Comunicata Scientiae
Horticultural Journal

ORIGINAL ARTICLE
published: 07 August 2023
https://doi.org/10.14295/CS.v14.3973

Thermal requirements and estimates of number of leaves of Annona squamosa L. grown under different shading conditions

Angélica Alves Gomes[1], Matheus Marangon Debastiani[1], Mariana Pizzatto[1], Andréa Carvalho Da Silva[1], Adilson Pacheco De Souza[1]

[1]Federal University of Mato Grosso, Sinop, Brazil
*Corresponding author, e-mail: pachecoufmt@gmail.com

Abstract

The objective of this study was to determine the thermal requirements and compare methods for estimating leaf emergence in *Annona squamosa L.* under different shading conditions during the dry and rainy seasons in a transition region between the Cerrado Amazon biomes, Mato Grosso, Brazil. Seedlings were grown under full-sun conditions (reference) and black polyolefin screens with 35%, 50%, 65%, and 80% attenuation of global radiation. Basal temperatures were determined using the method of least standard deviation; accumulated thermal sum was estimated using the method described in Ometto (1981); the relationship between number of leaves and thermal sum were evaluated using the phyllochron and Wang & Engel (1998) models. The minimum and maximum basal temperatures for the growth of A. squamosa were 11.0 and 38.0 °C, respectively. The accumulated thermal sum presented small variation between shading conditions and seasons, resulting in means of 1744±44 and 4434±118 degree-days at 113 and 260 days after transplanting (DAT), corresponding to the end of the dry and rainy seasons, respectively. The thermal requirement for leaf emergence varied among the different shading conditions, with higher phyllochrons under full sun conditions and 80% shading (109.8 °C day leaf^{-1}) and lower phyllochrons under 50% shading (91.74 °C day leaf^{-1}). The phyllochron model presented higher efficiency in estimating leaf emergence compared to the Wang & Engel model. Growing A. squamosa seedlings under 50% shading is recommended as it resulted in higher degree-day accumulation and lower phyllochron for leaf emergence.

Keywords: cardinal temperatures, phyllochron, sugar apple

Introduction

Plants exposed to high temperatures usually respond by causing changes such as increasing reactive oxygen species (Jedrzejuk et al., 2016), destabilizing membranes and increasing their fluidity (Nazdar et al., 2019; Amaral et al., 2020), and damaging the cell membrane and chloroplast structures (Guo et al., 2017).

However, plants have basal and acquired thermotolerances, which enable them to respond to high-temperature stress by increasing the activity of antioxidants such as superoxide dismutase, catalase, and peroxidase (Qin et al., 2018; Zhao et al., 2018) and by increasing proline contents (Qin et al., 2018; Amaral et al., 2020) and the activity of heat shock proteins (HSPs) (Zhang et al., 2015).

The use of thermal units or degree-days is one alternative for analyzing interactions among climate, plant, and atmosphere, as it can be applied to characterize phenological stages or the total cycle regarding thermal requirements or duration (Souza et al., 2009; Zeist et al., 2019). It also can be applied to estimate the cumulative number of leaves, which has been used as an excellent measure of plant development (Streck et al., 2003; Xue; Weiss & Baenziger, 2004) and is directly connected with leaf area, determining the interception of the solar radiation used for photosynthesis (Martins & Streck, 2007).

Cumulative number of leaves can be estimated through the leaf emergence rate, which can be obtained by using several methods, however, the most used are the phyllochron model (Frank & Bauer, 1995; Xue et al., 2004) and the model proposed by Wang & Engel (1998).

Studies have used the phyllochron and Wang & Engel models, singly or in comparison, for different crops. However, studies using these models for Annona squamosa L. were not found in the literature, either for

Received: 05 April 2022
Accepted: 11 May 2023

evaluating thermal requirements during the seedling stage or for estimating the cumulative number of leaves, which are base information on the species development and essential for the management and production of high-quality seedlings.

Annona squamosa L., popularly known as sugar apple or custard apple, is a fruit species of the family Annonaceae and has a high commercial importance in Brazil, where the largest production of this crop is in semiarid areas of the Northeast region. The interest in growing this species is due to its high nutritional value and the potential of high income from the marketing of fresh fruits and fruit pulp (Braga Sobrinho, 2014).

Considering the lack of information on the ecophysiological aspects of this species and its economic importance, the objective of this study was to determine thermal requirements and compare methods for estimating leaf emergence in Annona squamosa L. seedlings grown under different shading conditions.

Material And Method

The study was conducted in the municipality of Sinop, in the northern Mato Grosso, Brazil (11°51'50"S, 55°29'08"W, altitude of 384 m), which is within the transition region between the Cerrado and Amazon biomes. The climate of the region is Aw, tropical hot and humid, according to the Köppen classification, with two well-defined seasons: dry (May to September) and rainy (October to April). The mean monthly temperatures vary from 24 to 27 °C and the mean annual rainfall depth is 1,940 mm (Souza et al., 2013).

The experiment was conducted from May 2020 to February 2021, using seedlings of Annona squamosa L., based on evaluation periods divided into dry season (May 21 to September 18, 2020) and rainy season (September 19, 2020 to February 5, 2021). A completely randomized experimental design was used, which consisted of absence of shading (full-sun conditions) and four shading levels (35%, 50%, 65%, and 80% attenuation of global radiation) using black polyolefin screens. The growth variable evaluated was number of leaves (NF) on the main stem every 15 days from 15 days after transplanting the seedlings to the environments (full-sun and shading conditions), with 19 replications.

The shading structures (above-ground metal nurseries) were aligned in an East-West direction, with dimensions of 3.0 × 1.0 × 1.0 m (length, width, and height) at a height 1.0 m from the ground. The upper, front, and side of the structures were covered with agricultural black polyolefin screens with 35%, 50%, 65%, and 80% attenuation of global radiation. Full-sun conditions were used as reference. Metal screens with a 1" mesh size were used as support for the seedlings to minimize the effects of excess water, whereas a sprinkler irrigation system was installed in the center of the above-ground shading nurseries to supply a water depth of 17.7 L h^{-1}, which was timed and divided into four irrigation periods of 15 minutes each.

