioneer	Amazon	M-L[11,12]	Native	Flona Jamari	May 2011	Yes	20 × 5
Senna multijuga (Rich.) H.S.Irwin & Barneby	Leguminosae	Pioneer	Widespread	S[13,14]	Urban garden	UNIR campus	Aug 2010	Yes	20 × 5
Stryphnodendron guianense (Aubl.) Benth.	Leguminosae	Pioneer	Amazon/ Caatinga	S[15]	Native	UNIR campus	Aug 2010	Yes	50 × 5
Theobroma cacao L.	Malvaceae	Early succession	Widespread	L[16]	Cultivated	Ouro Preto do Oeste	Dec 2011	No	25 × 4

[1]Reis *et al.* (2016); [2]Ferraz *et al.* (2004); [3]Cornejo and Janovec (2010); [4]Pereira *et al.* (2017); [5]Angeli *et al.* (2005); [6]Ramos and Ferraz (2008); [7]Bonadeu and Santos (2013); [8]Camargo *et al.* (2008); [9]Carvalho (2009); [10]Díaz-Bardales (2001); [11]Souza *et al.* (2003); [12]Braga *et al.* (2013); [13]Amorim *et al.* (2008); [14]Carvalho (2004); [15]Freitas *et al.* (2014); [16]Venial *et al.* (2017). Successional status was classified according to Ferraz *et al.* (2004) and Amaral *et al.* (2009). Species distribution was classified according to the vegetation domain described in *Flora do Brasil* 2020 (http://floradobrasil.jbrj.gov.br). Seed size was classified from the literature (see below), following the criteria proposed by Cornejo and Janovec (2010) that is based on seed length: S = small = 0.5–0.99 cm; M = medium = 1–1.99 cm; L = large ≥ 2 cm. Approximate GPS coordinates of sites where seeds were collected: Flona Jamari (9°0′S; 62°44′W); UNIR campus (8°50′S; 63°56′W); Ouro Preto do Oeste (10°44′S; 62°12′W).

the *x*-axis ($y = 0$), thus ceasing the germination process (Steinmaus *et al*., 2000). Thermal time (θ_T) requirement was calculated as the reciprocal of the slope (1/b values) in the regression lines in the sub-optimal range (Garcia-Huidobro *et al*., 1982; Bradford, 2002). Ceiling temperatures (T_c) could not be precisely obtained mostly due to the small number of points found in the supra-optimal range. Therefore, T_c values were estimated based on which temperature G% was reduced to below 5%.

Data analysis

We used linear models to evaluate how temperatures affected seed germination for each species separately, considering a significance level of $\alpha = 0.05$. Linear models were carried out with the *lme4* package (Bates *et al*., 2015) in R software version 3.2.5 (R Core Team, 2016). *Post-hoc* Tukey's tests were performed to evaluate multiple comparisons among temperatures using the *multcomp* package (Hothorn *et al*., 2008). Likewise, we used regression analysis and linear models to evaluate how the different temperatures affected GR_{50} for each species. T_b, θ_{50} and optimal t_{50} values were compared between species using linear models after log transformations to fit model assumptions.

Results

For all species, there was a wide range of temperatures at which germination reached 80–100% (Fig. 1). All species showed germination ≤60% under the lowest temperature tested (10°C), except for *E. schomburgkii*, which already had germination of over 80% at this treatment. Most species started to show high germination percentages at 13°C; however, *Parkia* spp. required 17°C and *A. molaris* required 20°C to reach G% ≥80%. Regarding the hotter temperatures tested, only *C. fissilis* showed reduced germination (56%) at 30°C, while the other species showed reduced germination only at 37–40°C. Nevertheless, seeds of three species kept high germination at 40°C: *Astronium lecointei* (82%), *Parkia nitida* (81%) and *Schizolobium amazonicum* (71%).

