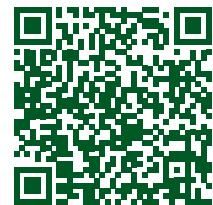


Nonlinear modeling of the growth of ornamental pepper accessions under high-temperature stress conditions

**Maria Clara Alencar Rodrigues^{1*} , Patricia da Silva Rodrigues¹,
Antonia Maiara Marques do Nascimento², Artur Mendes
Medeiros¹, Fabio Sandro dos Santos¹ and Priscila Alves
Barroso¹**

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Abstract: Describing the growth of pepper plants is essential for efficient management and the selection of superior genotypes. The objective of this study was to fit nonlinear growth models for the height and crown diameter of ornamental pepper accessions under heat stress. Height and crown diameter were evaluated every four days in two environments: (i) a greenhouse with humidity and temperature control and (ii) a greenhouse without control of these factors. The Logistic, Exponential, Gompertz, Richards, and Von Bertalanffy models were fitted. The results indicate that the choice of model depends on the characteristic measured and on the environment. The Gompertz, Richards, and Logistic models satisfactorily described plant height, while the Von Bertalanffy ($R^2=0.99$) model better represented the behavior of crown diameter under heat stress, characterizing a gradual deceleration of growth. These models should be used to estimate parameters that assist in the selection and management of ornamental pepper plants.

Keywords: *Capsicum annuum*, morphological traits, heat stress, growth modeling

INTRODUCTION

Pepper plants (*Capsicum* spp.) have high ornamental value due to the variety of colors and shapes of the fruits, as well as the different shades of flowers and foliage (Stommel and Bosland 2006). The ornamental plant sector has a recurring demand for compact varieties that are suitable for pots and indoor environments (Thakur et al. 2025). For this reason, pepper breeding programs aim to select plants with the desired architecture, which includes a balance between plant height and crown diameter in relation to the size of the pot used (Rêgo and Rêgo 2018).

The architecture of ornamental pepper plants and overall growth are directly related to environmental conditions. This relationship is associated with genotype \times environment interaction, which explains why genotypes respond differently to different environmental conditions, leading to variations in crop performance (Megerssa et al. 2024). High temperatures are one of the environmental factors with the greatest negative impact on crop growth and development, potentially

*Corresponding author:

E-mail: maria.alencar.ma@ufpi.edu.br

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¹ Universidade Federal do Piauí, Departamento de Engenharia Agronômica, Avenida Manoel Gracindo, km 01, s/n, 64900000, Bom Jesus, PI, Brazil

² Universidad de Burgos, Escuela Politécnica Superior, Departamento de Digitalización, Grupo de Inteligencia Computacional Aplicada (GICAP), Av. Cantabria, s/n., 09006, Burgos, Spain

causing various morphological and physiological changes, as well as losses in yield (Rosmaina et al. 2021, Roy et al. 2023). When plants are exposed to high-temperature stress, some changes are observed, such as reduced length, flower and leaf abortion, as well as significant loss in production (Rosmaina et al. 2021).

The analysis of growth, conducted through regression models and nonlinear models, is considered a valuable method that aids in the more efficient management of crops and is widely used in agronomic studies (Jane et al. 2019). Nonlinear models are more suitable for studying the growth of linear measurements such as height and diameter obtained from non-destructive plant assessments, as they provide better fits with fewer parameters and may also offer practical or biological interpretation (Sousa et al. 2014, Archontoulis and Miguez 2015, Jane et al. 2019). In this way, this technique allows for an understanding of the causes of variation in crop development, helping in the selection of more appropriate management practices.

Several models can be used to describe growth in plants. The logistic model describes symmetrical and limited growth and is widely used to represent controlled biological processes, such as the growth of organisms, populations, or plant tissues (Tjørve and Tjørve 2017). The exponential model assumes a continuous, unlimited growth rate and is therefore more suitable for the initial stages of development (Gerbi and Said-Houari 2013). The Gompertz model is asymmetric and describes growth processes in which the rate gradually decreases over time, finding various applications in growth analysis within the biotechnology field (Winsor 1932, Wang and Guo 2024). A generalization of the logistic and Gompertz models is the Richards model, which is widely used to describe growth processes due to its greater flexibility in representing the shape of the curve (Tjørve and Tjørve 2010). The most studied and commonly applied Von Bertalanffy model incorporates physiological principles of growth and metabolism, making it especially suitable for multicellular organisms (Bajzer and Vuk-Pavlović 2000, Lester et al. 2004, Katsanevakis 2006, Sogut et al. 2016, Janampa-Sarmiento et al. 2020).