Meteorological monitoring in the treatment under full-sun conditions was carried out by a portable Automatic Weather Station approximately 20 m from the experimental area. Digital thermo-hygrometers (model HT 4000 ICEL) were installed in the center of the above-ground shading structures to monitor temperature and relative air humidity in these treatments, providing protection against direct incidence of luminosity and exposure to water.

Fruits of Annona squamosa L. were collected on February 20, 2020 and subjected to pulping and cleaning of the seeds, which were then subjected to physical dormancy breaking using a sandpaper (no. 80 grit). The seeds were sown in a bed with commercial substrate at a depth of 3 cm on March 13, 2020. Plantlets were transplanted 30 days after germination to 820 cm³ tubes containing a substrate composed of forest soil and commercial substrate (2:1 ratio, respectively) under full-sun conditions. Seedlings were transferred to the shading environments on May 21, 2020 and, 82 days later, they were transplanted into 8,000 cm³ pots containing a substrate composed of sand and commercial substrate (2:1 ratio, respectively).

Meteorological data from each growing environment were used to estimate the minimum basal temperature (Tb) and maximum basal temperature (TB), using the method of least standard deviation (Souza et al., 2011). Temperatures ranging from 6 to 16 °C were considered for Tb simulations and from 30 to 40 °C for TB simulations, with a 2 °C discretization. These random values enabled to obtain the accumulated thermal sum (TSa) and, subsequently, the standard deviation (SDd) in degree-days, between May 21, 2020 and February 05, 2021. The method predicts that the basal temperature should correspond to the lowest standard deviation (SD), in days. TSa was obtained using the method described in Ometto (1981), recommended by Souza et al. (2011), considering the following cases:

Case 1: $T_m > T_b$; $T_B > T_M$

$$DD = \frac{T_M - T_m}{2} + (T_m - T_b) \quad (1)$$

Case 2: $T_b > T_m$; $T_B > T_M$

$$DD = \frac{(T_M - T_b)^2}{2(T_M - T_m)} \quad (2)$$

Case 3: $T_b < T_m$; $T_B < T_M$

$$DD = \frac{2[(T_M - T_m)(T_m - T_b)] + (T_M - T_m)^2 - (T_M - T_B)^2}{2(T_M - T_m)} \quad (3)$$

where: DD is the degree-day; TM is the maximum daily mean temperature (°C); Tm is the minimum daily mean temperature (°C); Tb is the minimum basal temperature (°C); TB is the maximum basal temperature (°C).

The values obtained for TSa were analyzed together with the cumulative number of leaves, generating a linear regression (Equation 4) (Frank & Bauer, 1995), which enabled the application of the phyllochron model (°C day leaf–1) through the inverse relationship of the regression slope coefficient (1/a) (Xue et al., 2004; Streck et al., 2006). The TSa to phyllochron ratio (Streck et al., 2006) was used to estimate the cumulative NF for the A. squamosa, as follows:

$$NF = a^* STa + b \qquad (4)$$

Additionally, cumulative NF was also estimated using the Wang & Engel (WE) model (Wang & Engel, 1998), through a function of nonlinear response to temperature f(T), multiplied by the maximum leaf emergence rate (LERmax) (Xue et al., 2004). The WE model is expressed by a general formula (Martins & Streck, 2007), according to the Equation 5:

$$LER = LER_{max} f(T) \qquad \text{(leaves by day)} \quad (5)$$

where: LER is the leaf emergence rate (leaves by day); LER_{max} is the maximum LER that occurs under the optimal temperature conditions for the species (leaves by day); *f*(T) is the temperature beta function, where f(T) has a null value when $T_{med} < T_b$ or $T_{med} > T_B$, and when T_b < Tmed ≥ TB (Martins & Streck, 2007), it is defined by the Equation 6:

$$f(T) = \frac{[2(T_{med} - T_b)^{\alpha} (T_{opt} - T_b) - (T_{med} - T_b)^{2\alpha}]}{(T_{opt} - T_b)^{2\alpha}} \qquad (6)$$

where: Topt is the optimal temperature for the species (°C); the coefficient a was obtained based on the neperian logarithm (ln) (Martins & Streck, 2007), according to the Equation 7:

$$\alpha = \frac{\ln(2)}{\ln[(T_B - T_b) / (T_{opt} - T_b)]} \qquad (7)$$

The cumulative NF by the WE model was obtained by summing the daily LER (NF = ∑LER) from the dates of transplanting the seedlings to full-sun and shaded environments (Wang & Engel, 1998; Xue et al., 2004).

The experiment was conducted between May 2020 and February 2021, with an evaluation period divided into the dry season (05/21/2020 to 09/18/2020) and rainy season (09/19/2020 to 02/05/2021). The experimental design used was completely randomized (DIC), using four levels of shading, provided by black polyolefin screens, with 35, 50, 65 and 80% of radiation attenuation, and in the absence of shading (full sun). The number of leaves (NF) on the main stem was evaluated fortnightly, in 19 repetitions, starting 15 days after the application of the treatments (DAT).

Results an Discussion

Climate characterization

The monthly mean temperature and relative air humidity under full-sun conditions during the dry season were 25.38 °C and 64%, respectively (**Table 1**), with the highest amplitudes of temperature (28.07 °C) and relative air humidity (79.40%) occurring in August and September, respectively.

The 2020 rainy season started on September 19 (121 days after transplanting - DAT) (**Figure 1**), with rainfall depths ranging from 4.8 to 69 mm (180 DAT); the cumulative rainfall depth throughout the experimental period (260 DAT) was 844.6 mm. The monthly mean temperature and relative air humidity under full-sun conditions were 26.23 °C and 80.93%, respectively, with the highest amplitudes (21.45 °C and 78.90%) occurring in October. The highest monthly mean temperatures (28.46 and 27.97 °C) and, consequently, the lowest monthly means of relative air humidity (49.36% and 67.25%) under full-sun conditions were recorded in September and October, respectively.

