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Growth, development and quality of *Passiflora tripartita* var. *mollissima* fruits under two environmental tropical conditions

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Summary

The curuba (*Passiflora tripartita* var. *mollissima*) is an important Andean fruit in bioprospecting industries because of its pleasant taste and aroma, antioxidant potential and sedative action. The objective of this study was to evaluate the development of curuba plants and the physicochemical characteristics of fruits under two environmental tropical altitudinal conditions. Crops were established in a low zone (2,006 m.a.s.l.) and a high zone (2,498 m.a.s.l.) in the municipality of Pasca (Cundinamarca, Colombia). Phenological monitoring was carried out in the principal growth stages. The weight, length, diameter, color, firmness, pH, total soluble solids, total titratable acidity and organic acid content were measured in the fruits. Climatic parameters were monitored during the crop cycle, and base temperatures and thermal times were estimated. The temperature and photosynthetically active radiation (PAR) were the climatic factors that had the greatest effect on plant development. The base temperatures of growth of the primary branches, floral buds and fruits were 4.3 °C, 3.1 °C and 0.01 °C, respectively. In the lower zone, the plants accumulated more growing degree days than in the upper zone. The fruits in the upper zone presented a higher weight, total titratable acidity and ascorbic acid content. The plants presented a marked response to the differential agroecological conditions of the two sites.

Introduction

The curuba or banana passionfruit (*Passiflora tripartita* var. *mollissima*) is a semi-perennial fruit plant with a climbing habit that is native to the Andean zone and belongs to the Passifloraceae family, *Passiflora* genus and *Tacsonia* subgenus (PRIMOT et al., 2005; CAMPOS and QUINTERO, 2012). The species *P. tripartita* var. *mollissima* is grown commercially in Colombia along the Andes mountain range (SEGURA et al., 2005) between 2,000 and 3,200 m.a.s.l. Curuba fruits are desired for their organoleptic properties (YOCKTENG et al., 2011), providing a source of vitamins A, B, C and niacin, calcium, iron, phosphorus, potassium, zinc, and fiber (LETERME et al., 2006; CHAPARRO-ROJAS et al., 2014; CONDE-MARTÍNEZ et al., 2014). In addition, it has a high antioxidant activity and a high content of phenolic compounds (VASCO et al., 2008; SIMIRGIOTIS et al., 2013), especially tannins, flavonoids and phenolic acids (ROJANO et al., 2012; CHAPARRO-ROJAS et al., 2014).

According to LARCHER (2003), "phenology is the study of the times of recurring phenomena of life history of plants and animals in relation to climate" and is one of the simplest ways to assess changes during life cycles (MENZEL, 2002). Phenological observations are important in agriculture for evaluating the good development of plants and making agronomic management decisions related to the date of carrying out crop tasks; they are also used in agrometeorological studies to analyze the relationships between crop development and

climate (CHMIELEWSKI, 2013).

One method widely used to predict growth and plant development is growing degree days (GDD), which express the amount of energy that a species requires to successfully complete a certain phenological stage or crop cycle (NUNES et al., 2016) and consist of the cumulative difference between the average ambient temperature and the base temperature, below which the plant cannot develop (PEDRO-JÚNIOR and SENTELHAS, 2003). For this reason, the base temperature of each phenological stage of a species is a tool that allows better management and control of a crop (MADAKADZE et al., 2003).

Physical (light, photoperiod, temperature, precipitation), edaphic and biotic factors continuously affect the physiology of plants and are determinants of plant growth (MENZEL, 2002; GALLÉ et al., 2015), fruit quality (KULLAJ, 2016) and post-harvest life because they modify the physiology, morphology and chemical composition (AHMAD and SIDDIQUI, 2015). Understanding how the phenology of a plant responds to climatic variations is important for predicting adaptive changes in response to climate change (MILLER-RUSHING et al., 2007); however, these responses differ not only between individuals but also depend on developmental adaptation to regionally differing factors (DOI et al., 2010); therefore, it is important to conduct comparative studies between zones for the same species.

Information on the growth and phenological development of *P. tripartita* var. *mollissima* is scarce, as is knowledge on the effect of climatic factors on its development. Some studies have been carried out on other passion fruits of economic interest, such as sweet granadilla (*Passiflora ligularis* Juss.) (RODRÍGUEZ-LEÓN et al., 2015), yellow passion fruit (*Passiflora edulis* Sims f. *flavicarpa* Degener) (MENZEL et al., 1987; GÓMEZ et al., 1999; FREITAS et al., 2015; SANTOS et al., 2016) and gulupa *Passiflora edulis* Sims (LEDERMAN and GAZIT, 1993; CARVAJAL et al., 2012; FLÓREZ et al., 2012; FRANCO et al., 2014; RODRÍGUEZ et al., 2019). Furthermore, studies evaluating the characteristics of fruits produced under different environmental tropical conditions have been carried out in fruit trees, such as purple passionfruit (FLÓREZ et al., 2012), sweet granadilla (ESPINOSA et al., 2015; ESPINOSA et al., 2018), cape gooseberry (FISCHER et al., 2007), guava (SOLARTE et al., 2014) and grapevine (GREER and WEEDON, 2012; MARTÍNEZ-LÜSCHER et al., 2015). There is little research on the physicochemical characterization of curuba fruits, and the few studies there are have focused on evaluating the effect of different postharvest treatments (TÉLLEZ et al., 2007; BOTIA-NIÑO et al., 2008), which is very important to improving quality conservation and commercialization of the fruit; however, knowledge on how environmental growing conditions affect fruits is important to generating agronomic management practices aimed at improving quality and production characteristics.

Accordingly, this research aimed to determine the base temperature for four phenological stages of the curuba, its duration in terms of thermal time, and the physicochemical characteristics of the fruits under two different altitudinal tropical conditions.

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Material and methods

Plant material and growth conditions

In two areas in the municipality of Pasca (Cundinamarca, Colombia), a high zone and a low zone, three-month-old curuba seedlings (*P. tripartita* var. *mollissima*), which had the first tendril emitted, were planted. The plants were obtained from a commercial nursery in the region. In the high zone, the crop was established in the Santa Teresita village on the “El Refugio” farm, located at 4°16′ 20.9″ N - 74°19′ 21.7″ W, at an altitude of 2,498 m.a.s.l. In the low zone, the crop was established in the San Pablo village on the “Bellavista” farm, located at 4°18′ 45.52″ N - 74°19′ 21.7″ W, at an altitude of 2,006 m.a.s.l.