Therefore, considering G%, *A. lecointei* displayed the broader range of optimal temperatures, ranging from 13 to 40°C. The optimal range for *S. amazonicum* and *T. cacao* was from 13 to 37°C, while *S. guianense* and *S. multijuga* showed higher G% from 13 to 35°C. The species with the shorter optimal range was *A. molaris* (from 20 to 35°C) and *C. fissilis* (from 13 to 25°C) (Fig. 1; Table 2). GR values showed a more specific thermal dependence, increasing linearly with temperature up to an optimal point or range (Fig. 1). *Astronium lecointei* and *P. nitida* maintained a high G% and relatively high GR_{50} even under 40°C. For these two species, GR_{50} increased with increasing temperatures. A similar pattern was found in *T. cacao*, with increased GR_{50} up to 37°C, but at 40°C germination abruptly declined to zero (Fig. 1).

The shortest germination times (lowest numerical value of t_{50}, in days) were found under the temperatures of 20 to 37°C. In the hottest temperatures, *P. nitida* and *T. cacao* showed the fastest germination times (t_{50}) under 37°C, while *A. lecointei* and *P. multijuga* exhibited fastest t_{50} under 35°C (Table 2). For most species, t_{50} varied between 2 and 4 days. Only *C. fissilis* showed a slower germination time ($t_{50} = 10$ days at 20°C), contrary to *E. schomburgkii*, for which 50% of seeds germinated within 1 day of the experiment (Table 2). Likewise, thermal time requirement (θ_{50}) varied from 32 to 75°C.days in all species, except for *C. fissilis*, which showed $\theta_{50} = 157$°C.days, and *E. schomburgkii*, which showed the lowest θ requirement ($\theta_{50} = 19$°C.days, see Table 2).

Most values of base temperature (T_b) varied from 7.2 to 9.5°C (Table 2), not differing among each other. The only difference was found between *A. molaris*, which had the highest T_b value (12.7°C), in relation to *C. fissilis* and *P. nitida* (both with T_b ~6°C, see Table 2). Ceiling temperatures (T_c) could not be precisely determined due to small number of temperatures falling in the supra-optimal range. Nevertheless, most species were tolerant to the hotter temperatures tested and would show T_c values >40°C, given that they still germinated more than 30% under the hottest treatment (Fig. 1; Table 2). *Senna multijuga*, *S. guianense* and *T. cacao* showed T_c limits around 40°C, temperature at which G% was nearly zero. For *A. molaris* and *C. fissilis*, germination was close to zero at 37°C.

Discussion

In the forest understory, temperatures may vary from 20 to 30°C (Benítez-Malvido and Martínez-Ramos, 2003). However, forest gap openings alter the microclimate, enhancing sunlight availability and temperatures (Denslow, 1980; Chazdon and Pearcy, 1991; Pearson *et al*., 2002). Our data show that seeds maintain high G% and low germination times under a wide range of temperatures, with most optimal temperatures varying from 20 to 40°C (see also Ferraz and Varela, 2003). Although temperature is a fundamental aspect of niche breadth (Thompson *et al*., 1999), our studied species do not seem to be particularly demanding with regard to their thermal requirements. Therefore, temperatures found in the forest would not be a limiting factor for seed recruitment. Cooler temperatures might cause a decrease in germination time, but G% is maintained >80% for most species, even under 13°C. Even though Amazon seeds rarely face temperatures below 20°C, their base temperature is around 9°C. However, such values are higher than T_b found in temperate species, which face severe winters and tolerate temperatures close to zero (Dürr *et al*., 2015). Under hotter conditions, T_c values were commonly higher than 40°C, indicating their capacity to tolerate high temperatures.

Even though rainforest species often have non-dormant and large seeds (Vázquez-Yanes and Orozco-Segovia, 1984; Baskin and Baskin, 2014; Rubio de Casas *et al*., 2017), seven of our species (all legumes) required scarification as they had water-impermeable seed coats (physical dormancy). The occurrence of this type of dormancy is related to seed size (Rubio de Casas *et al*., 2017), given it offers physical protection to the embryo (Rolston, 1978; Tweddle *et al*., 2003; Dalling *et al*., 2011), and is strongly clustered within tropical legumes (Dayrell *et al*., 2017). Under natural conditions, physical dormancy is usually alleviated as a result of the higher temperatures found in gaps (Moreno-Casasola *et al*., 1994; Geisler *et al*., 2017), but might also be related to their storage time in soil seed banks (Rodrigues-Junior *et al*., 2018). Once scarified, seeds behave as non-dormant species, allowing germination parameters based on thermal time models to be calculated (Daibes and Cardoso, 2018).

