

Understanding the Temperature Range for Foliar Development of Neotropical Forest Species during the Seedling Stage: Implications for Biology and Ecology

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Abstract

This study aimed to estimate the cardinal temperatures for the foliar development of seedlings from four forest species native to Brazilian biomes: *Handroanthus heptaphyllus*, *Tabebuia roseoalba*, *Ceiba speciosa*, and *Schinus terebinthifolia*. An experiment was conducted with ten sowing times between December 2019 and April 2021. Seven methods were employed to estimate the inferior cardinal temperature, the phyllochron concept for the optimal temperature, and mathematical models for the superior temperature. The results indicated significant variations in the inferior cardinal temperatures among the four species, ranging from 9.8°C to 11.5°C, as well as distinct optimal temperatures ranging from 22.7°C to 25.7°C. Furthermore, disparities were observed between species and sowing times concerning the determination of the phyllochron, with *Ceiba speciosa* exhibiting an average phyllochron ranging from 75.6 to 246.2 °day⁻¹. These findings offer valuable insights into the biological and ecological aspects of native forest species and enhance our understanding of key parameters for modeling vegetal growth. However, the limited availability of species-specific information in the Brazilian biome raises concerns regarding the applicability of these models. In conclusion, this study successfully estimates the cardinal temperatures (inferior, optimal, and superior) for foliar development of four important forest species native to Brazilian biomes, thereby contributing to the knowledge base of forestry research.

INTRODUCTION

The rise in temperature affects all life forms, particularly plants, which are sessile organisms with physiological activities directly influenced by temperature (Fagundes et al. 2021). Therefore, there is a growing concern about the potential impacts of temperature increases on plant development, specifically in Brazil, where projections indicate temperature increases ranging from 1.5°C to 5°C (IPCC 2013; Reis et al. 2021; Torres et al. 2021). Recent studies have demonstrated that these temperature increases are sufficient to alter the initial development rate of forest species, specifically during the seedling and sapling phases. As a result, the length of time that seedlings spend in nurseries and the management practices involved, such as increased irrigation frequency and the utilization of shading, may be affected (Lin et al. 2019; Fagundes et al. 2021; Reis et al. 2021). These changes have the potential to increase the operational costs of nurseries and compromise the quality of seedlings, thereby posing challenges for forest restoration and recovery programs (Costa and Streck 2018; Grossnickle and MacDonald 2018; Ferreira et al. 2019b; Florêncio et al. 2019; Martins et al. 2007; Martins and Streck 2007; Reis et al. 2021).

To project species behavior under different temperature scenarios, development models have been utilized (Fagundes et al. 2021; Reis et al. 2021; Martins et al. 2022). However, the accurate estimation of cardinal temperatures, which are species-specific thermal limits for plant development, is crucial as input data for these models (Ferreira et al. 2019a; Florêncio et al. 2019; Reis et al. 2021; Martins et al. 2022). Cardinal temperatures include the minimum (T_b) and maximum (T_B) temperatures at which plant development ceases or becomes negligible respectively, while the optimal temperature (T_{ot}) represents the maximum temperature for development (Martins et al. 2014; Freitas et al. 2017). Despite their importance, limited studies have determined the cardinal temperatures for forest species, particularly those native to Brazil. For instance, Fagundes et al. (2021), Ferreira et al. (2019a), and Martins et al. (2022) noted that the primary challenge in using development models for native species lies in the lack of input data, such as T_b, T_{ot}, and T_B.

To estimate T_b, various methods have been employed, including the minimum standard deviation method, the minimum coefficient of variation method (in days or degree days), regression coefficient, relative development (RD), and the least mean square error (MSE) method (Ferreira et al. 2019a, b; Freitas et al. 2017; Souza and Martins 2014; Yang et al. 1995). The phyllochron concept, which represents the thermal accumulation for leaf emergence, can be utilized to estimate T_{ot} (Fagundes et al. 2021; Martins et al. 2007 and 2022). T_B can be estimated using multiple functions based on plant development data under high-temperature conditions (Ferreira et al. 2019b; Silva et al. 2020). Typically, these methods require exposing plants to a wide range of temperatures, especially for T_b and T_B, through multiple sowing dates (Freitas et al. 2017; Martins et al. 2014; Silva et al. 2020). Despite the widespread application of these methods (Bartz et al. 2017; Ferreira et al. 2019a, b; Freitas et al. 2017; Martins et al. 2007; Souza and Martins 2014), the specificities of each method under different climatic conditions and their suitability for native forest species in Brazilian biomes remain scarce.

Knowledge of cardinal temperatures for forest species of significant importance in the Brazilian forestry context, such as *Handroanthus heptaphyllus* (Vell.) Mattos, *Tabebuia roseoalba* (Ridl.) Sandwith, *Ceiba speciosa* (A. St. Hil.) Ravenna, and *Schinus terebinthifolia* Raddi, is essential for understanding the biological responses of these species to temperature, determining developmental thresholds, and facilitating the use of development models under current and future climatic conditions (Fagundes et al. 2021; Reis et al. 2021; Martins et al. 2022; Silva et al. 2020).

Given the significance of the aforementioned forest species combined with the limited information available regarding their cardinal temperature values (T_b, T_{ot}, and T_B) for development, the present study aims to estimate the minimum, optimal, and maximum cardinal temperatures for foliar development in seedlings of *H. heptaphyllus*, *T. roseoalba*, *C. speciosa*, and *S. terebinthifolia* using widely employed methods described in the existing literature.

METHODS

The experimental procedure was performed in the forest nursery (22°46'27" S, 43°41'10" W, 26 m a. s. l.) of the Forest Institute of the Federal Rural University of Rio de Janeiro (UFRRJ), located in the municipality of Seropédica, southeastern Brazil (Fig. 1). The region is characterized by a tropical

climate with a dry season in winter and autumn (classified as Aw by the Köppen-Geiger climatic classification system (Alvares et al. 2013). The weather data employed in the study originated from an automatic weather station (ID A601) at the National Institute of Meteorology (INMET), which is situated approximately 1 km away from the experimental area. The data consisted of hourly maximum air temperature (T_x – °C), instantaneous temperature (T_m – °C), minimum air temperature (T_n – °C), relative air humidity (RU – %), and precipitation (prec – mm)."

Study species

H. heptaphyllus, a native species of Brazil, is distributed across the Amazônia, Caatinga, Cerrado, Mata Atlântica, Pampa, and Pantanal biomes (Lohmann 2020a). It has diverse applications, including as a source of timber, for forest restoration, and in traditional healing practices (Lima et al. 2014). Due to its remarkable flowering, it is frequently utilized as an ornamental plant in urban afforestation projects (Lima et al. 2014).

T. roseoalba is found in the Caatinga, Cerrado, and Mata Atlântica, with a slightly more limited distribution compared to *H. heptaphyllus* (Lohmann 2020b). The wood of *T. roseoalba* is highly regarded in the construction industry and widely employed in reforestation, landscaping, and urban afforestation projects (Santos et al. 2005).

C. speciosa is present in all Brazilian biomes, including the Amazon, Caatinga, Cerrado, Mata Atlântica, Pampa, and Pantanal (Carvalho-Sobrinho 2020). Its fruit, known as "paina," is utilized in the textile industry due to its similarity to cotton. Despite having thorns, the wood of *C. speciosa* holds significant value in various industries and is frequently used as an ornamental species in urban areas. It is also extensively employed in reforestation projects.

S. terebinthifolia is a species found in the Caatinga, Cerrado, Mata Atlântica, and Pampa biomes (Silva-Luz et al. 2020), with remarkable potential for timber production, ornamental use, degraded area rehabilitation, and reforestation purposes. It is particularly recognized for its fruit, Brazilian pepper, which is used in culinary endeavors (Marangoni et al. 2023).