In order to estimate the base temperatures for the main stages of development of the curuba, plantings were made at different times. In the high zone, a crop was established in December 2014 and another in May 2015; while in the low area, the planting was done in July, 2015. In each area, the plants were established with distances of 3 m between rows and 4 m between plants in a 600 m² area, for a total of 50 plants and a planting density of 834 plants/ha.

The soil in the upper zone was characterized by a sandy-loam texture, with a pH of 4.7; cation exchange capacity of 4.53 meq/100 g; 0.82% of N; 2.1 meq/100 g of Ca; 0.51 meq/100 g of K; 0.48 meq/10 g of Mg; 33.9 mg/kg of P; 11 mg/kg of S; 1.19 mg/kg of Cu; 103 mg/kg of Fe; 1.53 mg/kg of Mn; 2.05 mg/kg of Zn; and <0.12 mg/kg of B.

The soil of the low zone was characterized as having a clayey texture, with a pH of 4.5; cation exchange capacity of 10.96 meq/100 g; 0.24% of N; 8.74 meq/100 g of Ca; 0.31 meq/100 g of K; 2.02 meq/100 g of Mg; 0.34 mg/kg of P; 24.56 mg/kg of S; 0.033 mg/kg of Cu; 2.51 mg/kg of Fe; 0.18 mg/kg of Mn; 0.17 mg/kg of Zn; and 0.14 mg/kg of B. The climatic conditions of the two zones are described in Tab. 1.

A tutored system was used, which consisted of the installation of two horizontal wires for the conduction of the primary branches, one located at 1.5 m and the other at 2 m above the ground level. When the plants reached the second wire (2 m), a pinch was made in order to break the apical dominance and promote growth of the primary branches. With the pruning management, four primary branches were left on each plant: two at the level of each wire on opposite sides. When the primary branches reached the length of 1.8 m, they were pruned to promote the growth of secondary branches, which in turn were pruned when they reached a length of 0.75 m.

Weather stations (Coltein Ltda., Bogota, Colombia) with dataloggers (Coltein Ltda., Bogotá and Hobo U12-006, Onset Computer Corporation, Bourne, MA, USA) were installed in each of the two study areas for recording temperature, relative humidity (sensors VP-3,

Decagon Devices, USA) and photosynthetically active radiation (PAR) (sensors LI 190 B, LI-COR Inc. Lincoln, NE, USA). The data logging was configured for 15 min. intervals. The vapor pressure deficit (VPD) was calculated from the air temperature and relative humidity data with the method proposed by ALLEN et al. (1998). The daily light integral (DLI) was calculated from the average daily PAR during daylight hours and expressed in mol m⁻² day⁻¹.

Phenological monitoring

The phenological monitoring of the plants was done from December 2014 to June 2016. The measurements were done weekly, using the phenological stages described by RODRÍGUEZ-LEÓN et al. (2015) for *Passiflora ligularis* because there is no defined phenological scale for curuba. To carry out the monitoring, 15 plants were randomly selected in each study area, considering that FOURNIER-ORIGGI and CHARPANTIER-ESQUIVEL (1975) recommended a minimum sample size of 10 plants for phenological studies on tropical trees. During the growth of the main stem (BBCH-scale 3), the length of the stem and the number of knots were evaluated, until more than half of the sampled plants reached the final length of the stem (2 m). In the evaluation of the branch development (BBCH-scale 2), 15 primary branches, 3 cm in length, were marked, and the length and number of nodes of each marked branch were recorded until reaching the final preassigned length of 1.8 m. Subsequently, when the secondary branches were developed, 15 branches, 2 cm in length, were marked, and length and number of nodes were evaluated weekly until they reached the final length of 0.75 m.

During the development of the floral bud (BBCH-scale 5), 10 buds of approximately 1 cm in length in the apical part of the growing secondary branches were marked on eight plants, for a total of 80 floral buds per zone. With each marked bud, the length and diameter were recorded until the opening of the flower. During the fruit development (BBCH-scale 7), five fresh fruits of approximately 2 cm in length were marked on the secondary branches of eight plants, for a total of 40 fruits per zone. In each marked fruit, the length and diameter were recorded until the fruits reached harvest maturity, characterized by growth cessation and a slight loss of the firmness of the fruit.

Determination of base temperatures and thermal times

The base temperatures (BT) and thermal times (growing degree days, GDD) of four phenological stages of the curuba were estimated: stem and primary branch growth, secondary branch growth, flower

Tab. 1: Average climatic conditions of the two cultivation areas in the municipality of Pasca (Cundinamarca, Colombia): high zone (2,498 m.a.s.l.) from December 2014 to April 2016 and low zone (2,006 m.a.s.l.) from July 2015 to June 2016.

Climate variable		Low zone	High zone
Average temperature (°C)	Daytime (6:00-18:00 h)	19.4	14.9
	Nighttime (18:01-5:59 h)	16.1	12.9
Average low temperature (°C)		11.5	8.6
Average high temperature (°C)		26.7	23.8
Relative humidity (%)	Daytime (6:00-18:00 h)	80.5	90.2
	Nighttime (18:01-5:59 h)	87.3	90.3
PAR in hours of maximum radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$ of photons - 10:00 h)		620	680
Daily light integral (DLI, mol m ⁻² day ⁻¹)		15.2	17.5
Vapor pressure deficit (VPD; kPa)	Daytime (6:00-18:00 h)	0.68	0.41
	Nighttime (18:01-5:59 h)	0.52	0.38
Precipitation during growth (mm)		681	696

development, and fruit growth, using the methodology described by PARRA-CORONADO et al. (2015).

The base temperature (BT) for each of the phenological stages was determined from the sum of the average daily temperatures, recorded in each locality. The coefficient of variation (CV) of the estimated thermal times (GDE) was then minimized, considering a temperature range between 0 and 12 °C with increments of 0.1 °C, for each of the phenological stages. The BT for each phenological stage was obtained using the Solver tool for Excel® with a quadratic regression model, and corresponded to that temperature for which the lowest CV for the GDE was obtained (PARRA-CORONADO et al., 2015).

