

Preference and Performance of the Tomato Leafminer, *Tuta absoluta* (Lepidoptera - Gelechiidae) Towards Three Solanaceous Host Plant Species

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Received: 03 July 2018

Published: 17 July 2018

Keywords: *Ovipositional Preference; Development; Performance; T. absoluta*

Abstract

The tomato leaf-miner, *Tuta absoluta* Meyrick (Lepidoptera - Gelechiidae), is a widespread insect develops on many important solanaceous crops. The preference and performance of its host range could help in understanding and preventing the dispersion behavior of this pest in the environment. A choice experiment with whole plants was conducted with three selected hosts: tomato (*Lycopersicon esculentum* Mill), potato (*Solanum tuberosum* L.), eggplant (*Solanum melongena* L.) to examine adult ovipositional preference. *T. absoluta* performances taking into consideration larval, pupal and adult development and survival parameters were conducted. The females preferred tomato to lay their eggs in the triple- or dual-choice experiments. Also, performance of larvae showed growth preference with tomato plants. Survivorship of larvae, pupae and adults with tomato plants was also the most profound. A significant correlation was obtained between the ovipositional preference and fitness levels (performance) of larvae, pupae and adults.

This study indicates high ovipositional preference was correlated with short developmental times and high survival rates of *T. absoluta* which may relate to a suitable food quality.

Introduction

The tomato leafminer, *Tuta absoluta* (Meyric) (Lepidoptera - Gelechiidae) is a pest of great economic importance in a number of countries. Its primary host is tomato although potato, egg-plant, common weed and various wild solanaceous plants are also suitable hosts [1,2]. It is known to be a devastating pest of tomato originating from South America and has now invaded various European countries and dispersed throughout the Mediterranean basin [3].

Little is known about the trophic relationship between *T. absoluta* and its potential host-plants other than tomato. Different patterns of host-plants used by insect pests are related to differences in physiology, morphology, chemical and physical defenses of the plants, with subsequently differences in the insect life history traits [1,4].

Quality and quantity of food consumed by herbivores insects affect growth, survival and fecundity of individuals; and hence their population improvement [5]. Host plant choice is important for fitness of Lepidoptera [6]. The neonate larvae of many species are unable to move to an alternative food source and are dependent on their mother's choices. Classically females are attracted to the odor blends released by plants which signal oviposition site and so larval food sources [7,8,9]. Consequently, insect management strategies based on preference and performance of host plants involve the development of cultivars that have enhanced direct or indirect defense mechanisms [10], the use of polyculture [11], or the extraction of plant volatiles to develop products that lure insects [12].

The objective of this study was firstly studying the ovipositional preference of *T. absoluta* female towards the three different solanaceous plant cultivars. Secondly, evaluating the relative preference affects the performance of *T. absoluta* life stages on the three solanaceous hosts which are tomato (*Lycopersicon esculentum* Mill), potato (*Solanum tuberosum* L.) and eggplant (*Solanum melongena* L.).

Materials and Methods

The Insect Rearing

The tomato leaf-miner, *T. absoluta* colony was established as larvae collected from tomato growers at EL-Natron Valley area (30° 30' 26" N, 13° 30' 03" E). Collected larvae were reared on tomato leaves, fresh leaves were provided daily till pupation. Emerging moths were sexed, 15 pairs of both sexes of the moth were kept inside a plastic oviposition container (25 x 15 x 10 cm) sealed at the top with a fine mesh net and provided by small foliage of tomato for oviposition. After 24 h, the eggs laid were collected and divided into three groups. Within the group, each egg was transferred into 10 cm-Petri dish.

Fresh host plant leaves (tomato, potato or eggplant) were provided for larval feeding in dishes and were replaced every other day. The fourth instar larvae were transferred into small plastic tubes (3 cm diameter, 6 cm depth) for pupation.

Experiments have conducted after rearing *T. absoluta* for three generations. The insect colony and the experiments were conducted in a greenhouse (3 x 4 x 2 m) greenhouse equipped with a drip irrigation system located at Biological Control Department, Agricultural Research Center, Giza. The laboratory conditions during the experiments were: an average temperature of $25\pm 3^{\circ}\text{C}$; relative humidity ranging from 70% to 85% and a photoperiod of 14:10 h (L: D).

The Host Plants

Seeds of tomato, eggplant and tubers of potato were cultivated in a greenhouse condition and in seedling trays containing peat moss until the growth of the first leaves. Thereafter, the seedling were transferred to 5 L pots (one plant/pot) containing the main substrate of the greenhouse. The plants were fertilized firstly with cattle manure and after two weeks a mixture of ammonium sulfate and potassium chloride (3:1) were used weekly to fertilize the plants. Other cultural practices, such as staking and irrigation, were performed daily throughout the plant developmental area. The experimental design was completely run with 30-45-day-old plants.