Experimental design

The experiment was conducted following a completely randomized design, with four forest species (*Handroanthus heptaphyllus*, *Tabebuia roseoalba*, *Ceiba speciosa*, and *Schinus terebinthifolia*) cultivated in 280 cm³ tubes, across ten sowing periods (Table 1), with 15 replications for each period, totalling 600 repetitions (4 species × 10 sowing dates × 15 replications). The sowing periods were set at intervals of approximately 45 d to allow the seedlings to develop under a wide range of temperatures (Freitas et al. 2017; Ferreira et al. 2019a,b; Martins et al. 2022).

Table 1

Sowing, emergence, and end of the seedling phase dates (Day/Month/Year) of the experiment were carried out at the forestry nursery, Seropédica, Rio de Janeiro.

Species	Sowing date	Sowing	Emergence	End	Species	Sowing date	Sowing	Emergence	End
<i>H. heptaphyllus</i>	SD1	16/12/2019	23/12/2019	07/04/2020	<i>C. speciosa</i>	SD1	16/12/2019	30/12/2019	06/05/2020
	SD2	15/01/2020	22/01/2020	22/07/2020		SD2	15/01/2020	29/01/2020	12/08/2020
	SD3	17/02/2020	28/02/2020	12/08/2020		SD3	17/02/2020	04/03/2020	09/09/2020
	SD4	07/04/2020	20/04/2020	29/09/2020		SD4	07/04/2020	20/04/2020	09/09/2020
	SD5	06/05/2020	19/05/2020	29/09/2020		SD5	06/05/2020	10/06/2020	29/09/2020
	SD6	10/06/2020	24/06/2020	29/10/2020		SD6	10/06/2020	24/06/2020	29/10/2020
	SD7	21/07/2020	12/08/2020	17/12/2020		SD7	21/07/2020	12/08/2020	03/12/2020
	SD8	09/09/2020	15/09/2020	01/03/2021		SD8	09/09/2020	29/09/2020	08/01/2021
	SD9	29/10/2020	03/12/2020	11/02/2021		SD9	29/10/2020	15/11/2020	20/02/2021
	SD10	03/12/2020	17/12/2020	01/03/2021		SD10	03/12/2020	17/12/2020	26/03/2021
<i>T. roseoalba</i>	SD1	16/12/2019	23/12/2019	19/05/2020	<i>S. terebinthifolia</i>	SD1	16/12/2019	30/12/2019	06/05/2020
	SD2	15/01/2020	22/01/2020	24/06/2020		SD2	15/01/2020	29/01/2020	22/07/2020
	SD3	17/02/2020	28/02/2020	20/09/2020		SD3	17/02/2020	04/03/2020	09/09/2020
	SD4	07/04/2020	20/04/2020	29/09/2020		SD4	07/04/2020	20/04/2020	15/11/2020
	SD5	06/05/2020	19/05/2020	21/10/2020		SD5	06/05/2020	29/05/2020	17/12/2020
	SD6	10/06/2020	24/06/2020	17/12/2020		SD6	10/06/2020	24/06/2020	20/02/2021
	SD7	21/07/2020	04/08/2020	08/01/2021		SD7	21/07/2020	12/08/2020	21/01/2021
	SD8	09/09/2020	15/09/2020	21/01/2021		SD8	09/09/2020	29/09/2020	11/02/2021
	SD9	29/10/2020	15/11/2020	26/03/2021		SD9	29/10/2020	22/11/2020	26/03/2021
	SD10	03/12/2020	17/12/2020	06/04/2021		SD10	03/12/2020	17/12/2020	14/04/2021

Seeds were manually sown on a substrate composed of composted pine bark and vermiculite. Basal fertilization was performed following the procedure proposed by Gonçalves et al. (2000). For every 1m³ of substrate, 150 g of ammonium sulfate (N), 300 g of P2O5 (superphosphate), and 100 g of K₂O (potassium chloride) were homogenized. Additionally, for micronutrient supply, 150 g of FTE Br12 (1.8% B, 0.8% Cu, 3.0% Fe, 2.0% Mn, and 0.1% Mo) was added per 1m³. The substrate-fertilizer mixture was homogenized before filling the tubes. After 30 days of sowing, topdressing fertilization was carried out by applying approximately 10 ml of a nutrient solution composed of 200 g of N and 180 g of K₂O in 100 L of water monthly to each replicate. This nutrient solution was also supplemented with ammonium sulfate and potassium chloride (Gonçalves et al. 2000). This procedure is commonly used in nurseries to produce native Brazilian forest species (Calzavara et al. 2015). Daily irrigation was carried out using a sprinkler system to ensure that the plants developed without experiencing any water deficiency.

Cardinal Temperature Estimation

The cardinal temperatures (T_b, T_{ot}, and T_B) were estimated based on the data of number of leaves (NL) measured for each species, sowing period, and replication, as well as temperature data. T_b, T_{ot}, and T_B were estimated using widely used methodologies in the literature (Bartz et al. 2017; Souza and Martins 2014; Monteiro et al. 2014; Silva et al. 2020). To estimate T_b, data from the four sowing periods were considered, as they presented lower values of T_{min} and T_{med}, according to the recommendations of Souza and Martins (2014), Ferreira et al. (2019a), and Silva et al. (2020). For T_{ot}, NF data from all sowing periods were used, and for T_B, data from two sowing dates with the highest T_m values were used (Martins et al. 2014; Ferreira et al. 2019).

Base temperature (T_b)

The methods used to estimate T_b were the least standard deviation in degree days (SD_{dd}), least standard deviation in days (SD_d), coefficient of variation in days (CV_d), coefficient of variation in degree days (CV_{dd}), regression coefficient (RC), relative development (RD) (Arnold, 1959; Yang, Logan, Coffey, 1995), and lowest mean square error (MSE) (Sinclair et al. 2004). T_b values ranging from 0°C to 20°C at ± 0.5°C were chosen to calculate the SD_{dd}, SD_d, CV_{dd}, CV_d, RC, and MSE methods. The T_b methods are described in Table 2 and require daily degree days (DD_d = T_m - T_b × 1 d) and cumulative degree days (T_m - T_b × 1 d) values (DD = Σ(i = 1)ⁿ DD_d), obtained according to Sharratt et al. (1989) and Farias et al. (2015), in

which DDd = degree days (°C day), Tm = mean air temperature (°C), obtained by the arithmetic mean of hourly temperature from automatic weather station (A601 – Seropédica-Ecologia Agrícola), Tb = series of base temperature (°C) values ranging from 0°C to 20 (+ 0.5°C).

Table 2 presents an overview of the methods employed to estimate the base temperature for leaf development. These methods include several calculation approaches. The SDdd, SDd, CVdd and CVd are used as a measure of variability of GDD (SDdd and CVdd) or in days (SDd and CVd) for development stage. Using a range of Tb values from 0°C to 20°C, the correct Tb is the one resulting in the lowest standard deviation or coefficient of variation in GDD or in days required for the seedlings development. Additionally, the regression coefficient method (RC) consist of calculating the linear regression using the GDD as function of mean air temperature in the SD. Using a range of Tb values from 0°C to 20°C, the correct Tb is where the slope of regression equals zero. The linear regression analysis of the rate of seedlings development, defined as the ratio between 100 and number of days taken to reach the end of the seedling phase for each sowing date (n), as function of mean air temperature in the SD is the relative development method. Lastly, the lowest value of the mean square error (MSE) method use the linear regressions between the mean NL and the accumulated degree days (DD) during the SD and the Tb value for each SD was the one that showed the lowest MSE value of the linear regressions (Martins et al., 2012). The correct Tb is considered the arithmetic mean of the Tb values observed at different sowing dates.

Table 2

Traditional methodologies were used for the Tb estimation: standard deviation in degree days (SDdd), standard deviation in days (SDd), coefficient of variation in days (CVd), coefficient of variation in degree days (CVdd), regression coefficient (RC), relative development (RD) and lowest mean square error (MSE).