The duration of each phenological stage in terms of thermal time (GDD) was determined from the estimated BT values for each stage. The GDDs were calculated as the daily sum of the difference between the average temperature and the BT for each stage (Equation 1).

$$GDD = \sum_{i=1}^n (T_i - BT) = \sum_{i=1}^n T_i - nBT \quad (1)$$

Where, GDD is the thermal time (°C) accumulated during the n days of duration of the phenological stage, T_i is the average daily temperature (°C) for day i and BT is the base temperature (°C). GDDs were calculated taking into account the following considerations presented as (2), (3), (4) (PARRA-CORONADO et al., 2015):

$$T_i = \frac{T_{max} + T_{min}}{2} \quad (2)$$

$$T_i > BT, \quad GDD_i = T_i - BT \quad (3)$$

$$T_i < BT, \quad GDD_i = 0 \quad (4)$$

Where, T_{max} and T_{min} are the maximum and minimum temperature for day i, respectively.

Physicochemical characterization of fruits

In each study area, 40 fruits were collected in the harvest maturity stage (firmness 61-63 N corresponding to 6.2-6.4 kg/f), maintained at room temperature (18 °C) and transported to the Plant Physiology and Biochemical Laboratory of the Department of Biology of the Universidad Nacional de Colombia, Bogotá, to take the different physicochemical measurements.

The length and diameter of the fruits were measured using a digital calibrator (Fischer Scientific 0-150 mm); the fresh weight was measured on an analytical balance (Mettler AB204); and the firmness was measured with a penetrometer (0-13 kg) using a 2 mm head, with which force was applied in three points of the central part of each fruit. The colorimetric coordinates $L^*a^*b^*$ were evaluated at three points in the equatorial zone of the fruit exocarp, using a tristimulus colorimeter (Hunter Associates Laboratory, Mini Scan XE Plus, Reston, VA, USA), and the coordinate values were estimated, $L^*C^*H^*$ (L^* : brightness, C^* : chroma or saturation, and H^* : color circle tone), as indicated by SUI et al. (2016) and BARRERA et al. (2008).

Subsequently, the fruit juice was extracted, and the total soluble solids (TSS) measurements were taken with the use of a digital refractometer (Hanna Instruments, Woonsocket, USA). The total titratable acidity (TTA), expressed as meq-g of oxalic acid in 100 g of pulp, was determined by titration with 0.1 N NaOH, as indicated by HERNANDEZ et al. (2010). The content of organic acids (malic, citric, oxalic and ascorbic) of the fruit juice was determined as described by SOLARTE et al. (2014), for which 2 g of juice were placed in a 15 ml falcon tube covered with aluminum foil, and 12 ml of 5 mM phosphoric acid were added. The mixture was homogenized with

vortexing and then centrifuged at a centrifugal force of $2,817 \times g$ at 12 °C for 30 min; after which, a 2 ml sample of the supernatant was taken, filtered through 0.2 µm drum filters, and placed in a vial. The samples were analyzed in HPLC system equipped with a UV-visible detector (Waters, Milford, MA, USA) with an HPLC ROA organic acid H^+ column of 30 cm \times 7.8 mm. To obtain the calibration curves, a standard mixture of ascorbic acid, citric acid, malic acid, and oxalic acid, at five concentration levels between 0.01-1 mg·ml⁻¹, were used. Chromatogram peaks were identified by comparing retention times of the samples with external standards (HPLC grade, Sigma, USA).

Statistical analysis

For each major evaluated phenological stage, the trend of growth was adjusted to seven different mathematical models: linear, polynomial of the second degree, exponential of two parameters, exponential of three parameters, Gompertz, logistics of three parameters and monomolecular; based on studies by PAINE et al. (2012), who demonstrated that nonlinear models are appropriate for modelling plant growth.

The linear model has an absolute growth rate that is constant (PAINE et al., 2012); in the polynomial model, growth follows a smooth curve, potentially with great complexity (POORTER, 1989; HEINEN, 1999). The logistic model is characterized as having a sigmoidal shape and results from the combination of the exponential and monomolecular models, separated by an inflection point (FRANCO et al., 2014). The exponential model is useful for describing continuous growth or decreases when growth conditions remain favorable (ROJAS-LARA et al., 2008). The monomolecular model has no inflection point and its shape is concave downwards, the growth with this model is characterized by being fast at the beginning and, later, slow (PAINE et al., 2012). In the Gompertz model, growth declines exponentially over time (HEINEN, 1999) and differs from the logistic model in that the inflection point is first presented (PAINE et al., 2012). In each case, the model that presented the highest coefficient of determination (R^2) and the lowest Root Mean Square Error (RSME) was selected using statistical software Statistix 9.0®. The parameterization of the Gompertz model was carried out as indicated by WINSOR (1932), with the polynomial model by RODRÍGUEZ and LEIHNER (2006), and the monomolecular model by SEBER and WILD (1989).

In order to establish the differences between the BT of each phenological phase to estimate the GDD and to compare means, a Tukey test was used with the statistical package SPSS v.17 (SPSS Inc., Chicago, IL, USA).

Additionally, Spearman's correlation coefficients between the daily growth rates of each evaluated structure and the climatic variables for each zone were estimated. In relation to the physicochemical characteristics of the fruits, the assumptions of normality and homocedasticity were checked, and T-Student tests ($p \leq 0.05$) were carried out with SAS® software version 9.2.

Results

Climatic conditions of study areas

Fig. 1 shows that the high zone was characterized by a higher relative humidity and PAR, and the lower zone was characterized by a higher temperature and VPD. In both zones, the months of March and June had higher and lower temperatures, respectively. While the month of May had the highest relative humidity, and the month of September had the lowest relative humidity, the opposite of the VPD. In the lower zone, the highest PAR occurred in the month of September and, in the upper zone, in the month of January. The rainfall regime in the municipality of Pasca is bimodal, presenting two rainy seasons: the first in the months of April and May and the second in the months of October and November.