Effect of the host plants on some biological aspects of *T. absoluta*

Oviposition Preference of T. absoluta Towards Host Plants

Two flying tunnel types; three arms-tunnels (Figure 1) and two arms-tunnels (Figure 2) were used to study the oviposition preferences of *T. absoluta* towards different solanaceous plants (tomato, potato and eggplant). Both three-choice and dual-choice oviposition tests were conducted. The flying tunnel consists of three or two arms and central area. Each arm has length \times width \times high of $90 \times 60 \times 60$ cm. The central zone ($40 \times 60 \times 60$ cm) has an open up hole for insect release. Each tunnel arm has an open hole (20×20 cm) to facilitate the air follow. The flying tunnels were made from the transparent glass to facilitate light pass. Each tunnel arm hole is coated with a thin mesh that allows the air to pass and prevents the exit of the female moth. Three-day-old females were used in this experiment after they allowed mating with males.

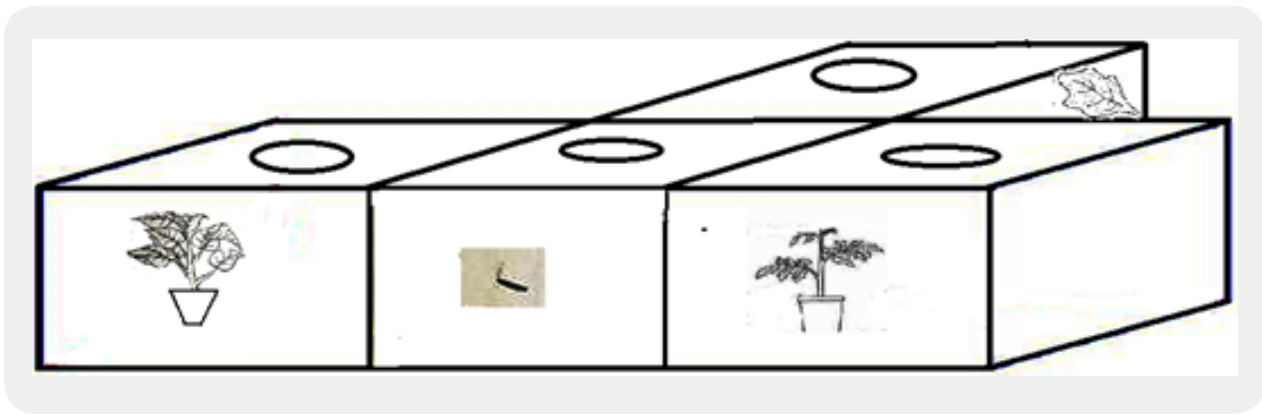


Figure 1: *Three arms flying tunnel*

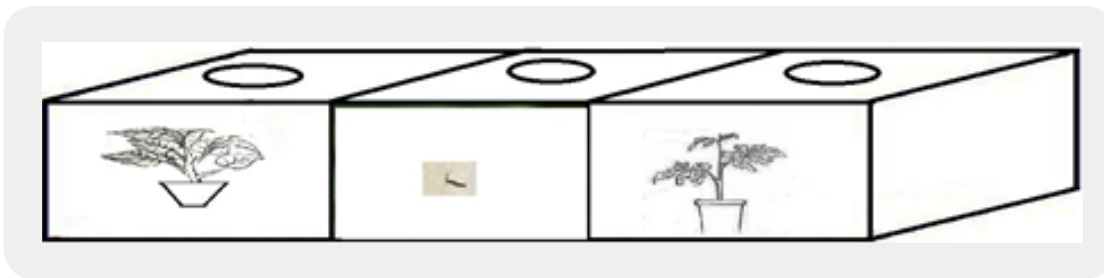


Figure 2: *Two arms flying tunnel*

At the beginning of the experiment, the plants (4-week-old) were put in the arms (one plant in each arm). The three and two different host plants were used in the triple and dual choice experiments, respectively. The female was released through the central zone hole and allowed to choose its oviposition site (host plant) for 24h, and then the number of eggs laid on each host plant was counted. The position of host plant in the arm site was reciprocal changed. Both the host plant and so the female moth were used only once. Fifteen females (emerged from larvae fed on tomato, potato or eggplant in an equal numbers) were used for each experiment.

Eggs, Larval and Pupal Survival and Developmental Assessment

Three generations of *T. absoluta* were reared on each of the selected host plants (tomato, potato or eggplant) before beginning of the experiments. Adults of the third generation were transferred to ovipositional cylinders containing fresh leaves of host plant and a thin layer of 10% honey on pepper ribbons. Eggs were collected daily with a moistened brush and kept individually in Petri dishes lined with moistened filter paper to establish the experimental colony for each host plant species. Eggs laid on the same day were placed individually into separate Petri dishes (4 cm diameter) containing host plant leaves (tomato, potato or eggplant). Thirty eggs per host plant were used. Fresh foliage was provided for newly emerged larvae and observed daily till pupation and adult emergence.

