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Node appearance model for Lulo (*Solanum quitoense* Lam.) in the high altitude tropics

Sandra Pulido[a,*], Carlos Ricardo Bojacá[a], Melba Salazar[b], Bernardo Chaves[c]

[a]Centro de Investigaciones y Asesorías Agroindustriales, Facultad de Ciencias Naturales, Universidad de Bogotá Jorge Tadeo Lozano, Bogotá, Colombia
[b]Universidad de La Sabana, Colombia
[c]Facultad de Agronomía, Universidad Nacional de Colombia, Colombia

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Lulo (*Solanum quitoense*) is an exotic fruit that originated and is cultivated in the high Andean tropics. The plant exhibits a very low growth rate and the growth period can extend to up to 2 years. A node appearance model based on thermal time approach was calibrated for this plant, by using datasets coming from field experiments conducted under different climate conditions. Plants, grown according to local management practices, were planted under greenhouse conditions at Bogotá Plateau (2560 m elevation) and Miraflores municipality (1850 m elevation) while a field crop was planted in an open field on the Bogotá Plateau. Base temperature (Tb) for node appearance was estimated as 9.61 °C according to the regression methodology proposed for this parameter. An exponential model was fitted for node appearance rate (δn) giving a good agreement between observed and simulated values for each dataset. Sensitivity analysis for estimated parameters of the model showed that Tb exerted a major influence on model response. Model validation was carried out using an independent dataset and, in general, showed that the model had good performance. However, at the end of the simulation period the model under estimated node appearance. Thus, the thermal time approach proved to be a reliable tool in order to represent node appearance for tropical species such as Lulo.

1. Introduction

The Lulo plant (*Solanum quitoense*) is a native fruit species from South America. It is widely consumed in Colombia because of its nutritional value, juice quality and has uses in agro industry (Angulo, 2003). Two botanical varieties are recognised for this species: *Solanum quitoense* var. *septentrionale*, which has thorns along the stem and the leaves and *Solanum quitoense* var. *quitoense*, without thorns (Whalen *et al.*, 1981; Morton, 1987). Lulo is considered as an uncompleted domesticated plant because of its narrow ecological adaptation, the presence of thorns in a large numbers of populations, the presence of trichomes around the fruit, the anthocyanin content in diverse organs, seed latency, and the high number of seeds per fruit (Lobo, 2000).

Plant growth rate is very low compared to other fruit species such as tomato (*Lycopersicon esculentum*) or cape gooseberry (*Physalis peruviana*) that are from the same botanical family.

* *Corresponding author.*
E-mail addresses: sandra.pulido@utadeo.edu.co (S. Pulido), melba.salazar@unisabana.edu.co (M. Salazar), bchavesc@unal.edu.co (B. Chaves).
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Cooman (2002) calibrated a crop growth model for greenhouse tomato at Bogotá Plateau and found a node appearance rate of 0.62 nodes day^{-1} at 20 °C. Salazar *et al.* (2006), working on cape gooseberry in the high altitude tropics, found a node appearance rate of 0.35 nodes day^{-1} at 21.3 °C. A local study conducted by Angulo *et al.* (2006) found a node appearance rate of 0.17 nodes day^{-1} at 18 °C for Lulo plant.

Studies on leaf appearance rates have been carried out on other Solanaceous crops like potato (*Solanum tuberosum* L.) and tropical soda apple (*Solanum viarum* Dunal). Recently, Fleisher *et al.* (2006) modelled the leaf appearance rate of potato by using two different approaches. The leaf appearance rate was 0.71 leaves day^{-1} for plants in a growth chamber with a CO_2 concentration of 370 μmol mol^{-1} and a temperature regime of 20/15 °C (day/night). Patterson *et al.* (1997) studied the effect of temperature and photoperiod on tropical soda apple, another species native from South America which is considered a noxious perennial weed in the United States. In this study, leaf appearance rate exhibited a closely linearly correlation with time-weighted temperature over the range of 11–29 °C. The authors found a leaf appearance rate of 0.36 leaves day^{-1} at 20 °C.