Method	Equation	Description
Least standard deviation, in degree days (SD _{dd})	$SD_{dd} = \left[\sum_{i=1}^n (D_i - GDD)^2 \right]^{\frac{1}{2}}$	Tb is the one that results in the lowest standard deviation in degree days from the set of assumed Tb values (Arnold, 1959; Sharratt et al. 1989; Souza; Martins, 2014).
Least standard deviation, in days (SD _d)	$SD_d = \frac{SD_{dd}}{T_m}$	Tb is the one that results in the lowest standard deviation in days from the set of assumed Tb values (Sharratt et al. 1989; Souza; Martins, 2014).
Coefficient of variation in degree days (CV _d)	$CV_d = \frac{SD_d}{\bar{D}} \cdot 100 \text{ (3)}$	Tb is the one that results in the lowest coefficient of variation in degree days from the set of assumed Tb values (Sharratt et al. 1989; Yang et al. 1995).
Coefficient of variation in days (CV _{dd})	$CV_{dd} = \frac{SD_{dd}}{\bar{D}} \cdot 100 \text{ (4)}$	Tb is the one that results in the lowest standard deviation in days from the set of assumed Tb values (Sharratt et al. 1989; Yang et al. 1995).
Regression coefficient (RC)	$GDD_i = a + b \cdot T_m \text{ (5)}$	Tb is the one that results in an angular coefficient closer to zero from the set of assumed Tb values. (Sharratt et al. 1989; Yang et al. 1995).
Relative Development (RD)	$DR = a + b \cdot T_m \text{ (6)}$	Tb is found by prolonging the equation to the X-axis, where the relative development is null. (Ferreira et al. 2019b)
Lowest mean square error (MSE)	$LN = a + b \cdot DD \text{ (7)}$	The Tb value is the one that presented the lowest MSE value obtained from a series of linear regressions between LN and DD calculated using the set of tb values (Freitas et al. 2017)

Optimum Temperature (Topt) Estimation

Topt was estimated based on the average Tm values obtained from sowing dates that presented the highest leaf development, that is, the lowest phyllochron (°C day leaf⁻¹) values (Freitas et al. 2017a; Ferreira et al. 2019a; Silva et al. 2020). To determine the optimal temperature for each forest species, phyllochron values were calculated using Eq. 8, which involved inverting the slope of the linear regression between the number of accumulated leaves on the main stem and the accumulated degree days. This calculation was performed for each forest species, sowing date, and replication. (Sharratt, Sheaffer and Baker, 1989).

$$NL = a \cdot DD + b \text{ (8)}$$

where NL represents the number of accumulated leaves on the main stem, and DD represents the accumulated degree of days (°C days).

Maximum Temperature (TB) Estimation

The TB of each forest species was estimated by considering the condition TB > Tm > Tb (Ferreira et al. 2019b), using 10 equations (Lima and Silva 2008):

$$A = N_2 \cdot Tx_1 \cdot Tx_2 - N_2 \cdot Tx_2 \cdot Tn_1 \text{ (9)}$$

$$B = -N_1 \cdot Tx_1 \cdot Tx_2 + N_1 \cdot Tx_1 \cdot Tn_2 \text{ (10)}$$

$$C = (-Tx_1 + Tn_1) \cdot (-Tx_2 + Tn_2) \text{ (11)}$$

$$D = N_1 \cdot Tn_2^2 \cdot N_2 - 2 \cdot Tn_2 \cdot N_1 \cdot N_2 \cdot Tb - Tn_2 \cdot Tn_1 \cdot N_1^2 \text{ (12)}$$

$$E = -Tn_2 \bullet Tx_1 \bullet N_1^2 + N_2^2 \bullet Tx_1 \bullet Tn_2 - Tn_1 \bullet N_2^2 \bullet Tn_2 + 2 \bullet Tn_2 \bullet N_2^2 \bullet Tb)$$

$$F = Tn_1 \bullet N_1^2 \bullet Tx_2 - 2 \bullet N_2^2 \bullet Tx_1 \bullet Tb - 2 \bullet N_1^2 \bullet Tx_2 \bullet Tb (14)$$

$$G = Tx_1 \bullet N_1^2 \bullet Tx_2 + Tx_1^2 \bullet N_2 \bullet N_1 - 2 \bullet Tn_1 \bullet N_2 \bullet N_1 \bullet Tb (15)$$

$$H = 2 \bullet Tn_1 \bullet N_2^2 \bullet Tb + 2 \bullet N_1 \bullet Tx_2 \bullet N_2 \bullet Tb + 2 \bullet N_2 \bullet Tx_1 \bullet N_1 \bullet Tb (16)$$

$$I = -2 \bullet N_2 \bullet Tx_1 \bullet N_1 \bullet Tx_2 + N_2^2 \bullet Tx_1 \bullet Tx_2 - Tn_1 \bullet N_2^2 \bullet Tx_2 (17)$$

$$J = -N_1 \bullet Tx_2 + N_1 \bullet Tn_2 + N_2 \bullet Tx_1 - N_2 \bullet Tn_1 (18)$$

$$TB = \frac{A + B \pm \sqrt{C \cdot (D + E + F + G + H + I)}}{J} (19)$$

Here, N_1 and N_2 are the duration (in days) of the seedling phase considering the two dates (1 and 2, respectively) with the highest temperature, Tx_1 and Tx_2 average of maximum air temperature ($^{\circ}\text{C}$), and Tn_1 and Tn_2 average of minimum air temperatures ($^{\circ}\text{C}$) during one and two sowing dates, respectively.

Statistical analysis

Spearman's correlation coefficient (rs) was used to verify the relationship between the duration of each sowing date and Tx , Tm , and Tn values. A hypothesis test was conducted to determine whether the sample correlation coefficient was significantly different from zero or close to zero using a 5% probability ($\alpha = 5\%$). The effects of forest species and sowing date (as sources of variation) were verified using analysis of variance. The mean values of the phyllochrons were compared using the Scott-Knott test at 5% probability. Before conducting the statistical analysis, the normality assumption for the phyllochron values was verified using the Shapiro-Wilk test at 5% probability. If the data did not follow a normal distribution, they were transformed using $\text{Ln}(\text{phyllochron})$.

RESULTS

The experiment exhibited variations in average meteorological conditions across different sowing seasons (Fig. 2), which is beneficial for accurate estimation of cardinal temperatures and reducing uncertainty in estimates. Uniform air temperatures and stable environmental conditions during certain periods can hinder the analysis, comparison of scenarios, and estimation of cardinal temperatures in plant development research (Ferreira et al. 2019b; Silva et al. 2020).

The lowest daily average temperature recorded during the experiment was 16.1°C in August (winter), while the highest daily average temperature was 32.2°C in October (spring). The absolute maximum air temperature reached 40.3°C (summer), and the minimum absolute temperature was 11.3°C (winter). December 2019 and 2020, as well as January and February 2020, had the highest accumulated precipitation, exceeding 150 mm in each of these months. Conversely, June and July 2020 experienced the lowest accumulated precipitation, with a total below 46 mm. The monthly average relative humidity (RH) ranged from 65.6–77.4%, with higher values observed in February and March 2020, exceeding an average RH of 76.0%. July 2020 and January 2021 had the lowest average RH, falling below 66.5%.

The sowing dates of SD3, SD4, SD5, and SD6 were used to estimate Tb values, as they had the lowest air temperatures, with the exception of *S. terebinthifolia*, which used SD2, SD3, SD4, and SD5 (Table 1). Generally, the coldest sowing dates result in longer seedling phases and less foliage development, making them ideal for estimating cardinal temperatures. Conversely, the two sowing dates with the highest temperature values, SD9 and SD10, resulted in the shortest seedling phase duration or the most rapid development for all four forest species.

