



Thermal and photoperiodic requirements of the seedling stage of three tropical forest species

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Received: 16 February 2022 / Accepted: 23 July 2022 / Published online: 5 September 2022
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Abstract Air temperature and photoperiod play an important role in the seedling development for tropical forest species. Both variables are sensitive to climate, and so evaluating thermal and photoperiodic effects on seedling development is fundamental, especially for climate change studies. Methods to quantify thermal time and the energy required for plants to reach a development stage include air temperature and cardinal temperatures. The photoperiod will also affect physiological reactions of a plant and thus its development. Here we evaluated the six thermal time methods widely used to compute thermal requirement, and identified the influence of the photoperiod from the 2015 and 2016 growing seasons and 12 sowing dates in Itajubá, Minas Gerais state, Brazil, on seedling development of three native tropical forest species *Psidium guajava* L. (Myrtaceae), *Citharexylum myrianthum* Cham. (Verbenaceae), and *Bixa orellana* L. (Bixaceae). The method used to quantify thermal

time influenced the analytical results of seedling development; the one that considered three cardinal temperatures and compared them with the mean air temperature (Method 5) performed better in computing thermal requirements. The influence of photoperiod on seedling development was inconclusive for the three species, but all three developed better in mild temperatures (between 13.3 °C and 26.9 °C) with a photoperiod shorter than 13 h.

Keywords Phyllochron · Thermal time · Day length · Seedling stage · Phenology

Introduction

The seedling stage of plant growth is the most sensitive and least tolerant to climatic conditions and extremes (Morin et al. 2010; Rawal et al. 2014; Ferreira et al. 2019a, b; Silva et al. 2020; Fagundes et al. 2021; Martins et al. 2022b), especially to air temperature variability (Costa and Streck 2018; Florêncio et al. 2019; Reis et al. 2021). Gradual or abrupt changes in climate can alter physiological processes, and if persistent, can change morphological and phenological patterns (Bahuguna and Jagadish 2015; Reis et al. 2021) and impact seedling quality and survival. Since seedlings may have limited access to soil moisture and nutrients (Abreu et al. 2022) and solar radiation, which hinders their growth, whereas faster development will improve their competitive ability and survival (Williams and Dumroese 2014; Reis et al. 2021). Therefore, studies that provide a greater understanding of the developmental responses of a species to climate conditions will help guide growers to select forestry and silvicultural practices in order to optimize seedling production, as well as assess and predict plant responses in future climate scenarios (Rawal et al. 2015; Ferreira et al.

Project funding: This work was financially supported by the Minas Gerais Research Support Foundation (FAPEMIG, APQ-01392-13 and APQ 01258-17), the Coordination for the Improvement of Higher Education Personnel (Capes, process numbers 88887.613734/2021-00, and 1827878), the FAPEMIG (process number ID14029), and National Council for Scientific and Technological Development (CNPq, process number 306845/2021-0).

Guest editor: Srđan Stojnić

The online version is available at <http://www.springerlink.com>.

Corresponding editor: Yanbo Hu

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2019b; Freitas and Martins 2019; Fagundes et al. 2021; Reis et al. 2021; Martins et al. 2022b).

Air temperature and photoperiod are critical factors for seedling development of tropical forest species (Rawal et al. 2014; Ferreira et al. 2019a, b; Freitas and Martins 2019; Silva et al. 2020; Martins et al. 2022b, c). Air temperature influences physiological and metabolic activities, photosynthesis and photorespiration, the transport of solutes, and the balance between transpiration and water consumption (Freitas et al. 2017; Ferreira et al. 2019a; Martins et al. 2022b). The photoperiod or day length affects the amount of solar radiation and the timing of photosynthesis and biomass production (Rawal et al. 2015; Langner et al. 2016; Mantai et al. 2017; Freitas and Martins 2019).

One way to assess the influence of air temperature and photoperiod on seedling development is using the phyllochron model (Martins et al. 2007, 2022c; Lisboa et al. 2012; Freitas et al. 2017; Reis et al. 2021). The phyllochron is the time between the visible emergence of successive leaf tips, assuming a linear relationship between leaf emergence rate (the phyllochron) and daily thermal accumulation (i.e., thermal time [TT] °C·d); thus, the phyllochron is the cumulative TT between successive leaves (or, number of leaves [NL]) and is thus measured as °C·d per leaf (Streck et al. 2011; Ferreira et al. 2019a). TT can be calculated using different methods (Rosa et al. 2009; Daibes et al. 2019; Freitas and Martins 2019), but all require air temperature and the cardinal temperatures, which are called base (T_b), optimum (T_{opt}), and maximum (T_B) temperatures. These thermal thresholds (T_b , T_{opt} and T_B) are specific for each tropical forest species and establish the temperature ranges at which a seedling can develop (Freitas et al. 2017; Ferreira et al. 2019a, b; Silva et al. 2020). Each TT method can result in different thermal time values, especially when air temperature is below the T_b or above the T_B of the species (Rosa et al. 2009; Ferreira et al. 2019a; Freitas and Martins 2019), thus affecting the phyllochron values (Rosa et al. 2009; Martins et al. 2022c).

Similar to air temperature, one way of assessing the influence of the photoperiod on seedling development is using the linear relationship between the phyllochron and photoperiod (Streck et al. 2007b; Rosa et al. 2009; Silva et al. 2020). By this approach, the seedlings can be classified based on their response to the photoperiod as short-day plants (SDP), long-day plants (LDP), or day-neutral plants (DNP) (Streck et al. 2006, 2007b; Rosa et al. 2009; Freitas and Martins 2019; Silva et al. 2020), the three most used classifications for seedlings of forest species (Ferreira 2017; Freitas and Martins 2019; Martins et al. 2022c). Controlled environments such as growth chambers (Baath et al. 2022) can be set for different air temperature and photoperiod conditions, but their air temperature, photoperiod, radiation, wind and air humidity regimes can deviate substantially from field

conditions (Rosa et al. 2009; White et al. 2012; Freitas and Martins 2019). Thus, the relationship between NL and photoperiod needs to be assessed using field experiments with several sowing dates (SD) over a year (Rosa et al. 2009; White et al. 2012; Freitas et al. 2017; Freitas and Martins 2019; Fagundes et al. 2021).

Of the studies on the influence of air temperature and the photoperiod on plant growth, most have been carried out on agricultural crops, like strawberry (Tazzo et al. 2015), sunflower (Souza et al. 2016), rice (Steinmetz et al. 2017), potato (Bisognin et al. 2017), grape (Pedro Júnior and Hernandez 2018), lettuce (Tezza and Minuzzi 2019), and arugula (Barreiros et al. 2021) and focused on germination, seedling establishment, budding, flowering, fruiting, and ripening. However, studies of this nature on tropical forest species are still scarce and have focused only on those of commercial interest, such as *Eucalyptus* at the seedling (Martins and Streck 2007; Freitas and Martins 2019) and flowering stages (Rawal et al. 2015), and some Brazilian forest species at the germination (Daibes et al. 2019) and seedling stages (Martins et al. 2022c).

