

# Determination of levels of damage caused by different densities of *Tuta absoluta* populations (Lepidoptera: Gelechiidae) under greenhouse conditions

Determinación de niveles de daño ocasionados por diferentes densidades de población de *Tuta absoluta* (Lepidoptera: Gelechiidae) en tomate bajo invernadero

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## ABSTRACT

In order to determine the effect of infestations with *Tuta absoluta* on the growth and development of tomato plants under greenhouse conditions, six densities of the pest were evaluated (0, 2, 4, 6, 8, and 10 females/plant). A completely random design with three replicates per treatment was employed. The percentage of leaf area and number of fruits damaged were estimated and those variables were used to construct a damage curve. The plants exposed at infestation levels between 6 and 10 females presented the highest percentages of leaf area consumed (between 27 and 43%), damage on fruits (between 45 and 100%), and loss of apical leaves in comparison with the treatments with two and four females/plants. The height, number of internodes, number of leaves and leaflets, number and biomass of fruits were differentially affected by the densities of *T. absoluta* infestation ( $P \leq 0.05$ ). The leaf area and the biomass of stems and leaves did not vary with the infestation levels evaluated. On the damage curve, we observed that with more than two females per plant, the variables biomass, quality and number of fruits, result affected in an important way.

**Key words:** infestation densities, damage curve, tomato budworm, *Solanum lycopersicum*.

## RESUMEN

Con el fin de determinar el efecto de infestaciones con *Tuta absoluta* sobre el crecimiento y desarrollo del tomate bajo invernadero, se construyó una curva de daño a partir de la evaluación de seis densidades de la plaga (0, 2, 4, 6, 8 y 10 hembras/planta) empleando un diseño completamente al azar con tres repeticiones. Se estimó el porcentaje de área foliar y número de frutos afectados y a partir de esta variable se generó la curva de daño. Las plantas sometidas a niveles de infestación entre 6 y 10 hembras presentaron mayores porcentajes de área foliar consumida (entre 27 y 43%), daño en fruta (entre 45 y 100%) y pérdida de hojas apicales en comparación con los tratamientos con dos y cuatro hembras/planta. La altura, número de entrenudos, número de hojas, número de folíolos, área foliar, biomasa total y biomasa de fruta fueron afectados diferencialmente por las densidades de infestación de *T. absoluta* ( $P \leq 0,05$ ). Por el contrario, las biomásas de tallos y hojas no fueron afectadas. En la curva de daño se observó que a partir de 2 hembras/planta se da un efecto negativo importante en el número de frutos totales y fruto sano, pudiendo generarse pérdidas importantes de producción con densidades por encima de esta cantidad de hembras.

**Palabras clave:** densidades de infestación, curva de daño, cogollero del tomate, *Solanum lycopersicum*.

## Introduction

In Colombia, the tomato crop (*Solanum lycopersicum* L.) under greenhouse conditions has grown considerably. Currently, in the Bogota savanna and in other regions of the country like Boyaca and Santander, this crop is affected by a great amount of plagues, with the most important ones in the Bogotá savanna being the whitefly (*Trialeurodes vaporariorum* West.) and the tomato budworm (*Tuta absoluta* Meyrick). The latter affects the terminal bud of tomato plants and perforates the fruits, rendering them not apt for market. Farmer response to plagues and disease has been the frequent application of pesticides, even if the crop is

in harvest, generating a final product with high contents of chemical waste (De Vis *et al.*, 2001).

Integrated Pest Management programs (IPM) are a set of control strategies stemming from a technical, socio-economic, and environmental conservation reaction against the unilateral and indiscriminate use of synthetic pesticides (Luna and Luna, 1998). It includes strategies that contemplate the importance of insects and other harmful organisms as part of an agro-ecosystem in which other components are the crop and the environmental and socioeconomic factors; thus, it is of interest to learn of the crop responses to plague activities and the economic consequences of these responses (Andrews and Navas,

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1989). The amount of damage to crops caused by arthropods is a function of the density of the plagues, eating habits and oviposition of each species and the biological characteristics of the plants. Besides, other factors like environmental variations, age of the crop and the presence of other interacting organisms cause complex relationships, which hinder the estimation of its effects and its economic implications (Gómez, 1999). Hence, it is important to study the ecological parameters, which permit determining the plant-phytophagous relationship to establish control decision criteria. Because of this, this project permitted establishing the level of damage caused by different *T. absoluta* population densities to the growth and development of greenhouse tomato plants at levels that permit making control decisions. To accomplish this, the following specific objectives were suggested: quantify the damage caused by five densities of *T. absoluta* in greenhouse tomato plants and establish the relationship between the damage caused by five infestation densities of *T. absoluta* with the degree of decreased indices in growth and development variables of greenhouse tomato plants.

## Materials and methods

The study was conducted between June and December 2005 in research greenhouses at the Río Grande Experimental Station in Universidad Militar Nueva Granada (UMNG), located in the municipality of Cajica (Cundinamarca). To carry out the work, Durinta variety tomato seeds were planted. Then, the seedlings in formation were placed in transplant bags and kept isolated in entomological cages to avoid infestation by insects. During plant development, these were traditionally fertilized, disbudding and tutoring, and received an application of insecticide and fungicide at the start of each planting.