The polynomial, logistic, and Gompertz models were used to describe the growth of sweet pepper cultivar plants, and the authors concluded that the logistic model was the most suitable (Jane et al. 2019). Demirel et al. (2012) used linear and nonlinear models to describe the height, diameter, and chlorophyll content of pepper plants (*Capsicum annuum* cv. Kapija) under deficit irrigation conditions, finding that the Linear, Logistic, and Gompertz models were suitable for determining the growth rate and that these characteristics were affected by water stress. Authors have also used nonlinear models to describe the length and width of chili peppers and bell peppers (Oliveira et al. 2021, Teixeira et al. 2023).

The application of nonlinear models to describe the growth of ornamental pepper plants, in which height and crown diameter are essential criteria for genotype selection, and especially the approach to plant growth under high-temperature stress conditions have not yet been investigated. The objective of this work was to fit growth models for the height and crown diameter of ornamental pepper accessions in two environments.

MATERIAL AND METHODS

Plant material

In this study, two pepper (*Capsicum* spp.) plant accessions were used, belonging to the Active Germplasm Bank of the Federal University of Piauí, *Campus Professora Cinobelina Elvas* (UFPI/CPCE). The accessions used in these experiments, namely CPCE 010 and CPCE 011, here referred to as accession 1 and 2 respectively, were previously described and evaluated for ornamental potential (Nascimento et al. 2025).

Initially, the seedlings were produced using the commercial substrate Terra Nova® (Flor da Serra do Sul/Paraná), in trays of 200 cells, by sowing 3 seeds per cell. After germination and once 2 to 3 pairs of true leaves had developed, the best seedlings were selected and transplanted into No. 15 pots (height of 10.5 cm, upper diameter of 14.5 cm, lower diameter of 10 cm, and volume of 1.16 L), containing the same substrate.

Three pots of each of the accessions were arranged in completely randomized blocks in two environments covered with 150-micron transparent diffusing film: (i) a greenhouse with humidity and temperature control, and (ii) a greenhouse without humidity and temperature control. In the second environment (uncontrolled greenhouse), the plants were kept under high-temperature stress due to the hot climate typical of the location where the experiments were conducted.

The facilities where the experiments were conducted are located in the experimental area of UFPI/CPCE in the city of Bom Jesus, Piauí (Brazil), corresponding to the coordinates WGS84 lat 9° 5' 3" S, long 44° 19' 33" W and alt 290 m asl. The air temperature and relative humidity conditions in the greenhouses were monitored twice a day, in the morning and afternoon (09:00 a.m. and 03:00 p.m. respectively - Brasília Time - BRT, UTC-3) using a digital thermo-hygrometer TH-50 from Incoterm®. In the greenhouse with uncontrolled conditions, air temperatures of 38.3 ± 3.2 °C and relative humidity of $16.3 \pm 0.1\%$ (mean value \pm standard deviation) were observed. In contrast, in the greenhouse with controlled conditions, an average air temperature of 26.2 ± 1.6 °C and relative humidity of $45 \pm 0.6\%$ (mean value \pm standard deviation) were recorded. Irrigation was performed three times a day until the substrate's maximum water-holding capacity was reached. Once a week, 10 g of Forth® Hortaliças (Cerquilho Velho — Cerquilho/São Paulo, Brazil) fertilizer were applied to each plant, diluted in 200 mL of water.

Assessments of plant height and crown diameter

The morphological assessments of plant height and crown diameter began on the day of transplanting (August 23, 2024) and were carried out every four days until the flowering period of all accessions corresponding to the date of October 22, 2024. A total of 16 evaluations were conducted over 60 days. Plant height was measured using a graduated ruler, from the base of the plant to the highest leaf/branch in the central region of the plant. Crown diameter was measured with the aid of a forestry caliper positioned horizontally, with the diameter measured in two different positions on the plant (longitudinal diameter and transverse diameter). These measurements were then averaged to obtain a more accurate representation of the plant's crown. Evaluations were performed on three plants from each accession. The average of each accession for each evaluation day was used to fit the growth curves. All analyses were performed in R version 4.0.5.

Growth models

Five classic nonlinear growth models were fitted for height and crown diameter: Logistic, Exponential, Gompertz, Richards, and Von Bertalanffy. The fitted curves were obtained through non-linear regression procedures implemented in the software R, which uses the maximum likelihood function to obtain the fits. The visualization of the results was performed using graphs that present the observed values and the fitted curves. The fitted growth models were evaluated separately for the accessions and the two environments, as described in the previous section.