Table 3
Variations in maximum (Tx), mean (Tm) and minimum air temperature (Tn) and seedling phase duration for each sowing date for four forest species in a forestry nursery experiment at Seropédica, Rio de Janeiro, Brazil.

Species	Sowing date	N (days)	Tx (°C)	Tm (°C)	Tn (°C)
<i>H. heptaphyllus</i>	E1	106	30.75	25.48	21.22
	E2	182	30.75	23.46	18.08
	E3	166	28.22	22.70	18.08
	E4	162	28.62	22.49	16.14
	E5	133	28.62	22.45	16.14
	E6	127	32.23	23.14	16.14
	E7	149	32.23	24.05	16.14
	E8	167	32.23	25.44	19.06
	E9	70	31.21	25.70	19.61
	E10	74	31.21	26.56	21.24
<i>T. roseoalba</i>	E1	148	30.75	24.56	19.15
	E2	154	30.75	24.11	19.15
	E3	205	28.62	22.83	16.14
	E4	162	28.62	22.49	16.14
	E5	155	32.23	22.87	16.14
	E6	176	32.23	23.45	16.14
	E7	157	32.23	24.16	16.14
	E8	128	32.23	25.00	19.06
	E9	131	31.21	26.34	20.75
	E10	110	31.21	26.48	21.24
<i>C. speciosa</i>	E1	128	30.75	24.84	20.73
	E2	196	30.75	23.23	18.08
	E3	189	28.22	22.68	16.14
	E4	142	27.52	22.18	16.14
	E5	111	28.62	22.72	16.14
	E6	127	32.23	23.11	16.14
	E7	113	32.23	23.84	16.14
	E8	101	32.23	25.14	19.61
	E9	97	31.21	26.35	20.75
	E10	113	31.21	26.65	21.24
<i>S. terebinthifolia</i>	E1	128	30.75	24.83	20.73
	E2	175	30.75	23.41	18.08
	E3	189	28.22	22.68	16.14
	E4	209	32.23	22.79	16.14
	E5	202	32.23	23.34	16.14
	E6	241	32.23	24.36	16.14
	E7	162	32.23	24.61	16.14
	E8	135	32.23	25.14	19.61

Species	Sowing date	N (days)	Tx (°C)	Tm (°C)	Tn (°C)
	E9	124	31.21	26.50	21.24
	E10	118	31.21	26.31	21.24

The mean air temperature and duration of the seedling phase showed an inverse relationship, as indicated by the Spearman's correlation coefficient for the four forest species (Table 3). *T. roseoalba* and *S. terebinthifolia* showed a particularly strong negative correlation ($r_s = -0.88$ and -0.81 , respectively), with moderate negative correlation values noted in *H. heptaphyllus* and *Ceiba speciosa* ($r_s = -0.50$ and -0.52 , respectively). These negative correlations suggest that as the mean air temperature increases, the duration of the seedling phase in the nursery decreases, accelerating plant development. Conversely, at cooler temperatures, seedling development was delayed, resulting in longer seedling phases. The maximum air temperature did not correlate significantly with DFM, whereas the minimum air temperature showed a negative correlation with seedling phase duration, except for *H. heptaphyllus* and *C. speciosa*.

Table 4
Spearman's correlation values between air temperature and the seedling phase duration for four forest species, where significance codes were attributed as follows: 0.01 '***'; 0.05 '**'; 0.1 '*'; ns indicating 'non-significant'. SPD stands for the seedling phase duration.

Correlation between temperature and SPD	Tx (°C)	Tm (°C)	Tn (°C)
<i>Handroanthus heptaphyllus</i>	-0.27 ^{ns}	-0.50 [*]	-0.38 ^{ns}
<i>Tabebuia roseoalba</i>	-0.23 ^{ns}	-0.88 ^{***}	-0.86 ^{***}
<i>Ceiba speciosa</i>	-0.53 ^{ns}	-0.52 [*]	-0.35 ^{ns}
<i>Schinus terebinthifolia</i>	-0.35 ^{ns}	-0.81 ^{**}	-0.89 ^{***}

The different methods applied for estimating Tb yielded similar results in terms of the value range, with the exception of the CR and RD methods, which displayed values outside the expected range for *H. heptaphyllus* and *T. roseoalba* (between ≥ 6.5 °C and ≤ 20.0 °C, as indicated by Ferreira et al. 2019b). These anomalous values were excluded from the arithmetic mean calculation to obtain Tb values for each forest species. The estimation methods exhibited mean Tb values ranging from 9.8 °C to 11.3 °C, with corresponding standard deviations ranging from 0.5 °C to 3.3 °C. For *H. heptaphyllus*, the estimated Tb was 11.3 °C $\pm$ 3.3; for *T. roseoalba*, it was 10.0 °C $\pm$ 0.5; for *C. speciosa*, it was 11.5 °C $\pm$ 2.6; and for *S. terebinthifolia*, it was 9.8 °C $\pm$ 1.8 (Table 2). Overall, the Tb estimation methods proved effective, with a graphical representation presented in Fig. 3.

Table 5
The estimated base temperature values were obtained using different methods, and the average and standard deviation between these methods were calculated.

Species	SD _{gd}	SD _d	CV _{gd}	CV _d	RC	RD	MSE	Mean $\pm$ SD
<i>H. heptaphyllus</i>	9.5	9.0	9.5	9.0	14.5	17.9	9.5	11.3 ± 3.3
<i>T. roseoalba</i>	10.5	9.5	10.5	9.5	20.0*	39.3*	9.8	10.0 ± 0.5
<i>C. speciosa</i>	10.0	9.5	10.0	9.5	15.5	15.7	10.0	11.5 ± 2.6
<i>S. terebinthifolia</i>	10.5	9.5	10.5	9.5	9.0	13.3	7.0	9.8 ± 1.8

*Values outside the appropriate temperature range for the base temperature according to Ferreira et al. (2019). SD is the standard deviation.

The CR and DR methods were unsuitable for estimating Tb for *H. heptaphyllus* and *T. roseoalba*, as they generated higher Tb values than the other methods. Additionally, the slope of the linear regression between the accumulated degree days and DR as a function of mean air temperature was not significant ($p \geq 0.05$; Table 3), indicating that there was no significant increase in DR with increasing mean air temperature (Fig. 3 and Table 5).

Table 6

Regression coefficients and p-values for the relative development and mean air temperature, as well as the degree-days and mean temperature. RD = relative development; DD = degree days accumulated; b = linear and slope coefficients, respectively; H_0 = null hypothesis for the t-test, in which the regression coefficient is equal to zero; r^2 = coefficient of determination; ^{ns} = non-significant.