A preliminary assay was conducted to determine a range of *T. absoluta* density in which considerable damage was observed on the growth and development of the plant. The preliminary assay was carried out under relative humidity conditions between 58 and 75% and temperature between 15 and 21°C; a complete random block design was used with three repetitions in which five *T. absoluta* pair densities were liberated (0, 10, 15, 20, and 25), which had just emerged in six-week old tomato plants under control conditions. Each eight days and during five weeks, evaluations were performed to determine the effect of the different infestation densities on plant development. The following plant growth and development variables were recorded: height, number of leaves, number of leaflets per plant, distance of internodes and biomass. To assess the effect of

the *T. absoluta* densities on these variables, we conducted analyses of variance and Tukey's multiple comparison tests through the R statistical program version 2.12.0 (R Foundation for Statistical Computing, Vienna, Austria). Based on the results of the preliminary assay, a second assay was conducted under relative humidity conditions between 52 and 90% and temperature between 16 and 21°C, keeping in mind six infestation densities (0, 2, 4, 6, 8, and 10 insect pairs just emerged from breeding *T. absoluta* at UMNG, bred on greenhouse tomato plants) with three repetitions. Each experimental unit was made up of a six-week old Durinta variety tomato plant in an entomological cage (1 m wide x 1 m deep x 2 m high). As with the preliminary assay, the variables were recorded on a weekly basis but this time until obtaining a new generation of the plague in pupal stage (during seven weeks). Additionally, each week we quantified the number of larvae and mines per leaf in each experimental unit to determine oviposition habits and consequently the parts of the plant most susceptible to damage; the plants were divided into three parts, lower third, medium third, and upper third where the larvae and mines were counted. A digital photographic record was made of the foliar area of all the open leaves of the plants to estimate the percentage of damage caused by the plague on the foliage through image analyses with the Scion Image program (Scion Corp., Frederick MD). To record the damage caused by the different *T. absoluta* densities in greenhouse tomato plants, we kept in mind the number of berries affected to the second cluster and upon completing the experiment we calculated the total biomass and by parts of the plants through the difference of dry weight and fresh weight.

To determine damage levels, plant response to the different infestation densities of the plague was analyzed in order to identify a linearity phase, which, according to Pedigo (2006), is that where there is the greatest rate of damage caused by the pest.

To generate the damage curves, in some instances the Gompertz model (Seber and Wild, 1989) was used, which is a sigmoid model applied to size measurements like weight, foliar area, and length that can present asymmetric growth with relation to the curve's point of inflection. Equation (1) corresponds to the model.

$$f(x) = \alpha \exp[-e^{-k(x-\gamma)}] \quad (1)$$

Where  $\alpha$  is the curve asymptote or the growth limit for the variable,  $\gamma$  is the curve's point of inflection, where there is the maximum rate of growth and  $w_n = k\alpha/e$  is the maximum

rate of growth (Seber and Wild, 1989). In those cases in which there was overcompensation, the growth curve was more similar to a parable than to the sigmoid curve of the Gompertz model, reason why a quadratic polynomial was fitted. For other variables like total fruit and affected fruit, linear regression models were used because they were more appropriate to the tendency observed in the data. The parameters of the Gompertz model were estimated through nonlinear regression by using the Newton algorithm, employing the R statistical language. For the quadratic polynomials, the parameters were estimated via simple regression using the software mentioned. During the whole experiment, temperature and relative humidity were monitored with Hobo-type digital sensors (data loggers Onset computer).

## Results and discussion

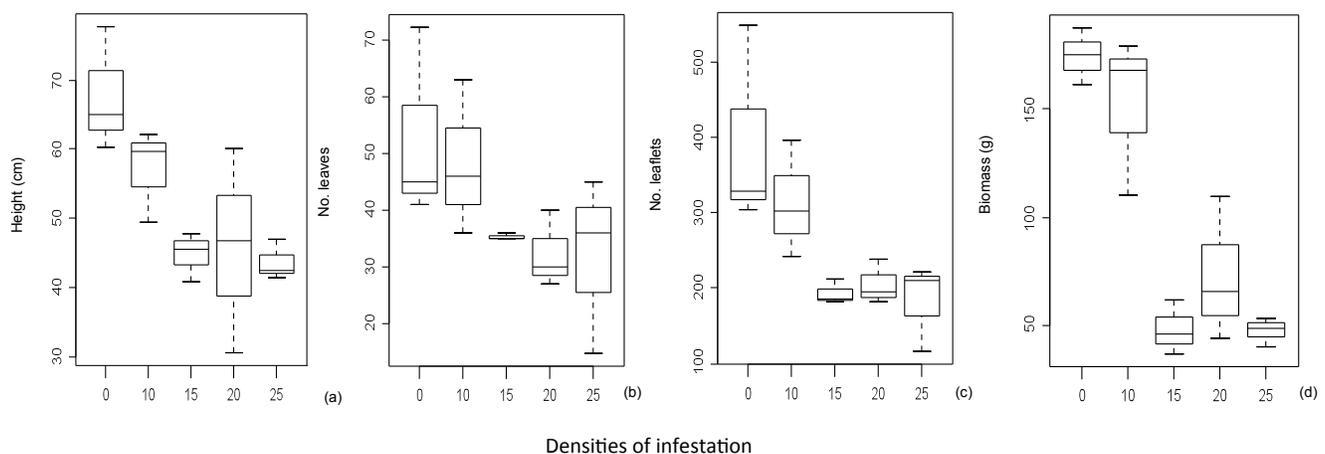
In all the variables evaluated, a negative effect was noted in the plant's development and growth as plague density increased (Fig. 1). For the variables of plant height, number of leaflets, and total plant biomass significant differences were present among densities according to the analysis of variance ( $F_{4;10} = 4.47$   $p = 0.024$ ;  $F_{4;10} = 4.50$   $p = 0.024$  and  $F_{4;10} = 19.16$   $p = 0.00011$ , respectively), while for the number of leaves variable there were no statistical differences ( $F_{4;10} = 1.86$   $p = 0.194$ ). The Tukey test presented differences only between treatment without plague and treatment of greatest infestation (25 females/plant) for the variables of height and number of leaflets. For total biomass, differences were found between treatment with 10 couples/plant and the rest of the treatments. The effect of the liberated pest

densities were evidenced on the number and distance of the internodes; the treatment without plague and the one with the lowest number of females liberated presented only one internode of difference whereas the distance between them was not marked. However, there is a greater difference of these two treatments from those of 15, 20, and 25 females/plant. Visually, differences were also noted in the aspect and vigor of the plants exposed to the different plague densities, plants presented deterioration signals as plague exposure densities increased.

Although in the vegetative variables mentioned there were no significant differences between the control and the density of 10 females per plant, in this density and all those higher, the larvae destroyed the apical meristem, which in the age evaluated (6 weeks) implies the impossibility of generating new inflorescences and, thus, the loss of the whole production above the first cluster. For this reason it was concluded that to generate the damage curve phases in the production variables it would be necessary to employ lower densities than those evaluated in the preliminary assay. Because of this, we selected densities between 0 and 10 females per plant.