Among the tropical forest species, three deserve particular attention due to their economic and ecological importance (Ferreira et al. 2019a, b; Reis et al. 2021; Martins et al. 2022b): *Psidium guajava* L. (Myrtaceae; guava), *Citharexylum myrianthum* Cham. (Verbenaceae; fiddlewood, *pau-viola*) and *Bixa orellana* L. (Bixaceae; annatto or achiote). *P. guajava* is native to tropical regions of Central and South Americas (Singh 2018). Its fruits are widely consumed (Ferreira et al. 2019a, b) because they are rich in compounds that benefit health (e.g., vitamin C, lycopene and phenolic compounds) (Reis et al. 2021). *C. myrianthum*, native to Brazil, facilitates gene flow of native biota, increases long-term income generation (Reis et al. 2021), and has therapeutic properties (e.g., *p*-coumaric and salicylic acids and hispidulin) with antimicrobial potential (Tenfen et al. 2018). *B. orellana* is native to Central and South Americas and widely used in the cosmetic (e.g., lipsticks, creams, sunscreens), food (e.g., dairy products, ice creams, meat, and condiments), pharmaceutical (e.g., antimicrobial, antioxidant, antiviral, anti-inflammatory), and textile industries (e.g., fiber dyeing) for pigments from its seeds (Ferreira et al. 2019a; Pandey et al. 2019; Silva et al. 2019; Reis et al. 2021).

Previous studies on *P. guajava* (Ferreira et al. 2019a), *C. myrianthum* and *B. orellana* (Ferreira et al. 2019b) provided crucial input data for thermal thresholds (T_b , T_{opt} , and T_B). However, the studies disregarded the thermal time methods and the influence of photoperiod on the development of the three species. Given the scarcity of studies of this nature and the economic and ecological importance of *P. guajava*, *C. myrianthum*, and *B. orellana*, here we evaluated six methods to determine thermal times and studied influence of

photoperiod on seedling development for the three tropical forest species.

Materials and methods

Experimental design

Field experiments were carried out at the Federal University of Itajubá, Itajubá, Minas Gerais, Brazil (Fig. 1), during the 2015 and 2016 growing seasons. This site has a typical monsoon climate, with a dry austral autumn/winter (April to September) and humid austral spring/summer (October to March) (Alves et al. 2020; Reis et al. 2021). The experiments were carried out in a completely randomized design with seeds of *P. guajava*, *C. myrianthum* and *B. orellana* sown in 8.0-L white polyethylene pots on 12 sowing dates (SD) (Table 1), and five replications (replication = pot) per species for a total of 15 pots per SD, totaling 540 pots. The 12 SDs were performed at ± 30 -d intervals, so that the plants developed in different thermophotoperiodic conditions (Rosa et al. 2009; Ferreira et al. 2019b; Freitas and Martins 2019; Fagundes et al. 2021).

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 2.50 g kg^{-1} of organic matter (Walkley–Black), 0.6 mg dm^{-3} of P and 5.0 mg dm^{-3} of K obtained using Mehlich extractor 1 (Mehlich 1953). About 90 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 12.20 g calcium carbonate, 6.45 g magnesium carbonate, 8.40 g simple-superphosphate (18%), 0.26 g potassium chloride (60%), and 0.35 g ammonium sulfate (20%) in each pot. At around 90–120 d after sowing, a cover fertilizer (0.58 g potassium chloride, and ammonium sulfate) was applied to each pot.

The seeds for each species were obtained from trees (isolated and embedded) during two dispersion periods (2015–2016) in forest fragments in cities close to Itajubá (Fig. 1). The seeds were sown in outdoor pots at the forest nursery. Details on collecting and storing the seeds were described by Ferreira et al. (2019a, b) and Martins et al. (2022b).

Phyllochron approach and thermal time methods

The phyllochron is given by the inverse of the slope of linear regression between the accumulated number of leaves on

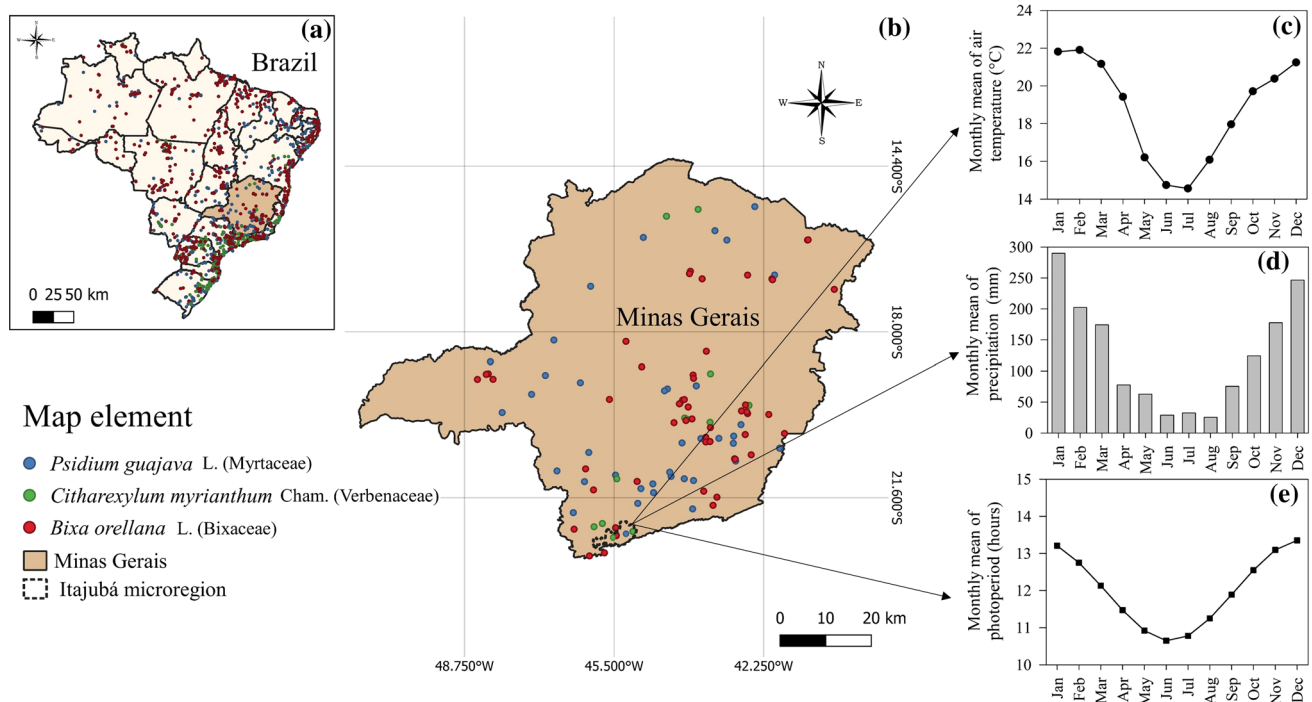


Fig. 1 a, b Location of study area and distribution of the three tropical forest species in Brazil and Minas Gerais state, respectively. The distribution data are available at <https://specieslink.net/>. c–e Climatological monthly averages for (c) air temperature, d accumulated precipitation, and e photoperiod from 1985 to 2014 for Itajubá. The

monthly mean values for air temperature and precipitation were calculated using a high-resolution gridded weather data set provided by Xavier et al. (2016); available at <https://utexas.app.box.com/v/Xavier-et-al-IJOC-DATA>) due to weather data gaps before 2002 for Itajubá. The photoperiod was obtained using Eq. 9