Species	RD = a + bTm				
	a	p-value (H_0 : a = 0)	b	p-value (H_0 : b = 0)	r^2
<i>H. heptaphyllus</i>	-2.55 ^{ns}	0.60	0.14 ^{ns}	0.52	0.23
<i>T. roseoalba</i>	1.39 ^{ns}	0.66	0.04 ^{ns}	0.80	0.04
<i>C. speciosa</i>	-0.73 ^{ns}	0.37	-0.05 ^{ns}	0.19	0.66
<i>S. terebinthifolia</i>	-1.65 ^{ns}	0.82	0.11 ^{ns}	0.75	0.06
Species	DD = a + bTm				
	a	p-value (H_0 : a = 0)	b	p-value (H_0 : b = 0)	r^2
<i>H. heptaphyllus</i>	3839.12 ^{ns}	0.65	-115.69 ^{ns}	0.75	0.06
<i>T. roseoalba</i>	-3940.29 ^{ns}	0.26	194.29 ^{ns}	0.22	0.61
<i>C. speciosa</i>	2736.97 ^{ns}	0.81	1.46 ^{ns}	0.99	0.00
<i>S. terebinthifolia</i>	1077.96 ^{ns}	0.92	-2.41 ^{ns}	0.10	0.00

Estimated base temperature (TB) values were 50.3 °C for *H. heptaphyllus*, 53.2 °C for *T. roseoalba*, 57.6 °C for *C. speciosa*, and 52.6 °C for *S. terebinthifolia*. As determined by ANOVA ($p \geq 0.05$), a significant interaction was detected between the studied species and sowing date for the phyllochron values. Differences in phyllochron values were observed between the times for *H. heptaphyllus* and *S. terebinthifolia*, whereas no difference was found among sowing dates for *T. roseoalba* and *C. speciosa* (Scott-Knott test). The lowest phyllochron values for *H. heptaphyllus* occurred during SD3, SD7, SD9, and SD10, whereas for *S. terebinthifolia* they occurred during E2, E5, E6, E7, and E10 (Table 7). The T_{opt} values for *H. heptaphyllus*, *T. roseoalba*, *C. speciosa*, and *S. terebinthifolia* were obtained using the arithmetic mean of the mean air temperatures of the sowing dates with the lowest phyllochron values. The Estimated T_{opt} values were 25.7°C for *H. heptaphyllus*, 24.2°C for *T. roseoalba*, 24.8°C for *S. terebinthifolia*, and 22.7°C for *C. speciosa*.

Table 7

Comparison of Mean Phyllochron Values (°C day per leaf) for Four Forest Species Across Ten Sowing Dates. The table displays a comparison of means for phyllochron values across ten sowing dates for the four forest species. Means marked with the same lowercase letter within a column (representing the sowing date) and uppercase letter within a row (representing the forest species) indicate no statistically significant differences between them, as determined by the Scott-Knott test ($p \geq 0.05$).

Sowing date	<i>H. heptaphyllus</i>	<i>T. roseoalba</i>	<i>C. speciosa</i>	<i>S. terebinthifolia</i>	Mean
E1	103.56aA	128.08aA	131.09aA	104.35bA	117.69b
E2	194.70aA	127.27aA	175.38aA	148.58aA	162.35a
E3	84.18bB	128.54aA	145.95aA	110.67bA	117.74b
E4	109.20aA	114.99aA	150.74aA	121.25bA	122.44b
E5	143.76aA	155.01aA	100.51aA	142.59aA	138.47b
E6	115.09aB	130.03aB	246.22aA	204.22aA	177.25a
E7	122.71bA	117.76aA	159.92aA	132.10aA	129.70b
E8	149.43aA	120.38aA	148.41aA	148.93bA	142.15b
E9	75.64bB	128.88aA	135.90aA	90.32bA	108.96b
E10	81.20bB	124.94aA	175.31aA	145.54aA	130.68b
Mean	122.51C	127.39B	154.82A	134.86B	

The *H. heptaphyllus* displayed the lowest phyllochron value among the forest species examined (Table 7) at a value of 122.5°C day leaf⁻¹. Conversely, the *C. speciosa* displayed the highest phyllochron value at 154.8°C day-leaf⁻¹, signifying that it requires a greater degree of energy accumulation to produce a leaf, leading to slower seedling development. The adjusted linear regressions between the NL and DD, computed by using the three cardinal temperatures previously mentioned for each forest species, showed an adjusted coefficient of determination greater than 0.75 ($R^2 \text{ adj} > 0.75$) with slope coefficients that were statistically significant ($p < 0.05$). This outcome indicates a positive and direct linear connection between the number of leaves and thermal sum (Fig. 4).

The phyllochron value exhibited substantial variability among the examined forest species, as indicated by the non-overlapping notched boxplot, signifying significant differences in medians. Notably, *C. speciosa* demonstrated the highest phyllochron value, followed by *T. roseoalba* and *S. terebinthifolia*. Conversely, *H. heptaphyllus* displayed the lowest phyllochron value (Fig. 5 and Table 5).

DISCUSSION

The results of our experiment revealed that the T_n , T_m , and T_x values exceeded those reported in previous studies with similar objectives for various species, such as *Psidium guajava* L. (Ferreira et al. 2019a), *Citharexylum myrianthum* Cham., *Bixa orellana* L. (Ferreira et al. 2019b), *Caesalpinia ferrea* Mart. ex. Tul. var. *leiostachya* Benth, *Anadenanthera macrocarpa* (Benth), Brenan (Silva et al. 2020), *Eucalyptus* sp. (Martins and Streck 2007; Freitas et al. 2017), and olive trees (Souza and Martins 2014). These studies employed similar methods for estimating the cardinal temperatures and observed wider temperature variations, ranging from 3.6°C to 34.6°C (Silva et al. 2020a), 2.3°C to 35.7°C (Ferreira et al. 2019a), and - 3.7°C to 32°C (Souza and Martins 2014), resulting in thermal amplitudes of approximately 30°C (between the absolute minimum and maximum air temperature). In contrast, our study exhibited a thermal amplitude of around 20°C.

A study conducted by Monteiro et al. (2014) with *Hymenobium petraeum*, *Parkia pendula*, *Anadenanthera pavonina*, and *Cassia fistula* presented temperature variations similar to our study, confirming the applicability of most of the methods employed to estimate T_b and the phyllochron approach to T_{opt} . Literature reports T_b ranging from 10.0°C to 12.9°C and T_{opt} ranging from 17.3°C to 25.1°C for perennial species (Ferreira et al. 2019a; Lima and Silva 2008; Martins et al. 2007; Monteiro et al. 2014), which aligns closely with the range found in our study.

In general, the methods used in our study were effective in estimating T_b , except for CR and RD, which produced T_b values outside the expected range ($> 20^\circ\text{C}$) for *T. roseoalba*. While the T_b values for the other forest species examined fell within the expected range, the slope coefficient for the linear regression between RD and T_m was found to be insignificant (Table 3). The relative development method relies on the correlation between T_m and RD ($RD = 100/N$) to estimate T_b . Thus, higher RD values are expected during periods of higher mean temperatures. However, the mean temperature values considered in T_b estimation using sowing dates exhibited limited variation ($\sim 2^\circ\text{C}$). As cautioned by Yang et al. (1995), extrapolating the regression line in such cases poses a limitation to the comparative development method, leading to a tendency of RD to approach zero. This can result in inaccurate basal temperature readings when temperature variation is minimal.

The RC method was employed to associate the number of days required for leaf emergence with T_m . It is generally expected that as temperature increases, the accumulated number of days for leaf emergence remains relatively constant. Although the slope coefficients for *H. heptaphyllus* and *T. roseoalba* did not support the null hypothesis ($H_0: b = 0$; $p\text{-value} > 0.05$), the values deviated significantly from zero, indicating a higher T_b for *H. heptaphyllus* (positive slope coefficient) and a lower T_b for *T. roseoalba* (negative slope coefficient).

Regarding T_b , our method established higher thresholds compared to those estimated for other perennial species, including *Parkia pendula* (Monteiro et al. 2014), *Corymbia citriodora*, and *Eucalyptus urophylla* (Freitas et al. 2017), *Citharexylum myrianthum*, *Bixa orellana*, *Libidibia ferrea*, *Anadenanthera macrocarpa* (Silva et al. 2020), *Ceiba speciosa*, and *Psidium guajava* (Ferreira et al. 2019a), with values ranging from 36.5°C to 46.4°C.

In conclusion, our experiment demonstrated higher T_n , T_m , and T_x values compared to previous studies for various species. The temperature variations observed in our study were relatively lower, resulting in a narrower thermal amplitude. The methods employed for estimating T_b proved effective, except for CR and RD, which produced unexpected T_b values for *T. roseoalba*. The RC method provided insights into the relationship between T_m and the number of days for leaf emergence, highlighting the contrasting T_b values for *H. heptaphyllus* and *T. roseoalba*. These findings contribute to the current understanding of cardinal temperatures and their implications for the growth and development of forest species. It is important to note that our study aligns with the established ranges of T_b and T_{opt} reported in the literature for perennial species.