Considering the shaded environments (Table 1) during both seasons, the lowest monthly mean temperatures and the highest monthly means of relative air humidity were found for the environments with 65% and 80% shading, whereas the opposite was found for 35% and 50% shading. However, the comparison between full-sun and shaded environments during the rainy season showed that the full-sun environment had the lowest monthly mean temperature and relative air humidity (25.81 °C and 72.47%, respectively).

The seasonality of these two meteorological elements (**Figure 2**) indicates higher daily thermal amplitudes during the dry season; however, the daily mean temperature and relative air humidity increased during the rainy season, presenting increases of 0.43 °C and 8.47% under full-sun conditions (Figure 2A), 1.74 °C and 16.07% under 35% shading (Figure 2B), 1.57 °C and 15.89% under 50% shading (Figure 2C), 1.67 °C and 14.81% under 65% shading (Figure 2D), and 2.01 °C and 14.4% at 80% shading (Figure 2E).

Considering the entire experimental period (Figure 2), the daily mean temperatures in descending order were 26.58 (50% shading), 26.39 (full-sun conditions), 25.98 (35% shading), 25.88 (80% shading), and 25.65 °C (65% shading), whereas the daily means of relative humidity in descending order were 72.68% (65% shading), 72.66% (80% shading), 70.65% (full-sun conditions), 70.28%

Table 1. Monthly mean temperature and relative air humidity under different shading conditions, during the dry and and rainy seasons. Sinop, MT, Brazil, 2021

Months	Shading (%)									
	Full sun		35		50		65		80	
	T (°C)	UR (%)	T (°C)	UR (%)	T (°C)	UR (%)	T (°C)	UR (%)	T (°C)	UR (%)
May*	23.58	77.99	23.79	67.66	24.31	76.51	23.10	79.30	23.37	73.31
June	24.31	74.88	24.74	72.31	24.89	67.96	24.16	74.02	24.54	74.00
July	24.29	65.78	24.47	64.23	24.88	63.45	23.72	66.16	23.93	66.43
August	26.27	52.01	26.08	56.32	26.18	56.20	25.11	60.23	25.12	59.98
September	28.46	49.36	28.21	54.13	28.48	53.44	27.43	54.82	27.21	57.56
Mean	25.38	64.00	25.46	62.93	25.75	63.51	24.70	66.91	24.83	66.25
October	27.97	67.25	28.17	69.84	28.40	69.57	27.44	71.94	27.51	72.86
November	26.74	78.42	27.58	77.60	27.69	78.06	26.93	78.24	27.35	78.26
December	25.47	85.54	26.33	82.98	26.40	83.79	25.68	84.13	26.02	84.73
January	25.28	86.72	26.30	83.86	26.38	85.00	25.55	86.81	26.05	85.46
February**	25.70	86.73	27.60	80.72	27.75	80.57	26.28	87.48	27.29	82.03
Mean	26.23	80.93	27.20	79.00	27.32	79.40	26.38	81.72	26.85	80.67
Overall mean	25.98	70.65	26.39	70.96	26.62	71.45	25.68	74.31	25.85	73.45

* **Period** from May 21 to 30, 2020. ** Period from February 1 to 05, 2021 (260 days after transplanting).
Dry season (May 21 to September 18, 2020); Rainy season (September 19, 2020 to February 05, 2021).

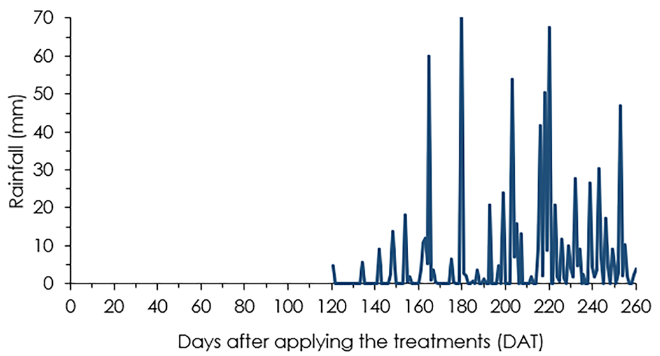

Figure 1. Daily rainfall depths between May 21, 2020 to February 05, 2021, Sinop, MT, Brazil.

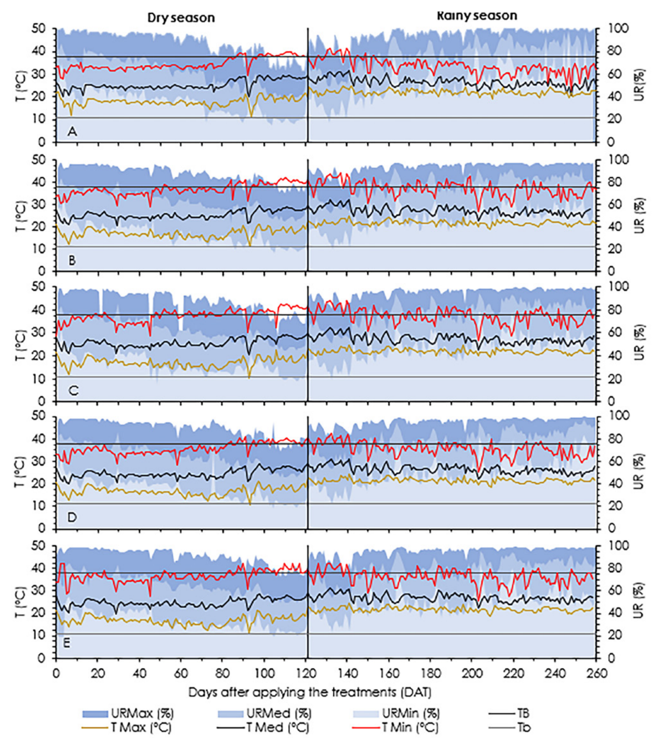

Figure 2. Daily temperature and relative air humidity in environments under different shading conditions for growing *Annona squamosa* L. seedlings, during the dry season (May 21 to September 18, 2020) and rainy season (September 19, 2020 to February 05, 2021): full-sun conditions (A) and 35% (B), 50% (C), 65% (D), and 80% shading (E). Sinop, MT, Brazil

(35% shading), and 70.22% (50% shading).