The logistic model is defined by the following mathematical expression:

$$y(t) = \frac{A}{1 + \exp[-k(t - t_0)]}$$

where $y(t)$ represents the response variable (for example, plant height or crown diameter) at time t , A is the maximum asymptotic value, corresponding to the upper limit of growth, k is the growth rate, and t_0 is the inflection point, that is, the moment when the growth rate reaches its maximum value.

The exponential model is defined by the expression:

$$y(t) = A \exp(kt)$$

where $y(t)$ represents the response variable at time t , A is the initial value (when $t = 0$) and k is the growth rate.

The Gompertz model is given by:

$$y(t) = A \exp[-\exp(-k(t - t_0))]$$

where $y(t)$ represents the response variable at time t , A is the maximum asymptotic value, k is the growth rate and t_0 is the inflection point.

For the Richards model, the mathematical formulation is expressed by:

$$y(t) = A[1 + ve^{-k(t - t_0)}]^{-1/v}$$

where $y(t)$ represents the response variable at time t , A is the parameter associated with the upper asymptote or maximum growth value, indicating the limit toward which the variable tends as $t \rightarrow \infty$, k corresponds to the intrinsic growth rate, controlling the slope of the curve and the speed at which growth occurs, t_0 denotes the inflection point of

the curve, that is, the moment when the growth rate is maximum and the concavity changes, and v is a shape parameter that gives flexibility and asymmetry to the model (Tjørve and Tjørve 2010).

The Von Bertalanffy model is represented by the following equation:

$$y(t) = A(1 - b \exp(-kt))^3$$

where A is the asymptotic maximum value, b is a shape parameter related to the initial condition, and k is the growth rate.

Evaluation metrics

The quality of the fit for each model was evaluated using four complementary statistical metrics (Table 1): Mean Absolute Percentage Error (MAPE), Root Mean Squared Error (RMSE), Mean Absolute Error (MAE), and Coefficient of Determination (R^2) (Nascimento et al. 2023). These metrics were selected because they offer different perspectives on the model's performance in terms of relative accuracy, robustness to outliers, average error magnitude, and explanatory power.

RESULTS AND DISCUSSION

The comparative evaluation of quality metrics for fitting nonlinear growth models for pepper cultivation shows that the adequacy of each model depends on the morphological characteristic analyzed, the accession, and the environment under study (Table 2).

For the variable plant height in accession 1, the logistic and Richards models showed the best performance in both environments, with MAPE values below 7.5%, RMSE less than 0.74, MAE below 0.62, and R^2 above 0.996, which demonstrates high predictive power and robustness in describing the growth dynamics (Table 2). The similarity between the results of the logistic model and the Richards model suggests that, for this type of variable, the additional flexibility of the Richards model does not translate into significant improvements in fit (Figure 1A, 1B). In accession 2, the Gompertz and Richards models showed better performance in both environments. The logistic model also provides good fits in both environments, with R^2 above 0.997. When working with different sowing times for the sunflower crop, Mello et al. (2022) concluded that the logistic model described plant height best, reinforcing the model's ability to describe this trait under different environmental conditions.

Similar results were observed by Demirel et al. (2012) and Jane et al. (2019) when evaluating the height growth of pepper plants, with the Gompertz and Logistic models showing the highest R^2 values, leading the authors to conclude that these models are suitable for describing this variable. The Richards model had not yet been used to describe the height of pepper plants; however, it was used to fit the growth of fruit length, presenting the best results according to AIC (412.61), BIC (432.82), MSE (2.32), MAE (1.06), and R^2 (0.9957) compared to the Gompertz and Logistic models (Teixeira et al. 2023). In this way, the Richards model can be used to describe the height of the pepper plant regardless

Table 1. Metrics used for evaluating growth models

Metric	Equation	Description
Mean Absolute Percentage Error (MAPE)	$\text{MAPE} = \frac{100\%}{n} \frac{\sum_{i=1}^n y_i - \hat{y}_i }{y_i}$	Measures the mean percentage error, allowing comparison between variables of different scales. Lower values indicate higher relative accuracy.
Root Mean Squared Error (RMSE)	$\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2}$	Expresses the average magnitude of errors in the same unit as the variable analyzed. It is sensitive to large deviations and useful for detecting extreme discrepancies.
Mean Absolute Error (MAE)	$\text{MAE} = \frac{1}{n} \sum_{i=1}^n y_i - \hat{y}_i $	Represents the mean absolute error, being less influenced by outliers than the RMSE and easy to interpret.
Coefficient of Determination (R^2)	$R^2 = \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2}$	Quantifies the proportion of variability explained by the model. Values close to 1 indicate excellent explanatory power.