The limitations of our study include the restricted temperature variation during the estimation of T_b using sowing dates, leading to potential inaccuracies in the basal temperature readings. The extrapolation of the regression line in cases of minimal temperature variation can further impact the accuracy of the relative development method. These limitations highlight the need for caution when applying these estimation methods in experiments with low temperature variability.

Overall, our study contributes to the knowledge of cardinal temperatures and their estimation methods for forest species. Further research is warranted to validate these findings and explore additional factors that may influence the growth and development of these species under varying temperature conditions. Such investigations will enhance our understanding of the physiological responses and adaptive mechanisms of forest species to temperature fluctuations, facilitating more accurate predictions and management strategies in the face of changing climate conditions.

Additionally, future studies could also investigate the potential interactions between cardinal temperatures and other environmental factors, such as light intensity, humidity, and soil moisture, to gain a more comprehensive understanding of the growth and development processes.

The results obtained from this study suggest that the four forest species examined in this study are well-suited to high-temperature conditions, which is consistent with their occurrence in Brazil (Lohmann 2020a; Lohmann 2020b; Carvalho-Sobrinho 2020; Silva-Luz et al. 2020). These regions are known to experience high daily mean air temperatures (Alvares et al. 2013). Studies projecting temperature increases and modeling the growth of tropical species under future climates have reported the potential for changes in specific leaf area and leaf lifespan, depending on the season (Reis et al. 2021; Fagundes et al. 2021), particularly in species with limited thermal amplitude.

The TB values obtained in this study were influenced by experimental conditions, but certain constraints were observed in the operation of the TB techniques at different temperatures. The slightly elevated TB values found in our investigation compared to other perennial species (Martins et al. 2014; Freitas et al. 2017; Ferreira et al. 2019a, b; Silva et al. 2020) may be attributed to the narrow range of T_n, T_m, and T_x values between the two sowing dates used in the TB estimation, similar to the duration (in days) (Table 3).

The measured T_{opt} values for the analyzed species (ranging from 22.5°C to 26.0°C) were comparable to those reported for *Anadenanthera macrocarpa* (T_{opt} = 23°C) (Silva et al. 2020a), *Hymenolobium petraeum* (T_{opt} = 24.9°C), *Parkia pendula* (T_{opt} = 25.1°C), *Adenanthera pavonina* (T_{opt} = 24.4°C), and *Cassia fistula* (T_{opt} = 24.9°C) (Monteiro et al. 2014). These values were also higher than those reported for other forest species such as *Citharexylum myrianthum*, *Bixa orellana* (Ferreira et al. 2019b), *Caesalpinia ferrea* (Silva et al. 2020a), *Psidium guajava* (Ferreira et al. 2019a), *Corymbia citriodora*, and *Eucalyptus urophylla* (Freitas et al. 2017), which ranged from 17.1°C to 20.7°C.

The average phyllochron values for the species in our study were statistically significant ($p \leq 0.05$). However, there was limited variation between the sowing dates, with no significant difference observed for *T. roseoalba* and *C. speciosa*. This lack of difference may be attributed to the minimal variation in T_m during the experimental period, as it was close to the T_{opt}. The species exhibited differences in leaf emergence speed according to the sowing dates, with higher phyllochron values observed in the sowing dates with intermediate temperatures for *S. terebinthifolia* (SD5 and SD6) and higher T_m for *H. heptaphyllus* (SD2 and SD8). These findings align with previous studies that reported similar trends in *H. heptaphyllus* and *S. terebinthifolia*, with *H. heptaphyllus* displaying a higher phyllochron and an inverse relationship with T_m, while *S. terebinthifolia* exhibited faster maturation and a lesser phyllochron, with less reliance on daily mean temperatures (Monteiro et al. 2014). This suggests that *H. heptaphyllus* requires a lower degree of energy accumulation (in degree days) to produce a leaf on the main stem, resulting in faster leaf generation and seedling development, as reported by Martins et al. (2023). The lower T_b estimated for *S. terebinthifolia* compared to other forest species may contribute to greater thermal accumulation under similar environmental conditions (Fagundes et al. 2021; Freitas et al. 2017; Martins et al. 2023).

CONCLUSIONS

Our findings highlight the importance of considering temperature variability and its effects on *Handroanthus heptaphyllus*, *Tabebuia roseoalba*, *Ceiba speciosa*, and *Schinus terebinthifolia*. Deviations from their optimal temperature ranges, as revealed by our observations of T_{opt}, T_b, and TB values, could severely affect their growth and survival, particularly under climate change scenarios. The variations in cardinal temperature values among species have implications for their phenology, growth, and overall adaptation to different environmental conditions. The methods employed in our study proved effective in estimating cardinal temperatures, although certain limitations exist for specific species. This knowledge contributes to the broader field of plant physiology and can inform management and conservation efforts for forest ecosystems. Thus, careful management and monitoring of these plant species are imperative to ensure their long-term viability. Consequently, our research highlights the thermal requirements of these plant species, allowing for the development of suitable models that require cardinal temperatures as inputs.

Declarations

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Figures

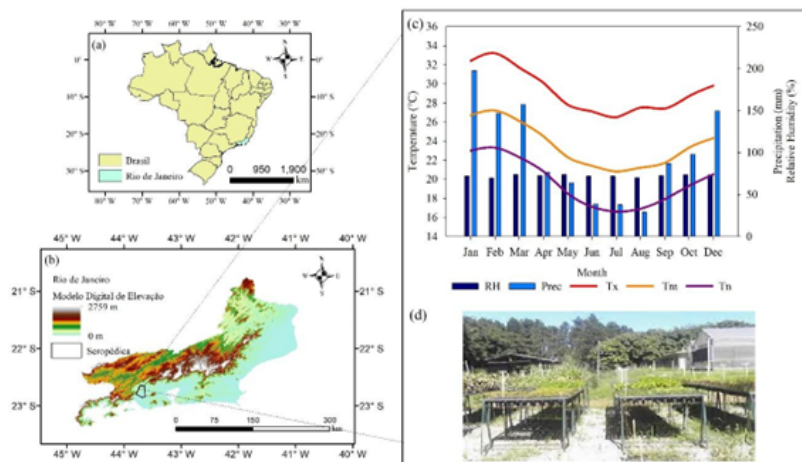


Figure 1

Forest Nursery "Luiz Fernando de Oliveira Capellão" Location and Experiment Details. (a) Location of the Rio de Janeiro State, Brazil. (b) Location of Seropédica city. (c) Average climatological mean (1981-2010) air temperatures - maximum (Tx), mean (Tm), and minimum (Tn) - relative humidity (RH), and precipitation (Prec) in Seropédica. (d) Benches used for placing the seedlings at the forest nursery.

