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Predicting temperature ranges for the initial development of two native Brazilian tree species using multiple sowing dates

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ABSTRACT

Accurate data on development responses to air temperature are essential to feed development and productivity models through which it is possible to analyze the global warming impacts. The cardinal temperatures – base (Tb), optimum (Topt), and maximum (TB) - delimit the temperature range in which development occurs, while the phyllochron (ºC day per leaf) defines the thermal requirements necessary for leaf appearance and development rate of tree species. Field experiments employing multiple sowing dates provide a wide range of temperature regimes closer to natural field conditions and, at the same time, allow obtaining accurate and reliable estimates of cardinal temperatures and phyllochron values. This study estimated the cardinal temperatures – Tb, Topt, and TB – and the phyllochron of tree species *Cybistax antisyphilitica* (Mart.) Mart. and *Platycyamus regnellii* Benth., both native to Brazil, using multiple sowing dates. For this, leaf appearance data from field experiments conducted outdoors during the 2017 and 2018 growing seasons with twelve sowing dates were used. *C. antisyphilitica* develops properly among 13 °C (Tb), 20 °C (Topt), and 48.4 °C (TB) temperature ranges, and *P. regnellii* among 13.7 °C (Tb), 21.5 °C (Topt) and 43.4 °C (TB). The phyllochron for leaf appearance was different between the two species. On average, *C. antisyphilitica* needs to accumulate 88.2 °C day to emit a leaf on the main stem, while *P. regnellii* needs to accumulate 109.7 °C day per leaf, and both values correspond to a development rate of 0.0134 and 0.0091 leaf per ºC day, respectively. Information about cardinal temperatures provides valuable insights into the development patterns and thermal requirements, which can be used in development models to project the development under future climates.

1. Introduction

Air temperature is the key variable in the development of forest tree species, influencing processes related to the appearance of leaves (Ferreira et al., 2019a; Freitas et al., 2017; Martins et al., 2007, 2022b; Silva et al., 2020), floral primordia, flowers and fruits (Di Lucchio et al., 2018; Kumar et al., 2019; Rawal et al., 2014), as well as geographic distribution of plant species (Baath et al., 2020, 2022; Florêncio et al., 2022;

Martins et al., 2022a; Pirovani et al., 2018; Silva et al., 2019). Exposure (gradual or abrupt) to high temperatures negatively influences the formation of molecular (proteins and DNA) or supramolecular (membranes and chromosomes) structures, in addition to causing physiological stresses (Bahuguna and Jagadish, 2015; Nievola et al., 2017; Ruelland and Zachowski, 2010), disrupting the carbon balance in plants (Fagundes et al., 2021; Florêncio et al., 2022; Ruelland and Zachowski, 2010). On the other hand, exposure to low temperatures can result in

development inhibition or delay or lead to irreversible damage and/or cell death (Baath et al., 2022; Hatfield and Prueger, 2015; Martins et al., 2022b, 2023a; Silva et al., 2020). Such impacts can be more drastic during the initial development stage of forest tree species (Costa and Streck, 2018; Fagundes et al., 2021; Florêncio et al., 2019; Martins et al., 2022b, 2023b, 2023c; Morin et al., 2010; Rawal et al., 2014; Reis et al., 2021), since the seedling phase is the most sensitive and least tolerant to air temperature variability (Fagundes et al., 2021; Martins et al., 2022b, 2023a,b,c).

In order to predict the responses of forest tree species to air temperature variability, firstly, it is necessary to define the appropriate thermal thresholds for the development (Ferreira et al., 2019a,b; Freitas et al., 2017; Martins et al., 2007; Silva et al., 2020). Three cardinal temperatures (base – Tb, optimum – Topt, and maximum – TB) delimit the temperature range in which development occurs (Freitas et al., 2017; Ferreira et al., 2019a; Hatfield and Prueger, 2015; Kamkar et al., 2012; Martins et al., 2007), being specific values to each forest species. Tb and TB represent, respectively, the temperatures below and above physiological and metabolic processes are reduced, and where there is practically no appearance of new leaves (Martins et al., 2023b; Silva et al., 2020). I.e., air temperature values close to Tb reduce all metabolic reactions, including photosynthesis (Baath et al., 2020; Ferreira et al., 2019b), while values close to TB affect membrane fluidity, metabolism, cytoskeletal rearrangement and lead to an increase in the photorespiration/photosynthesis ratio (Ruelland and Zachowski, 2010; Slot and Winter, 2017). Topt represents the temperature at which the development rate is maximum (Baath et al., 2020; Hatfield and Prueger, 2015), and consequently, more new leaves emerge (Ferreira et al., 2019a,b; Freitas et al., 2017; Martins et al., 2007; Silva et al., 2020).

Tb, Topt, and TB are mandatory input data in development models of forest tree species (Fagundes et al., 2023; Ferreira et al., 2019a; Martins and Streck, 2007; Martins et al., 2022b; Monteiro et al., 2014), such as the phyllochron, which describes development by the relationship between leaf appearance rate and thermal time (TT, ºC day) (Fagundes et al., 2023, 2021; Martins and Streck, 2007; Martins et al., 2014, 2022b, 2023a,b). With the phyllochron approach (ºC day per leaf), it is possible to quantify the thermal requirement to reach a certain development stage, being used for multiple purposes, such as comparing the development among several forest species under current climate (Ferreira et al., 2019a; Martins et al., 2022b, 2023a,b), predicting the initial development stage duration in forest nurseries and seedling sales date (Fagundes et al., 2021, 2023; Martins et al., 2022b), as well as projecting development under future climate conditions (Costa and Streck, 2018; Fagundes et al., 2021; Martins et al., 2023c; Reis et al., 2021). I.e., by applying the cardinal temperatures on the phyllochron model, it is possible to project the development of a species under climate change scenarios (Fagundes et al., 2021; Martins et al., 2023c).

Cardinal temperatures are predicted by specific statistical methods, which use development and air temperature data (Ferreira et al., 2019a, b; Freitas et al., 2017; Lago et al., 2009; Lisboa et al., 2012; Souza and Martins, 2014). For example, the leaf number (LN) during the seedling phase is a widely used variable to measure the initial development of forest species (Ferreira et al., 2019b; Freitas et al., 2017; Silva et al., 2020; Martins et al., 2007, 2022b). In this type of study, it is mandatory that plants are subjected to a wide range of air temperatures (Freitas et al., 2017; Kamkar et al., 2012; Sinclair et al., 2004), which can be accurately obtained in controlled environment such as growth chambers (Baath et al., 2020, 2022). However, such systems impose regimes of temperature, radiation, photoperiod, wind, and humidity that deviate substantially from field conditions (Freitas et al., 2017; Martins et al., 2023a; Silva et al., 2020; White et al., 2012). Two complementary options for exposing plants to a range of air temperatures are to use: i) infrared warming with a T-FACE system (Kimball, 2005; Kimball et al., 2008; White et al., 2012), or ii) field experiments with multiple sowing dates (SD) (Erpen et al., 2013; Ferreira et al., 2019a, b; Freitas et al., 2017; Freitas and Martins, 2019; Lago et al., 2009; Martins et al., 2014,

2023a). In this sense, the second option ends up being widely used due to the lower cost and the ability to generate reliable estimates of Tb, Topt, and TB in forest tree species (Ferreira et al., 2019a, 2019b; Freitas et al., 2017; Martins et al., 2007; Silva et al., 2020).