The temperature data recorded for each shading condition were used to estimate the minimum basal temperature (Tb) and maximum basal temperature (TB): 11.0 and 38.0 °C, respectively (**Figures 3**A and 3B). The estimated optimal temperature for full development of Annona squamosa L. seedlings was 25.9 °C, which was used to estimate the cumulative number of leaves through the Wang & Engel (WE) model.

The environments with 50% and 65% shading presented lower temperatures than the estimated Tb (10.49 and 10.9 °C, respectively) during the dry season, but only on a single day in August (Table 1 and Figures

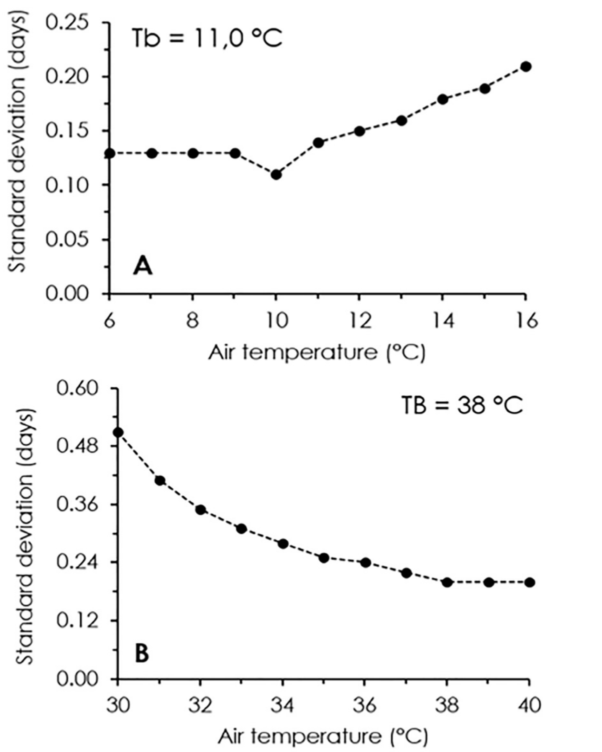

Figure 3. Minimum basal temperature - Tb (A) and maximum basal temperature - TB (B) for the growth of Annona squamosa L. seedlings. Sinop, MT, Brazil, 2021.

Table 2. Accumulated thermal sum for *Annona squamosa* L. seedlings grown under different shading conditions, during the dry and rainy seasons. Sinop, MT, Brazil, 2021

		Accumulated thermal sum (°C day)				
	DAT	Shading (%)				
		Full-sun	35	50	65	80
Dry season	15	236.49	248.90	255.05	240.25	263.62
	29	409.62	441.00	453.58	425.00	457.69
	43	623.66	657.25	666.25	631.53	667.64
	57	810.02	854.40	870.53	813.03	860.44
	71	1009.45	1067.15	1094.14	1011.85	1068.54
	85	1213.06	1277.90	1315.42	1212.78	1272.79
	100	1464.75	1533.69	1566.90	1462.58	1523.47
	113	1699.94	1771.24	1804.39	1690.66	1753.37
Rainy season	127	1952.91	2031.51	2069.49	1940.67	2007.22
	142	2250.89	2339.30	2376.87	2235.12	2303.69
	155	2480.02	2581.19	2619.94	2466.91	2532.44
	170	2737.03	2858.84	2900.34	2730.36	2800.09
	183	2960.03	3100.40	3139.55	2960.54	3037.85
	197	3204.48	3370.92	3114.13	3215.18	3304.87
	210	3403.84	3597.71	3640.70	3428.65	3525.29
	245	3969.20	4218.09	4268.43	4019.39	4131.21
	260	4197.52	4497.35	4550.41	4278.94	4409.83

Dry season (May 21 to September 18, 2020); Rainy season (September 19, 2020 to February 05, 2021). DAT = days after transplanting.

2C and 2D). However, the estimated TB was exceeded in all environments during both seasons, with a higher frequency in September (103 to 132 DAT) (Figure 2). The full-sun environment and those with 35%, 50%, 65%, and 80% shading presented maximum temperatures higher than the estimated TB for a total of 38, 94, 110, 59, and 66 days, respectively.

Accumulated thermal sum

The highest and lowest accumulated thermal sum (TSa) (113 DAT) during the dry season were found in the environments with 50% (1804.39 °C) and 65% shading (1690.66 °C), respectively. Regarding the rainy season, the highest TSa was also found for the environment with 50% shading (4550.41 °C), whereas the lowest TSa was found under full-sun conditions (4197.52 °C) (**Table 2**).

The results for daily mean accumulation during the dry season were 15.56, 16.18, 16.47, 15.46, and 15.97 °C and the accumulations for the entire dry period were 1716.42, 1782.61, 1814.44, 1700.42, and 1743.60 °C day) for full-sun conditions and 35%, 50%, 65%, and 80% shading, respectively. Regarding the the rainy season, the increased temperatures during this period resulted in higher daily mean accumulation, with means of 16.62, 18.32, 18.43, 17.36, 17.86 °C, whereas the accumulations for the entire period were 1946.63, 2158.05, 2173.54, 2043.82, and 2106.14 °C day) for full-sun conditions and 35%, 50%, 65%, and 80% shading, respectively.

The thermal requirement for emergence of one leaf on the main stem was estimated based on the data obtained for thermal sum and number of leaves (NF). Full-sun and 80% shading conditions presented the same thermal requirement (109.89 °C day leaf–1) (**Figure 4**), which was higher than those found for the other evaluated shading conditions. The lowest result for this variable (91.74 °C day leaf–1) was found under 50% shading.