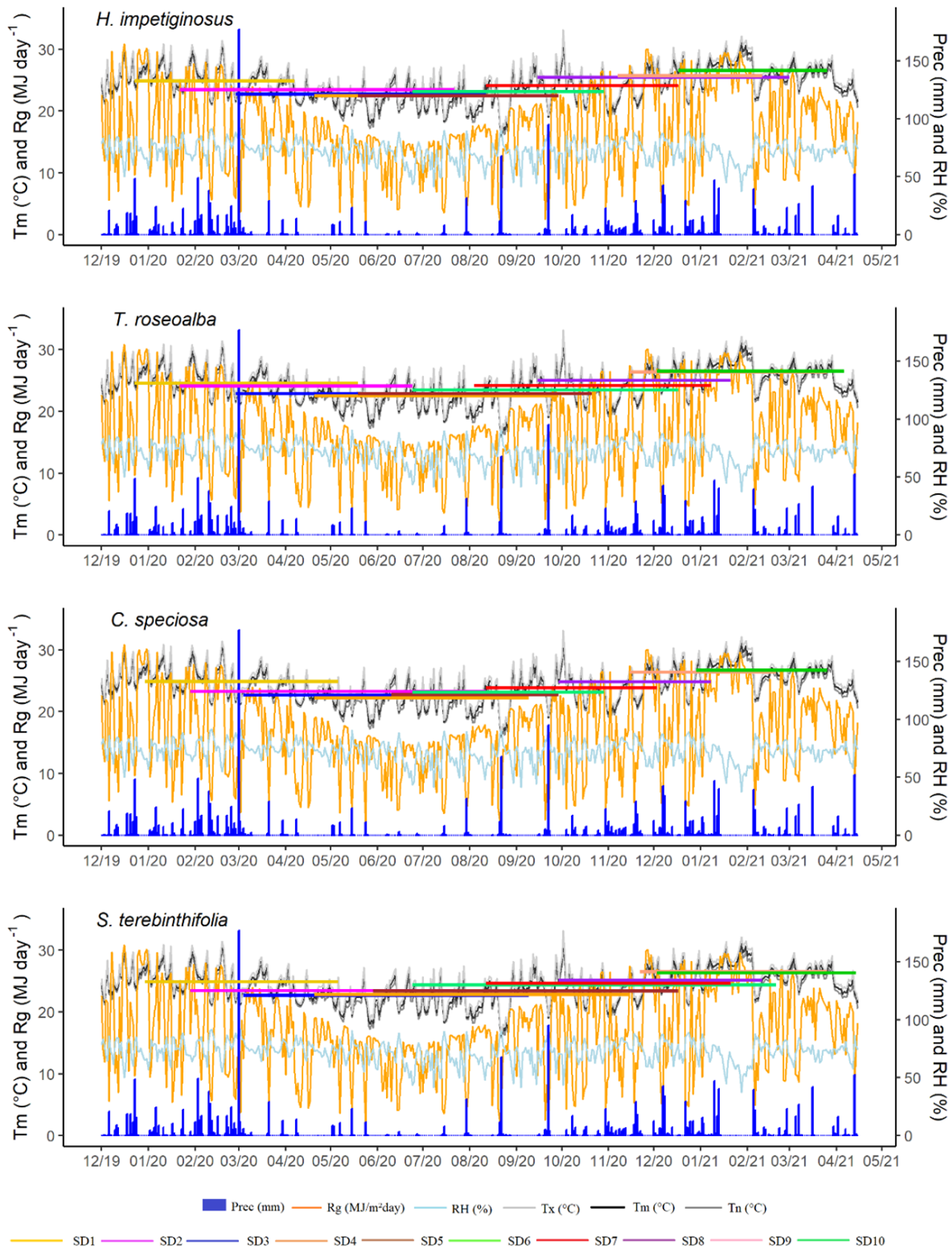


Figure 2

The maximum (T_x , °C), mean (T_m , °C), and minimum (T_n , °C) air temperatures, relative humidity (RH,%), precipitation (mm), global radiation (R_g , MJ/m²dia) and the duration of the seedling phase throughout the course of the experiment (SD1-SD10).

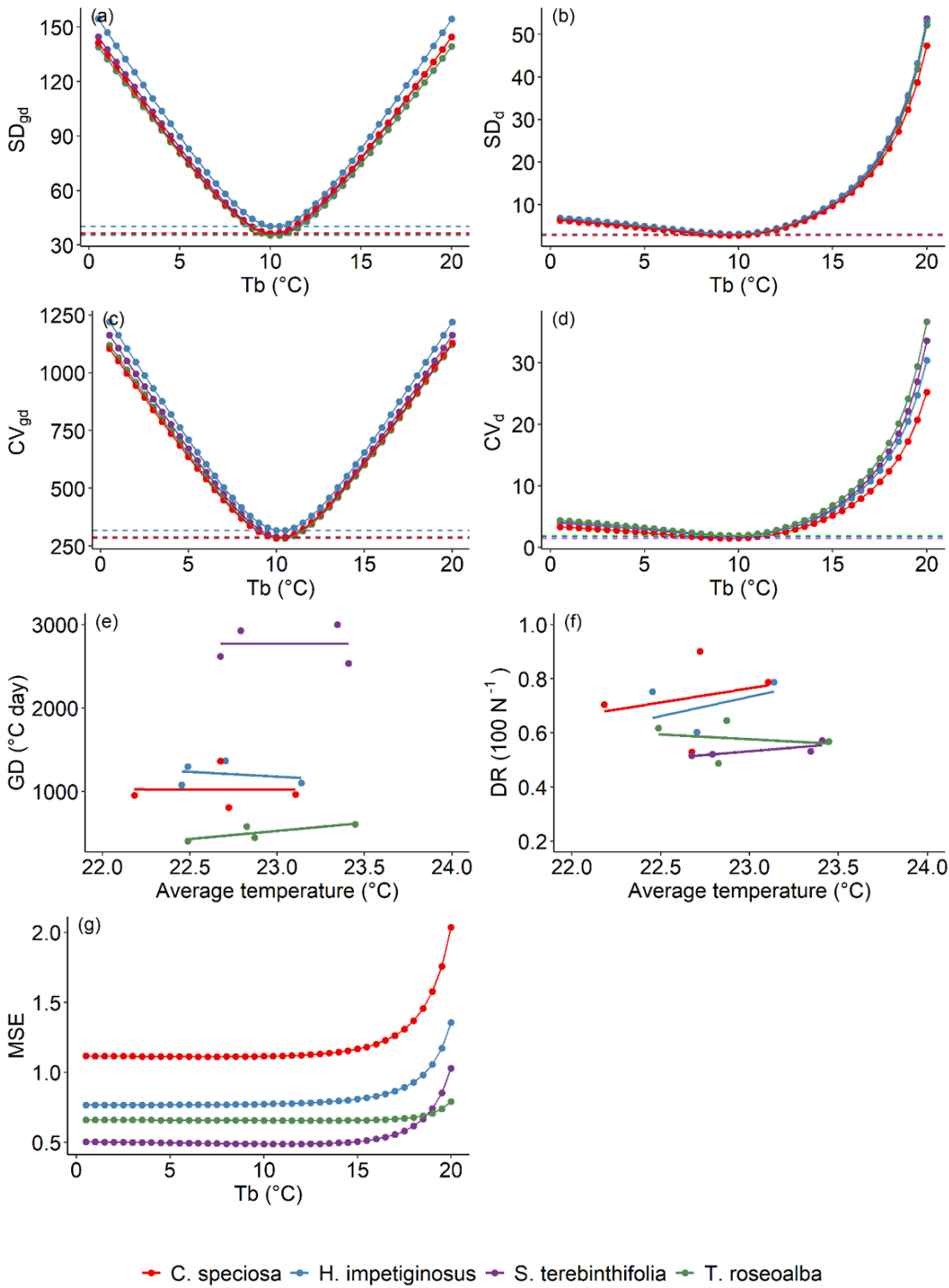


Figure 3

Methods utilized for estimating the base temperature (T_b) for *H. heptaphyllus*, *T. roseoalba*, *C. speciosa*, and *S. terebinthifolia*. These methods include: (a) the least standard deviation in degree days, (b) the least standard deviation in days, (c) the coefficient of variation in degree days, (d) the coefficient of variation in days, (e) the regression coefficient, and (f) the relative development. The parameter N denotes the number of days corresponding to each sowing date.