Table 1 Sowing and emergence dates for *Psidium guajava*, *Citharexylum myrianthum* and *Bixa orellana* during 2015 and 2016 growing seasons in Itajubá, Minas Gerais, Brazil

Sowing date (month day, year)	Emergence date ^a (month day, year)		
	<i>P. guajava</i>	<i>C. myrianthum</i>	<i>B. orellana</i>
SD1, May 12, 2015	Jun 15, 2015	Jun 10, 2015	Jun 12, 2015
SD2, Jun 12, 2015	Jul 17, 2015	Jul 15, 2015	Jul 10, 2015
SD3, Jul 10, 2015	Aug 05, 2015	Aug 05, 2015	Jul 28, 2015
SD4, Aug 11, 2015	Sep 04, 2015	Sep 02, 2015	Aug 26, 2015
SD5, Sep 10, 2015	Sep 30, 2015	Oct 05, 2015	Sep 30, 2015
SD6, Oct 09, 2015	Oct 28, 2015	Nov 04, 2015	Oct 19, 2015
SD7, Nov 13, 2015	Dec 04, 2015	Dec 08, 2015	Nov 27, 2015
SD8, Dec 11, 2015	Dec 30, 2015	Jan 04, 2016	Dec 28, 2015
SD9, Jan 12, 2016	Feb 02, 2016	Feb 07, 2016	Jan 27, 2016
SD10, Feb 11, 2016	Feb 29, 2016	Mar 04, 2016	Feb 19, 2016
SD11, Mar 11, 2016	Mar 30, 2016	Mar 30, 2016	Mar 24, 2016
SD12, Apr 12, 2016	Apr 28, 2016	May 05, 2016	May 03, 2016

^aDay when 50% of the seeds had germinated and a seedling was visible above the ground

the main stem (NL) and the accumulated TT (TTa, °C·d) (Fagundes et al. 2021; Martins et al. 2022b):

$$NL = a \cdot TTa + b, \text{ where } TTa = \sum_i^n TTd \quad (1)$$

where a = the slope of the linear regression (leaves per °C·d), TTa = accumulated thermal time (°C·d) calculated by each TT method, b = linear coefficient, i = emergence date (Table 1), n = day when NL = 20 leaves, and TTd = daily thermal time (°C·d) and the phyllochron is the number of °C·d per leaf, i.e., $1/a$.

New leaves ≥ 1.0 cm long were counted weekly during the seedling stage, which was considered to start at the emergence date (taken as the date that 50% of seedlings had emerged) (Table 1) until each species had reached an average of 20 NL (Ferreira et al. 2019a, b; Martins et al. 2022b). Any lateral shoots were removed so that only the main stem developed (Ferreira et al. 2019a, b).

The TT was calculated on a daily basis (TTd) using the six most widely methods described in the literature (Rosa et al. 2009; Tomazetti et al. 2015; Freitas and Martins 2019; Fagundes et al. 2021):

Method 1 (M1) considers the difference between mean air temperature (T_{mean}) and T_b :

$$TTd = (T_{\text{mean}} - T_b) \cdot D_1 \quad (2)$$

$$T_{\text{mean}} = \frac{T_{\text{max}} + T_{\text{min}}}{2} \quad (3)$$

when $T_{\text{mean}} < T_b$, T_{mean} is considered to equal T_b , then $TTd = 0$.

Method 2 (M2) is the same as M1, but penalizes the daily minimum air temperature (T_{min}) to obtain T_{mean} :

$$TTd = (T_{\text{mean}} - T_b) \cdot D_1 \quad (4)$$

when $T_{\text{min}} \leq T_b$, $T_{\text{min}} = T_b$.

Method 3 (M3) considers the T_{mean} and T_{opt} for each tropical forest species:

$$TTd = (T_{\text{mean}} - T_b) \cdot D_1 \quad (5)$$

when $T_{\text{mean}} < T_b$, $T_{\text{mean}} = T_b$, and when $T_{\text{mean}} > T_{\text{opt}}$, $T_{\text{mean}} = T_{\text{opt}}$.

Method 4 (M4) is the same as M3; however, T_{min} and the daily maximum air temperature (T_{max}) are penalized to obtain the T_{mean} :

$$TTd = (T_{\text{mean}} - T_b) \cdot D_1 \quad (6)$$

when $T_{\text{min}} \leq T_b$, $T_{\text{min}} = T_b$, and when $T_{\text{max}} > T_{\text{opt}}$, $T_{\text{max}} = T_{\text{opt}}$.

Method 5 (M5) considers the T_{mean} and three cardinal temperatures (T_b , T_{opt} , and T_B) of the tropical species:

$$TTd = \begin{cases} 0, & \text{when } T_{\text{mean}} < T_b \text{ or } T_{\text{mean}} > T_B \\ (T_{\text{mean}} - T_b) \cdot D_1, & \text{when } T_b \leq T_{\text{mean}} \leq T_{\text{opt}} \\ (T_{\text{opt}} - T_b) \frac{(T_B - T_{\text{mean}})}{(T_B - T_{\text{opt}})} \cdot D_1, & \text{when } T_{\text{opt}} < T_{\text{mean}} \leq T_B \end{cases} \quad (7)$$

Method 6 (M6) is the same as M5, but T_{min} and T_{max} are penalized to obtain the T_{mean}

$$TTd = \begin{cases} (T_{\text{mean}} - T_b) \cdot D_1, & \text{when } T_b \leq T_{\text{mean}} \leq T_{\text{opt}} \\ (T_{\text{opt}} - T_b) \frac{(T_B - T_{\text{mean}})}{(T_B - T_{\text{opt}})} \cdot D_1, & \text{when } T_{\text{opt}} < T_{\text{mean}} \leq T_B \end{cases} \quad (8)$$

when $T_{\text{min}} < T_b$, $T_{\text{min}} = T_b$; and when $T_{\text{max}} > T_B$, $T_{\text{max}} = T_B$.