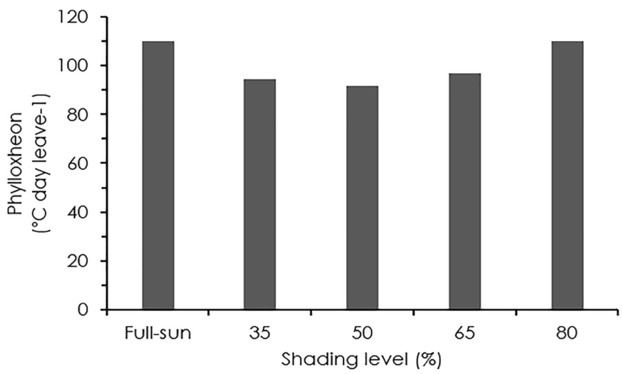

Figure 4. Phyllochron for the mean number of leaves in *Annona squamosa* L. seedlings grown under different shading conditions, during the period from May 21, 2020 to February 05, 2021. Sinop, MT, Brazil, 2021

Estimation of number of leaves (NF)

The WE model overestimated NF regardless of the shading environment (**Figure 5**), whereas the phyllochron model underestimated NF under full-sun conditions and 80% shading. In general, the phyllochron model presented closer alignment with the 1:1 line (simple linear regression passaging through the origin) and higher coefficients of determination (R2) than those adjusted for the WE model, thus resulting in better estimates of NF throughout the seedling development cycle.

The temperature and relative air humidity in full-sun and shaded environments vary between the dry

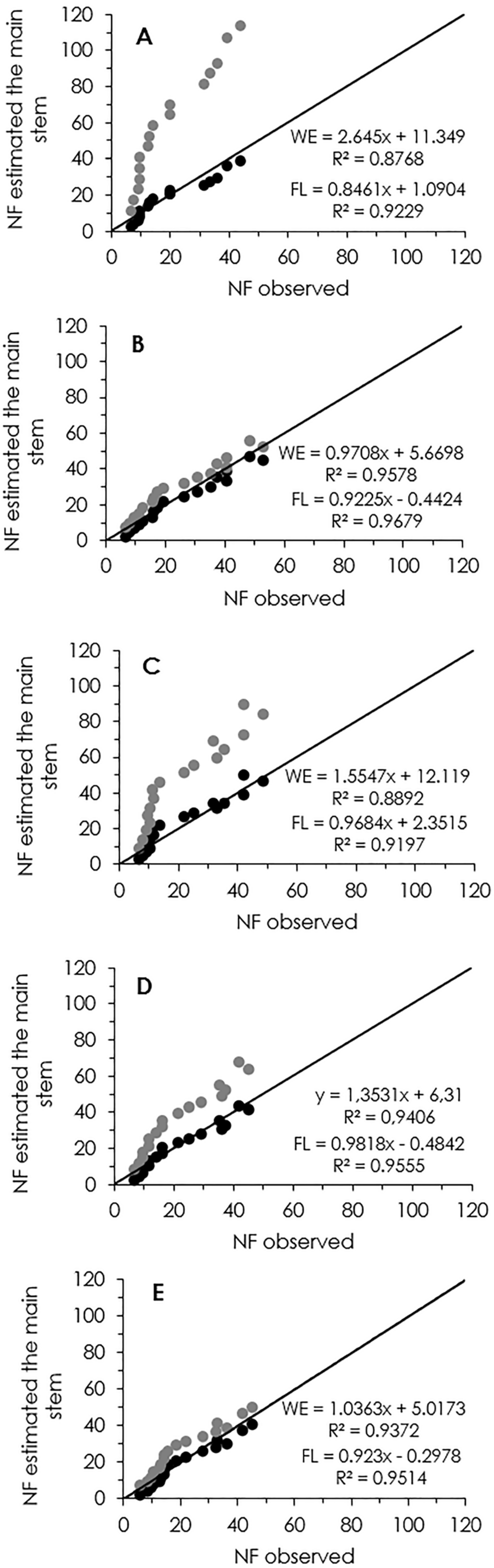

Figure 5. Number of leaves (NF) observed and estimated by the phyllochron and Wang & Engel models for *Annona squamosa* L. seedlings grown under full-sun conditions (A) and 35% (B), 50% (C), 65% (D), and 80% (E) shading, from May 21, 2020 to February 05, 2021. Sinop, MT, Brazil, 2021.

and rainy seasons in the transition region between the Cerrado and Amazon biomes (Monteiro et al., 2016). An increase of 1.10 °C was found for mean temperature under full-sun conditions during the rainy season (Figure 2), characterizing this period as the hottest season, as reported by Souza et al. (2013).

The lowest daily mean thermal amplitudes were also found during this season, resulting from the dynamics of water vapor and cloud formation in the region. Increased cloud cover decreases the incidence of global radiation during the daytime period and changes the longwave balance during the nighttime period, as the atmospheric longwave emissions increase; consequently, surface cooling decreases, i.e., resulting in lower air temperature reduction gradients at night, compared to the dry season (Santos et al., 2013). Thus, decreases in thermal amplitude under full-sun conditions during the rainy season can be correlated with increases in minimum daily temperatures and decreases in maximum daily temperatures.

Therefore, the highest daily thermal amplitudes were recorded during the dry season, which are explained by the highest indexes of atmospheric transmissivity during the daytime period, facilitated by the low attenuation of solar radiation by clouds, water vapor, and aerosols (Souza et al., 2016). Increased longwave (infrared) emission from the surface and decreased occurrence of attenuating agents result in significant variations in latent heat levels near the ground surface between the sunrise and sunset, increasing the maximum temperatures during the day and decreasing the minimum temperatures during the night due to heat losses caused by low atmospheric longwave emission.

Information on temperature dynamics under full-sun conditions is essential for understanding the dynamics of shaded environments (Table 1), as shade screens are primarily used to reduce direct sunlight incidence and, consequently, air temperature (Borella et al., 2021). The 65% and 80% shade screens decreased the mean temperatures compared to full-sun conditions. Contrastingly, all shaded environments presented higher mean relative air humidity compared to full-sun conditions.