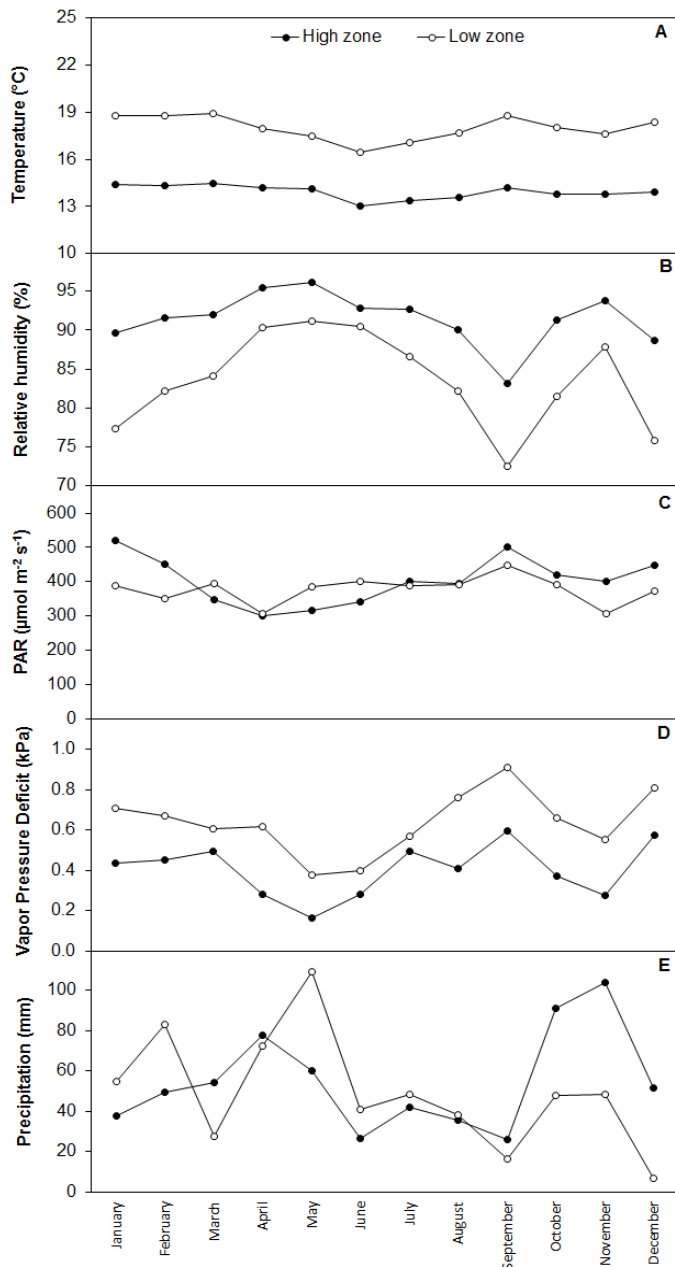


Fig. 1: Monthly behavior of climatic variables of the two cultivation areas in the municipality of Pasca (Cundinamarca, Colombia): high zone (2,498 m.a.s.l.), and low zone (2,006 m.a.s.l.).

Base temperature (BT)

The BT was different in each of the evaluated phenological stages. The growth of the primary branches was the stage that had the highest BT (4.3 °C), accumulating 1,204±69 growing degree days (GDD). The BT for the growth of the secondary branches was 1.5 °C, and the thermal time was 1,449±253 GDD. The development of a floral bud had a BT of 3.1 °C and an accumulation of 532±11 GDD, while the BT for fruit growth was 0.01 °C and the thermal time was 1,456±224 GDD. For the estimation of the thermal time in the growth stage of the main stem, the same BT was used as for the development of the primary branches (4.3 °C) since both structures have similar development processes (vegetative stage) and, probably, do not directly support the development of fruits (reproductive stage), contrary to the secondary branches where the fruits are developing.

Vegetative phase development

The increase in the length and number of nodes of the main stem as a function of the thermal time presented good adjustment to the *logistic model of three parameters*. In the low zone, the plants accumulated 1,799 GDD until reaching the final height of the stem, developing a total of 47 nodes; while in the high zone, the plants reached this height and the same number of nodes with 1,398 GDD, that is, 22% less GDD than in the lower zone (Fig. 2A and 2B).

This difference in thermal time does not indicate that the development of the stem in the upper zone occurred in a shorter calendar time; on the contrary, in the lower zone, the elongation and development of the stem nodes were more accelerated (data not shown), but the accumulation of GDD was greater because of the higher average temperature of this site, as explained in the second paragraph of the discussion chapter.

The increase in length and development of the nodes in the primary and secondary branches presented a good fit to the *polynomial model of second degree*. The primary branches in the low zone reached the final length with 1,084 GDD, and, in the high zone, the final length was reached with 1,177 GDD, indicating that, in spite of the lower temperature in the high zone, the plants there accumulated 8.6% more GDD in this stage (Fig. 2C), taking a longer calendar time. In both zones, the primary branches developed 31 nodes when they reached the final length (Fig. 2D).

In the development of secondary branches, in the high zone, they reached a length of 75 cm, accumulating 1,353 GDD; while in the low zone, they accumulated 1,798 GDD, 33.9% more GDD than in the high zone (Fig. 2E). As with the development of the main stem, the secondary branches developed faster in the lower zone, possibly because of the higher average temperature. In both zones, the secondary branches presented 21 nodes when they reached the length of 75 cm (Fig. 2F).

Reproductive phase development

The growth in length of the floral buds as a function of thermal time was adjusted to an *exponential model of three parameters*. The growth of the floral buds had a similar pattern and thermal times in the two zones. In the upper zone, the buds accumulated 517 GDD until reaching the floral opening, and, in the lower zone, they accumulated 537 GDD (Fig. 3A).

The emergence of the perianth from inside the bracts that encapsulate the fruit occurred in the low zone with 212 GDD, and, in the high zone, they emerged with 222 GDD (Fig. 3B), when the floral bud was 2.5 cm long.

The increase in length and diameter of the fruits as a function of thermal time was adjusted to the *monomolecular model*. In the low zone, the fruits completed their development when they accumulated 1,222 GDD, reaching a length of 8.4 cm and a diameter of 3.8 cm; in the high zone, the fruits accumulated 1,414 GDD to reach the point of harvest maturity (15.7% more GDD than in the low zone). However, the fruits in the high zone reached a greater length and diameter than low zone, 10.8 and 4.2 cm, respectively (Fig. 3C and 3D).