### Quantification of the damage caused by five *T. absoluta* densities in greenhouse tomato plants

A linear regression was performed relating the number of larvae per plant with the density of females liberated in each treatment, through which the proportion of larvae doing damage to the plant per treatment was obtained, *i.e.*, the larvae rate of growth per each density of adults of the plague liberated. A statistically significant linear regression



**FIGURE 1.** Effect of different densities of infestation with *T. absoluta* on height (a), number of leaves (b), number of leaflets (c) y Biomass (d) of greenhouse tomato plants.

was found ( $F_{1,12} = 4.79$   $p = 0.049$ ) where the rate of increase of larvae per each female of the plague liberated is of 12.89, approximately 13 larvae. This ratio of 13 larvae per female is used to express the equivalency between females and larvae per plant in the results shown previously in this work.

High densities affect leaf area development, while densities below four females per plant permitted the plants to have better foliar development (Tab. 1). When infestation densities are low (2 and 4 females/plant, approximately 26 and 52 larvae per plant) foliar area development is even higher than that presented by plants without plague, which could be interpreted as an effect of overcompensation. Retuerto *et al.* (2003) state that this effect, also called compensatory photosynthesis, could be the result of changes in factors external to the plant or in the plant's physiological processes. Some authors interpret the compensatory capacity as part of a tolerance strategy that minimizes the harmful effects of a determinate stress agent and conclude that under appropriated conditions, the plants can compensate the harmful effects of past unfavorable conditions, depending on the intensity, duration, and type of stress experienced. Although many plants tolerate herbivores or can compensate the losses caused by those, the damage induced by herbivores does not necessarily lead to benefits for the plant (Agrawal, 1999). This is noted in plants exposed to the density of 10 females/plant or 129 larvae per plant in which foliar area development is affected by the consumption of the plant's apical meristem limiting its growth and development.

An increased tendency in foliar damage was observed, which generated a curve where three phases were identified (Fig. 2): 1) Phase of increased foliar damage, there is foliage consumption by first-stage larvae on a given number of leaves. According to Borgorni *et al.* (2003), first-stage larvae consume up to 24.9% of the leaf mesophyll. Nevertheless, this percentage is conditioned to the plant variety. 2) Phase of maximum level of foliar damage, which presents the maximum consumption of foliar area

on leaves supporting larvae in advanced stages of development. This is corroborated by Borgorni *et al.* (2003) who observed that fourth instar larvae present the highest daily consumption of leaf mesophyll, reaching up to 78.9% of the total accumulated in the larval phase, explained by size increase, presenting an exponential growth tendency, and 3) Phase of foliar damage reduction at the end of the observation period. This phase presents a combined activity between the cease of foliar area consumption because the larvae have completed their development and increased foliar areas in not attacked zones or leaves. The apical leaves were affected in all the infestation densities. But, damage intensity was different in all cases. The damage cause on apical leaves by infestation densities between two and 6 females/plant or 26 and 52 larvae per plant, generated a subsequent development of real leaves with areas affected by larval consumption. The eating habits of the plague larva, make them mine not only leaves, but also tear and stick to the leaves of the apical bud, bore the stems and affect the fruit (García, 1993; Vallejo, 1999). When infestation was induced with 8 and 10 females/plant or greater than 100 larvae per plant, there was a total loss of the apical leaves. In these last cases, the presence of larva mining within the plant stalk was noted, altering general development of the plants.

The total number of fruit and healthy fruit produced per plant in the first and second cluster is reduced when increasing infestation density (Fig. 3). The greatest amount of perforated fruit was obtained in infestation densities of 8 and 10 females/plant, that is, densities over 100 larvae per plant with 55 and 100% damage, respectively. These damage percentages were the result of *T. absoluta* larvae consumption of fruit in formation still protected by sepals. The reduced number of fruit produced by plants subjected to these infestation densities may be the result of the consumption of organs of inflorescences. According to Fernández and Montagne (1990), the plague larvae can attack the fruit by making galleries, penetrating mainly at the base or near the peduncle insertion zone. Vélez (1997),

**TABLE 1.** Total leaf area (AFT) and percentage of leaf area affected (%AFA) by *T. absoluta* under greenhouse in tomato plants between eight to twelve weeks of age.

Female; larvae/plant	0; 0		2; 26		4; 52		6; 77		8; 103		10; 129	
Age (weeks)	AFT (cm <sup>2</sup> )	%AFA (cm <sup>2</sup> )	AFT (cm <sup>2</sup> )	%AFA (cm <sup>2</sup> )	AFT (cm <sup>2</sup> )	%AFA (cm <sup>2</sup> )	AFT (cm <sup>2</sup> )	%AFA (cm <sup>2</sup> )	AFT (cm <sup>2</sup> )	%AFA (cm <sup>2</sup> )	AFT (cm <sup>2</sup> )	%AFA (cm <sup>2</sup> )
8	229,8	0	504,3	0,22	407,2	0,81	437,6	3,84	401,5	4,89	335,2	4,83
9	535,6	0	914,3	2,23	841,6	1,11	712,0	10,78	361,8	28,94	581,9	16,65
10	500,4	0	1143,3	16,41	1054,5	2,54	851,7	53,70	713,5	77,60	773,6	49,23
11	1024,3	0	1322,9	29,68	1468,5	2,91	997,3	41,42	891,9	52,34	865,6	30,69
12	1177,9	0	1519,6	27,95	1642,4	2,62	1536,5	26,53	1060,6	43,38	824,6	33,29