The microclimate dynamics found in the environments with 35% and 50% shading, characterized by higher mean temperatures throughout the dry and rainy seasons, were similar to those reported by Monteiro (2015), Borella et al. (2021), and Bueno et al. (2021). The higher amount of retained radiation (energy storage) and higher wind attenuation in these environments, compared to full-sun conditions, contribute to a greenhouse effect in shaded crop environments. However, environments with 65% and 80% shading have increased radiation absorption by the shade screen due to the meshes; however, losses to the atmosphere through longwave emissions tend to be higher, decreasing heat under the shade screen.

Air temperature is still considered the main meteorological element affecting plant development and growth (Segantini et al., 2014). Plant species have an optimal temperature (Topt) for their physiological processes, as well as thermal limits know as minimum basal temperature (Tb) and maximum basal temperature (TB), which represent the minimum temperature required for the activation of metabolic processes in the plant and the maximum temperature above which the respiration rate exceeds the photosynthetic rate (Souza et al., 2009). The Tb (11.0 °C) and TB (38.0 °C) found for A. squamosa in the present study (Figure 3) are similar to those obtained for other fruit species, such as Theobroma grandiflorum (15 and 35 °C) (Ferraz et al., 2012) Mangifera denotes (13 and 32 °C) (Rodrigues et al., 2014), Anacardium occidentale (10 and 30 °C) (Matos et al., 2014), and Passiflora edulis (10 and 36 °C) (Hurtado-Salazar et al., 2015), respectively.

Determining basal temperatures in shaded environments enables the simulation of several climate conditions, thus accelerating the process of obtaining these thermal limits, enabling microclimate variations in a short time interval. One of the main limitations for determining basal temperatures is the need to subject crops (species/cultivar) to different microclimates, which can only be evaluated under normal field conditions in different years or regions, requiring the conduction of several simultaneous experiments and/or long-duration experiments.

The different microclimate dynamics among the evaluated environments affected the accumulation of thermal energy in A. squamosa seedlings, as the accumulated thermal sum (TSa) varied from 4197.52 (full-sun conditions) to 4550.41 °C day (50% shading) at 260 DAT (Table 2). TSa variations in seedlings growing under shading conditions were reported by Monteiro et al. (2014) for Adenanthera pavonina, Cassia fistula, Hymenolobium petraeum, and Parkia pendula, and by Borella et al. (2020) for Dipteryx alata.

Commonly, the thermal sum can vary for the same plant species growing in different regions and under different climate conditions and cultural practices, resulting in variations in the duration of phenophases and cycles. Ferreira et al. (2019) evaluated Psidium guajava considering 12 sowing times and found variation from 126 to 192 days in the duration of the seedling stage: the shortest stage occurred under higher maximum, mean, and minimum temperatures (29.0, 22.6, 18.0 °C), whereas the longest seedling stage occurred under lower maximum, mean, and minimum temperatures (27.6, 20.4, 15.0 °C, respectively).

The A. squamosa seedlings evaluated in the present study did not progress to a different stage, remaining in the vegetative stage throughout the experimental period. However, the results (Table 2) denote that seedlings under 50% shading could have shorter stages and, consequently, shorter cycles, which could lead to a shorter permanence of these seedlings in the nursery.

The environment with 50% shading presented higher TSa than that found in the other environments, as maximum temperatures higher than TB and higher daily mean temperatures were recorded in this environment for a total of 110 days during the experimental period. Plants can present molecular and biochemical sensitivity or tolerance responses to heat stress caused by temperatures higher than TB.

In this context, some deleterious effects caused by heat have been reported in the literature, such as increased reactive oxygen species in Syringa vulgaris (Jedrzejuk et al., 2016), destabilization of membranes with increased fluidity in Calendula officinalis and Vernonia ferruginea (Nazdar et al., 2019; Amaral et al., 2020), and damage to the cell membrane and chloroplast structures in Potentilla fruticosa (Guo et al., 2017). However, some plant resistance responses reported in the literature include increased activity of antioxidants such as superoxide dismutase, catalase, and peroxidase in Dahlia pinnata and miniature roses (Qin et al., 2018; Zhao et al. 2018), increased proline contents in V. ferruginea and D. pinnata (Qin et al., 2018; Amaral et al., 2020), and increased activity of heat shock proteins in Paeonia suffruticosa (Zhang et al., 2015).

All these responses to the heat stress assist the plant to improve its thermal tolerance to withstand higher temperatures that would otherwise be lethal. However, it is not possible to state that the evaluated A. squamosa seedlings presented tolerance or sensitivity responses to heat stress, as no biochemical and molecular analyses were carried out.

Nevertheless, temperature and microclimate effects on plant morphology were found, mainly regarding number of leaves (NF), which presented variations among the environments throughout the experimental period (260 DAT), with cumulative NF means of 44, 48, 42.3, 41.6, and 45 leaves for full-sun conditions and 35%, 50%, 65%, and 80% shading, respectively (Figure 5).

Light also affects the development of new leaves, as ontogenic initiation occurs at the apex of plants grown under light, through the negative regulation of KNOX genes and signaling of hormones such as cytokinins and auxins, which are responsible for maintaining the functions of the apical meristem of the stem and directing this meristem towards leaf initiation; under opposite conditions, the meristem ceases the leaf production (Byrne, 2012).

The leaf initiation process involves the action of cytokinins and auxins, but also involves the action of hormones such abscisic acid and ethylene, thus regulating NF through leaf senescence and abscission, which are processes that naturally occur to renew the leaf area or as a morphological strategy to overcome some abiotic stress, such as drought and high light intensity conditions (Pariz et al., 2010). These conditions may explain the difference between the observed NF and that estimated by the WE model for full-sun conditions, as the model considers cumulative NF and does not consider leaf abscission.

Cumulative NF is one of the main parameters for evaluating plant development in response to temperature and is directly connected to leaf area evolution, thus, directly affecting the interception of the solar radiation used in the photosynthetic process (Streck et al., 2003; Xue et al., 2004). Therefore, this parameter is highly important for ecophysiological studies.