Although Tb, Topt, and TB are mandatory variables in development models and are used for multiple purposes, their values are still unknown for most forest tree species, especially native species with less economic interest. Few existing studies were conducted for Brazilian native forest species such as *Hymenolobium petraeum* Ducke, *Parkia pendula* (Willd.) Benth. ex Walp. (Monteiro et al., 2014), *Citharexylum myrianthum* Cham., *Bixa orellana* L. (Ferreira et al., 2019b), *Libidibia ferrea* (Mart. ex Tul.) L. P. Queiroz (basionym *Caesalpinia ferrea* Mart. ex Tul.), *Anadenanthera peregrina* (L.) Speg. (Silva et al., 2020), and exotic species, such as *Eucalyptus grandis* (W. Hill ex Maiden), *Eucalyptus saligna* (Sm.) (Martins et al., 2007), *Eucalyptus urophylla* (S.T. Blake), *Corymbia citriodora* (Hook.) (K.D Hill and L.A.S Johnson) (Freitas et al., 2017), *Adenanthera pavonina* (L.), *Cassia fistula* (L.) (Monteiro et al., 2014), and *Psidium guajava* (L.) (Ferreira et al., 2019a).

Among the numerous native forest tree species to Brazil, two deserve attention due to their ecological and environmental importance: *Cybistax antisyphilitica* (Mart.) Mart. (Bignoniaceae; ipê-verde, ipê-caroba or caroba-verde) and *Platycyamus regnellii* Benth. (Fabaceae, pau-pereira, mangalô or folha-de-bolo). Both species are naturally distributed in the Cerrado, Caatinga, Amazon, and Pantanal phytogeographic domains (Fig. 1), which are characterized by a high vulnerability to biodiversity loss under expected future climates (Fagundes et al., 2023; Silva et al., 2019). Furthermore, both species have an essential role as ecological repairers, as they can establish in sandy, stony, and low-fertility soils and are successfully used in urban afforestation programs within the states of Rio de Janeiro, Paraná, and São Paulo (Fagundes et al., 2023).

C. antisyphilitica is a pioneer species (Ortolani et al., 2008) present in the six Brazilian phytogeographic domains (Fig. 1A) (Costa et al., 2019; Freitas et al., 2022; Lohmann, 2020). It has a perennial cycle and is a deciduous, heliophilous, and medium-sized tree (Ortolani et al., 2008). Its wood has a low density (0.59 g cm^{-3}) and low resistance to decay, it is used in the manufacture of slats, crates, and cellulosic pulp (Bittencourt et al., 2011; Guilherme et al., 2011; Ortolani et al., 2008). Its leaves and bark are used in folk medicine as both have anti-inflammatory, analgesic, antibiotic, antisyphilitic, antiepileptic, and antineoplastic actions (Bittencourt et al., 2011; Martins et al., 2023a) besides having larvicidal activity against the *Aedes aegypti* mosquito (Rodrigues et al., 2005). Its flowers have an important ecological function, mainly in Cerrado, providing nectar and pollen for bees during the dry season (Almeida et al., 2003; Bittencourt et al., 2011).

P. regnellii is endemic to Brazil and a secondary species in ecological succession (Moura et al., 2016; Saueressig, 2017), with natural distribution restricted to the Atlantic Forest and Cerrado phytogeographic domains (Moura, 2020). It has a perennial cycle, is deciduous, and heliophilous species. Its wood is exceptionally durable, with high density (0.81 g cm^{-3}), being used for furniture, civil construction, carpentry, and manufacturing purposes (Souza et al., 2021), and the flowers are attractive to bees (Saueressig, 2017). Its roots and bark have multiple usages in folk medicine against fever, poor digestion, and inappetence (Cury and Tomazello-Filho, 2011; Souza et al., 2021).

Given the scarcity of studies of this nature coupled with the lack of information about cardinal temperatures of *C. antisyphilitica* and *P. regnellii*, this study aimed to predict the Tb, Topt, and TB values and the thermal requirements, through the phyllochron model, for the initial development stage of two native Brazilian forest tree species using data from multiple SDs. Predicting cardinal temperatures can allow the improvement of development models, which in turn are useful tools to determine the adaptability of both tree species under different geographic locations and enhance their resource management under current and future climates. Also, this study provides valuable insights into the temperature ranges for development, which can be used in development models to project the development under future climates.
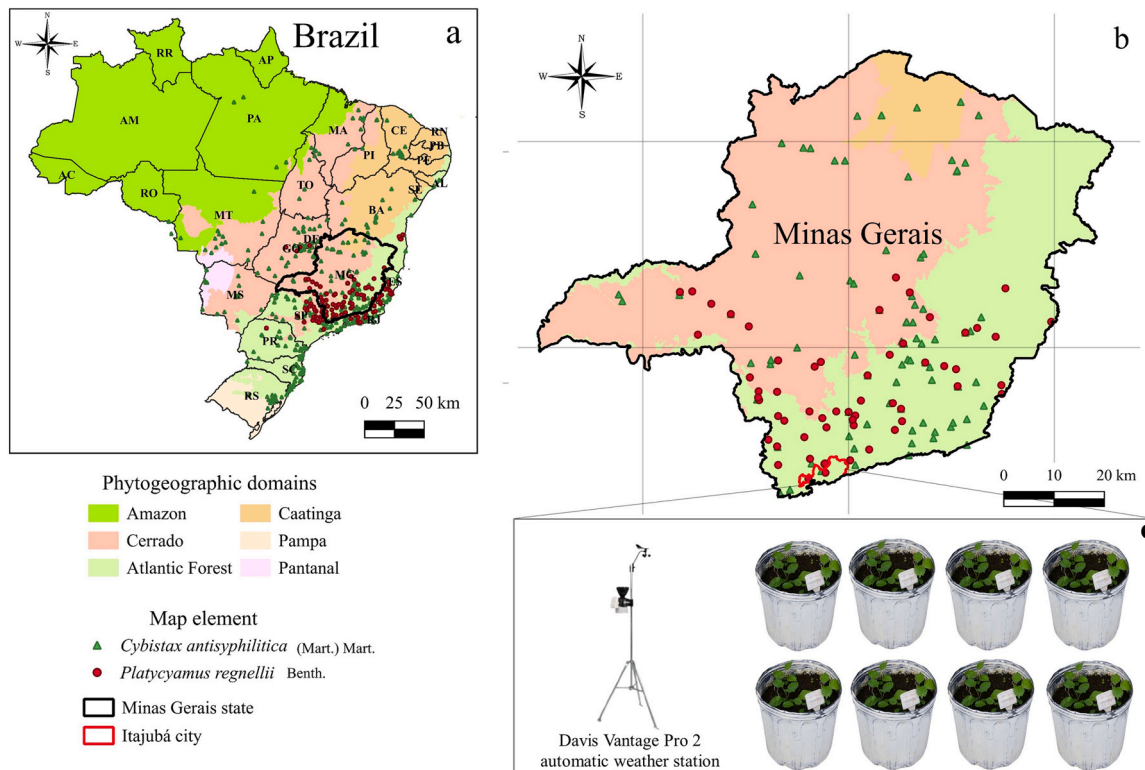
Fig. 1. Study area's location and occurrence of the two tropical forest species in Brazil (Panel a), Minas Gerais state (Panel b), and schematic representation of the experiment (Panel c). Phytogeographic domains (IBGE, 2014) and occurrence data of the tropical forest species are available at https://specieslink.net/.

2. Materials and methods

2.1. Data and field experimental design

The development data used in this study refer to the leaf number (LN), with 1.0 cm long, counted weekly from the emergence date (ED) to the end of the initial development stage date (n) of each forest species (Table 1). ED was considered as the date when 36% of the seeds emerged and were visible above ground, while the end of initial development stage date was regarded as the day when *C. antisyphilitica* reached LN = 20 leaves, and *P. regnellii* reached LN = 10 leaves on the main stem (Fagundes et al., 2023). Although a germination rate of 50% of seeds is commonly used for species with homogeneous germination coupled with long seed viability, the level of 36% is appropriate for the studied

species, as determined in a preliminary experiment conducted by Fagundes (2023). Both LN thresholds represent the ideal level for selling the two native species seedlings, which correspond to ~60 cm in height (Fagundes et al., 2023; Oliveira et al., 2011, 2016). Any lateral shoots were removed, so only the main stem developed (Martins et al., 2023a).