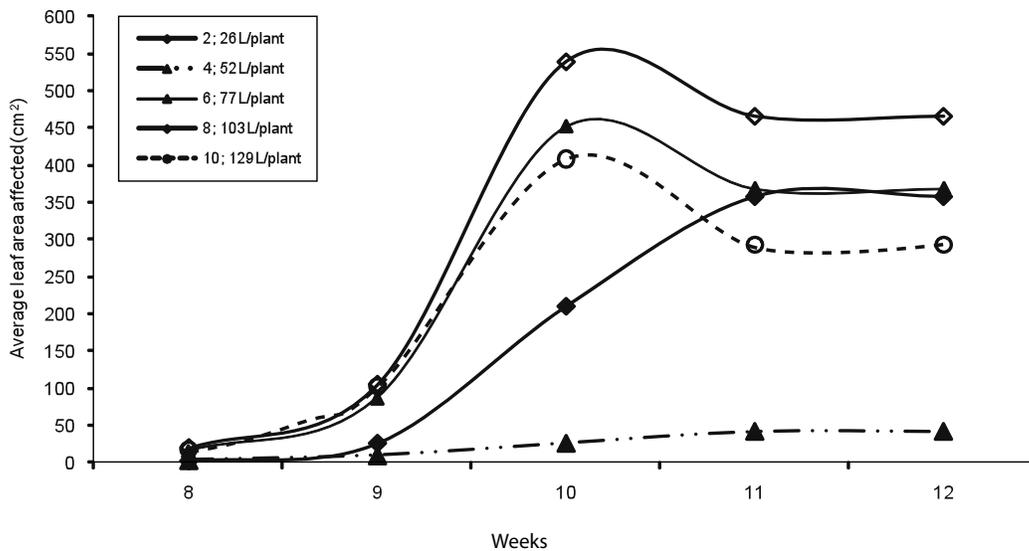


FIGURE 2. Average total leaf area affected by *T. absoluta* in greenhouse tomato plants between eight to twelve weeks of age. L, larvae.

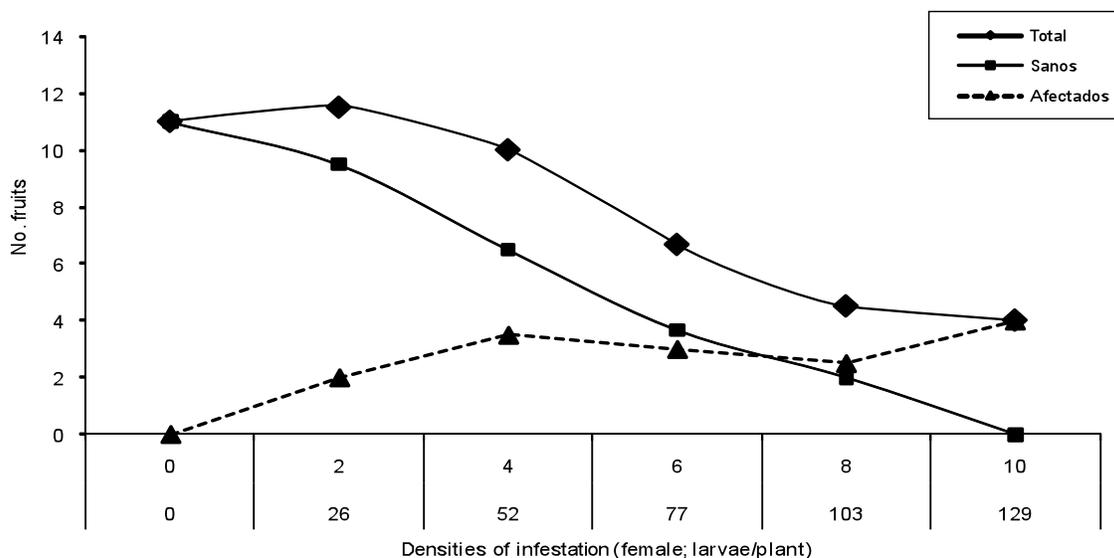


FIGURE 3. Average healthy and affected fruits by *T. absoluta* for the first two clusters in greenhouse tomato plants.

states that sometimes the larvae bore the ovary of the tomato flower promoting the fall of the buds and flowers. However, the diminished number of fruit produced by the plants exposed to these densities can also be in response to foliar area damage, as suggested by Marcano (1995) who stated that the average number of fruit per plant is affected by the percentage of defoliation in tomato plants.

#### Distribution of larvae

The plant was divided into three parts during the evaluation period, in which plague larvae were found, with the

greatest number of larvae in the lower third with relation to the medium and upper thirds, respectively (Fig. 4). The greatest number of larvae present in the lower third was counted at 20 days after infestation (nine-week old plants); while in the other two thirds, the greatest number was counted at 27 days after infesting the plants (10-week old plants), except for the treatments with 2 and 4 females/plant, where the number of larvae was greater in the medium third. These observations coincide with that cited by Torres *et al.* (2001) who stated that *T. absoluta* oviposits mainly on the apical and medial parts of the