Species that have a wide distribution range normally have a wide range of optimal temperatures for germination (see Marques *et al*., 2014). However, among the studied species, such a pattern remained unclear: *S. multijuga* was the only widespread species showing a broad plateau of optimal temperatures, while *A. lecointei*, a species restricted to the Amazon basin, showed a wide range of optimal temperatures. *Apuleia molaris,* considered to have a wide distribution range, showed the

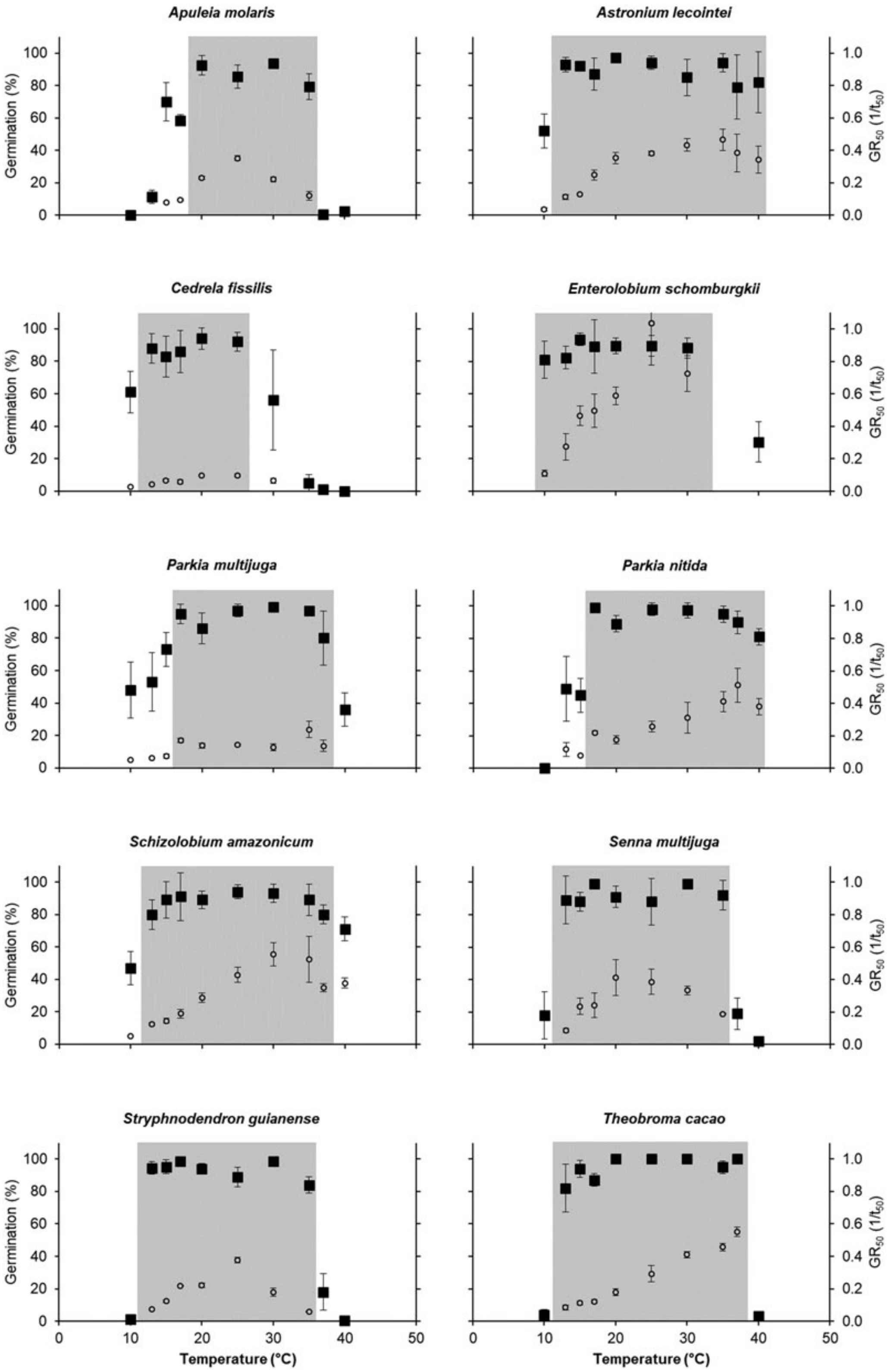

Fig. 1. Germination capacity (G%, black squares) and germination rate (GR_{50}, white circles, $1/t_{50}$) under a range of constant temperatures of ten tree species occurring in the western Brazilian Amazon. Optimal ranges for maximal G% are shaded in grey.

narrowest range of optimal G% (20–35°C), which suggests that germination niche breadth is not always linked to a broader distributional range (Thompson and Ceriani, 2003). Despite the narrow optimal range, the temperatures at which *A. molaris* germinates are still within the range of temperatures usually found in the understory. Nevertheless, in forest gaps where temperatures

Table 2. Thermal parameters of germination of ten tree species occurring in the western Brazilian Amazon

Species	Base temperature	Thermal time	Optimal range (G%)	Best t_{50} (and T)	Ceiling temperature
Apuleia molaris	12.7 ± 0.2^{a}	35 ± 2^{cd}	20–35	3 ± 0.1^{c} (25)	~37
Astronium lecointei	9.1 ± 0.5^{ab}	32 ± 3^{cd}	13–40	2 ± 0.3^{cd} (35)	>40