Effect of climatic conditions on phenology

In the plants in the lower zone, the growth rate in diameter and length of the fruits showed an inverse and significant correlation with the DLI; while fruit diameter had a direct correlation with daytime and nighttime temperature (Tab. 2).

In the plants grown in the upper zone, the rate of development of node numbers in the secondary branches showed a significant and inverse correlation with the daytime temperature and DLI. The fruit growth, both length and diameter, showed a significant and direct correlation with the DLI, but an inverse correlation with the nighttime temperature (Tab. 2).

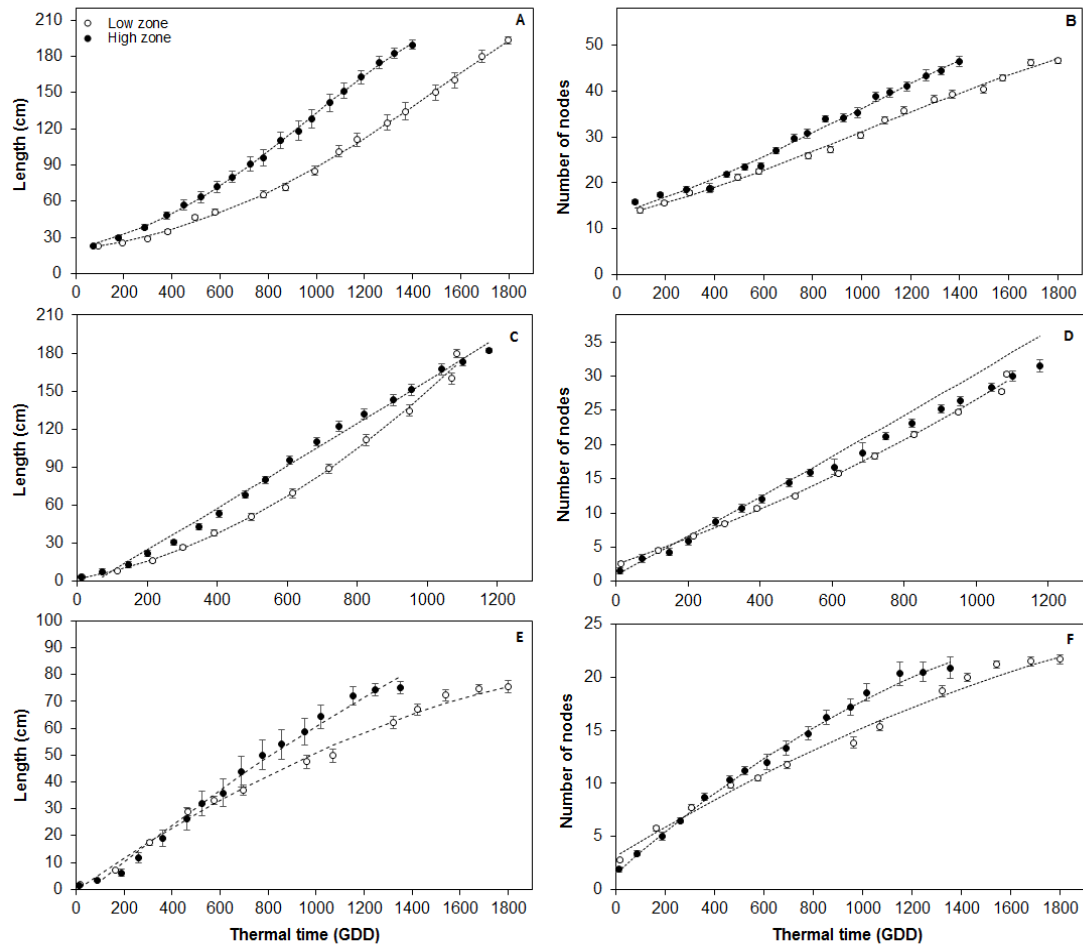


Fig. 2: Node length, growth and development of node number as a function of thermal time in the main stem (A and B), primary branches (C and D) and secondary branches (E and F) of *P. tripartita* var. *mollissima* in a high zone (2,498 m.a.s.l.) and a low zone (2,006 m.a.s.l.) in the municipality of Pasca (Cundinamarca, Colombia). Vertical bars indicate the standard error ($n = 15$).