where n is the number of observations in the set of observations, y_i is the observed (actual) value for the i -th sample, \hat{y}_i is the value estimated by the model for the i -th sample, \bar{y} is the average of the observed values.

of the environment or accession, adequately depicting the initial phase of slow growth, the intermediate exponential phase, and the subsequent stabilization of growth, as observed in Figures 1A and 1B for accession 1 and Figures 2A and 2B for accession 2.

According to the results obtained in this study, the exponential model shows limitations regarding height adjustment in both accessions and both environments evaluated, demonstrating little adherence to the observed values over time (Figures 1 and 2). The model overestimated growth in both early and more advanced stages (Table 2, Figures 1 and 2), as evidenced by the high MAPE values (above 21.85% in accession 1, and above 45.05% in accession 2), although it still maintained R^2 above 0.92. This confirms that the height growth of pepper plants follows a sigmoidal pattern, and is not adequately represented by purely exponential functions.

For the crown diameter of the pepper plants, a distinct dynamic was observed. In the controlled environment, the Richards and Gompertz models showed better performance with MAPE of 8.94% and 9.54%, respectively, RMSE of 0.942, MAE below 0.750, and R^2 above 0.99 (Table 2). The logistic model was slightly inferior to Richards and Gompertz for all metrics studied, except for MAPE, equal to 8.35%, and was also considered to have a good fit. In accession 2, the logistic and Richards models showed better fit, with MAPE below 5.25% and R^2 of 0.992. For this accession, the Gompertz model was slightly inferior, but still showed good fit according to all metrics evaluated. In this context, for both accessions, in the controlled environment the sigmoid models (Gompertz, Richards, and logistic) once again stood out, as was also observed for plant height (Figure 1C and Figure 2C).

On the other hand, in the uncontrolled environment under high-temperature stress, the Von Bertalanffy model showed remarkably superior performance for both accessions studied (Table 2), followed by the Gompertz model, both with R^2 values close to 0.992–0.998 and significantly lower errors (MAPE between 6% and 8.4%). The Richards model presents metrics closer to those of the Gompertz and Von Bertalanffy models. In this environment, the Logistic model

Table 2. Quality of fit of growth models for plant height and crown diameter of ornamental pepper plants in two environments

Accession 1									
Traits	Model	Controlled environment				High-temperature stress environment			
		MAPE	RMSE	MAE	R^2	MAPE	RMSE	MAE	R^2
Plant height	Logistic	5.441	0.739	0.541	0.997	7.447	0.696	0.617	0.996
	Exponential	36.418	2.796	2.507	0.954	21.859	1.805	1.475	0.972
	Gompertz	8.821	0.901	0.663	0.995	8.826	0.797	0.706	0.995
	Richards	5.423	0.739	0.541	0.997	7.133	0.689	0.595	0.996
	Von Bertalanffy	11.608	1.049	0.812	0.994	9.717	0.870	0.753	0.994
Crown diameter	Logistic	8.357	1.102	0.8714	0.989	13.596	0.895	0.769	0.992
	Exponential	58.834	3.658	3.227	0.886	43.400	2.382	2.112	0.946
	Gompertz	9.548	0.942	0.750	0.992	6.151	0.567	0.478	0.997
	Richards	8.942	0.942	0.742	0.992	7.627	0.632	0.540	0.996
	Von Bertalanffy	12.891	1.004	0.819	0.991	6.253	0.477	0.409	0.998
Accession 2									
Traits	Model	Controlled environment				High-temperature stress environment			
		MAPE	RMSE	MAE	R^2	MAPE	RMSE	MAE	R^2
Plant height	Logistic	8.680	0.935	0.775	0.998	7.925	0.726	0.577	0.997
	Exponential	45.059	3.627	3.187	0.964	60.214	3.819	3.425	0.926
	Gompertz	6.353	0.910	0.655	0.998	8.308	0.643	0.553	0.998
	Richards	6.005	0.865	0.669	0.998	6.292	0.591	0.487	0.998
	Von Bertalanffy	8.400	1.039	0.727	0.997	12.350	0.812	0.679	0.997
Crown diameter	Logistic	5.106	0.819	0.585	0.992	10.157	1.153	0.987	0.989
	Exponential	35.627	2.837	2.579	0.902	30.547	2.350	2.072	0.953
	Gompertz	7.511	0.885	0.690	0.990	8.324	0.941	0.771	0.992
	Richards	5.250	0.812	0.587	0.992	8.560	0.972	0.813	0.992
	Von Bertalanffy	9.606	0.984	0.801	0.988	8.371	0.912	0.724	0.993

Mean Absolute Percentage Error (MAPE), Root Mean Squared Error (RMSE), Mean Absolute Error (MAE) and Coefficient of determination (R^2).