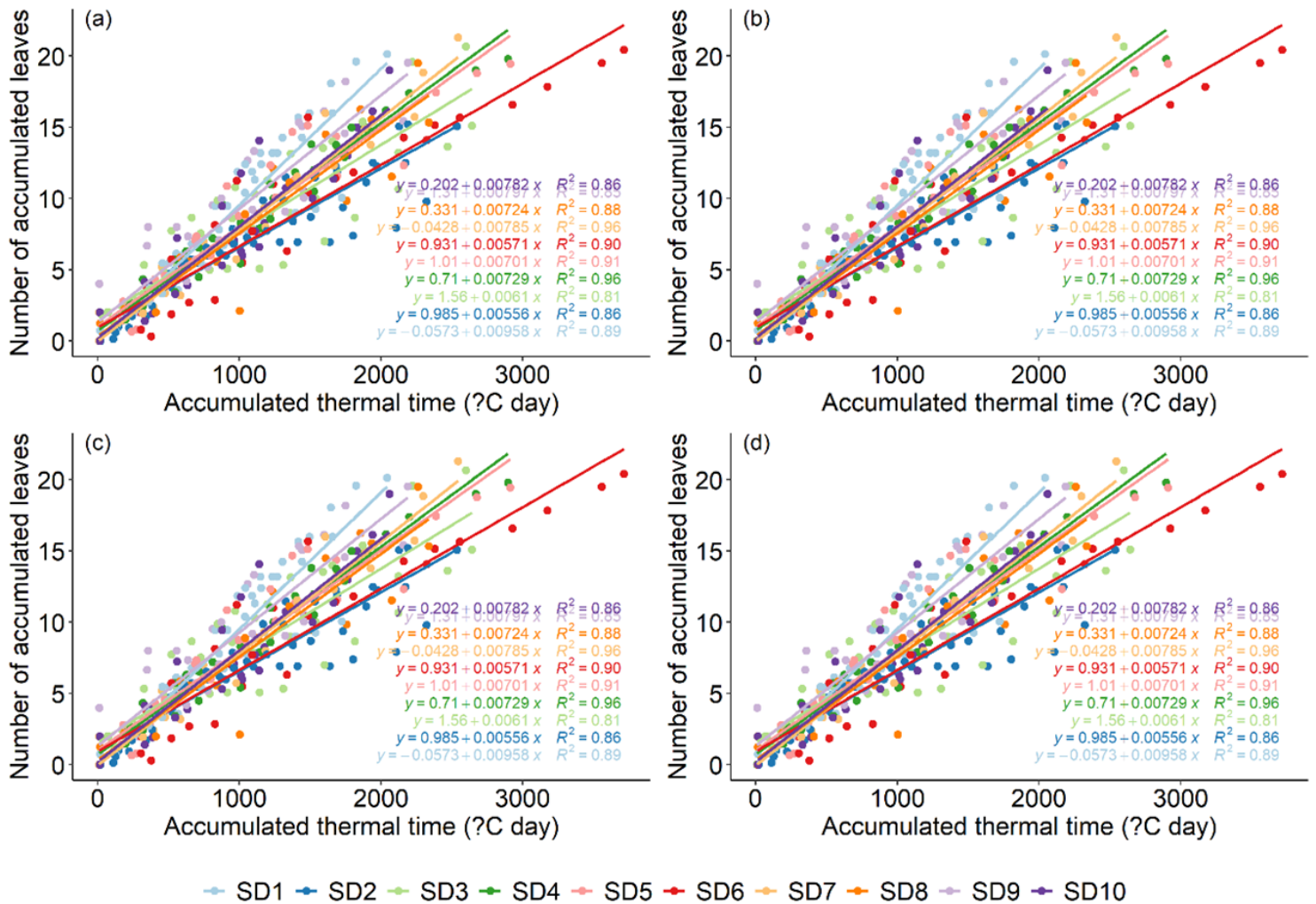


Figure 4

Accumulated number of leaves versus accumulated degree days were calculated for the following forest species: (a) *H. heptaphyllus*, (b) *T. roseoalba*, (c) *C. speciosa*, and (d) *S. terebinthifolia*.

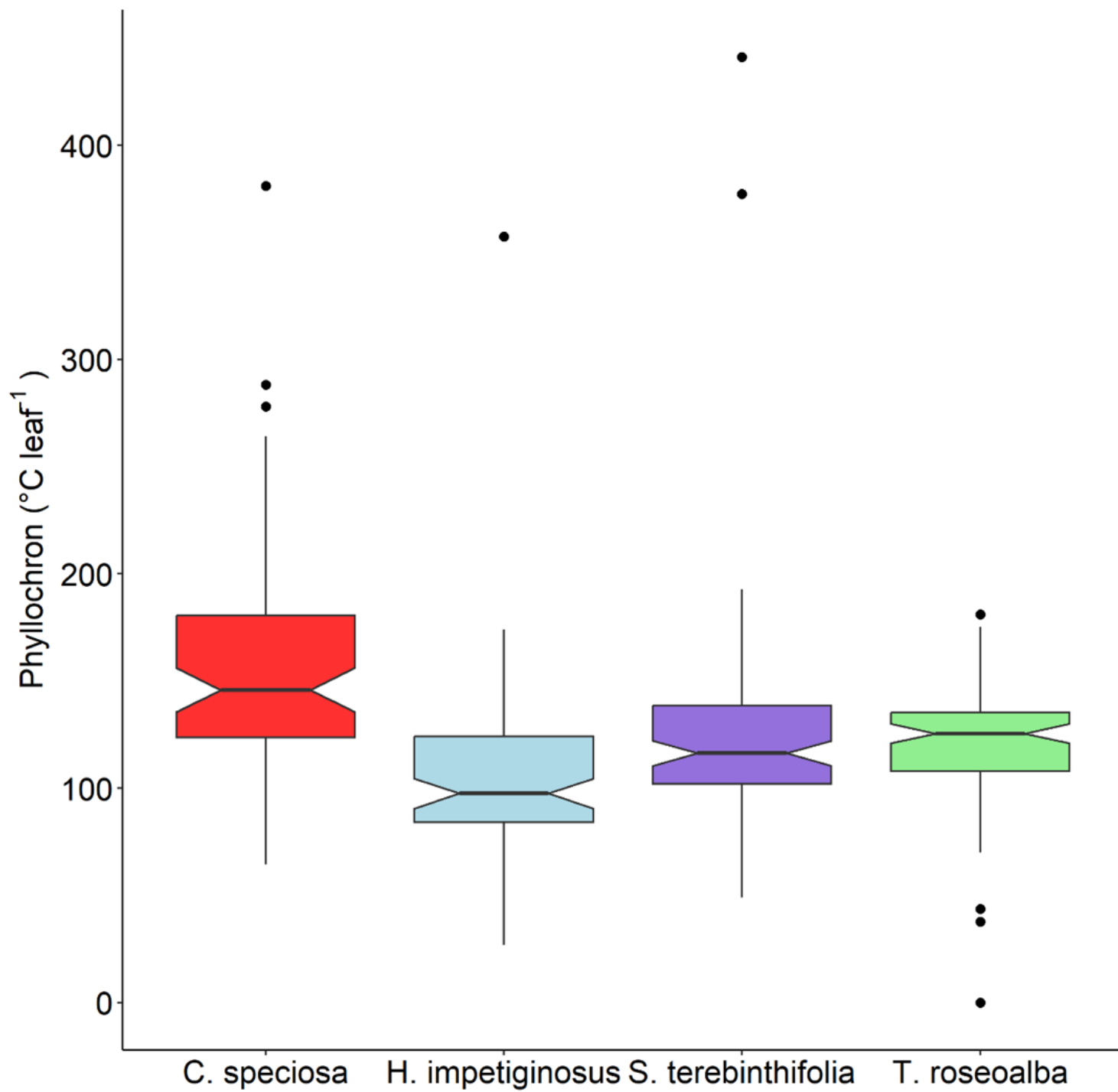


Figure 5

The boxplot of the phyllochron values for *H. heptaphyllus*, *T. roseoalba*, *C. speciosa*, and *S. terebinthifolia*.