Accurate prediction of crop phenology is a major requirement for crop simulation models (Soltani *et al.*, 2006). Researchers have found that air temperature is a dominant factor controlling crop development (Yang *et al.*, 1995; Trudgill *et al.*, 2005). The number of nodes on the stem can represent the development stage of plants such as Lulo. Phyllochron, or interval between the appearance of two successive nodes, can be expressed either in terms of time (d) or, more commonly, thermal time (°C d) (Campbell *et al.*, 1998). Thermal time approach has been used to estimate or predict the duration of phenological stages based on temperature. Methodologies and the mathematical formulae used for degree day sums and cardinal temperatures have been widely discussed (Yang *et al.*, 1995; Bonhomme, 2000; Normand & Léchaudel, 2006). Heat unit models have been developed for a broad range of crop species such as corn, muskmelon, cotton, pastures, chickpea, broccoli (Tan *et al.*, 2000; Moot *et al.*, 2000; Baker & Reddy, 2001; Ruiz-Corral *et al.*, 2002; Viator *et al.*, 2005; Soltani *et al.*, 2006), considering not only the estimation of phenological stages but also the rate of dry matter accumulation. For fruits growing in the high altitude tropics, research on this topic is limited and only a few reports on fruits such as cape gooseberry (Salazar *et al.*, 2006) are available in the scientific literature.

The objectives of this work were to determine the base temperature for rate of node appearance, calibrate a node appearance model based on field trials conducted under different climate conditions, analyse the sensitivity of such model to variations in parameters values and validate the model under the specific condition of the high altitude tropics using an independent dataset.

2. Materials and methods

2.1. Field experiments

In order to calibrate the node appearance model, three crop growth cycles were conducted in two different locations in Colombia during 2002 and 2003. Two experiments were established under greenhouse (BG) and open field (BO) conditions at Bogotá Plateau (04°53′N–74°00′W and 2560 m elevation). A greenhouse experiment (MG) was planted at Miraflores municipality (5°11′N–73°09′W and 1850 m elevation). The durations of cultivation were 469, 442 and 434 days for BO, BG and MG, respectively. Hourly average temperatures for each experiment are shown in Fig. 1. The botanical variety *Solanum quitoense* var. *septentrionale* was used for all the experiments with a planting density of 0.25 plants m^{-2}. Plants were planted in single rows, leaving 2 m among rows and the same distance among plants. Plants were transplanted from the nursery to experimental fields after 55 days and were pruned in order to have four stems per plant after the main stem reached a height of 0.5 m.

Before each experiment was planted, soil samples were analysed and soil fertility was corrected according to general practice. Black polyethylene mulch was applied to all rows for weed control. Plants were watered using a drip irrigation system and nutrients were supplied with the irrigation. Diseases and pests were controlled using only minimal corrective applications of pesticides.

From 20 randomly selected plants, the number of nodes on one of the stems was periodically determined. A node can produce a leaf or an inflorescence and was defined from the moment that a leaf or truss bud reached a minimum length of 5 mm. Copper-constantan thermocouples coupled to a datalogger were placed in the central part of each experimental area, in the upper third of the crop, and monitored continuously; air temperature was registered every 10 min. The thermocouples were placed in an aspirated box and shielded from direct solar radiation. For all temperature data, daily averages were computed before further analysis.

2.2. Model calibration and evaluation

The von Bertalanffy equation, which is a variant of the exponential growth curve, was used to propose the node appearance model. In this type of exponential curve exhibits a rapid initial growth followed by a levelling-off (Karkach, 2006). By

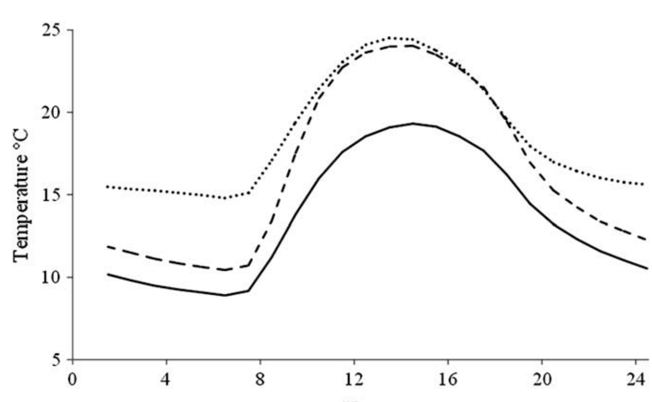

Fig. 1 – Average daily course of air temperature during the field trials at BO (—), BG (- - -) and MG (· · ·). Average temperature for the entire data acquisition period was 13.6, 16.4 and 18.6 °C for BO, BG and MG, respectively.