Phyllochrons of 109.89 and 91.74 °C day leaf-1 (Figure 4) were found for 80% and 50% shading, respectively, based on linear regressions. These results are lower than the mean phyllochrons found for D. alata (191.04 °C day leaf-1) (Borella et al., 2020) and for Fragaria ananassa in the second cycle (122.73 °C day leaf-1) (Zeist et al., 2019); however, they are higher than those found for P. guajava (76.06 °C day leaf-1) (Ferreira et al., 2019), A. pavonina (11.40 °C day leaf-1), C. fistula (19.54 °C day leaf-1), H. petraeum (26.72 °C day leaf-1) and P. pendula (30.30 °C day leaf-1) (Monteiro et al., 2014), and for F. ananassa in the first cycle (50.8 °C day leaf-1) (Zeist et al., 2019). These results show the diversity among plants regarding thermal requirements for leaf emergence, which may extend to other phenological stages or the entire plant cycle. Thus, thermal sum is an essential parameter for predicting the growth dynamics and planning crop seasons and agricultural activities.

The phyllochron model provided better NF estimates (higher R2 and closer to the 1:1 line) in all crop environments (Figure 5). Contrastingly, the WE model was more efficient for estimating NF in Eucalyptus grandis and Eucalyptus saligna (Martins & Streck, 2007), Manihot esculenta (Samboranha et al., 2013), and Olea europaea (Martins et al., 2014).

Despite showing higher efficiency in estimating NF for the evaluated environments, the phyllochron model is significantly questionable as it considers a linear growth response to air temperature, which is not fully accepted from the biological point of view, as leaf emergence has a nonlinear response near cardinal temperatures (minimum, optimum, and maximum) (XUE et al., 2004). However, this model presents some advantages, such as a small number of coefficients and ease of application, making it efficient for estimating NF in different crops, such as eucalyptus (Martins et al., 2007), O. europaea (Martins et al., 2012), Brassica spp. (Dalmago et al., 2013), P. guajava (Ferreira et al., 2019), F. ananassa (Zeist et al., 2019), and Avena sativa (Delatorre et al., 2021).

Conclusion

The minimum and maximum basal temperatures found for the growth of Annona squamosa L. were 11.0 and 38.0 °C, respectively. Increasing shading levels in the growing environment affected the accumulation of thermal energy and the leaf emergence in A. squamosa seedlings. Leaf emergence in this species was best estimated using the phyllochron model.

The production of A. squamosa seedlings seedlings under 50% shading is recommended as it resulted in higher degree-day accumulation and lower phyllochron for leaf emergence.

References

Amaral, C.L., Santos, J.I., Portugal, C.R.S., Braga, A.F., Alves, P.L.C.A. 2020. Growth of Vernonia ferrugínea seedlings submitted to thermal stress. Planta Daninha 38: 1-12.

Borella, D.R., Souza, A.P., Silva, A.C., Felipe, R.T.A., Silva, K.N.C., Souza, J.H.G. 2020. Exigências térmicas e filocrono de Dipteryx alata sob níveis de sombreamento na transição Cerrado-Amazônia. Scientia Plena 16: 1-15.

Borella, D.R., Souza, A.P., Silva, K.N.C., Santos, L.M.M., Ximenes, E.S.O.C., Anjos, A.M. 2021. Dinâmica e estimativas da temperatura e umidade relativa do ar em viveiros protegidos com diferentes sombreamentos. Nativa 9: 62-75.

Braga Sobrinho, R. 2014. Produção integrada de Anonáceas no Brasil. Revista Brasileira de Fruticultura 36: 102–107.

Bueno, M.M., Leles, P.S.S., Pinto, M.F., Resende, A.S., Couto, B.R.M., Carvalho, D.F. 2021. Water use in the growth of atlantic forest tree species seedlings under different shading levels. Ciência e Agrotecnologia 45: 1-14.

Byrne, M.E. 2012. Making leaves. Current Opinion in Plant Biology 15: 24-30.

Dalmago, G.A., Fochesatto, E., Kovaleski, S., Tazzo, I.F., Bolis, L.M., Cunha, G.R., Nied, A.H., Bergamaschi, H., Santi, A. 2013. Filocrono e número de folhas da canola em diferentes condições ambientais. Pesquisa Agropecuária Brasileira 48: 573-581.

Delatorre, C.A., Duarte, V.F., Wairich, A., Fraga, G.P., Ribeiro, M.P., Lazzari, H.E. 2021. Oat development in response to temperature. Ciência Rural 52: 1-18.

Ferraz, I.D.K., Albuquerque, M.C.F., Calvi, G.P., Farias, D.L. 2012. Critérios morfológicos e temperatura para avaliação da germinação das sementes de cupuaçu. Revista Brasileira de Fruticultura 34: 905-914.

Ferreira, M.C., Martins, F.B., Florêncio, G.W.L., Pasin, L.A.A.P. 2019. Cardinal temperatures and modeliing of vegetative development in guava. Revista Brasileira de Engenharia Agrícola e Ambiental 23: 819-825.

Frank, A.B., Bauer, A. 1995. Phyllochron Differences in Wheat, Barley and Forage Grasses. Crop Science 35: 19-23.

Guo, Y., Wang, Z., Guan, X., Hu, Z., Zhang, Z., Zheng, J., Lu, Y. 2017. Proteomic analysis of Potentilla fruticosa L. leaves by iTRAQ reveals responses to heat stress. Plos One 12: 1-23.

Hurtado-Salazar, A., Silva, D.F.P., Sediyama, C.S., Bruckner, C.H. 2015. Physical and chemical characterization of yellow passion fruit grafted onto wild species of genus passiflora cultivated in greenhouse. Revista Brasileira de Fruticultura 37: 635-643.

Jedrzejuk, A., Lukaszewska, A., Rabiza-Swider, J., Skutnik, E. 2016. Low temperature forcing reduces oxidative stress in lilac flowers. Horticulture, Environment and Biotechnology 57: 625-632.

Martins, F.B., Pereira, R.A.A., Pinheiro, M.V.M., Abreu, M.C. 2014. Desenvolvimento foliar em duas cultivares de oliveira estimado por duas categorias de modelos. Revista Brasileira de Meteorologia 29: 505-514.