The LN data come from experiments conducted outdoors at the forest nursery of the Natural Resources Institute at the Federal University of Itajubá, Itajubá, Minas Gerais, Brazil (Fig. 1), measured in several sowing dates (SDs) during the 2017 and 2018 growing seasons. Itajubá has a typical monsoon climate, with two well-defined seasons: dry austral autumn/winter (April to September) and humid austral spring/ summer (October to March) (Martins et al., 2023c), with the natural occurrence of *C. antisyphilitica* and *P. regnellii*.

The orthodox seeds of both species were collected from different

Table 1
Sowing, emergence, and end dates of initial development stage for *Cybistax antisyphilitica* and *Platycyamus regnellii* during the period in which the experiments were conducted in Itajubá, Minas Gerais, Brazil.

Sowing dates (month day, year)	*Cybistax antisyphilitica*		*Platycyamus regnellii*	
	Emergence[a] (ED)	End of initial development[b](n)	Emergence[a](ED)	End of initial development[b](n)
SD1, Jan 20, 2017	Feb 17, 2017	Oct 27, 2017	Feb 10, 2017	Jun 02, 2017
SD2, Feb 20, 2017	Mar 10, 2017	Nov 17, 2017	Feb 24, 2017	Nov 10, 2017
SD3, Mar 20, 2017	Mar 31, 2017	Oct 20, 2017	Mar 24, 2017	Dec 01, 2017
SD4, Apr 20, 2017	May 12, 2017	Nov 03, 2017	May 05, 2017	Oct 20, 2017
SD5, May 19, 2017	Jun 16, 2017	Jan 12, 2018	Jun 02, 2017	Nov 17, 2017
SD6, Jun 20, 2017	Jul 07, 2017	May 25, 2018	Jul 14, 2017	Dec 22, 2017
SD7, Jul 20, 2017	Aug 18, 2017	May 11, 2018	Aug 11, 2017	Dec 08, 2017
SD8, Aug 29, 2017	Sep 22, 2017	Mar 02, 2018	Sep 08, 2017	Dec 08, 2017
SD9, Sep 20, 2017	Oct 06, 2017	Jun 01, 2018	Oct 06, 2017	Mar 02, 2018
SD10, Oct 20, 2017	Nov 10, 2017	Apr 13, 2018	Nov 03, 2017	Jan 19, 2018
SD11, Nov 20, 2017	Dec 01, 2017	Apr 13, 2018	Nov 24, 2017	Mar 02, 2018
SD12, Dec 20, 2017	*	*	Dec 29, 2017	Mar 23, 2018

[a] Day when 36% of the seeds germinated and were visible above ground.

[b] Day when *Cybistax antisyphilitica* reached 20 leaves, and *Platycyamus regnellii* reached 10 leaves on the main stem.

* Sowing date where all repetitions were lost for reasons unrelated to the experimental conditions.

matrices (isolated and embedded) located in forest fragments close to Itajubá (Fig. 1b) during two dispersion periods (May/October for *C. antisyphilitica* and August/September for *P. regnellii*) in 2016 and 2017. To preserve the viability of the seeds throughout the experiments, we followed the recommendations provided by Fowler and Martins (2001), Medeiros (2001), Melo (2009), and Lorenzi (2014) for their collection, drying, packaging, and storage. I.e., the seeds were stored in plastic bags in a dry cold chamber at 7–12°C and a relative humidity of 38–48%.

The experiments were carried out in a completely randomized design with seeds of *C. antisyphilitica* and *P. regnellii* sown in 11 L white polyethylene pots, in twelve SDs (Table 1) performed at approximately 30-day intervals in five repetitions (= pots), totaling 10 pots per SD. Approximately 10 seeds of both species were sown in each pot. When the germination rate of both species reached 36%, thinning was performed, leaving two seedlings in each pot. Using multiple SDs ensures that plants develop closer to natural field conditions (Freitas et al., 2017; Ferreira et al., 2019b; Silva et al., 2020; Martins et al., 2022a, 2023a), and in different weather conditions, especially air temperature (Fig. 2). Such conditions are imperative requirements in estimating base (Tb), optimum (Topt) and maximum (TB) temperatures (Ferreira et al., 2019a,b; Martins et al., 2014; Rosa et al., 2009; White et al., 2012) and phyllochron (Fagundes et al., 2021, 2023; Martins et al., 2023a, c).

The pots were filled with moderate type A horizon subsoil of a Rhodic Hapludox Oxisol (Santos et al., 2018), which was collected in Itajubá, Minas Gerais state. The soil contained 2.45 g kg^{-1} of organic matter (Walkley-Black), 0.5 mg dm^{-3} of P and 4.0 mg dm^{-3} of K obtained using Mehlich extractor 1 (Mehlich, 1953). About 40–50 days before each SD, acidity and fertility were corrected according to the Soil Fertility Commission of the State of Minas Gerais (CFSEMG, 1999) by applying (in each repetition) 17.63 g calcium carbonate (CaCO$_3$), 5.88 g magnesium carbonate (MgCO$_3$), 8.86 g simple-superphosphate (18%), 1.52 g potassium chloride (60%) and 2.28 g ammonium sulfate ((NH$_4$)$_2$SO$_4$). Around 90–120 days after sowing, a cover fertilizer (0.76 g potassium chloride and 1.14 g ammonium sulfate) was applied to each repetition. Furthermore, except on rainy days, daily irrigations were performed by replenishing the water lost by evapotranspiration. For this, the daily evapotranspiration was first determined by weighing pots and then watering them to 80 – 100% of the pot weight capacity. This procedure is aligned with methodological choices employed in experiments involving container-grow plants (or pots), as per Abreu et al. (2022), Fagundes et al. (2023), and Sinclair et al. (2005). I.e., the plants grew under optimal fertilization and soil moisture conditions.

2.2. Estimating the base temperature (Tb)

To estimate Tb, the lowest mean square error (MSE) method was used (Sinclair et al., 2004) considering the SDs that presented the lowest air temperature values (Tmin, Tmean, and Tmax) coupled with longer initial development stage duration (days between ED and n) (Table 1 and Fig. 2) (Freitas et al., 2017; Martins et al., 2012, 2014; Silva et al., 2020). For selecting these SDs, the Scott- Knott test was used, which in
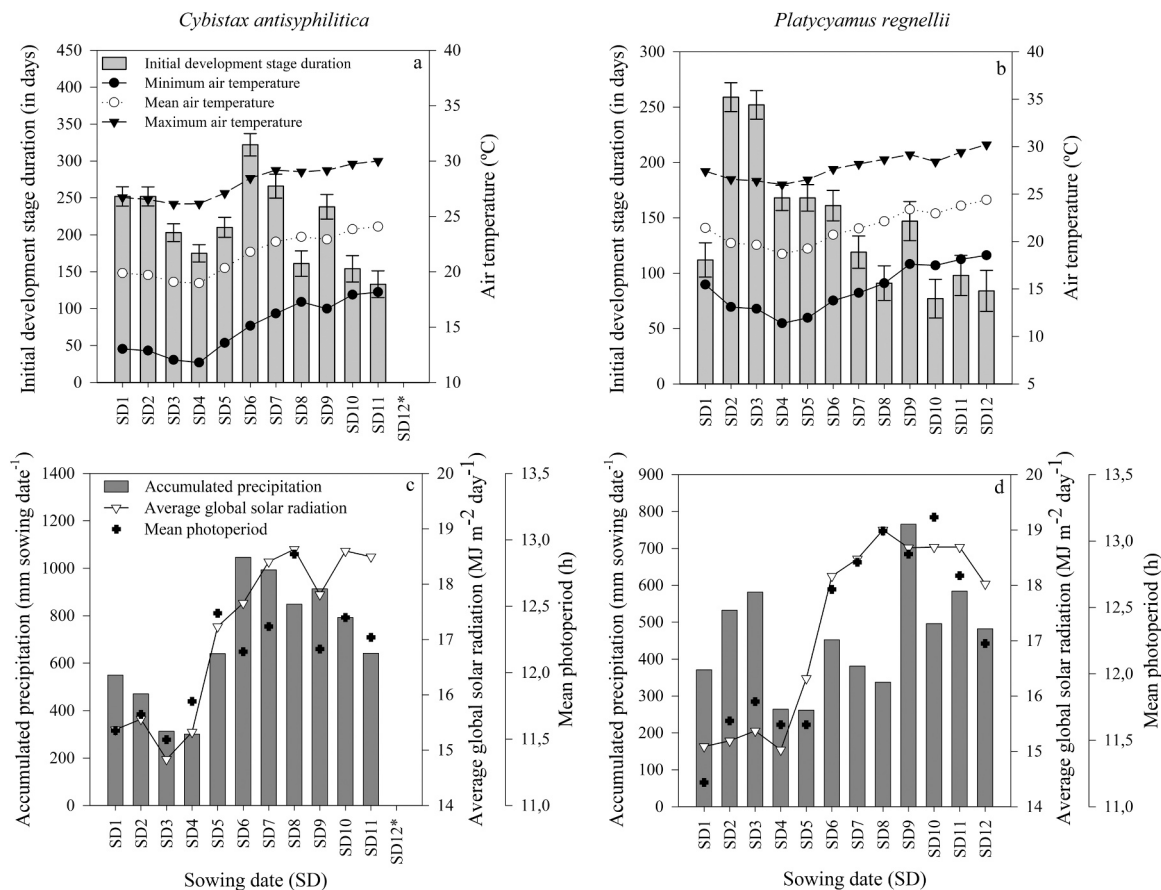