inverting the time and size scales from the exponential growth curve, an asymptotic approach to the maximum node number b can be obtained:

$$N = b(1 - e^{-a(\text{gdd})}), \tag{1}$$

a (nodes °C d^{-1}) is the rate at which b (nodes) is achieved. Growing degree days (gdd) were calculated as the accumulation of the average daily temperature above the base temperature,

$$\text{gdd} = \sum_{i=1}^{n} (Ti - \text{Tb}), \tag{2}$$

where Ti (°C) is the average daily air temperature; Tb (°C) is the theoretical base temperature at which the stem node appearance stops and n is the number of days of temperature observations used in the calculation of gdd.

Tb for node appearance was determined applying the regression coefficient method proposed by Hoover (1955) and reported by other authors. Parameters a, b and Tb were determined by the nonlinear least square method using the NLIN Procedure (Marquardt method) from the SAS System software (SAS, 2003).

By deriving Eq. (1), daily node appearance rate (δn, nodes day^{-1}) was estimated by $\delta n = abe^{-a\text{gdd}}$. The simulation for each climate condition was numerically solved using the Euler method (Jones & Luyten, 1998) for solving ordinary differential equations with a step size of 1 day. The integration was carried out using,

$$N_t = N_{t-1} + \delta n \times \Delta t, \tag{3}$$

where N_t is the number of simulated nodes on time t; N_{t-1} is the number of simulated nodes on previous step, and $\Delta t = 1$. Simulations were carried out for periods of 469, 442 and 434 days after transplanting for BO, BG and MG, respectively.

The goodness of the fit of the simulations was evaluated comparing the root mean square error of the predictions compared with the average observed values (N_i). For each observation (i) the error was divided by the average observed value and a root mean square of the relative deviations was obtained (RRMSE).

$$\text{RRMSE} = \left[\sum_{i=1}^{n}\left(\frac{(N_i - N_t)^2}{N_i^2}\right)\Big/ n\right]^{1/2} \times 100. \tag{4}$$

A sensitivity analysis of the model output parameters a, b and Tb was performed using a factorial design considering three levels for each parameter. Estimated values and 95% confidence limits were used as levels for parameters a and b while for Tb the upper and lower values were set to ±1 °C from the estimated value. A total of 27 daily simulations were carried out for each climate condition over a 300 day period. A definite integral was computed using a recursive adaptive Simpson quadrature numerical method to find the area below the curve described by the simulated data. An analysis of variance using a general linear model (SAS, 2003) was performed on the area under the curve considering parameters a, b, Tb and its interactions as sources of variation. In order to decompose the response variability among contributions from each parameter and their interactions, sensitivity indices for each level and interactions were calculated by dividing each one of the sums of squares by the total sum squares.

An additional Lulo crop was planted under greenhouse condition (BGV) at Bogotá Plateau, starting on August, 2006 for model validation. The node number count followed the same principles as those from the calibration experiments. Non-stressed conditions were used for this experiment and agronomic practices were the same as for the calibration experiments. Performance of model simulation was evaluated by calculating RRMSE, as already described.

3. Results and discussion

The relationship between measured node number and temperature was initially checked by graphing the observed nodes number per stem *versus* accumulated temperature for each location as shown in Fig. 2. The crop, under the coldest climate (BO), registered an observed δn of 0.062 nodes day^{-1} while for BG, δn was 0.096 nodes day^{-1}. The plants with the highest δn were found at MG with an average value of 0.103 nodes day^{-1}. The δn found for each location is even lower than that reported by Angulo (2003) indicating the lower growth rate for this species.