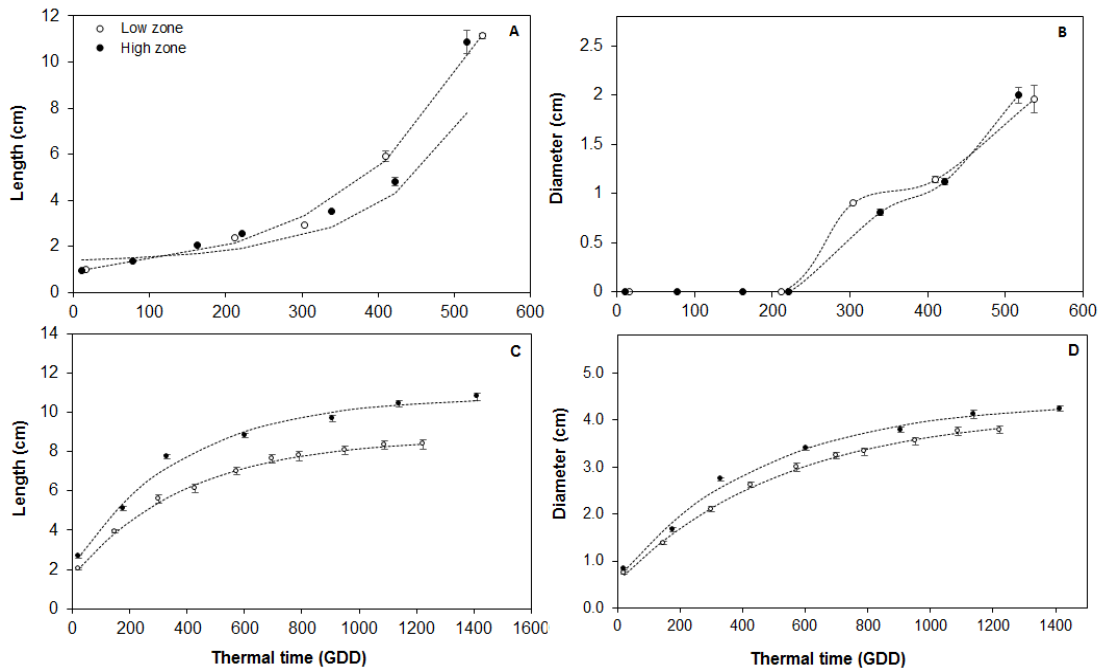


Fig. 3: Growth in length (A) and diameter (B) of flower buds; length (C) and diameter of fruits (D) as a function of the thermal time of *P. tripartita* var. *mollissima* in a high zone (2,498 m.a.s.l.) and a low zone (2,006 m.a.s.l.) in the municipality of Pasca (Cundinamarca, Colombia). The vertical bars indicate the standard error ($n=80$ floral buds and $n=40$ fruits).

Tab. 2: Matrix of correlations between phenological development indicators and climatic variables evaluated in *P. tripartita* var. *mollissima* in a high zone (2,498 m.a.s.l.) and a low zone (2,006 m.a.s.l.) in the municipality of Pasca (Cundinamarca, Colombia). The number in each box indicates Spearman's correlation coefficient and * the level of significance: * $p \leq 0.05$, ** $p < 0.01$.

Development indicator	Low zone				High zone			
	Temperature nighttime	Temperature daytime	VPD daytime	DLI	Temperature nighttime	Temperature daytime	VPD daytime	DLI
Length of main stem (cm/day)	0.02	-0.003	-0.17	-0.09	-0.45	-0.05	-0.001	-0.04
Nodes of main stem (nodes/day)	0.20	0.17	0.15	0.27	-0.23	-0.06	-0.27	-0.08
Length of primary branches (cm/day)	0.44	0.59	0.35	0.47	0.12	0.25	0.41	0.17
Nodes of primary branches (nodes/day)	0.23	0.37	0.23	0.28	0.01	0.30	0.29	0.38
Length of secondary branches (cm/day)	0.07	0.42	0.53	0.41	-0.16	-0.42	-0.31	-0.49
Nodes of secondary branches (nodes/day)	0.21	0.46	0.51	0.28	-0.18	-0.56*	-0.36	-0.52*
Floral bud length (cm/day)	-0.27	-0.24	-0.18	-0.24	0.17	0.33	-0.09	0.04
Fruit length (cm/day)	0.58	0.68	0.36	-0.71*	-0.94**	0.23	0.78	0.88*
Fruit diameter (cm/day)	0.70*	0.79*	0.34	-0.81*	-0.97**	0.11	0.75	0.83*

The responses of fruit development to the environmental conditions were contrary in the two zones, possibly because of the adaptation process of the plants since, in the site with a lower average temperature (high zone), high nocturnal temperatures negatively affected the development of the fruits, while, in the area with least DLI (low zone), high levels of DLI negatively affected development.

Physicochemical characteristics of fruits

The fruits produced in the high zone presented a greater fresh weight, length and diameter than the fruits in the low zone (Tab. 3), suggesting that the differential climatic conditions during the growth and development of the two crops influenced the final size of the fruits.

The color of the fruits in the low zone presented greater luminosity (L) and saturation (Chroma) than those in the high zone, and their tone ($^{\circ}$ H) corresponded to an intermediate shade between green and yellow, with a greater tendency towards yellow (Tab. 3). The firmness of the fruits at the point of harvest maturity did not show significant differences between the two zones. In the low zone, the fruits presented a higher TSS content, and those of the higher zone

Tab. 3: Physicochemical characteristics of *P. tripartita* var. *mollissima* fruits in a high zone (2,498 m.a.s.l.) and a low zone (2,006 m.a.s.l.) in the municipality of Pasca (Cundinamarca, Colombia). The values indicate the means \pm the standard error ($n=40$). The * indicates significant differences according to the t-student test ($p \leq 0.05$), ns: not significant.

Variable	High zone	Low zone	Significance
Fresh weight (g)	109.4 \pm 2.2	94.8 \pm 1.5	*
Length(cm)	11.1 \pm 0.1	9.5 \pm 0.1	*
Diameter (cm)	4.4 \pm 0.03	4.0 \pm 0.03	*
Tone ($^{\circ}$ H)	115.6 \pm 0.7	111.9 \pm 0.6	*
Brightness	36.4 \pm 0.6	44.8 \pm 0.8	*
Saturation (Chroma)	14.9 \pm 0.4	20.5 \pm 0.6	*
Firmness (N)	63.1 \pm 3.8	60.74 \pm 3.16	ns
TSS ($^{\circ}$ Brix)	8.3 \pm 0.1	9.65 \pm 0.17	*
pH	3.2 \pm 0.02	3.44 \pm 0.01	*
Total titratable acidity (%)	1.7 \pm 0.03	0.94 \pm 0.04	*
Citric acid (mg/100 g)	445 \pm 14	120 \pm 10	*
Malic acid (mg/100 g)	20 \pm 1	37 \pm 1	*
Oxalic acid (mg/100 g)	8525 \pm 439	17365 \pm 465	*
Ascorbic acid (mg/100 g)	189 \pm 18	37 \pm 6	*

had a higher TTA (Tab. 3).

The predominant organic acid in the curuba fruits was oxalic acid, with levels above 8,000 mg/100 g, followed by citric, ascorbic and malic acids (Tab. 3). The fruits in the upper zone had a higher content of ascorbic and citric acids than the fruits in the lower zone; while the fruits in the lower zone had a higher content of malic and oxalic acids than those in the upper zone (Tab. 3).