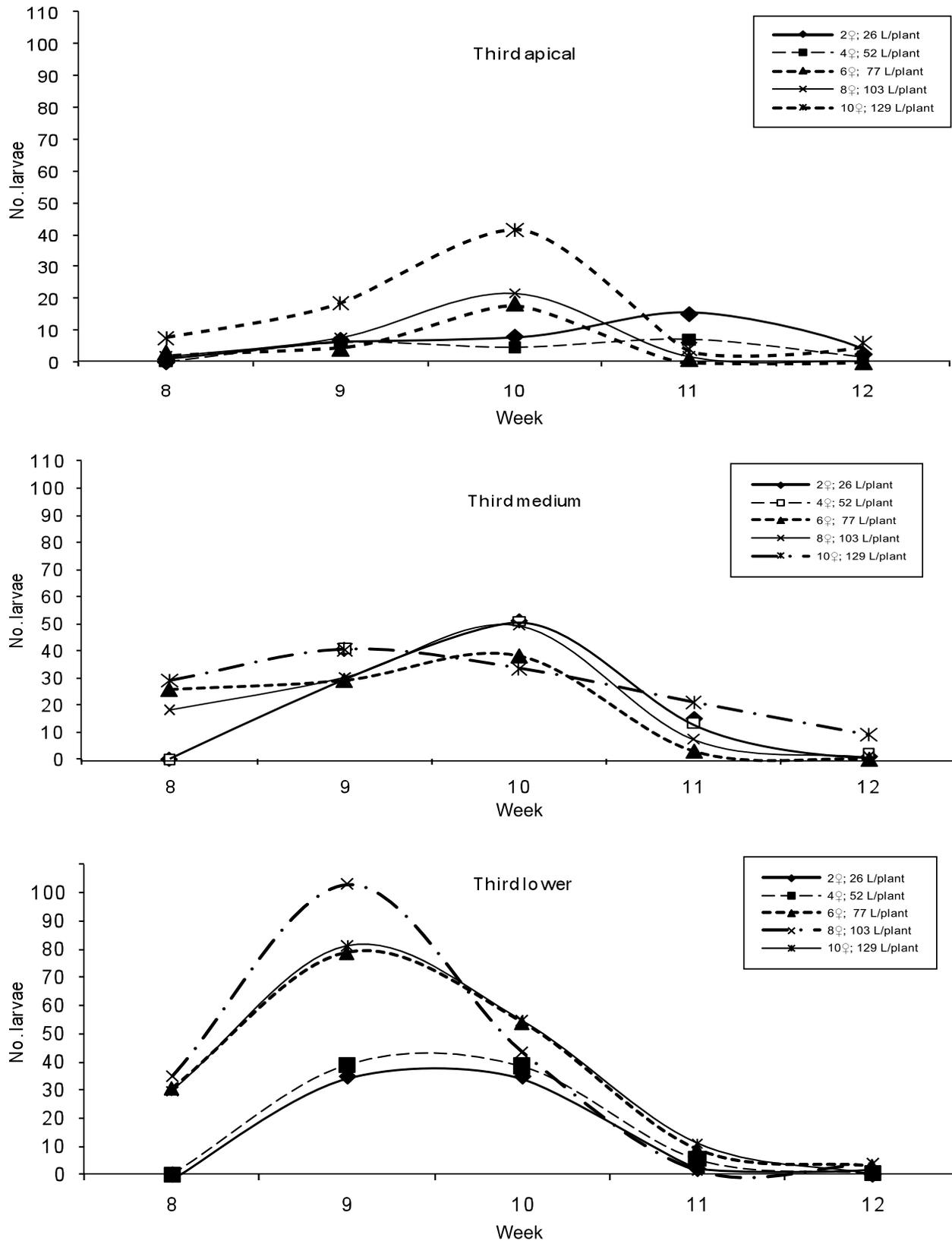


FIGURE 4. Distribution of larvae of *T. absoluta* from different densities of females of the pest strata in greenhouse tomato plant. L, larvae.

plant and that besides there is high oviposition of the plague on petioles and meristems of young plants prior to blooming. This explains that most larvae being found in the lower and medium thirds given that, they are the tissues that, at the moment of infestation, were part of the apical third and medium part of the plant. With the presence of mines in the whole plant until the end of the plague cycle, it can be deduced that as the larvae develop, some seek young tissue and elaborate more than one mine on different plant organs. This confirms reports by Torres *et al.* (2001), who stated that third and fourth instar larvae move to other parts of the plant diminishing their mobility in the prepupal stage. Authors like Coelho *et al.* (1984), Haji *et al.* (1988), and Torres *et al.* (2001) state that second stage instar larvae frequently leave the mines and walk on the leaves especially during the morning hours. These observations are important to generate control strategies given that the plague can be attacked in larval state before it again penetrates the plant tissue.

**Relationship between the damage caused by five *T. absoluta* infestation densities with the decreased degree of indices in growth and development variables of greenhouse tomato plants**

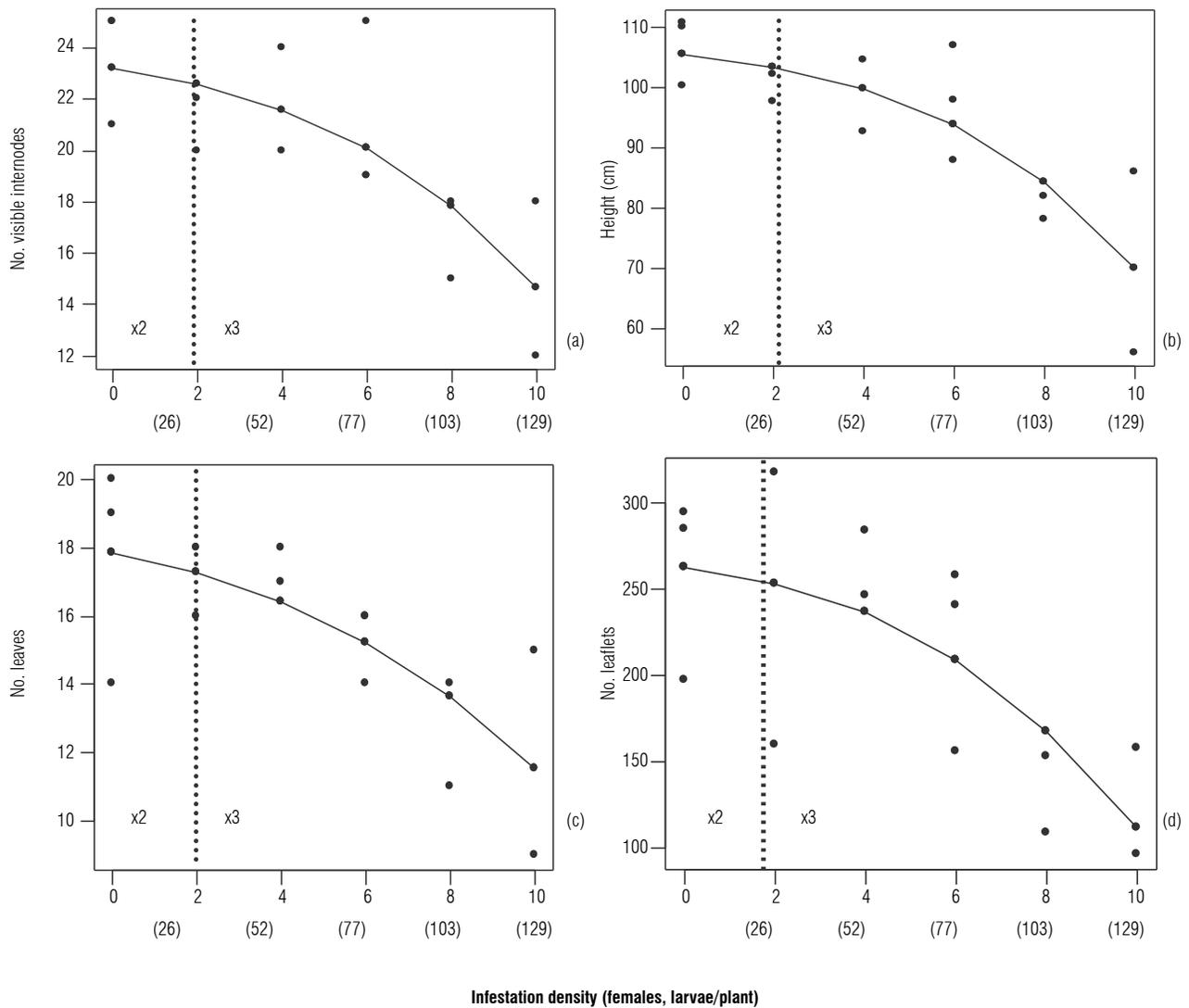
Variation of *T. absoluta* infestation densities significantly affected the plant's growth and development variables, as can be confirmed via probabilities associated to the F statistic of the fitted Gompertz models. That effect was noted for height ( $F_{2,11}=12.23 P=0.001598$ ), visible number of internodes ( $F_{2,11}=7.96 P=0.00727$ ), number of leaves ( $F_{2,11}=6.48 P=0.01377$ ), and number de leaflets ( $F_{2,11}=5.91 P=0.01804$ ). The  $\gamma$  parameter of the Gompertz model indicates the density of females in which the rate of damage is maximum, which is between 10 and 13 females/plant for the variables mentioned ( $\gamma = 13.01$ ;  $\gamma = 12.78$ ;  $\gamma = 13.35$ , and  $\gamma = 10.34$ , respectively). This is verified when observing Fig. 6, where the greatest slope is presented when the density is closed to 10 females/plant, in all cases. The  $\alpha$ -parameter values correspond to the behavior expected from the variables in the absence of the plague. Hence, when there is no plague damage, height reaches a value around  $\alpha = 108$ , 67 cm; the number of internodes corresponds to  $\alpha = 24.19$ ; the number of leaves developed is approximately  $\alpha = 19.10$  and a number of leaflets around  $\alpha = 275.00$  per plant. Fig. 5 clearly shows that these variables diminished as infestation density increased. Once the model is fitted, it permits identifying the phases of damage for each variable, showing that these levels of *T. absoluta* infestation affect the quality of the plants and with densities above two females per plant there is a negative effect on the growth of those plants. Variation of infestation