Fig. 2. Initial development stage duration (in days), average air temperature (minimum = Tmin, mean = Tmean, and maximum = Tmax, °C) (Panels a and b), accumulated precipitation (mm sowing date^{-1}), average global solar radiation (MJ m^{-2} day^{-1}), and average photoperiod (P, hours) variations (Panels c and d) in each sowing date during experiments carried out in Itajubá for *C. antisyphilitica* (Panels a and c) and *P. regnellii* (Panels b and d). *Sowing date where all repetitions of *C. antisyphilitica* were lost. Error bars in panels a and b refer to the standard deviation of initial development stage duration for each sowing date. The weather variable values refer to average values between the emergence (ED) and the end of the initial development stage dates (n). Except for the photoperiod, all variables were recorded from an automatic weather station at the experimental area.

turn was applied to initial development stage duration and air temperature values, in addition to analyzing the frequency distributions of air temperature values. For statistical purposes, at least five SDs must be selected to estimate the Tb, following the procedures from Sinclair et al. (2004), Martins et al. (2007), Freitas et al. (2017), and Ferreira et al. (2019a,b). By using groups of SDs, it is possible to cover a wide range of development conditions and temperature regimes (Ferreira et al., 2019b; Silva et al., 2020; White et al., 2012), which are important requirements in accurately estimating the Tb value.

The MSE method consists of simple linear regression fits (Eq. 1) between LN and accumulated thermal time (TTa, °C day) (Eq. 2), adjusted for each species and SD. In these fits, we considered the mean LN obtained by the arithmetic mean of the five repetitions was considered (Freitas et al., 2017; Martins et al., 2023a; Silva et al., 2020):

$$LN = a * TTa + b \qquad (1)$$

$$TTa = \sum_{i=VE}^{n} (Tmean - Tb), \text{ when } Tmean \le Tb, Tmean = Tb \qquad (2)$$

Where: LN = leaf number accumulated on the main stem (from ED to n); a = slope of linear regression (leaves per °C day); TTa = accumulated thermal time (°C day); b = linear coefficient; Tmean = daily mean air temperature (°C) obtained from the automatic weather station at the experimental area, Tb = base temperature (°C) using a series of values (from 0 °C to 20 °C, at increments of +0.5 °C), ED = emergence date (Table 1); n = end of initial development stage date (Table 1).

For each species and SD, 40 linear regressions were adjusted (Eq. 1), one for each Tb value (from 0°C to 20 °C at + 0.5 °C), as recommended by

Sinclair et al. (2004), Martins et al. (2007), Freitas et al. (2017) and Silva et al. (2020). Thus, the Tb value for each SD was obtained by the regression that presented the lowest MSE value. The Tb estimated value of each species was obtained by the arithmetic mean of the Tb values of the selected SDs (Freitas et al., 2017; Martins et al., 2012; Silva et al., 2020).

2.3. Estimating the optimum temperature (Topt) and phyllochron approach

The Topt was estimated following the recommendations proposed by Lisboa et al. (2012), Freitas et al. (2017), and Ferreira et al. (2019a) that involves two steps: i) first, the phyllochron for each species, replication and SD (SD1 to SD12) is obtained, and ii) the SD in which the lowest phyllochron value occurs is identified. In step i, the phyllochron is given by the inverse of the slope (1/a) of the linear regression between LN and TTa (Eq. 1), calculated using the Tb previously estimated. In practice, the phyllochron values indicate the thermal requirements (°C day per leaf) necessary to emit a leaf on the main stem, i.e., to produce leaves

and develop (Fagundes et al., 2021, 2023; Streck et al., 2011). That is, the lower (higher) the phyllochron value, the lower (higher) the amount of energy required by the plant to emit a leaf (Ferreira et al., 2019a,b; Martins and Streck, 2007; Martins et al., 2022b, 2023a), and consequently, higher (lower) the initial development rate.

In step ii, to identify the SD in which the lowest phyllochron value occurs, i.e., the highest development rate, the phyllochron values were submitted to analysis of variance (ANOVA) two-way test, considering 12 SDs x 2 native forest tree species. Subsequently, the mean values of phyllochron were compared by the Scott-Knott test (p = 0.05). The Topt value of each species was obtained by the arithmetic mean of the Tmean from SD in which the highest development rate occurred, i.e., the SD with the lowest phyllochron value (Ferreira et al., 2019a,b; Freitas et al., 2017; Lisboa et al., 2012; Silva et al., 2020).

2.4. Estimating the maximum temperature (TB)

The TB of each native forest species was estimated using data from the two SDs that simultaneously present higher Tmean and Tmax values and longer initial development stage duration (days between ED and n) (Table 1 and Fig. 2). TB was estimated considering ten conditions (A to J) using the equation (Ferreira et al., 2019a,b; Freitas et al., 2017; Lima and Silva, 2008; Martins et al., 2014; Silva et al., 2020):

$$TB = \frac{A + B \pm \sqrt{C * (D + E + F + G + H + I)}}{J} \text{ where} \qquad (3)$$

$$
\left\{
\begin{array}{l}
A = Nb * TMa * TMb - Nb * TMb * Tma \\
B = -Na * TMa*TMb + Na * TMa*Tmb \\
C = (-TMa + Tma)*(-TMb + Tmb) \\
D = Na * Tmb^2 * Nb - 2 * Tmb * Na*Nb*Tb - Tmb*Tma*Na^2 \\
E = -Tmb*TMa * Na^2 + Nb^2 *TMa * Tmb - Tma * Nb^2 * Tmb + 2 * Tmb * Na^2 *Tb \\
F = Tma*Na^2 *TMb - 2*Nb^2 * TMa*Tb - 2*Na^2 * TMb*Tb \\
G = TMa * Na^2*TMb + Tma^2*Nb * Na - 2 * Tma * Nb * Na * Tb \\
H = 2*Tma * Nb^2 *Tb + 2 *Na*TMb * Nb*Tb + 2 *Nb*TMa*Na*Tb \\
I = -2*Nb*TMa * Na * TMb + Nb^2 *TMa * TMb - Tma*Nb^2 *TMb \\
J = -Na * TMb + Na * Tmb + Nb * TMa - Nb * Tma
\end{array}
\right.
\qquad (4)
$$

Where: 'a' and 'b' indices refer to the two sowing dates with the highest temperature and initial development stage duration; N_a and N_b = duration, in days, from emergence (ED) to the end of initial development stage dates (n); TM_a and TM_b = average of maximum air temperature (°C) during a and b sowing dates, respectively; Tm_a and Tm_b = average of minimum air temperature (°C) during a and b sowing dates, respectively.