3.1. Model calibration and evaluation

For the present work the modified exponential model represented accurately the node appearance of the plants grown under the three temperatures (Fig. 3a). Parameters for the exponential model were estimated statistically (Table 1). According to the behaviour exhibited by von Bertalanffy equation, b represents the maximum number of nodes that can be produced by one stem. Under commercial conditions, Lulo plants will not reach the maximum node number per stem estimated by this function since the crop growth period is around two years. Tb for high altitude tropical fruits has not been widely studied and only Tb for cape gooseberry has been estimated as 6.29 °C by Salazar *et al.*, (2006). Based on the parameters of the linear equation to determine leaf appearance rate as function of temperature for tropical soda apple, it

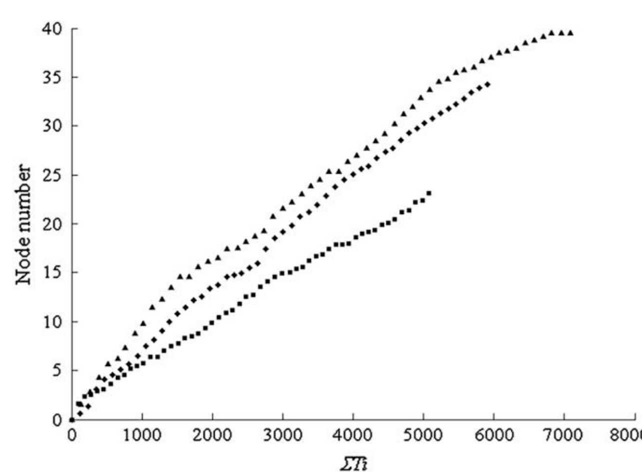

Fig. 2 – Observed node number *versus* accumulated temperature ($\sum Ti$) for Lulo grown under three different climate treatments: BO (■), BG (◆) and MG (▲).

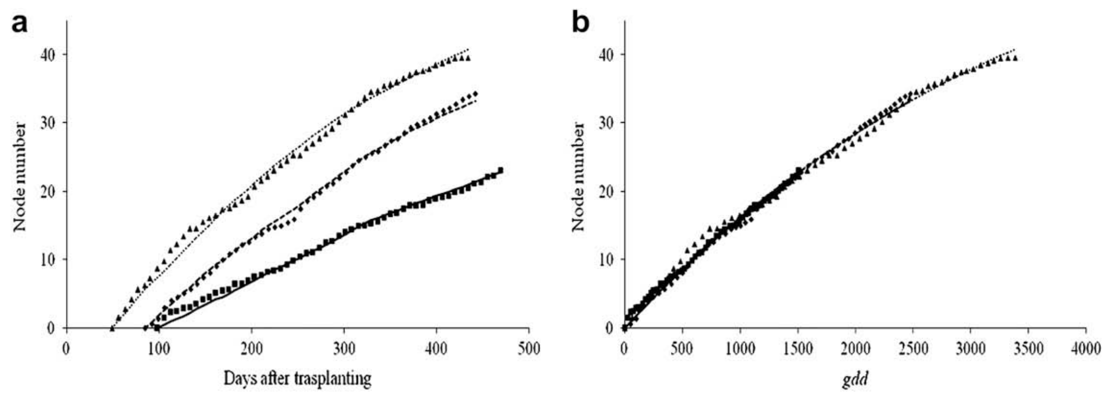

Fig. 3 – Comparison of simulated node number (BO: —, BG: - - -, MG: · · ·) and observations (BO: ■, BG: ◆, MG: ▲) *versus* days after transplanting (a) and gdd (b) for Lulo grown under three different climate treatments.

can be deduced a Tb of 1.78 °C (Patterson *et al.*, 1997). The higher Tb value (9.61 °C) found for Lulo in the present work reflects the adaptation of the species to lower altitude environments compared to the cape gooseberry. It is important to point out that Tb was estimated by statistical means and it is not possible to interpret the estimated value as a physiological Tb, according with reviews made by other authors (Yang *et al.*, 1995; Wielgolaski, 1999; Bonhomme, 2000; Normand & Léchaudel, 2006).