density significantly affected the foliar area ( $F_{2,11}=10.9 P=0.024$ ), as well as the accumulation of total biomass in the plant ( $F_{2,11}=9.69 P=0.0037$ ) (Fig. 6). The quadratic model fitted to these variables permitted generating and identifying in the damage curve the overcompensation stages (X2a) and linearity (X3). The overcompensation phase was noted with the damage induced by densities between 2-6 females/plant or 26-77 larvae/plant, which produces a stimulus generating an increase in foliar area, which is reflected by the total biomass increase.

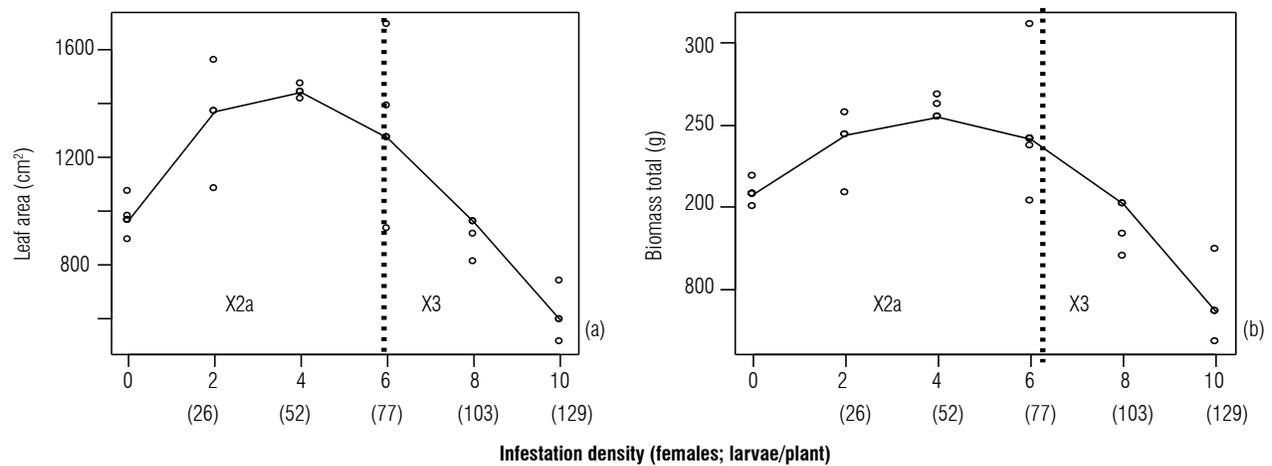
The effect of the densities of females evaluated on stem biomass and leaves was not statistically significant, as corroborated by the probabilities associated to the Gompertz model F statistic ( $F_{2,11}=3.3216 P=0.074$ ;  $F_{2,11}=0.98 P=0.4036$ ). However, upon interpreting the parameters for these two variables we find that the maximum rate of damage is around 10 females per plant ( $\gamma = 10.65$ ,  $\gamma = 10.90$ , respectively), similar behavior to that found for height, number of internodes, number of leaves, and number of leaflets. The  $\alpha$  values indicate that without the plague's attack, stem biomass corresponds to approximately 130 g and leaf biomass to 200 g ( $\alpha = 129.68$  and  $\alpha = 202.34$ , respectively). In these initial variables, the linearity phase can be identified around 8 females/ plant. There were significant differences in the biomass of the reproductive part (flowers and fruit) ( $F_{2,10}=8.38 P=0.0072$ ) and densities above 4 females/plant affecting the fruit biomass (Fig. 7). With the model fitted, we were able to identify the phases of tolerance, compensation, linearity, and insensitivity for this variable.