Cedrela fissilis	5.8 ± 1.1^{b}	157 ± 20^{a}	13–25	10 ± 0.3^{a} (20)	~37
Enterolobium schomburgkii	7.2 ± 2.2^{ab}	19 ± 6^{d}	10–?	1 ± 0.2^{e} (25)	>40
Parkia multijuga	9.5 ± 2.8^{ab}	52 ± 22^{bc}	17–37	4 ± 1^{b} (35)	>40
Parkia nitida	5.9 ± 2.9^{b}	75 ± 22^{b}	17–40	2 ± 0.5^{cd} (37)	>40
Schizolobium amazonicum	8.3 ± 0.9^{ab}	40 ± 5^{bc}	13–37	2 ± 0.3^{d} (30)	>40
Senna multijuga	8.7 ± 3.4^{ab}	32 ± 19^{cd}	13–35	3 ± 1^{cd} (20)	~40
Stryphnodendron guianense	8.9 ± 0.4^{ab}	44 ± 3^{bc}	13–35	3 ± 0.1^{c} (25)	~40
Theobroma cacao	9.2 ± 0.7^{ab}	53 ± 3^{bc}	13–37	2 ± 0.1^{d} (37)	~40
Mean	8.5 ± 2.4	56 ± 42	—	3 ± 3	—
F-value	3.25 ($P = 0.006$)	20.54 ($P < 0.001$)	—	64.25 ($P < 0.001$)	—

Base temperature (T_b, °C), thermal time requirement (θ_{50}, °C.days), optimal range (temperature intervals, in °C, showing G% ≥80% with no statistical difference among them), best germination time (lowest numerical value of t_{50}, in days; optimal temperature (T) where the best germination time was found is shown in parentheses), and approximate value of ceiling temperature (T_c, °C). All values are means ± standard deviation. Different superscript letters in the columns indicate significant differences among species ($P \leq 0.05$). The question mark for *E. schomburgkii* indicates that optimal range could not be precisely determined for this species, given that temperatures of 35 and 37°C were not tested.

could reach over 40°C (Pearson *et al.*, 2002; Geisler *et al.*, 2017), seed germination would be hampered as G% of *A. molaris* falls after 35°C.