In the equations, TTd = daily thermal time (°C·d), T_{mean} = daily mean air temperature (°C), T_{min} = daily minimum air temperature (°C), T_{max} = daily maximum air temperature, T_b , T_{opt} and T_B = cardinal temperatures (base, optimum

and maximum, respectively) for seedling development. $D_1 = 1$ day. T_{mean} , T_{min} and T_{max} were obtained from the automatic weather station at the experimental area. The cardinal temperatures for *P. guajava* are $T_b = 10.9$ °C, $T_{\text{opt}} = 17.3$ °C, and $T_B = 51.2$ °C (Ferreira et al. 2019a), for *C. myrianthum* are $T_b = 11.4$ °C, $T_{\text{opt}} = 18.1$ °C, and $T_B = 36.6$ °C, and for *B. orellana* are $T_b = 12$ °C, $T_{\text{opt}} = 18.4$ °C, and $T_B = 46.4$ °C (Ferreira et al. 2019b).

The choice for the best TTd method was based on the lowest standard deviation (SDev) and coefficient of variation (CV, %) for the phyllochron value, as per Streck et al. (2006), Rosa et al. (2009), and Freitas and Martins (2019). The phyllochron ($1/a$) was estimated for each TTd method, tropical species, and pot for the 12 SDs. Both SDev and CV values were calculated for each TTd method (and tropical species), considering the overall phyllochron values obtained for each pot for the 12 SDs. To verify the influence of SDs and species on seedling development, the phyllochron values of each tropical species were analyzed using the analysis of variance (ANOVA) two-way test, i.e., 12 sowing dates $\times$ 3 tropical forest species. Subsequently, mean values of phyllochron were compared by the Scott-Knott test ($P = 0.05$).

Influence of photoperiod

To verify the influence of the photoperiod on the phyllochron of the three species, the methodology of Freitas and Martins (2019) was used. Linear regressions between mean phyllochron (average of 5 pots) and mean photoperiod (P_{med}) were fitted for each SD and species. The P_{med} was obtained using the arithmetic mean of the daily photoperiod (P) from the emergence date (Table 1), to the end of the seedling stage, using the Keisling algorithm (1982):

$$P = \frac{2}{15} \arccos(\cos \alpha \cdot \sec \varphi \cdot \sec \delta - \tan \varphi \cdot \tan \delta) \quad (9)$$

$$\alpha = 90 + B \quad (10)$$

$$\delta = \arcsin(0.39779) \cdot \sin \lambda \quad (11)$$

$$\lambda = M + 1.916 - \sin M + 0.020 \cdot \sin 2M + 282.565 \quad (12)$$

$$M = 0.985600 \cdot \text{NDA} - 3.251 \quad (13)$$

where P = daily photoperiod (h), α = zenith angle (degrees), λ = latitude (degrees), δ = solar declination (degrees), 0.39779 = sine of 23°27', M = mean solar anomaly (degrees); NDA = day of the year (between 1 and 365/366), and B = angle below the horizon plane (6°).

The positive, and significant values for the slope of the linear regression ($P < 0.05$) indicate typical SDP photoperiodic responses, while negative and significant values

indicate typical LDP photoperiodic responses (Rosa et al. 2009; Freitas and Martins 2019; Martins et al. 2022c).

Since this methodology does not allow one to exclude the effect of air temperature, given by TTa, from the effect of P_{med} on the phyllochron, the partial correlation ($r_{x,y}$) was calculated using the phyllochron values from the 12 SDs. The $r_{x,y,z}$ allows the degree of association between two (x,y) or three variables to be obtained, by removing the co-effects among them (z) (Snedecor and Cochran 1989). This approach resulted in a TTa (2) effect on phyllochron (1) excluding the P_{med} (3), and vice versa, as per Eq. 14:

$$r_{12.3} = \frac{r_{12} - r_{13}r_{23}}{\sqrt{1 - r_{13}^2} \sqrt{1 - r_{23}^2}}, \quad (14)$$

where r_{12} = simple correlation between the phyllochron and the accumulated thermal time (TTa, °C·d), respectively, r_{13} = correlation between the phyllochron and the mean photoperiod (P_{med} , h), respectively, r_{23} = correlation between TTa and P_{med} , respectively, using $P = 0.05$.

Results and discussion

Different SDs allowed the tropical forest species to develop at different temperature and photoperiod conditions (Fig. 2). In general, air temperatures ranged from 2.3 °C (minimum absolute value) to 35.7 °C (maximum absolute value), and P ranged from 9.6 h to 14.3 h, which is important for evaluating the TTd methods and the influence of P_{med} on the phyllochron.

The differences among weather conditions also influenced the seedling stage duration (SSD). The plants that developed from seeds sown at SD1 to SD3, when the air temperatures were lowest, developed slower, so the SSD was longer. For these SDs (SD1 to SD3), the daily T_{min} values were close to the T_b of the three species (10.9 °C, 11.4 °C, and 12 °C). By contrast, at SD7 (*P. guajava*), SD9 (*C. myrianthum*), and SD8 (*B. orellana*) the T_{mean} values were close to the T_{opt} (17.3 °C, 18.1 °C, and 18.4 °C), and the plants developed faster, so the SSD was shorter. This pattern was similar to that reported for *Eucalyptus urophylla* S.T. Blake and *Corymbia citriodora* (Hook.) K.D Hill & L.A.S Johnson (formerly known as *E. citriodora* – basionym) (Freitas et al. 2017), *Libidibia ferrea* (Mart. ex Tul.) L. P. Queiroz (basionym *Caesalpinia ferrea* Mart. ex Tul.), *Anadenanthera macr carp a* (Benth.) Brenan (Martins et al. 2022c), and agricultural crops during the seedling stage, such as MGS ASC315 and Arbequina olive cultivars (Lisboa et al. 2012), and arugula (Barreiros et al. 2021). During our experiments, none of the SDs had a T_{mean} or T_{max} equal to or greater than the T_B of the three tropical forest species (36.6 °C to 51.2 °C).