It is important to highlight that the maximum rate of damage for the reproductive weight is around 7 ( $\gamma = 7.21$ ), a value clearly lower than that observed for the vegetative variables, which were always at 10 or more. This bears an important implication regarding the damage caused by the insect, given that the critical densities of the plague are lower in the case of direct damage than in indirect damage. According to this, it would be common to see situations in which the plant's vegetative growth is not visibly affected, and there may have already been important damage to the flowers and fruit. When observing Fig. 8c, it is clear that a level of four females per plant or less does not reduce the reproductive biomass.

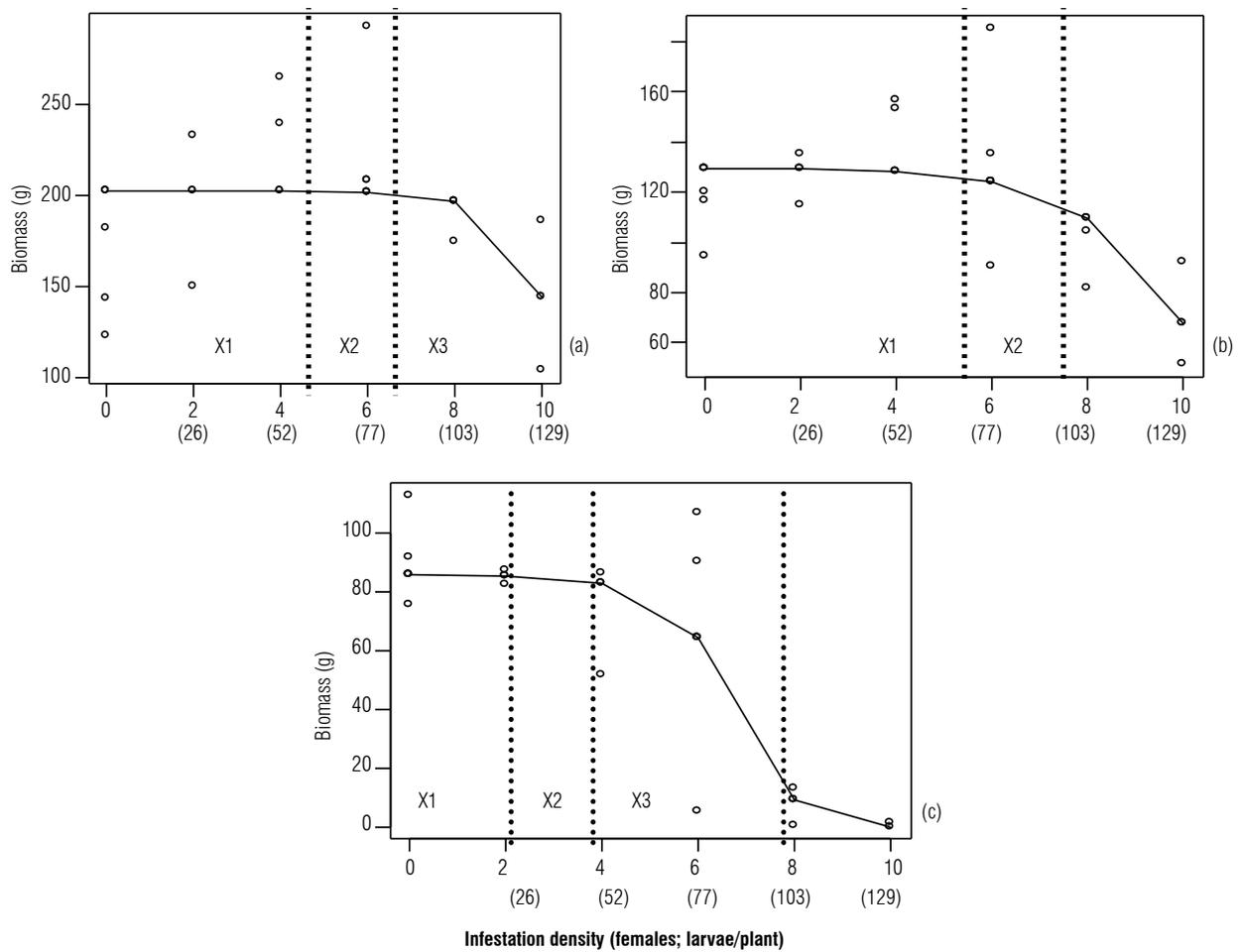
Both the total number of fruit as the number of healthy fruit are affected by the different infestation densities, as shown by probabilities associated to the F statistic for the linear regression models ( $F_{1,4} = 40.5 p = 0.0031$  y  $F_{1,4}=409.5 p = 3.52 \cdot 10^{-05}$ , respectively). When observing the behavior