The Scott-Knott test (p = 0.05) and frequency distributions of air temperature values were used to select the two SDs coupled with longer initial development stage duration and higher air temperature values.

3. Results

Using multiple SDs allowed forest species to develop under different weather conditions (Fig. 2). In general, air temperature values ranged from 3.6 °C (minimum absolute value) to 34.6 °C (maximum absolute value), global solar radiation ranged from 2.6 MJ m^{-2} day^{-1} (minimum absolute value) to 29.8 MJ m^{-2} day^{-1} (maximum absolute value), and photoperiod ranged from 10.6 h to 13.4 h. In addition, accumulated

precipitation varied among SDs, with the lowest values in SD3–SD5 (~264 mm sowing date^{-1}) and highest values in SD6 (1046 mm sowing date^{-1}). Overall, the lowest (highest) average air temperature values occurred in the SDs, where plants developed during the cold (hot) months, while the lowest (highest) accumulated precipitation values occurred in the SDs, where plants developed during the dry (rainy) season. These values are coherent with climatological averages of monthly temperature, global solar radiation, and precipitation for Itajubá (Alves et al., 2020; Fagundes et al., 2023; Ribeiro et al., 2024). Such variations, mainly related to air temperature, are important requirements for reliably estimating of Tb, Topt and TB and phyllochron.

The distinct weather conditions also influenced the leaf appearance speed and the initial development stage duration (days from ED to n), making it possible to properly select the SDs to be used at estimating Tb and TB values. A significant difference was observed among all SDs (p ≤ 0.05) when comparing the initial development stage duration and air temperatures means (Table S1). Three coupled patterns can be observed when analyzing the results of both comparisons of means (Table S1) coupled with the frequency distributions of air temperature (Table S2). The first pattern refers to the groups of SDs on which seedlings had a significantly longer initial development stage duration in significantly lower air temperature (Tmin and Tmean) conditions. The second pattern refers to the groups of SDs where seedlings had a longer initial development stage duration, however, in significantly higher air temperature (Tmax) conditions. Finally, a third pattern is for the groups of SDs in which seedlings had a significantly shorter initial development stage duration even higher (or milder) air temperature conditions. By grouping these patterns, it was possible to cover a wide range of development conditions and temperature regimes, which are important requirements in accurately estimating the cardinal temperature values (Ferreira et al., 2019b; Freitas et al., 2017; Silva et al., 2020; Sinclair et al., 2004; White et al., 2012).

The first pattern is for the groups formed by SD1 to SD5 (for *C. antisyphilitica*) and SD2 to SD6 (for *P. regnellii*). Plants that developed during these SDs, when Tmin and Tmean values were significantly lower and the highest frequency of lower Tmin (≤ 15 ºC) and Tmean values (≤ 20 ºC) were observed (Table S2), developed slower and had longer initial development stage duration (Table 1 and Table S1).

In SD6, the *C. antisyphilitica* developed slower than SD1 to SD5 (and SD7 to SD11), reaching the end of the initial development stage at ~322 days after emergence. However, in SD6, Tmin, Tmean, and Tmax means were significantly higher than SD1 to SD5 and lower than SD7 to SD11. I.e., none of the three coupled patterns were observed for *C. antisyphilitica* seedlings that developed during SD6. For these reasons, we opted not to use SD6 to estimate Tb or TB values for *C. antisyphilitica*.

These conditions justify the selection of SD1 to SD5 to estimate the

Tb of *C. antisyphilitica* (duration ~219 days and Tmin ~12.1 ºC), and of SD2 to SD6 of *P. regnellii* (duration ~202 days and Tmin ~11.9 ºC). At SD1, *P. regnellii* developed significantly faster (Table S1), reaching the end of the initial development stage at 112 days; in addition, Tmin value (15.5 °C) was significantly superior to the other SDs (SD2 to SD6). Therefore, SD1 was not used in Tb estimates of *P. regnellii*, since in SD1, both coupled conditions did not occur simultaneously, i.e., lower Tmin and longer initial development stage duration.

Analogously, however, in the opposite way, the plants that developed in SD7 and SD9 had longer initial development duration coupled with the highest air temperature values (Tmean and Tmax) and with a higher frequency of occurrence of Tmean ≥ 20 ºC and Tmax ≥ 25 ºC (Fig. 2 and Tables S1 and S2). Both SDs represent the second coupled development pattern. Therefore, SD7 and SD9 were selected for the TB estimate of *C. antisyphilitica* (duration ~262 days), and of *P. regnellii* TB (duration ~138 days).

The third pattern is for the groups formed by SD8, SD10, and SD11 for *C. antisyphilitica*, and SD1, SD8, S10 to SD12 for *P. regnellii*. Plants that developed during these SDs, had significantly shorter initial development stage duration even when air temperature values were significantly higher (or milder). i.e., in these SDs, the frequency of higher Tmean (~ 25 ºC) and Tmax values (~30 ºC) were observed (Table S2), along with the lower frequency of lower Tmin (~20 ºC) values.

Regarding Tb estimates, all linear regressions between LN and TTa showed high adjusted coefficient of determination values ($R^2 \geq 0.73$ for both species) (Fig. S1 and S2, Supplementary material), low MSE values (< 1.4027 for *C. antisyphilitica* and 0.3504 for *P. regnellii*), and significant slope coefficients (p ≤ 0.05). Using a series of Tb values generated different TTa values, which in turn influenced the fit of linear regressions, and so the MSE values (Fig. 3). Such variation is a desirable characteristic for estimating Tb by the MSE method. Moreover, there was variation between the estimated Tb values among the SDs for both species (Fig. 3a and b). For *C. antisyphilitica* in SD1, the lowest MSE value (0.7975) was for Tb = 16 °C, in SD2 the lowest MSE value (0.4923) was for Tb = 5.5 °C, in SD3 (0.2102) was for Tb = 12.5 °C, in SD4 (0.5326) and SD5 (1.4027) was for Tb = 15.5 °C. It is worth highlighting that even using SD6 to estimate the Tb value for *C. antisyphilitica*, the lowest mean square error value (7.6018) was for Tb = 0°C. I.e., the estimated value of Tb = 0 ºC in SD6 should be discarded in calculating the arithmetic mean to obtain the Tb for *C. antisyphilitica*. Thus, the estimated Tb for *C. antisyphilitica* was 13 ºC, obtained by the arithmetic mean of the Tbs from SD1 to SD5.

Considering *P. regnellii*, the lowest MSE value found in SD2 (0.1844) was for Tb = 13.5 °C, in SD3 (0.1688) was for Tb = 16.5 °C, in SD4 (0.3504) was for Tb = 11 °C, and in SD5 (0.2119) and SD6 were for Tb =
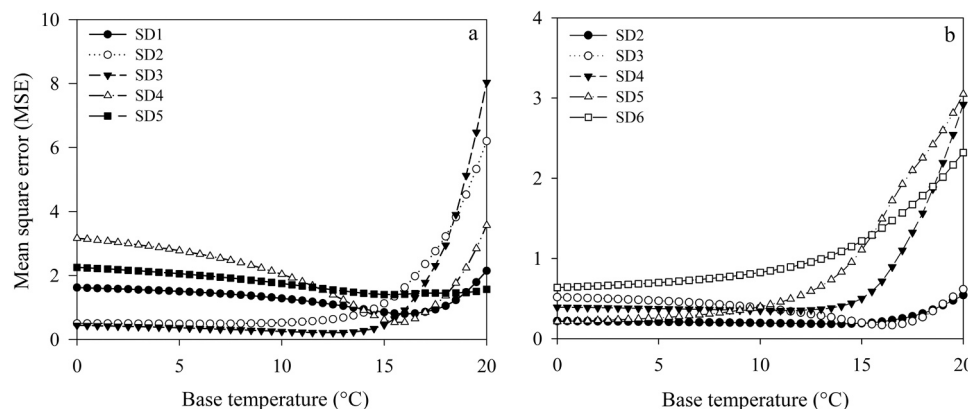

Fig. 3. Mean square error (MSE) values obtained from regressions between the leaf number accumulated on the main stem and the accumulated thermal time, calculated with different base temperature values (ranging from 0 °C to 20 °C), for *Cybistax antisyphilitica* (panel a) and *Platycyamus regnellii* (panel b). See Table 1 for sowing dates (SD).