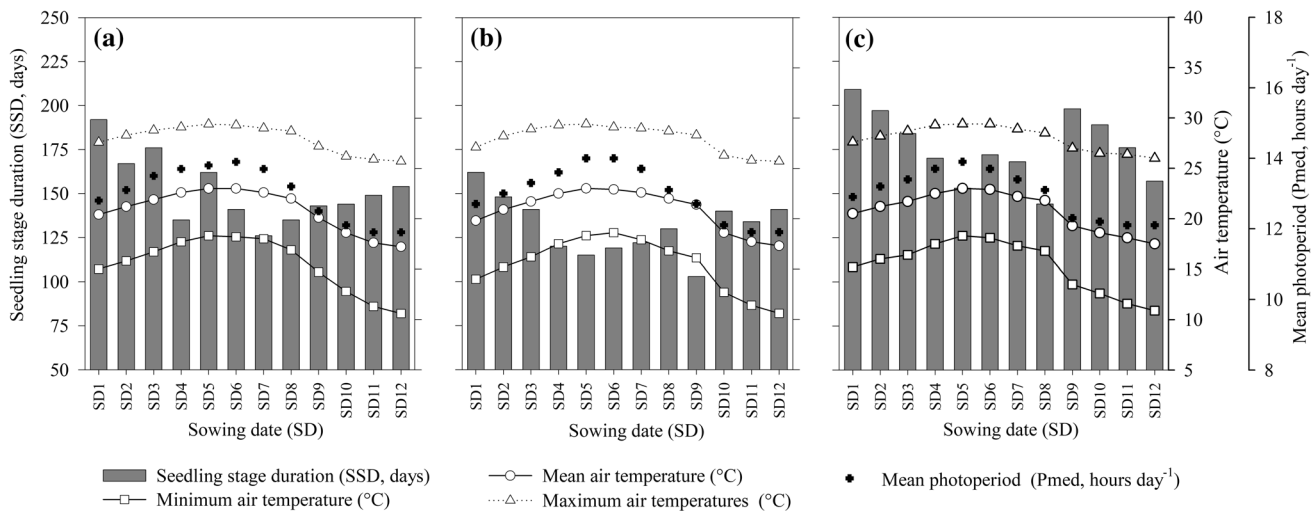


Fig. 2 Variation in minimum, mean and maximum air temperatures (°C), seedling stage duration (SSD, d), and mean photoperiod (P_{med} , h) for each sowing date (SD) for three tropical forest species in field

experiments at Itajubá, Minas Gerais, Brazil. **a** *Psidium guajava*, **b** *Citharexylum myrianthum*, **c** *Bixa orellana*

Phyllochron approach and thermal time methods

The adjusted regressions between NL and six TTd methods (M1 to M6) (Fig. 3) for the three species showed a high coefficient of determination ($R^2 > 0.9613$), and low standard error of estimate ($Sy_x < 0.9790$), which are ideal biologically and statistically (Martins et al. 2007; Freitas and Martins 2019). This result suggests that the seedling development presents a linear trend with air temperature, and one can quantify by the phyllochron approach. Similar results were observed for exotic forest species, like *Eucalyptus grandis* (W. Hill ex Maiden), *Eucalyptus saligna* Sm. (Martins et al. 2007), *E. urophylla*, *C. citriodora* (Freitas and Martins 2019), and also for Brazilian native forest species such as *L. ferrea* and *A. macrocarpa* (Fagundes et al. 2021; Martins et al. 2022c).

The phyllochron values varied among the six TTd methods and three species, with means between 39.6 °C·d and 79.8 °C·d per leaf for *P. guajava*, 33.5 °C·d and 68.2 °C·d per leaf for *C. myrianthum*, and 47.0 °C·d and 87.4 °C·d per leaf for *B. orellana* (Table 2), being all values for M5 and M2 methods, respectively. Phyllochron values were progressively lower using methods M1 and M2 to those using methods 5 and 6, a pattern also reported by Streck et al. (2007a), Rosa et al. (2009), and Freitas and Martins (2019). This decrease occurs when T_{opt} is included in M3 and M4, and when T_{opt} and T_B are included in M5 and M6 methods, leading to reductions in the TTd and TTA values. This reduction occurred mainly for SDs at the warmest times of the year, when the T_{mean} was above the T_{opt} for *P. guajava* (17.3 °C), *C. myrianthum* (18.1 °C) and *B. orellana* (18.4 °C) (Ferreira et al. 2019a, b; Martins et al. 2022c).

Despite this expected variation and the progressive phyllochron reduction toward M6 method, the phyllochron values obtained were closer between methods M1 and M2, between M3 and M4, and M5 and M6. These results are because there were fewer cases for daily air temperature in which T_{mean} was lower than T_b and T_{min} was lower than T_b . In this sense, T_{mean} was $\leq T_b$ in only four cases for *C. myrianthum*, six cases for *B. orellana*, and none for *P. guajava*. Furthermore, T_{min} was $\leq T_b$ in 114 cases for *P. guajava*, 145 cases for *C. myrianthum*, and 162 cases for *B. orellana*, which occurred on SDs during the winter (SD2, SD3 and SD4). T_{max} or T_{mean} were never $> T_b$ for the three tropical forest species, even for SDs during the summer (SD8 to SD11).

Despite the expected difference between the phyllochron values among the six TTd methods (Streck et al. 2007a; Freitas and Martins 2019), the overall SDev and CV values for phyllochron were greater using methods M1 and M2. When the six TTd methods were compared, M5 and M6 yielded lower SDev (3.7–3.9) and CV values (14%–21.8%) (Table 2) with a small difference between the SDev (not exceeding ± 0.1 °C·d) and the CV (not exceeding 0.6%) values. Thus, M5 and M6 are considered the best methods to be used for computing the thermal energy required by seedlings to produce leaves and develop. When the results using the three cardinal temperatures are compared with those using the daily T_{mean} (or T_{min} and T_{max}), M5 and M6 more accurately account for TTd and TTA than do M1 and M2, which consider only T_b , and also M3 and M4, which consider T_b and T_{opt} . Similar results were found for Brazilian native forest species *A. macrocarpa* and *L. ferrea* (Martins et al. 2022b) and for agricultural crops such as wheat (Rosa et al. 2009), soybean (Streck et al. 2009), and grape (Tomazetti

et al. 2015). However, the results differ from those of Freitas and Martins (2019), who obtained lower SDev values using method M4 for *C. citriodora* and *E. urophylla*.

The processes responsible for leaf production, such as leaf primordia differentiation and cell division depend on enzymes (Rosa et al. 2009; Soltani and Sinclair 2012), which denature at high temperatures, especially above supraoptimal temperatures (between T_{opt} and T_{B}), so fewer new leaves emerge (Fagundes et al. 2021; Reis et al. 2021). Therefore, to quantify seedling development using the phyllochron approach, air temperature functions (TTd and TTa) must include T_{b} , T_{opt} and T_{B} as per M5 and M6 methods. Although both methods were efficient and had small differences in the SDev values (between ± 0.08 to 0.1 °C·d) and CV values (0.1% – 0.6%) for the phyllochron, method M5 is the most widely used for the air temperature functions (Ferreira et al. 2019b; Florêncio et al. 2019; Fagundes et al. 2021; Reis et al. 2021; Martins et al. 2022b). For one reason, it only considers T_{mean} , which is readily available from weather stations or other databases and is commonly included in the outputs of climate models and reanalysis data (Monteiro et al. 2021; Martins et al. 2022a, b).

The interaction between the species and sowing date was significant ($P \leq 0.05$) (Table 3). Since each species was found to develop differently based on the SD, there may be a combined influence of the temperature and the photoperiod on the phyllochron (Streck et al. 2007b; Lisboa et al. 2012; Freitas and Martins 2019) for each of the three tropical forest species. Lower phyllochron values for a particular SD indicates that less energy was needed for leaf development; thus, leaves were generated quicker, and seedlings developed faster. *P. guajava* developed faster when seeds were sown on SD2, SD4, SD7 to SD10 and SD12; *C. myrianthum* developed faster from SD3 to SD5, SD9, SD10 and SD12; and *B. orellana* developed faster when sown on SD4, SD8, SD11 and SD12 (Table 3).