Martins, F.B., Reis, D.F., Pinheiro, M.V.M. 2012. Temperatura base e filocrono em duas cultivares de oliveira. Ciência Rural 42: 1975-1981.

Martins, F.B., Silva, J.C., Streck, N.A. 2007. Estimativa da temperatura-base para emissão de folhas e do filocrono em duas espécies de eucalipto na fase de muda. Revista Árvore 31: 373-381.

Martins, F.B., Streck, N.A. 2007. Aparecimento de folhas em mudas de eucalipto estimado por dois modelos. Pesquisa Agropecuária Brasileira 42: 1091-1100.

Matos, V.A.T., Pivetta, F., Paiva Sobrinho, S., Tissiani, A.S.O., Pereira, A.P.M.S., Ramos, F.T., Campelo Júnior, J.H. 2014. Temperaturas basais e exigência térmica para a maturação de caju. Bioscience Journal 30: 969-977.

Monteiro, E.B. 2015. Crescimento e necessidades hídricas de mudas florestais tropicais em diferentes condições de sombreamento. 2015. 193 f. Dissertaçãode Mestrado) – Universidade Federal de Mato Grosso, Sinop, Brasil.

Monteiro, E.B., Silva, A.C., Souza, A., Tanaka, A.A., Fernanda, B.G., Martim, C.C. 2016. Water requirements and crop coefficients of tropical forest seedlings in different shading conditions. Revista Brasileira de Engenharia Agrícola e Ambiental 20: 709-715.

Monteiro, E.B., Silva, C.C., Silva, A.C., Souza, A.P. 2014. Estimating emission of leaves seedlings forest in different shading levels, at conditions of transition Amazon-Cerrado, Brasil. America Journal of Plant Sciences 5: 2330-2341.

Nazdar, T., Tehranifar, A., Nezami, A., Nemati, H., Samiei, L. 2019. Physiological and anatomical responses of calendula (Calendula officinalis L.) cultivars to heat stress duration. The Journal of Horticultural Science and Biotechnology 94: 400-411.

Pariz, A.R.C., Peiter, M.X., Robaina, A.D., Soares, F.C., Vivin, G.A., Ramao, C.J. 2010. Water levels in the culture of kalanchoe grown in protected. Ciência Rural 40: 854-861.

Qin, Y., Zhou, Z., Liu, H., Wang, Y., Lai, Y., Wang, Y., Mao, F., Zhang, L., Wang, H., Zhang, G. 2018. Effects of exogenous salicylic acid on physiological indexes in miniature rose under high temperature stress. Journal of Southern Agriculture 49: 2028-2033.

Rodrigues, J.C., Souza, P.J.O.P., Lima, R.T. 2014. Estimate of base temperature and thermal requirement in mango for the northeast of Para. Revista Brasileira de Fruticultura 35: 143-150.

Samboranha, F.K., Streck, N.A.A., Uhlmann, L.O., Gabriel, L.F. 2013. Modelagem matemática do desenvolvimento foliar em mandioca. Revista Ciência Agronômica 44: 815-824.

Santos, R.B., Souza, A.P., Silva, A.C., Almeida, F.T., Arantes, K.P., Siqueira, J.L. 2013. Planejamento da pulverização de fungicidas em função das variáveis meteorológicas na região de Sinop-MT. Global Science and Technology 6: 72-88.

Segantini, D.M., Leonel, S., Cunha, A.R.D., Ferraz, R.A., Ripardo, A.K.S. 2014. Thermal requirement and productivity in blackberry-function times of pruning. Revista Brasileira de Fruticultura 36: 568- 575.

Souza, A.P., Mota, L. L., Zamadei, T., Martim, C.C., Almeida, F.T., Paulino, J. 2013. Classificação climática e balanço hídrico climatológico no estado de Mato Grosso. Nativa 1: 34-43.

Souza, A.P., Ramos, C.M.C., Lima, A.D., Florentino, H.O., Escobedo, J.F. 2011. Comparison of methodologies for degree-day estimation using numerical methods. Acta Scientiarun Agronomy 33: 391-400.

Souza, A.P., Silva, A.C., Leonel, S., Escobedo, J.F. 2009. Temperaturas basais e soma térmica para a figueira podada em diferentes épocas. Revista Brasileira de

Fruticultura 31: 314-322.

Souza, A.P., Zamadei, T., Monteiro, E.B., Casavecchia, B.H. 2016. Transmissividade atmosférica da radiação global da região amazônica de Mato Grosso. Revista Brasileira de Meteorologia 3: 639-648.

Streck, N.A., Lago, I., Buriol, G.A., Heldwein, A.B., Tibola, T. 2006. A non-linear model to simulate node appearance in muskmelon (Cucumis melo L.) grown inside plastic greenhouse as a function of air temperature. Revista Brasileira de Agrometeorologia 14: 210-216.

Streck, N.A., Wiss, A., Xue, Q., Baezinger, P.S. 2003. Incoeporating a chronology response into the prediction of leaf appearance rate in winter wheat. Annals of Botany 92: 181-190.

Xue, Q.W., Weiss, A., Baenziger, P.S. 2004. Predicting leaf appearance in field-grown winter wheat: evaluating linear and non-linear models. Ecological Modelling 175: 261-270.

Wang, E., Engel, T. 1998. Simulation of phenological development of wheat crops. Agricultural Systems 58: 1-24.

Zeist, A.R., Resende, J.T.V., Lima Filho, R.B., Gabriel, A., Henschel, J.M., Silva, I.F.L. 2019. Phenology and agronomic components of first and second-cycle strawberry. Horticultura Brasileira 37: 29-34.

Zhang, Y.Z., Cheng, Y.W., Ya, H.Y., Han, J.M., Zheng, L. 2015. Identification of heat shock proteins via transcriptome profiling of tree peony leaf exposed to high temperature. Genetics and Molecular Research 14: 8431-8442.

Zhao, C., Guan, H., Yuan, X., Li, X., Gao, L., Shen, C., Tan, J. 2018. Effects of paclobutrazol on physiological parameters of dahlia under heat stress. Agricultural Biotechnology 7: 67-70.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.