Table 2
Comparison of means for the phyllochron values (1/a, ºC day per leaf) and development rate (a, leaf per ºC day) for *Cybistax antisyphilitica* and *Platycyamus regnellii* in twelve sowing dates.

Sowing dates	*Cybistax antisyphilitica* Phyllochron (development rate)	*Platycyamus regnellii* Phyllochron (development rate)
SD1	95.20 (0.0105) Ba	163.58 (0.0061) Cb
SD2	61.05 (0.0164) Aa	178.00 (0.0056) Cb
SD3	59.78 (0.0167) Aa	186.30 (0.0054) Cb
SD4	51.88 (0.0193) Aa	94.80 (0.0105) Bb
SD5	69.67 (0.0144) Aa	65.82 (0.0152) Aa
SD6	157.67 (0.0063) Cb	99.75 (0.0100) Ba
SD7	142.62 (0.0070) Cb	90.92 (0.0110) Ba
SD8	87.08 (0.0115) Ba	83.25 (0.0120) Ba
SD9	96.78 (0.0103) Ba	106.27 (0.0094) Ba
SD10	71.65 (0.0140) Aa	71.59 (0.0140) Aa
SD11	76.95 (0.0130) Ba	94.50 (0.0106) Ba
SD12	-	82.08 (0.0122) Ba
Overall mean (± standard deviation)	88.2 (± 33.9) a	109.7 (± 41.8) b

See Table 1 for sowing dates. Means followed by the same uppercase letter in the column (sowing dates) and lowercase letter in the row (native forest species) did not differ from each other by the Scott-Knott test (p ≥ 0.05). The values shown in the table refer to the original data. However, the data were transformed into Ln (phyllochron) given the non-normality assumption by the Shapiro-Wilk test (p < 0.05) (Freitas et al., 2017; Reis et al., 2021; Silva et al., 2020). The development rate refers to the inverse of the phyllochron, i.e., the coefficient 'a'. The letters (A to C, a or b) were set up in ascending order of phyllochron value.

0ºC. The estimated value of Tb = 0 ºC in SD5 and SD6 was discarded in calculating the arithmetic mean to obtain the Tb for *P. regnellii*. Since *P. regnellii* is an endemic species to Brazil and restricted to latitudes from −8° to −26° (Moura, 2020), estimated Tb values ≤ 4ºC can be considered unfeasible and unreliable. Thus, the estimated Tb value for *P. regnellii* was 13.7 °C.

The steps for estimating Topt involve obtaining the phyllochron (1/a) for each species, repetition and SD, performing ANOVA and comparison of means test to identify the SD where the lowest phyllochron value occurs. By ANOVA, a significant effect on the interaction among SDs and forest species was observed (p ≤ 0.05). However, there were differences in the magnitude and influence of each SD on the phyllochron (and development rate) of the two forest species (Table 2). This pattern shows that the air temperature influences the LN of both species, and therefore the recommendation from Lisboa et al. (2012) can be used to estimate Topt using multiple SDs.

Lower phyllochron values for a particular SD indicate that less energy is required for the leaf appearance (Fagundes et al., 2021; Martins et al., 2022a; Streck et al., 2011), which results in faster leaf emission due to the higher development rate (Fagundes et al., 2021; Martins et al., 2022b), and shorter duration (in days) to complete the initial development stage (Martins et al., 2023a). In other words, the lowest thermal requirement and highest development rate occur when the air temperature is close to the Topt of the species. Analyzing only *C. antisyphilitica*, the SDs that have the lowest phyllochron value were SD2 (ED = March), SD3 (ED = April), SD4 (ED= May), SD5 (ED = June), and SD10 (ED = November) (Table 2). That is, during these SDs, the thermal requirement of *C. antisyphilitica* was smaller, since the seedlings developed in air temperature conditions close to the Topt. I.e., the estimated Topt for *C. antisyphilitica* is 20 ºC. Similarly, the lowest phyllochron value for *P. regnellii* occurred in SD5 (ED = June) and SD 10 (ED = November), and therefore the estimated Topt for *P. regnellii* is 21.5 °C.

Comparing both species, regardless of SD, *P. regnellii* presented higher phyllochron value (109.7 ºC day per leaf) compared to *C. antisyphilitica* (88.2 ºC day per leaf). However, the slower development of *P. regnellii* occurred only from SD1 to SD3. Therefore, in these

SDs, *P. regnellii* is later and reaches the end of the initial development stage more slowly, while *C. antisyphilitica* is earlier. *C. antisyphilitica* developed slower only in SD6 and SD7, with phyllochron ~150ºC day per leaf, resulting in a longer initial development stage duration of ~294 days (Table 1).

Regarding TB, the estimated values were 48.4 ºC for *C. antisyphilitica* and 43.4ºC for *P. regnellii*. Despite both values being higher than the absolute maximum air temperature measured during the experiment periods (34.6 ºC), they can be considered coherent. The reasons are: (i) the use of multiple SDs increases the reliability of TB estimation, since it ensures that the species develop under a wide range of air temperature and in conditions closer to those measured in the field (White et al., 2012); (ii) data from the two SDs (SD7 and SD9 for both species) were used where was observed a significant higher air temperature (Tmean and Tmax) aligned with a significant longer initial development stage duration (Ferreira et al., 2019a,b; Freitas et al., 2017); (iii) high TB values (between 40 °C and 55 °C) are expected in tropical forest tree species (Ferreira et al., 2019a; Freitas et al., 2017; Silva et al., 2020), since they represent the maximum temperature threshold, above which damage to plant metabolic processes occurs (Fagundes et al., 2021; Reis et al., 2021).

4. Discussion

The processes responsible for leaf appearance, such as leaf primordia differentiation and cell division, depend on enzymatic activities (Bahuguna and Jagadish, 2015; Martins et al., 2023a; Parent and Tardieu, 2012; White et al., 2012), which in turn depend on air temperature (Ruelland and Zachowski, 2010). That is, the combined action of different enzymes in metabolic cycles, cascade and redox chains is disturbed when the temperature is changed (Bahuguna and Jagadish, 2015; Perdomo et al., 2017; Ruelland and Zachowski, 2010; Slot and Winter, 2017), especially above supra-optimum temperatures (between Topt and TB). Under these conditions, the leaf appearance rate is lower, and so fewer new leaves emerge (Costa and Streck, 2018; Fagundes et al., 2021; Florêncio et al., 2019; Reis et al., 2021).

This occurs because all metabolic reactions, including photosynthesis, are adjusted by plants to occur within the thermal thresholds delimited by Tb, Topt and TB (Baath et al., 2020; Bahuguna and Jagadish, 2015; Fagundes et al., 2021, 2023; Ferreira et al., 2019a, b; Hatfield and Prueger, 2015; Martins et al., 2022a). Although the physiological basis of cardinal temperatures is unclear (Hatfield and Prueger, 2015; White et al., 2012), the processes that drive development, such as leaf appearance and the initial development stage duration, are intrinsically associated to them (Baath et al., 2022; Hatfield and Prueger, 2015; Martins et al., 2023a, 2022a; Parent and Tardieu, 2012; White et al., 2012). Therefore, cardinal temperatures values estimated in this study for *C. antisyphilitica* (Tb = 13.0 °C, Topt = 20 °C and TB = 48.4 °C) and *P. regnellii* (Tb = 13.7 ºC, Topt = 21.5 °C and TB = 43.4 °C), describe the thresholds at which both species can develop properly under natural field conditions. Furthermore, they are mandatory input data on development models, e.g., the phyllochron model, which in turn are used to quantify the dynamics and rate of initial development, and the seedling phase duration (Fagundes et al., 2023; Ferreira et al., 2019a,b; Martins et al., 2023a), especially in studies on climate change (Fagundes et al., 2021; Freitas et al., 2017; Martins et al. 2022a, 2023c; Morin et al., 2010; Reis et al., 2021; Silva et al., 2020).