However, the lower phyllochron value did not result in shorter SSD in the field (Fig. 2). For example, for *B. orellana* with SD4, the phyllochron was lower (41.2 °C·d per leaf) with a SSD of 170 days than with SD5 (49.9 °C·d per leaf) with a SSD of 153 days. This same pattern was found for *P. guajava* (SD2, SD5, SD6, and SD11) and *C. myrianthum* (SD3, SD6, SD7, SD10, and SD12). That is, the data show that the phyllochron approach can be used to quantify leaf development, unlike the calendar day method that is commonly used by nurseries to determine when (the moment) seedlings are sold (Martins et al. 2007; Fagundes et al. 2021; Martins et al. 2022b, c). Despite the difference in temporal pattern (SD1 to SD12), in common, the three tropical species developed more rapidly in SD4 and SD12 (Table 3), when the air temperature was close to the T_{opt} for the species.

Among the three species, the phyllochron for *C. myrianthum* (34.8 °C·d per leaf) was lowest, *P. guajava*, 39.9 °C·d

per leaf; *B. orellana*, 47.0 °C·d per leaf; thus, in practice, *C. myrianthum* needs less energy accumulation (°C·d) to produce leaves. Therefore, it completes the seedling stage earlier. By contrast, the higher phyllochron value for *B. orellana* is due to slower development, since it prioritizes leaf growth earlier than leaf development (Fagundes et al. 2021; Martins et al. 2022b, c). It is important to emphasize that growth and development are independent processes that may occur simultaneously or not (Streck et al. 2011; Soltani and Sinclair 2012). While leaf growth involves irreversible increase in physical dimensions of leaves, such as area, length and width, development refers to ontogenetic processes at different levels of organization, such as cell differentiation, organ initiation (organogenesis), and appearance (morphogenesis), and extends to crop senescence (Soltani and Sinclair 2012). Based on the phyllochron approach, the TTa to finish the seedling stage (NL = 20 leaves) varies, approximately from 697 (*C. myrianthum*) to 940 °C·d (*B. orellana*). After the accumulated TTa, the seedlings are ready to be marketed; i.e., the seedlings will reach the marketable threshold with enough vigor for commercialization by the sales date (Fagundes et al. 2021). The phyllochron values for the three species (between 34.8 and 47.0 °C·d per leaf) are similar to those for other forest species such as *E. saligna* (30.7 °C·d per leaf) and *E. grandis* (32.0 °C·d per leaf) (Martins et al. 2007), *C. citriodora* (38.2 °C·d per leaf) (Freitas and Martins 2019), and *A. macrocarpa* (47 °C·d per leaf) (Martins et al. 2022c), but lower than that of *L. ferrea* (154.3 °C·d per leaf).

Influence of photoperiod

The regressions between the mean phyllochron versus P_{med} showed that *P. guajava* and *B. orellana* (Fig. 4a, c) have typical SDP behaviors since the slopes are positive and significant ($P < 0.05$), explaining the lower phyllochron value and the higher rate of leaf production, especially for SDs with milder temperatures and shorter days (≤ 12 h) (Fig. 2). Normally, the opposite is expected, that is, lower phyllochron values for warmer periods and higher phyllochron values for milder periods (Freitas and Martins 2019). These results are evidence that seedling development is strongly influenced by air temperature (Fagundes et al. 2021; Martins et al. 2022b), which interacts with the photoperiod (Rawal et al. 2015; Freitas and Martins 2019). By contrast, *C. myrianthum* had a negative slope coefficient that was not significant ($P > 0.05$) (Fig. 4b), with a shallower slope. In other words, seedling development of *C. myrianthum* was not well defined in relation to the photoperiod. The lowest phyllochron for *C. myrianthum* was for SD3 (i = August) to SD5 (i = October) when the photoperiod varied from 11.9 to 14.3 h and for SD9 (i = February), SD10 (i = March) and SD12 (i = May) when the photoperiod was < 13.8 h, resulting in faster development over a wider photoperiod range.