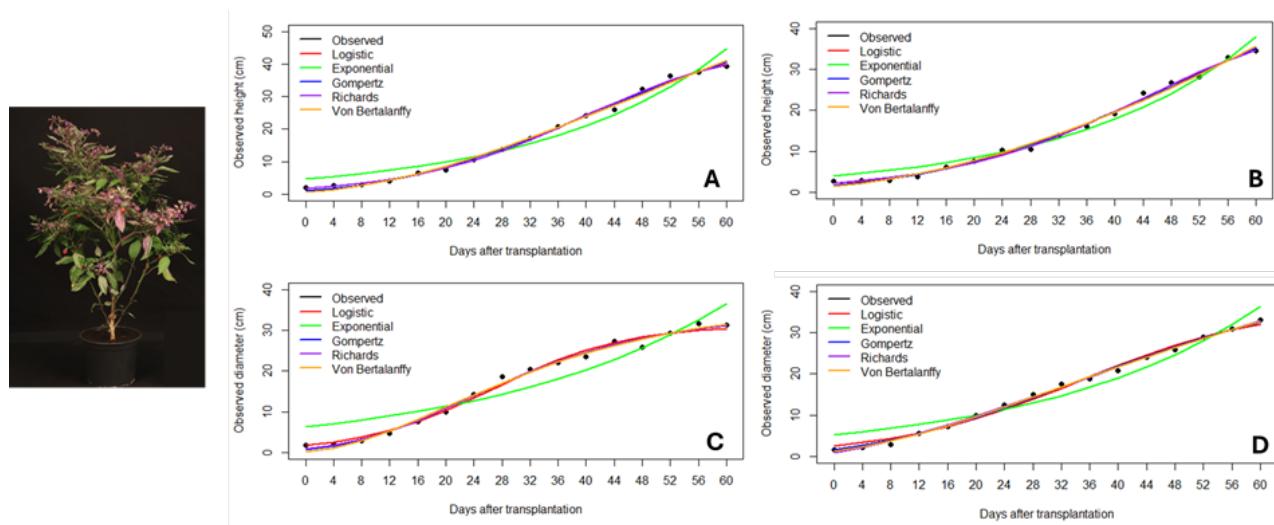


Figure 1. Fitting of growth models for accession 1 of ornamental pepper (A) Plant height in a controlled environment; (B) Plant height in a high-temperature stress environment; (C) Crown diameter in a controlled environment; (D) Crown diameter in a high-temperature stress environment.