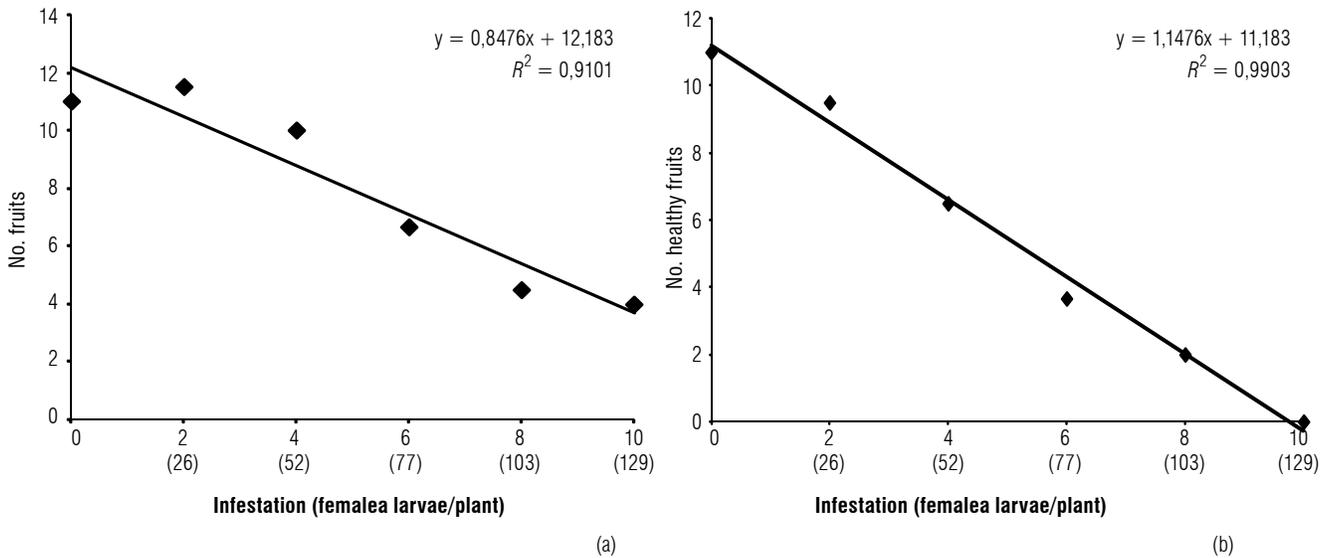
**FIGURA 5.** Effect of different densities of infestation with *T. absoluta* on the number of visible internodes (a), height (cm) (b), number of leaves (c) and number of leaflets (d) of greenhouse tomato plants and damage levels X<sub>2</sub>= Compensation, X<sub>3</sub>= Linearity.



**FIGURE 6.** Effect of different densities of infestation with *T. absoluta* on leaf area (cm<sup>2</sup>) (a) y total biomass accumulation of plants (g) of greenhouse tomato (b) and damage levels: X<sub>2a</sub>= Overcompensation y X<sub>3</sub>= Linearity.



**FIGURE 7.** Effect of different densities of infestation with *T. absoluta* on the biomass greenhouse tomato plants (a) leaves, (b) stems and (c) flowers and fruits, and levels of damage X1 = tolerance, X2 = compensation, X3 = linearity, X4 = desensitización.



**FIGURE 8.** Effect of different densities of infestation with *T. absoluta* on the total number of fruits (a) and number of healthy fruits (b) produced by greenhouse tomato plants and levels of damage X3 = linearity.

of the variables and those corresponding to regression model (Fig. 8), a linear reduction can be seen (X3) for the whole range of densities of females evaluated. This implies the nonexistence of the tolerance and compensation phases for these two variables. Thereby, there is an important reduction of the number of healthy fruit and the total number of fruit, even from the lowest density, corresponding to two females per plant, equivalent to 26 larvae/ plant. Note that even though the effect of the plague on the fruit biomass takes place when there are 4 females/plant, the effect on the number of fruit occurs as of 2 females/plant. Taking into account that for farmers, the perforated fruit imply losses even if the weight and size are appropriate, it may be concluded that densities of 2 females/plant onwards, imply an important loss in terms of production, even when there is no effect on the weight of the fruit and the plant's vegetative growth variables.

### Determination of levels of damage

According to the model by Pedigo (2006), the phases of the plant's response curve regarding the damage caused by a given density of plague insects, can be identified. Specific areas of this curve could be distinguished according to the rate of response of each of the variables evaluated when there is damage by *T. absoluta*.

The model fitted to the results for each of the variables permitted establishing the different phases on the damage curve (Tab. 2). The infestation density in which there is the maximum rate of damage ( $\gamma$  in the Gompertz model) is not the same for all the growth and development variables evaluated because the plague attacks the plant during all its stages of development, damaging stems, apical meristems, mining foliage; besides affecting flowers and fruit (Siqueira *et al.*, 2000).

The vegetative variables evaluated present a significant reduction with high densities of the insect, as evidenced

by the maximum attack rates between 10 and 13 females/plant. On the contrary, low levels of infestation caused evident damage to the reproductive part, where there is an important weight reduction of fruit when there are four or more females per plant. Although the most sensitive variables were the total number of fruit and the number of healthy fruit, where there is important damage when 2 females/plant are present. Hence, the control strategies implemented must lead to a plague density not surpassing two females per plant or 26 larvae/plant.

### Conclusions

In the variables of height, number of leaves, number of leaflets, and number of internodes there is a compensation effect in which the damage is minimal with up to 2 females/plant and even maintains a low level with 4 females/plant. For foliar area and total biomass, there is an overcompensation effect, presenting important damage levels with six or more females per plant.

From a density of 2 females/plant or 26 larvae/plant *T. absoluta*, there is a considerable production decrease expressed in terms of total number of fruit and healthy fruit per plant.

The curves for damage caused by *T. absoluta* present important differences depending on if the damage is direct or indirect. The variables quantifying vegetative growth were affected by insect densities much higher to those required to cause important damage in reproductive growth. This implies that there could be important losses related to the effect of the perforated fruit, although in the crop a negative effect on the plant vegetative growth may not be evident.

### Acknowledgements

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**TABLE 2.** Densities of *T. absoluta* to identify which stages of the damage curve of Pedigo (2006) obtained from the model fitted to each variable evaluated, females (larvae) per plant.

Variable	Tolerance (X <sub>1</sub> )	Overcompensation (X <sub>2a</sub> )	Compensation (X <sub>2</sub> )	Linearity (X <sub>3</sub> )	Desensitization (X <sub>4</sub> )
Height	_____	_____	0-2 (0-26)	2 (26)	>10 (>129)
No. leaves	_____	_____	0-2 (0-26)	2 (26)	> 10 (>129)
No. leaflets	0-2 (0-26)	_____	0-2 (0-26)	2 (26)	> 10 (>129)
Total biomass	_____	0-4 (0-52)	4-6 (52-77)	6 (77)	> 10 (>129)
Fruit biomass	0-2 (0-26)	_____	2-4 (26-52)	4-8 (52-77)	8 (103)
No. fruits	_____	_____	_____	<2 (<26)	
No. healthy fruit	_____	_____	_____	<2(<26)	
Leaf area	_____	0-4 (0-52)	4-6 (52-77)	6 (77)	> 10 (>129)

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