It is worth highlighting that emergence dates in both Brazilian native forest species may vary depending on the sowing dates, mainly when the seed propagation method is used (Martins et al., 2023c). Practical issues specific to Brazilian native forest species like reduced seed dispersal times (once or twice a year), seed viability losses over time, pathogens or excess impurities within seed lots (Michelon et al., 2021), and seeds that are hard to germinate (Fagundes et al., 2021, 2023; Lorenzi, 2014; Martins et al., 2023c; Michelon et al., 2021) hinder uniform germination, and consequently, affect the emergence date. However, to avoid

further damage to germination and development of both forest species in the SDs, seed collections were carried out at two different dispersal times (between May and October) in 2016 and 2017 as per Fagundes et al. (2023).

Regarding Tb, the differences between the estimated values for each SD in both species (Fig. 3) are common to occur in methods based on natural/real field conditions, such as those that use multiple SDs (Erpen et al., 2013; Ferreira et al., 2019a, b; Lago et al., 2009; Martins et al., 2007; Monteiro et al., 2014; Silva et al., 2020). The estimated values for the initial development stage of *C. antisyphilitica* (13.0 °C) and *P. regnellii* (13.7 ºC) were close to the other tropical forest species, such as: *A. pavonina* (15 °C), *C. fistula* (16.4 °C), *H. petraeum* (14.5 °C), *P. pendula* (14.6 °C) (Monteiro et al., 2014), *E. urophylla* (10 °C) (Freitas et al., 2017), *C. myrianthum* (11.4 °C), *B. orellana* (12 °C) (Ferreira et al., 2019b), *L. ferrea* (12.8 °C), *A. peregrina* (10.3 °C) (Silva et al., 2020), and *Dipteryx alata* Vogel (10 °C) (Borella et al., 2020).

Since the methods used to estimate Tb, including the MSE method, are statistical, it is normal to have (small) differences between the estimated and physiological base temperature of each species (Freitas et al., 2017; Silva et al., 2020; Sinclair et al., 2004; Souza and Martins, 2014). Therefore, it is important to verify whether the estimated Tb values are within the range of temperatures observed by weather stations in the SDs (Ferreira et al., 2019a), and whether Tb values are consistent with phenological observations measured (at the field) during experiments (Martins et al., 2019). Unfeasible Tb value and well below the air temperature measured at field conditions (Souza and Martins, 2014) was observed in the SD5 and SD6 for *P. regnellii* (Tb=0ºC, Fig. 3), including SD6 for *C. antisyphilitica*. In the SD6, *C. antisyphilitica* developed slower than all SDs, reaching the end of the initial development stage at ~322 days after emergence. The reduced physiological quality, germination, and vigor of *C. antisyphilitica* seeds after 6–8 months of storage (Melo, 2009; Ribeiro et al., 2018; Ribeiro-Oliveira et al., 2019) may have affected the germination speed, and initial development, contributing to the longer initial development stage duration in SD6. Since none of the three coupled patterns were observed for *C. antisyphilitica* seedlings that developed during SD6, we opted not to use SD6 to estimate Tb and TB values.

Moreover, Tb = 0ºC has already been estimated using statistical methods, such as the least coefficient of variation, least standard deviation in days (Ferreira et al., 2019a; Lago et al., 2009), and lowest MSE (Freitas et al., 2017; Martins et al., 2007). In all aforementioned cases, the unfeasible Tb values were disregarded, being common the exclusion of Tb values below 4°C in forest tree species that are naturally distributed in tropical and subtropical climates (Ferreira et al., 2019a,b; Freitas et al., 2017; Martins et al., 2007; Silva et al., 2020).

When air temperature is close to (or below) the Tb, there is a reduction in enzymatic activities, membrane fluidity, accumulation of reactive oxygen species, and impairment of photosynthesis (Bahuguna and Jagadish, 2015; Nievola et al., 2017; Ruelland and Zachowski, 2010). This leads to inhibition or slowness on processes related to leaf appearance, resulting in a delay in the appearance of new leaves, and an increase in initial development stage duration (Fagundes et al., 2021; Martins et al., 2023a, c; Reis et al., 2021). This exact pattern occurred in SD2 and SD3 (Fig. 2) for *P. regnellii*. In both SDs, there were more cases (number of days) in which Tmin (~144 days) and Tmean (~44 days) were close (or smaller) than Tb, resulting in a longer seedling phase duration, especially for *P. regnellii* (~255 days). Furthermore, close to Tb, seedlings can reduce root development, and water and nutrients uptake (Abreu et al., 2022; Nievola et al., 2017). i.e, all these changes combined inhibit leaf and root development, which may negatively affect the seedling quality at forest nurseries (Ferreira et al., 2019a; Martins et al., 2023a).

Otherwise, when air temperature is close to the estimated Topt for *C. antisyphilitica* (20 °C) and *P. regnellii* (21.5 °C), the higher the development rate and leaf appearance speed, and the shorter duration (in days) to complete the initial development stage of both species. For example, at SD10 there were more cases in which Tmean was close to Topt of *C. antisyphilitica* (46 days) and *P. regnellii* (64 days), reducing the initial development stage duration in both species (154 and 77 days, respectively) (Fig. 2). This pattern was also verified for *L. ferrea* and *A. peregrina* (Fagundes et al., 2021), *P. guajava* (Martins et al., 2023a), *C. myrianthum*, *B. orellana* (Martins et al., 2022b), and *E. urophylla* (Freitas et al., 2017). When the air temperature is close to Topt, the carboxylase activity of ribulose 1.5-bisphosphate carboxylase-oxygenase (RuBisCo) is favored due to the greater solubility of CO_2 relative to O_2 (Ruelland and Zachowski, 2010), which in turn contributes to increased photosynthesis and, consequently, net photosynthesis (Bahuguna and Jagadish, 2015; Perdomo et al., 2017; Reis et al., 2021), resulting in faster leaf appearance (Fagundes et al., 2021; Martins et al., 2023c; Parent and Tardieu, 2012). Both Topt values estimated in this study (20 and 21.5 °C) are similar to those for other tropical forest tree species, such as *A. pavonina* (24.4 °C), *C. fistula* (24.9 °C), *H. petraeum* (24.9 °C), *P. pendula* (25.1 °C) (Monteiro et al., 2014), *Ficus insipida* Willd. (23.9 ºC), *Ochroma pyramidale* (Cav. ex Lam.) Urb. (25.9 ºC), *Calophyllum longifolium* L. (24.9 °C) (Slot and Winter, 2017), *L. ferrea* (20.7 °C) and *A. peregrina* (23 °C) (Silva et al., 2020). That is, in most tropical forest species, the development rate is maximum between 20 °C and 25 °C.