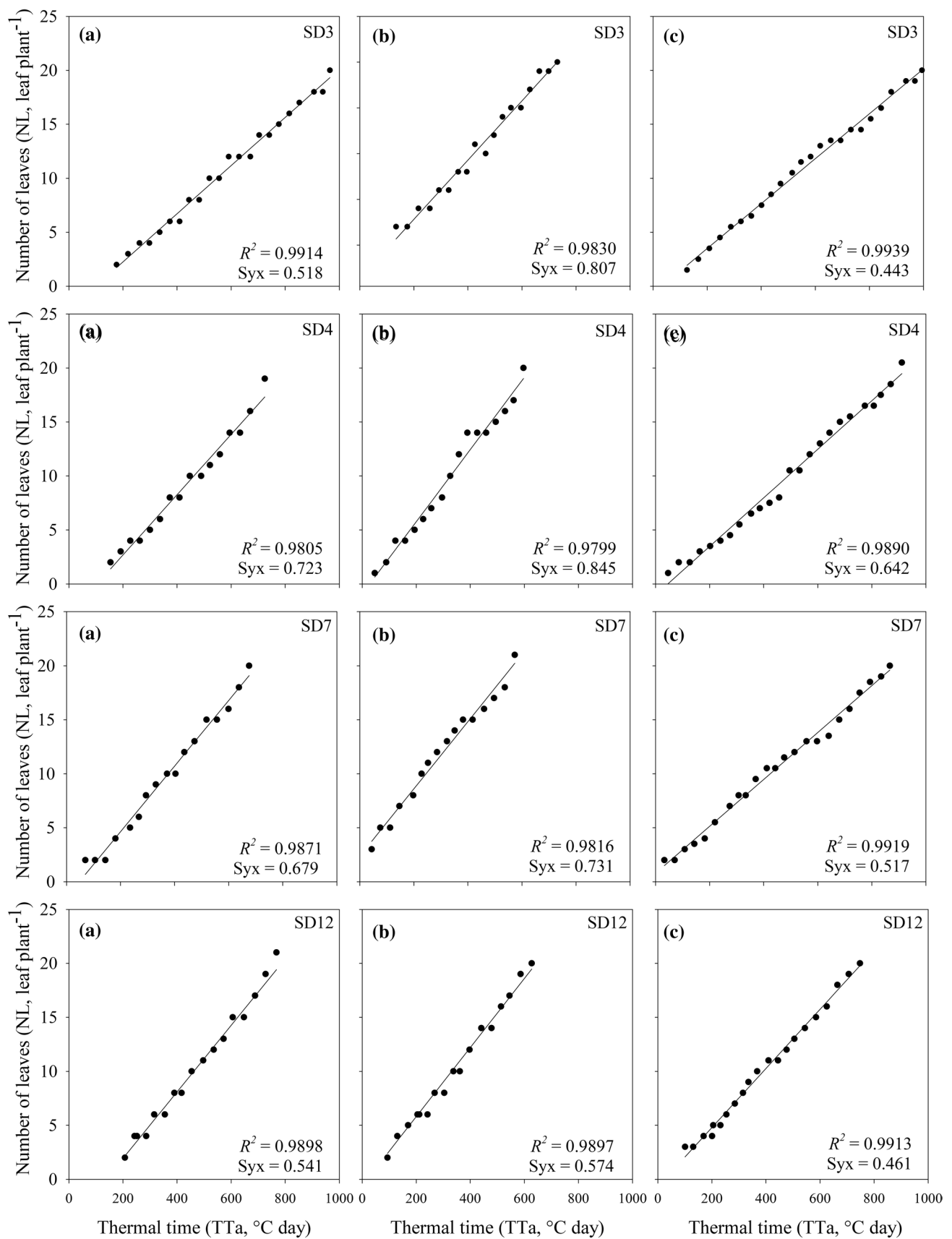


Fig. 3 Accumulated number of leaves on the main stem (NL) versus accumulated thermal time (TTa, °C·d), calculated using method M5 for *Psidium guajava* (a), *Citharexylum myrianthum* (b), and *Bixa orellana* (c) species for four sowing dates (SD3, SD4, SD7, and SD12). Data from each panel corresponds to one pot. R^2 is the coefficient of estimation given by $R^2 = \text{MSS}/\text{TSS}$, where MSS is explained by variation squares due to regression; TSS is total variation, i.e., total sum of squares ($0 \leq R^2 \leq 1$), Syx is standard error of the estimate given by $\text{Syx} = \sqrt{\text{SSE}/(n-2)}$, where SSE is sum of squares error; n is number of observations

All regressions between the mean phyllochron and P_{med} had low R^2 (~ 0.11) values, and they were lower than those fit between NL and TTa ($R^2 \geq 0.96$). By partial correlation, we observed that the air temperature (TTa) exerts a greater influence on the phyllochron than the photoperiod. Furthermore, all partial correlation values for the phyllochron and TTa disregarding P_{med} ($r_{12.3}$) were significant ($P < 0.05$) for *P. guajava* ($r_{12.3} = 0.77$), *C. myrianthum* ($r_{12.3} = 0.60$), and *B. orellana* ($r_{12.3} = 0.85$), while the values for phyllochron and P_{med} disregarding TTa ($r_{13.2}$) were not significant ($P > 0.05$) for any of the species. The $r_{13.2}$ values were 0.38 for *P. guajava*, 0.17 for *C. myrianthum*, and 0.29 for *B. orellana*. Therefore, the hypothesis regarding the combined effect of air temperature and photoperiod on the phyllochron, and the effect of the photoperiod must be discarded for *C. myrianthum*, as only temperature has an influence on the phyllochron. Regarding *P. guajava* and *B. orellana*, we cannot affirm that there is a combined effect of the two variables on the phyllochron.

Although the partial correlation was not significant for P_{med} , the slope coefficients of the regressions between the mean phyllochron and P_{med} were significant (Fig. 4). These regressions had low R^2 (~ 0.11), lower than those of Freitas and Martins (2019) for *C. citriodora* ($R^2 = 0.59$) and Martins et al. (2022c) for *A. macrocarpa* ($R^2 = 0.36$). Nonetheless, *P. guajava* and *B. orellana* developed faster (except for SD4) for SDs between January and September (SD8–SD12), with a $P_{\text{med}} < 13.2$ h and T_{mean} between 17.3 °C to 22.1 °C, i.e., close to the T_{opt} temperature for the species (17.3 °C, 18.1 °C, and 18.4 °C) (Ferreira et al. 2019a, b), explaining why seedling development was fastest during this period. A change in the photoperiod affects TTd and TTa, but whether the photoperiod imposes any constraints on the physiology of fully developed leaves (and SSD) during relatively favorable temperatures is unknown (Way and Montgomery 2015). There is evidence that the photoperiod can also regulate the physiological activity of leaves (Way and Montgomery 2015), as found for temperate deciduous trees, where seasonal variation in photosynthetic capacity is more closely correlated with photoperiod than with air temperature (Basler and Körner 2012).

Studies on the effects of the photoperiod on seedling development of forest species are still scarce. In Brazil, such

studies have been done for tropical forest species such as *E. urophylla*, *C. citriodora* (Freitas and Martins 2019), *L. ferrea* and *A. macrocarpa* (Martins et al. 2022c), which all have typical SDP behavior. Some reasons for the scarcity of these studies are that (1) they have long development cycles compared to annual crops (Fagundes et al. 2021); (2) phenological data are unavailable or unreliable (Reis et al. 2021), and (3) the developmental pattern of native forest species is completely different (Martins et al. 2022b, c). Furthermore, practical issues such as distinct seed dispersal habits, fewer seed dispersal periods (1 or 2 times a year), and loss of seed viability over time can make experiments to study the effects of photoperiods on the seedling development of forest species difficult (Ferreira et al. 2019a, b; Freitas and Martins 2019; Fagundes et al. 2021).

Even though the results of this study were inconclusive with respect to the effect of P_{med} on the phyllochron, we confirmed that air temperature had the greatest influence on seedling development of all three tropical forest species. Thus, seedlings may not be able to tolerate or adapt to projected increases in air temperature, slowing or halting seedling development (Ferreira et al. 2019a, b; Florêncio et al. 2019; Fagundes et al. 2021; Reis et al. 2021). Thus, to assess the impacts of increased air temperature on seedling development of *P. guajava*, *C. myrianthum*, and *B. orellana*, we need to use the M5 (or M6) TTd method with output data from the Earth System Models to determine the phyllochron. Moreover, we suggest that the threshold for selling forest species seedlings will be determined by the TTd and TTa, replacing calendar days. According to this approach, the TTa to finish the seedling stage is 800 °C·d for *P. guajava*, 697 °C·d for *C. myrianthum*, and 940 °C·d for *B. orellana*.

Conclusions

Assessments of seedling development of the three tropical forest species—*P. guajava*, *C. myrianthum*, and *B. orellana*—using the phyllochron approach were influenced by the method used to estimate thermal time. The most suitable method (M5) considers the three cardinal temperatures and compares these with the mean air temperature. However, we could not confirm the effect of photoperiod on the phyllochron. The phyllochron differed among the three tropical forest species and sowing dates. *C. myrianthum* developed the fastest of the three, needing less energy accumulation to produce new leaves on the main stem and end the seedling stage. The three tropical forest species developed best in months with mild air temperatures (between 13.3 °C and 26.9 °C) and day lengths < 13 h.