Discussion

In various studies on the phenology of fruit species, including passion fruits, thermal times have been determined using a standard base temperature of 10 $^{\circ}$ C; however, in some research on other tropical altitudinal commercial fruit plants such as feijoa (*Acca sellowiana*) and cape gooseberry (*Physalis peruviana*), variations of the BT according to the species and the phenological stage (PARRA-CORONADO et al., 2015; SALAZAR et al., 2008) have been reported. These findings coincided with the present study, in which the vegetative development phase had a higher BT than the phase of reproductive development, and the fruit development stage had the lowest BT (0.01 $^{\circ}$ C). This response could have been due to the fact that the fruits that started their growth were acclimated at low temperatures at the zone of growth (PARRA-CORONADO et al., 2015), such as the cape gooseberry, which has a BT of 1.9 $^{\circ}$ C for its fruit growth (SALAZAR et al., 2008). In addition, the curuba can tolerate temperatures up to -5 $^{\circ}$ C and is cultivated at altitudes up to 3,400 m in Peru (NATIONAL RESEARCH COUNCIL, 1989). Also, in strawberry plants, a BT as low as 0 $^{\circ}$ C was reported for leaf insertion (ROSA et al., 2011).

Temperature is one of the climatic variables that have the greatest influence on the growth and development of crops and, therefore, on their different phenological stages, whose duration is a good indicator of potential crop growth. Calendar time (days) has often been used to predict the beginning and end of phenological stages without considering the physiological aspects of plants for their development; however, its physiology is affected by the predominant temperature in the crop (PARRA-CORONADO et al., 2015). Methods have been used for a better prediction of the onset and end of phenological stages, which consider the effect of temperature on the development of plants (SALAZAR-GUTIERREZ et al., 2013). One of the more widely used methods is the accumulation of average daily temperature above a base temperature (BT), which is known as thermal time or growth degree-days (GDD). GDDs are defined as the number of day degrees needed to complete a phenological stage or a specific development process and are used to estimate the dates of appearance of knots, leaves, inflorescences, and fruit set, as well

as to estimate the growth of fruits, harvest date and potential crop production (PARRA-CORONADO et al., 2015).

Longer thermal times and fewer calendar days to complete each phenological stage in areas with higher average temperature (low zone) result from acceleration in phenology as a response to increases in temperature (MENZEL et al., 2006; MILLER RUSHING et al., 2007) because of the accumulation of heat units, as has been reported in other high zone fruit trees such as *Acca sellowiana* (PARRA-CORONADO et al., 2015) and for climbing habits, as in *Vitis vinifera* (MARTÍNEZ et al., 2015) and *Passiflora* sp., in which high temperature conditions increase the production of knots and the elongation of internodes (MENZEL et al., 1987).

The temperature and DLI were the only climatic variables that had an effect on the daily growth rates; however, the response was different and even inverse, depending on the stage of growth and the zone. BAHUGUNA et al. (2015) indicated that plants can alter their response to changes in temperature in the short- and long-term, depending on the phenological stage, the type of tissue and the metabolic composition.

The correlation coefficients between the temperature (daytime and nighttime) and the daily growth rate in the different phenological stages were in most cases positive and higher in the lower zone, which had the highest temperature and the greatest daily and annual temperature variation. MENZEL et al. (2006) indicated that phenophases exhibit a stronger response to temperature in warmer regions than in colder regions. Additionally, it is possible that, because of greater fluctuations in the climatic conditions in the low zone, the plants have developed different strategies of adaptation to this variability (DOI et al., 2010).

During the development of the main stem and primary branches, the growth was slower in the plants in the high zone, where a greater PAR was seen. Additionally, in the upper zone, the development of node numbers of secondary branches showed a negative correlation with the DLI. A short stem length under high solar radiation conditions may be due to an inhibitory effect of UV light on the synthesis of auxins (FISCHER, 2000). In *Passiflora alata*, vegetative growth has been stimulated with the use of a shading nets that decreased the incidence of light and UV rays (FREITAS et al., 2015).

The growth model during the development of the main stem in *P. tripartita* var. *mollissima* was similar to that reported for *P. ligularis*, which had a good fit to the logistic model of three parameters in the growth in length and nodes of the main stem, primary branches and secondary branches (RODRÍGUEZ-LEÓN et al., 2015).

The growth in curuba floral bud length was adjusted to the exponential model, while in sweet granadilla it was adjusted to the three-parameter logistic model (RODRÍGUEZ-LEÓN et al., 2015). The differential response between the two species may result from the morphology of the floral bud, where the curuba features a bud with an elongated hypanthium, and the granadilla has a rounded bud.

On the other hand, the growth of the curuba fruits was adjusted to the monomolecular model, while, in comparable studies, the fruits of sweet granadilla and yellow passionfruit have been adjusted to logistic models (RODRÍGUEZ-LEÓN et al., 2015; GÓMEZ et al., 1999). and purple passionfruits have been adjusted to logistic and monomolecular models (LEDERMAN and GAZIT, 1993; CARVAJAL et al., 2012; FLÓREZ et al., 2012; FRANCO et al., 2014). In all cases, these models are asymptotic, where growth rates are initially rapid and then gradually decrease as the fruits reach their final size.

Although the phenological development was more accelerated in the low zone, the fruits produced there were smaller, an effect that may have been due to the fact that, under high temperature conditions, allocation to fruits is reduced as a result of the shorter duration of the crop cycle, where photosynthesis rates do not compensate for reduced development times (PARENT and TARDIEU, 2014). In addition, there may be limited transport of sucrose and starch metabolism because

the genes involved in sucrose synthesis, sucrose transport, sucrose breakdown and starch synthesis are suppressed (BAHUGUNA and JAGADISH, 2015). *V. vinifera* fruits have also shown less weight in plants grown in greenhouses under high temperature conditions (28/18 °C), as compared to fruits in plants grown under ambient temperature conditions (24/14 °C) (MARTÍNEZ et al., 2015).

In the low zone, the smaller fruit size was also associated with the lower PAR of the zone, which is reflected in the negative correlation between the DLI and the length and diameter of the fruits since luminosity is the fundamental factor for photosynthesis and production of photoassimilates that support fruit development (MARTÍNEZ-VEGA et al., 2008).

The greater weight and size of fruits in the high zone is an indicator of better quality according to the Colombian technical standard for the curuba (NTC 1262), which established first quality fruits as those that exceed 11 cm in length, 4.5 cm in diameter and a 100 g weight. Second quality fruits have a length between 8 and 11 cm, diameter between 3.8 and 4.5 cm and weight between 70 and 100 g, characteristics of an average fruit produced in the low zone.