Regarding TB, the estimated values for *C. antisyphilitica* (48.4 ºC) and *P. regnellii* (43.4 ºC) represent the absolute maximum threshold, above which leaf development is negligible or null (Freitas et al., 2017; Hatfield and Prueger 2015; Martins et al., 2014; Ruelland and Zachowski, 2010), i.e., the new leaves emission is interrupted (Martins et al., 2023b). Both values are within the expected range for tropical species (between 39 ºC and 46 ºC) (Kositsup et al., 2009; Slot et al., 2016; Slot and Winter, 2017). Furthermore, they are close to the estimated values for seedlings of *P. pendula* (40.1 °C) (Monteiro et al., 2014), *B. orellana* (46.4 °C) (Ferreira et al., 2019b), *L. ferrea* (46.3 °C), *A. peregrina* (45.5 °C) (Silva et al., 2020), *C. citriodora* (41.3 °C), *E. urophylla* (40.5 °C) (Freitas et al., 2017), and *Eucalyptus globulus* Labill. (40.0 °C) (Sands and Landsberg, 2002). At supra-optimum temperatures several metabolic, and physiological changes can be observed due to (Baath et al., 2020; Mathur et al., 2014; Nievola et al., 2017; Perdomo et al., 2017; Ruelland and Zachowski, 2010): (1) favoring the oxygenase activity of RuBisCo with an increase in the photorespiration/photosynthesis ratio; (2) inhibited electron transport activity, ATP synthesis and regeneration of ribulose-1.5-bisphosphate (RuBP), limiting CO_2 fixation; (3) increased energy consumption or carbonate skeletons, raising cell maintenance costs. Furthermore, as the vapor pressure deficits increase (with increasing Tmean and Tmax), the stomata close, reducing the internal carbon concentration and latent heat loss from the leaf (Abreu et al., 2022; Fagundes et al., 2021; Martins et al., 2023a,c), which contributes to the reduction of net photosynthesis (Perdomo et al., 2017; Reis et al., 2021). Therefore, Tmean (or Tmax) values close to TB compromise the appearance of new leaves and increase the duration of the initial development stage. Similar pattern was observed by Costa and Streck (2018), Fagundes et al. (2021), Martins et al., 2023c, Morin et al. (2010), and Reis et al. (2021) in tropical forest species subjected to supra-optimum temperatures.

Several factors can explain the difference between these values (Tb, Topt, and TB), given their intricate and multifaceted relationships. For instance, weather conditions from an experimental area can interfere with cardinal temperature estimations when using the approach based on multiple sowing dates. For this reason, preference should be given to performing the experiments where these species naturally occur and, at the same time, present a wide variation (on a daily or monthly scale) in air temperature (Fagundes et al., 2023; Martins et al., 2023a).

Although the methods used in this study predicted Tb, Topt, and TB reliably, they need improvements mainly in terms of statistical procedures. Since cardinal temperatures are determined statistically rather than physiologically, owing to the criteria for selecting these values sometimes, Tb can be estimated below (above) to 0 ºC (20 °C), which is

challenging to explain mainly in tropical forest species (Ferreira et al., 2019a,b; Freitas et al., 2017). The same applies to Topt and TB estimates. In these cases, using artificial intelligence techniques could generate more realistic values and reduce the time spent on statistical procedures.

Moreover, it is essential that development data from experiments be consistent. However, some practical issues, e.g., fewer dispersal times, loss of seed viability over time, and presence of pathogens in the seeds, make it challenging to install experiments (Fagundes et al., 2021, 2023; Martins et al., 2023c; Michelon et al., 2021), providing unreliable development data for predicting Tb, Topt and TB purposes. For these reasons, predicting the cardinal temperature for some forest species like *Paubrasilia echinata* (Lam.) Gagnon, H.C.Lima and G.P.Lewis, and *Araucaria angustifolia* (Bertol.) Kuntze is virtually impossible. Despite their enormous ecological importance, they have recalcitrant seeds with short-lived storage (~ 2 months) (Carvalho, 2003).

The phyllochron values for the two species along the different SDs (between 52 and 186 ºC day per leaf) are higher than most tropical forest species, such as *C. myrianthum* (~35 ºC day per leaf), *B. orellana* (~47 ºC day per leaf), *P. guajava* (~40 ºC day per leaf) (Martins et al., 2023a), *L. ferrea* (~47 °C day per leaf) (Fagundes et al., 2021), *E. saligna* (32.2 °C day per leaf), *E. grandis* (30.9 °C day per leaf) (Martins and Streck, 2007), *C. citriodora* (from 38.2 to 41.5°C day per leaf) (Freitas and Martins, 2019; Martins et al., 2023c), *A. pavonina* (11.40 °C day per leaf), *C. fistula* (19.54 ºC day per leaf), *H. petraeum* (26.54 ºC day per leaf) and *P. pendula* (30.30 ºC day per leaf) (Monteiro el al., 2014), except for *A. peregrina* (171.5 ºC day per leaf) (Fagundes et al., 2021). When analyzing phyllochron value, it is expected that the lower (higher) phyllochron value, i.e., lower (higher) thermal requirement, results in a shorter (longer) duration of the initial development stage (Costa and Streck, 2018; Fagundes et al., 2021, 2023; Florêncio et al., 2019; Martins et al., 2014, 2023a). This pattern occurred in most SDs, such as SD4 and SD10 (and SD6 and SD7) of *C. antisyphilitica* and SD10 (SD2 and SD3) of *P. regnellii*. However, in some SDs the lower phyllochron value did not result in a shorter initial development stage duration in the field. For example, for *C. antisyphilitica* in SD2 and SD3, the phyllochron was lower (~60 °C day per leaf) with a duration of ~230 days, than in SD11 (~77 °C day per leaf) with a duration of 133 days. This pattern also occurred in SD5 and SD11 of *P. regnellii*, corroborating the selection of these SDs for estimating Tb and TB of both species.

It is worth mentioning that the phyllochron value is intrinsically related to the method of calculating TTa (and TT) (Freitas and Martins, 2019; Martins et al., 2023a; Rosa et al., 2009). Each TT method can result in different thermal time values (or TTa), especially when air temperature is above Topt (or close to TB) of the species, thus affecting the phyllochron values. Therefore, the TTa method that considers the three cardinal temperatures is the most suitable for tropical forest species (Martins et al., 2023a), reinforcing the importance of estimating the three cardinal temperatures (Tb, Topt and TB) and inserting them on phyllochron or other development model. Furthermore, the phyllochron approach is better suited to quantify initial development (and LN) compared to the civil calendar day approach (Fagundes et al., 2021; Martins et al., 2023a), which is commonly used to determine the end of initial development stage, and when (the moment) seedlings are sold (Martins et al., 2007, 2022b, 2023a).

As any change in air temperature can alter the initial development stage, *C. antisyphilitica* and *P. regnellii* may not be able to tolerate or adapt to projected increases in air temperature, reducing or inhibiting the leaf appearance, increasing the seedling phase duration, and impacting on a higher maintenance cost for seedlings production. Thus, future studies should assess the impacts of climate change using development models that are fed with the cardinal temperatures estimated in this study (Ferreira et al., 2019a,b; Freitas et al., 2017; Martins et al., 2007, 2022b, 2023a), as well as with outputs data from climate models (Fagundes et al., 2021; Florêncio et al., 2019; Martins et al., 2023c; Reis et al., 2021).

5. Conclusion

The cardinal temperatures estimated to initial development stage for *Cybistax antisyphilitica* (Mart.) Mart. were 13 °C (Tb), 20 °C (Topt) and 48.4 °C (TB), and for *Platycyamus regnellii* Benth. were 13.7 °C (Tb), 21.5 °C (Topt) and 43.4 °C (TB). Although *Cybistax antisyphilitica* presented, on average, a longer seedling phase duration (~215 days), it needs less energy accumulation (88.2°C day per leaf) to emit leaves on the main stem compared to *Platycyamus regnellii* (109.7 ºC day per leaf with ~145 days).

Both native forest tree species developed differently along the sowing dates, demonstrating that they have different development rates under the same field conditions, and that the cardinal temperatures can be estimated using multiple sowing dates.

CRediT authorship contribution statement

Fernando Yuri da Silva Reis: Visualization, Supervision, Data curation, Conceptualization. **Haroldo Felipe da Costa:** Supervision, Methodology, Data curation. **Flávia Fernanda Azevedo Fagundes:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Fabrina Bolzan Martins:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Code availability

Not applicable.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121912.

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