Simulated δn for BO was 0.0615 nodes day^{-1}, 0.93 nodes day^{-1} for BG and 0.106 nodes day^{-1} for MG. The proposed model described adequately the temperature effect on node appearance and the RRMSE for each dataset confirm it. The higher fit was obtained for MG with a RRMSE of 8.7% while for BG was 10.1%. The poorest value reported for BO (16.8%) was due to the underestimation of the observed nodes at the beginning of the measurement period (Fig. 3a). Calculated thermal time phyllochrons for each experiment were 60.2, 64.3 and 68.3 °C d node^{-1} for BO, BG and MG, respectively. For tropical soda apple (Patterson *et al.*, 1997) determined a thermal time phyllochron of 55.5 °C d node^{-1}, which can be considered a comparable value with the results obtained in the present work. The representation of simulated and observed values for node number *versus* gdd is shown in Fig. 3b.

Kirk and Marshall (1992) established a thermal time phyllochron of 31.3 °C d leaf^{-1} in potato, another Solanaceous crop, with a constant Tb equal to 0 °C. Fleisher *et al.* (2006) found a similar value when considering all the temperature treatments with the same Tb. Working with a Tb of 4 °C, they found a thermal time phyllochron of 28.2 °C d leaf^{-1}.

Sensitivity analysis showed that modification of parameters Tb and *a* resulted in the highest variation on the model output. Lower Tb value caused a higher simulated node number due to greater gdd accumulation. The average difference between lower and upper values and estimated Tb was 3.6 nodes, considering only simulations where Tb was varied. Increasing *a* value, higher node number was registered at the end of each simulation. Despite of the small changes in *a* values, 2.6 less nodes were found when the lower value was used and 1.6 more nodes when the upper value was used. The results of the analysis of variance of the model parameters *a*, *b* and Tb for the sensitivity analysis are summarised in Table 2. According to the analysis, parameter Tb was the only parameter that caused a significant variation in the model output. When decomposing the proportion of sum of squares of each parameter and their interactions with respect to the total sum of squares, Tb represented 63.7%, *a* and *b* 23.7% and 12.4%, respectively. The large impact of Tb indicates the importance of estimating Tb correctly in order to apply the model for other climatic conditions (Yang *et al.*, 1995; Baker & Reddy, 2001).

An additional 390 day simulation was performed in order to test the validity of the proposed model. The recorded average temperature for simulation period at BGV location was 16.2 °C, which represents a climatic condition close to the one registered for BG experiment (16.6 °C). The RRMSE was

Table 1 – Estimated parameters (*a*, *b*, Tb), standard error and 95% confidence limits of the fitted exponential regression for node appearance rate (δn) as a function of growing degree days (gdd)

Parameter	Estimate	Std. error	Approximate 95% confidence limits	
a	0.00027	0.00001	0.00029	0.00024
b	68.095	1.949	64.246	71.944
Tb	9.61	0.087	9.438	9.783

Table 2 – Analysis of variance of the model parameters *a*, *b*, Tb and its interactions using general linear models

Source	Df	Sum of squares	Mean square	*F* value	Pr > *F*
A	2	6 824 432.95	3 412 216.48	1.56	0.2184
B	2	3 574 040.07	1 787 020.03	0.82	0.446
Tb	2	18 360 259.1	9 180 129.54	4.21	0.02
*a**b*	4	14 535.85	3633.96	0	1
*a**Tb	4	50 387.75	12 596.94	0.01	0.9999
*b**Tb	4	39 106.86	9776.71	0	1
*a**b**Tb	8	107.33	13.42	0	1

11.6% representing close agreement between observed and simulated values. However, after day 235, the model tended to underestimate node number and at the end of the simulation period a difference of 6 nodes was observed.

4. Conclusions

A node appearance model for tropical high altitude plant Lulo was calibrated and evaluated using thermal time approach. The principles of the degree day approach were met allowing the methodology to be used.

The model was accurate enough to represent stem growth under non-limiting conditions. The proposed model based on degree day sum and statistical Tb determination proved to be a useful tool to predict plant growth in terms of node number for tropical species like Lulo. Although, the von Bertalanffy function has not been widely used to describe plant growth in terms of thermal time, for the present work this function was accurate enough to represent the node number accumulation under the calibration experiments. Validation of the model was performed using an independent dataset showing an adequate estimation of node appearance.

For future work, it is desirable to calibrate the model for a wider range of climate conditions, especially covering higher average temperatures than those recorded for the experimental crops used in the present study. This would allow the model to be used under a broad range of climatic conditions without using extrapolation.

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