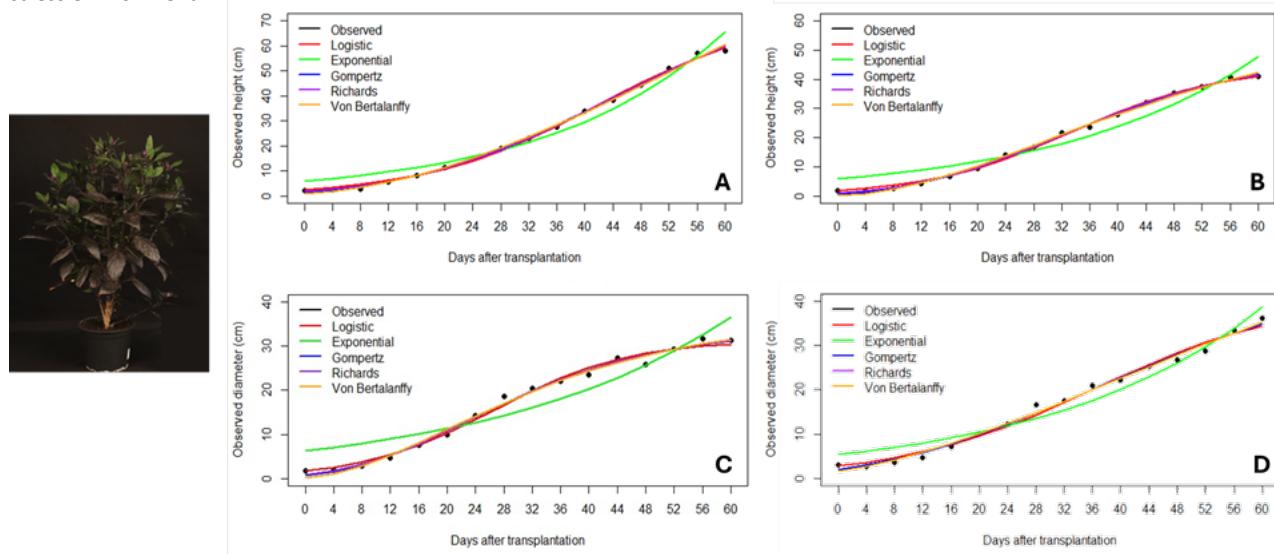


Figure 2. Fitting of growth models for accession 2 of ornamental pepper: (A) Plant height in the controlled environment; (B) Plant height in the high-temperature stress environment; (C) Crown diameter in the controlled environment; (D) Crown diameter in the high-temperature stress environment.

did not stand out. Oliveira et al. (2021) also recommended the von Bertalanffy model to describe the fruit diameter of five pepper genotypes.

This contrast between environments indicates that the plant's phenotypic plasticity, modulated by environmental factors such as high temperature, exerts a direct influence on the adequacy of mathematical models. The von Bertalanffy model describes growth as the result of the balance between anabolic and catabolic processes; in other words, growth is determined by the difference between gain and loss (Renner-Martin et al. 2018). This characteristic gives the model a physiological basis that can explain its good fit to the growth of the crown diameter of ornamental pepper plants under thermal stress conditions, as the increase in temperature tends to reduce the anabolic rate and intensify catabolic

processes, such as the activity of enzymes including RuBisCO, nitrate reductase, proteases, catalase, starch synthase, and ATP synthase, leading to impairments in photosynthesis, carbohydrate metabolism, protein synthesis, antioxidant defense, and phytohormone regulation (Mahajan et al. 2025). In these cases, the dynamics imposed by the Von Bertalanffy model, with an almost linear decrease in the growth rate as the plant approaches the asymptote (maximum size), adequately reflect the observed pattern of progressive deceleration under adverse conditions (Lee et al. 2020). The result is a smoothly asymptotic curve, without a pronounced inflection as seen in Figures 1D and 2D.

Under ideal temperature and humidity conditions, the growth of pepper plants is characterized by a more vigorous initial phase and a more abrupt slowdown (Figures 1C and 2C), a pattern that fits better with the Gompertz or Richards models, whose functions have floating inflection points and greater shape flexibility (Zeide 1993, Tsoularis and Wallace 2002). The Richards model, in particular, features a shape parameter that allows for shifting the position of the inflection point and modeling different degrees of asymmetry in the curve, which makes it capable of representing more complex growth patterns (Archontoulis and Miguez 2015). This structural difference explains why the von Bertalanffy model fits better under conditions of continuous and limited growth, such as under high-temperature stress observed in uncontrolled environments, while the Gompertz model tends to better represent growth under ideal conditions, with phases of rapid expansion and subsequent stabilization.

The results found in this study showed that: plant height is best represented by the Logistic and Richards growth models for accession 1, and by the Gompertz and Richards models for accession 2; crown diameter showed greater sensitivity to the environment, being better fitted by the Gompertz and von Bertalanffy models in the uncontrolled environment under high-temperature stress, and by the Richards model in the controlled environment; and the exponential model proved inadequate for both variables, accessions, and environmental conditions due to its inability to capture the stabilization phase of growth. These findings reinforce that the choice of growth model should be guided not only by statistical criteria but also by biological and physiological considerations of the cultivated species. Sigmoid models, which incorporate growth deceleration in advanced stages, better fit the actual pattern observed in pepper cultivation, characterized by rapid initial growth followed by stabilization. These models should be used with the aim of estimating parameters that assist in the selection and management of ornamental pepper plants exploring cross-validation and confidence intervals for predictive evaluation. Future studies could also prioritize the use of selected nonlinear models with mixed effects, which allow for the simultaneous incorporation of inter-plant variability and the structure of repeated measures over time.

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DATA AVAILABILITY

The datasets generated and/or analyzed during the current research are available from the corresponding author upon reasonable request.

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