For fruit color, the tone of the fruits from the low zone was closer to yellow than those of the high zone, which could indicate a lower chlorophyll content that occurs in low light conditions as a result of a lower synthesis of chlorophylls (KULLAJ, 2016) and in high temperature conditions because fruit ripening processes that include degradation or unmasking of chlorophylls are accelerated (HORNERO-MÉNDEZ and MÍNGUEZ-MOSQUERA, 2002; BARRERA et al., 2008).

The higher content of TSS in the curuba fruits from the lower zone was similar to that reported for *V. vinifera* fruits, which presented high rates of maturation and accumulation of TSS related to high temperatures during late stages of fruit development (GREER and WEEDON, 2012), probably because of higher hydrolysis of starch, giving rise to soluble sugars (sucrose, fructose and glucose) (TÉLLEZ et al., 2007). The lower TTA in the fruits of this same area can be associated with the fact that, under high temperature conditions, the respiration rates of curuba fruits increase (TÉLLEZ et al., 2007), a process that uses organic acids as a substrate (BOTIA-NIÑO et al., 2008; BATISTA-SILVA et al., 2018). Additionally, fruit ripening is accelerated, in which organic acids are converted into sugars through the gluconeogenesis process (PRASSANA et al., 2007; FAMIANI et al., 2015).

The lack of studies on the biochemical characterization of curuba fruits has led to the assumption that citric acid predominates in this fruit, as seen in other passionfruits (HERNÁNDEZ and FISCHER, 2009). However, the results of this study indicate a predominance of oxalic acid in curuba fruits.

The content of ascorbic acid in the fruits of the upper zone was much higher than that reported by TÉLLEZ et al. (2007) and by VASCO et al. (2008), while the fruits of the lower zone had a lower ascorbic acid content than those reported by these authors. The ascorbate pooling in fruit crops is affected by abiotic factors, such as light or temperature, because of its role in the antioxidant cellular system (FENECH et al., 2019). This, the higher content of ascorbic acid in fruits in the high zone, may be due to the conditions that included higher PAR and lower temperature. High light in particular is translated into a ROS burst caused by an increased photoreduction and photorespiration, which, in turn, leads to increased ascorbate biosynthesis in order to detoxify these ROS (ASADA, 1999).

The higher content of ascorbic acid in the high zone fruits is a favorable characteristic for the commercialization of the product, given the nutritional importance of this compound (vitamin C) because of its antioxidant activity and its function as cofactor in many enzymes, such as enzymes involved in the synthesis and stability of collagen and in the synthesis of carnitine (FENECH et al., 2019).

The response of the curuba plants under the two evaluated climatic

conditions and the effect of environmental factors on the quality and organoleptic characteristics of the fruits suggested agronomic management alternatives for changing climate environment scenarios, such as water management, pruning and radiation, in order to maintain good physiological performance.

Conclusions

The curuba plants showed a phenotypic response to adjusting their growth and development to the climatic conditions of each zone. The plants grown in the zone with a higher temperature (lower zone) presented a greater accumulation of growing degree days and a more accelerated phenological development; however, the fruits produced there were smaller because of the shorter accumulation time of photoassimilates and lower daylight integral. The temperature and DLI were the two climatic factors that had the greatest effect on plant phenology. The fruits produced in the two zones showed marked differences in their physicochemical properties, suggesting that the contrasting climatic conditions had an important effect on the quality of the fruits, with the fruits from the upper zone having a greater size, weight and content of ascorbic acid, conditions that infer better quality.

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Conflict of interest

No potential conflict of interest was reported by the authors.

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Supplementary material

Tab. S1: Growth adjustment equations of *P. tripartita* var. *mollissima* structures in a high zone (2,498 m.a.s.l.) and a low zone (2,006 m.a.s.l.) in the municipality of Pasca (Cundinamarca, Colombia).

PARAMETER	LOW ZONE	HIGH ZONE
Length of main stem	$Length (cm) = 308.39 / (1 + \text{Exp}(2.7110 - 0.00179 * GDD))$	$Length (cm) = 256.62 / (1 + \text{Exp}(2.4362 - 0.00251 * GDD))$
Number of nodes, main stem	$Nodes = 64.672 / (1 + \text{Exp}(1.4049 - 0.00133 * GDD))$	$Nodes = 71.876 / (1 + \text{Exp}(1.4811 - 0.00150 * GDD))$
Length of primary branches	$Length (cm) = 1.996 + 0.0505 * GDD + 0.0000973 * GDD^2$	$Length (cm) = -7.943 + 0.1627 * GDD + 0.00000335 * GDD^2$
Number of nodes, primary branches	$Nodes = 2.5417 + 0.0173 * GDD + 0.00000674 * GDD^2$	$Nodes = 0.9674 + 0.0279 * GDD + 0.00000151 * GDD^2$
Length of secondary branches	$Length (cm) = -0.401 + 0.0626 * GDD - 0.000011 * GDD^2$	$Length (cm) = -4.1602 + 0.0739 * GDD - 0.00000894 * GDD^2$
Number of nodes, secondary branches	$Nodes = 3.0797 + 0.0143 * GDD - 0.00000212 * GDD^2$	$Nodes = 1.5248 + 0.0206 * GDD - 0.00000435 * GDD^2$
Length of flower buds	$Length (cm) = 0.4242 + 0.5291 * \text{Exp}(0.0056 * GDD)$	$Length (cm) = 0.3097 + 0.0986 * \text{Exp}(0.0088 * GDD)$
Diameter of flower buds	$Diameter (cm) = 2.463 * \text{Exp}(-\text{Exp}(2.416 - 0.007 * GDD))$	$Diameter (cm) = 3.617 * \text{Exp}(-\text{Exp}(2.523 - 0.0058 * GDD))$
Fruit length	$Length (cm) = 8.719 * (1 - \text{Exp}(-0.0025 * (GDD + 86.988)))$	$Length (cm) = 10.793 * (1 - \text{Exp}(-0.0026 * (GDD + 86.691)))$
Fruit diameter	$Diameter (cm) = 4.189 * (1 - \text{Exp}(-0.002 * (GDD + 78.144)))$	$Diameter (cm) = 4.398 * (1 - \text{Exp}(0.0022 * (GDD + 69.928)))$