Table 2 Mean $\pm$ standard deviation and coefficient of variation (%) of the phyllochron values ($^{\circ}\text{C}\cdot\text{d}$ per leaf) for the three tropical forest species from the twelve sowing dates calculated using the six thermal time methods

Species	Thermal time methods (value $\pm$ standard deviation) ($^{\circ}\text{C}\cdot\text{d}$), CV (%)					
	M1	M2	M3	M4	M5	M6
<i>Psidium guajava</i>	77.7 $\pm$ 7.2, 31.3	79.8 $\pm$ 7.4, 27.7	45.9 $\pm$ 4.3, 20.4	48.4 $\pm$ 4.7, 22.0	39.9 $\pm$ 3.7, 18.4	40.4 $\pm$ 3.8, 18.3
<i>Citharexylum myrianthum</i>	65.7 $\pm$ 7.2, 25.3	68.2 $\pm$ 7.9, 25.5	42.3 $\pm$ 4.6, 22.3	43.2 $\pm$ 4.7, 21.4	33.9 $\pm$ 3.7, 21.6	34.5 $\pm$ 3.8, 21.8
<i>Bixa orellana</i>	82.6 $\pm$ 6.4, 31.1	87.4 $\pm$ 6.9, 19.5	53.6 $\pm$ 4.3, 16.9	55.8 $\pm$ 4.6, 14.7	47.0 $\pm$ 3.8, 14.6	48.0 $\pm$ 3.9, 14.0

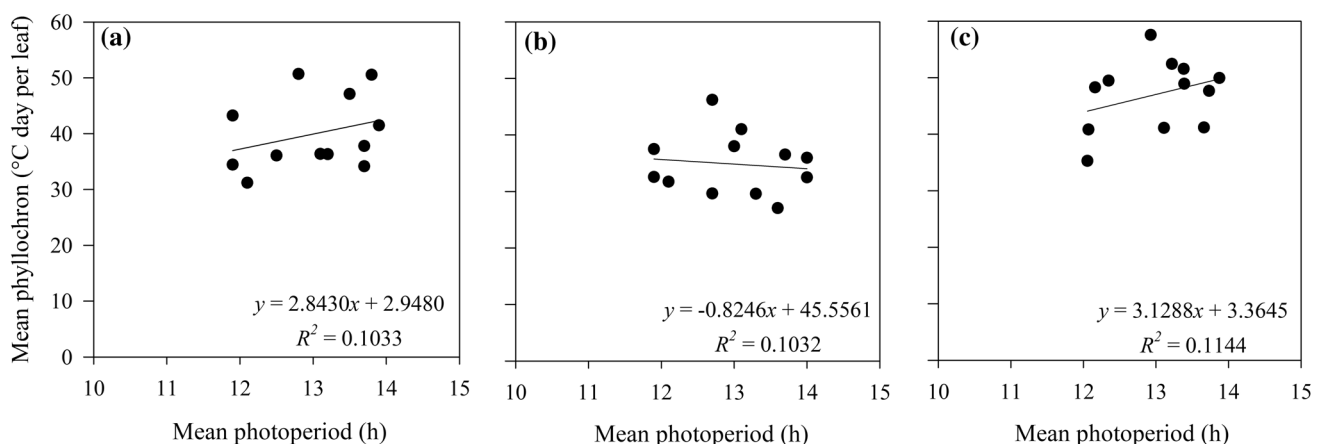
Itajubá, Minas Gerais, Brazil, 2015 and 2016 growing seasons

Phyllochron values were estimated using each thermal time method, tropical species and pot for 12 sowing dates. The data in the table refer to overall mean of phyllochron, standard deviation and coefficient of variation values

Table 3 Comparison of means for phyllochron values ($^{\circ}\text{C}\cdot\text{d}$ per leaf) calculated using the thermal time method M5 for tropical forest species *Psidium guajava*, *Citharexylum myrianthum* and *Bixa orellana* sown on 12 sowing dates performed during 2015 and 2016 growing seasons in Itajubá, Minas Gerais, Brazil

Sowing date	<i>P. guajava</i>	<i>C. myrianthum</i>	<i>B. orellana</i>
SD1	50.70 Ca	46.19 Ca	57.57 Bb
SD2	36.36 Aa	37.98 Ba	52.45 Bb
SD3	47.10 Cb	29.58 Aa	48.92 Bb
SD4	37.78 Ab	27.04 Aa	41.19 Ab
SD5	50.55 Cb	32.48 Aa	49.94 Bb
SD6	41.49 Ba	35.94 Ba	47.67 Bb
SD7	34.16 Aa	36.52 Ba	51.56 Bb
SD8	36.33 Aa	41.00 Ba	41.12 Aa
SD9	36.09 Ab	29.64 Aa	49.48 Bc
SD10	31.20 Aa	31.72 Aa	48.29 Bb
SD11	43.24 Ba	37.50 Ba	40.84 Aa
SD12	34.45 Aa	32.54 Aa	35.27 Aa
Overall mean	39.95 b (SDev $\pm$ 6.59)	34.84 a (SDev $\pm$ 5.43)	47.02 c (SDev $\pm$ 6.23)

See Table 1 for sowing dates. Means followed by the same uppercase letters in the column (sowing date), and lowercase letters in the row (tropical forest species) did not differ from each based on a Scott-Knott test ($P > 0.05$). Original data are shown, but the data were transformed (Ln phyllochron) because they did not meet the assumption of normality for the Shapiro–Wilk test ($P < 0.05$) (Freitas et al. 2017; Florêncio et al. 2019). Letters A to C and a to c were set up in ascending order according to the phyllochron value

**Fig. 4** Relationship between the mean phyllochron and the mean photoperiod for *Psidium guajava* (a), *Citharexylum myrianthum* (b), and *Bixa orellana* (c), Itajubá, Minas Gerais, Brazil. Each point marks a SD, and the line shows the linear regression. R^2 is the coefficient of determination

Acknowledgements The authors thank the Minas Gerais Research Support Foundation (FAPEMIG, APQ 01258-17 and APQ-01392-13) for financial support, the Coordination for the Improvement of Higher Education Personnel (Capes, process numbers 88887.613734/2021-00 and 1827878) for scholarships to FFAF and GWLF, the FAPEMIG (process number ID-14029) for scholarship to MdCF, and the National Council for Scientific and Technological Development (CNPq, process number 306845/2021-0) for a research fellowship to FBM. The authors also thank Alexandre Cândido Xavier PhD for providing the spatialized data on the Brazilian territory and the Natural Resources Institute at the Federal University of Itajubá for providing subsidies for experiments and publishing this article.

Author contribution Martins, F.B.: Conceptualization, methodology design, data analysis, writing, reviewing and editing, supervision, project administration, funding acquisition. Ferreira, M.C.de.: Conceptualization, data acquisition, data curation, data analysis, methodology design, data analysis, data curation, software, writing and reviewing. Fagundes, F.F.A.: Data analysis, software, writing, reviewing and editing. Florêncio, G.W.L.: Methodology design, data acquisition, data curation, data analysis.

Data availability The datasets generated during and/or analyzed during this study are available upon request from the corresponding author.

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