The most sensitive species to the hotter temperatures was the climax species *C. fissilis*, for which germination was reduced at 35°C and reached nearly zero at 37°C. Because *C. fissilis* showed a relatively high germination time ($t_{50} = 10$ days), it also had the highest thermal time requirement, irrespective of its widespread distribution. Highest thermal requirement could be related to larger seed size of climax species, which tend to show slow-growing (and shade-tolerant) seedlings (Foster, 1986; Swaine and Whitmore, 1988; Souza and Válio, 2001, 2003). In contrast, the small-seeded *E. schomburgkii* (a late-successional species) had the quickest germination time and lowest thermal time requirement. Other late-successional species, including the large-seeded *P. multijuga*, germinated most of their seeds within a few days after experiments began and showed similar θ values in comparison with the other species. The inclusion of more climax and late-successional species would be desired to unfold a clearer pattern regarding thermal requirements, successional status, and seed size in tropical forests.

Independent of the successional status, some species (see *A. lecointei* and *P. nitida*) showed an enhanced GR_{50} at the hottest temperatures, maintaining a germination of ≥ 80% even at 40°C. Such unique patterns differ from most theoretical thermal-dependence patterns that have been described, including those for tropical legumes (Daibes and Cardoso, 2018). Therefore, we argue that increasing kinetics of seed germination under hotter temperatures might be an ecological strategy to face forest gaps, thus favouring the rapid recruitment of understory species (Chazdon and Pearcy, 1991). However, GR-temperature dependence should increase linearly with temperature, reaching a point where it decreases from optimal to supra-optimal ranges until the ceiling temperature (Alvarado and Bradford, 2002; Bewley *et al.*, 2013). In *T. cacao*, GR increased up to 37°C and then germination dropped abruptly from 100% to zero at 40°C (Fig. 1). Hence, instead of slowly decreasing GR in the supra-optimal range, there was a short but decisive interval of 3°C that drove seed germination from its maximum capacity to death. Other species (see Table 2) showed T_c values greater than the hottest temperature tested, thus treatments testing temperatures over 40°C are necessary to stipulate their supra-optimal range limits.

Even though most species are tolerant to high temperatures, small differences in their germination requirements, especially of their supra-optimal range, could act as potential drivers of seed recruitment in tropical rainforests (see Daws *et al.*, 2002; Pearson *et al.*, 2002), especially in more disturbed sites where temperatures are usually higher. However, temperatures are normally lower than their supra-optimal range in forest understories and would not play such an important role in seed recruitment. At these sites, non-dormant seeds can be quickly recruited, forming seedling banks that compete for light in the understory. Therefore, seed and seedling traits might show complementary trade-offs contemplating all aspects of the regeneration niche in tropical forests (Osunkoya *et al.*, 1994; Daws *et al.*, 2007). Thus, intermediate-successional species would be able to germinate in the understory but would also be able to take advantage from forest gaps in disturbed sites and grow into the canopy (Denslow, 1980).

In conclusion, germination temperature limits may be similar among Amazon species but patterns in their thermal requirements seem to be different. Efficient thermal energy use throughout the germination processes leads to increasing germination with higher temperature, thus enhancing the chance of a successful establishment. On the other hand, in the supra-optimal range, delicate limits can be found as temperatures increase, with germination dropping to zero within a short interval of temperatures. This might be fundamental to understand germination responses in the context of habitat loss and fragmentation, given climate and microclimate conditions are altered (Laurence and Williamson, 2001). Climate change consequences could also affect the dynamics of forest understories as the Intergovernmental Panel on Climate Change (IPCC) predict, for the Amazon region, an increase in temperature of 3–5°C in the less pessimistic scenario and an increase of up to 8°C in the more pessimistic scenario (Ambrizzi *et al.*, 2007; Malhi *et al.*, 2008). Moreover, other aspects of seed germination should be examined, such as tolerance to moisture, as it may negatively affect germination, especially in large-seeded species (Daws *et al.*, 2008). Cardinal temperatures may also change according to the life cycle stage, differing between seed germination and seedling growth (Bastos *et al.*, 2017). Thus, it remains unclear how recruitment of Amazon species will respond to global change. Additional research is needed to understand whether seed size and successional status explain thermal parameters of seed germination, as well as how the thermal requirements change during seedling establishment. This study helps to start elucidating important questions regarding seed regeneration in the Amazon rainforest.

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