Insect individuals were checked daily for development and survival. Egg incubation periods (days), egg hatching (%), larval developmental periods (days) and pupal periods (days) were recorded. Survival rate for each stage was also recorded.

Adult Longevity

Newly emerged adults (one male and one female) were transferred into wooden rearing cage (30×30×20 cm) lined with tulle and containing host plant foliage (tomato, potato or eggplant) and fed on 10% sucrose solution. Fresh foliage was provided as ovipositional medium. Adult's longevity was recorded daily.

Statistical Analysis

Variables were first tested for normality before analysis. Data are presented as mean ± SEM and analyzed by one-way analysis of variance (ANOVA) followed by comparison of the means with Tukey test at $\alpha = 0.05$. Furthermore, a paired t-test was performed to detect the relation between ovipositional preference and developmental performance on various host plants using software Graphpad Instat (2009) [13].

Results

Oviposition Preference of *T. absoluta* Female Towards Different Host Plants

The number of eggs deposited by *T. absoluta* females on each of the three plant species (tomato, potato and eggplant) in the three-choice or dual-choice tests indicated a strong oviposition preference for tomato plants. Each female laid 8.50 ± 0.51 eggs/day (66.6%) on tomato plants in comparison with 2.66 ± 0.45 eggs/day (20.8%) on potato plants and 1.60 ± 0.25 eggs/day (12.5%) on eggplant as shown in table (1) and figure (3). Statistically, in the three-choice test, *T. absoluta* female significantly preferred tomato plants for egg deposition than potato and eggplant ($F_{(2,42)} = 79.34$; $P = 0.043$). In the dual choice test including tomato compared with potato, tomato compared with eggplant and potato compared with eggplant, the females of *T. absoluta* preferred tomato plant over potato or eggplant. They laid 10.07 ± 0.68 eggs/day (79.5%) on tomato plants compared with 2.60 ± 0.49 eggs/day (20.5%) on potato plants. Statistically significant differences ($t = 8.82$; $df = 28$; $P < 0.0001$) were obtained as shown in table (2) and figure (4). Percentage deposited eggs on tomato plant was increased to 91.23% with mean egg numbers of 10.40 ± 0.64 eggs/day when the dual-choice experiment included tomato and eggplant as shown in table (3) and figure (5). The females significantly preferred tomato to oviposition than eggplant ($t = 12.78$; $df = 28$; $P < 0.0001$). When females exposed to potato and eggplant in a dual-choice test, they preferred potato for oviposition than eggplant with a percentage of 81.67 % and a mean number of 8.60 ± 0.46 eggs/day as shown in table (4) and figure (6). Statistically, *T. absoluta* female significantly preferred potato for oviposition compared to eggplant ($t = 11.50$; $df = 28$; $P < 0.0001$).

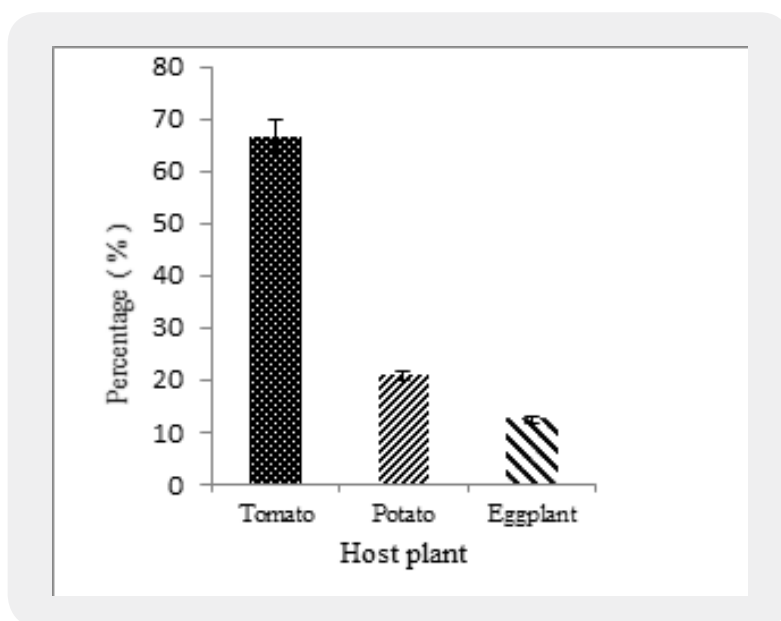


Figure 3: Ovipositional preference (%) of *T. absoluta* towards host plants (three-choice)

Table 1: Ovipositional preference of *T. absoluta* towards host plants (three-choice)

Host plant	No. of eggs (Mean±SE)
Tomato	8.50±0.51 a
Potato	2.66±0.45 b
Eggplant	1.60±0.25 b
F	79.34
df	2,42
P-value	0.043

-Means followed by the same letter, in the same column, are not significantly different ($P>0.05$).

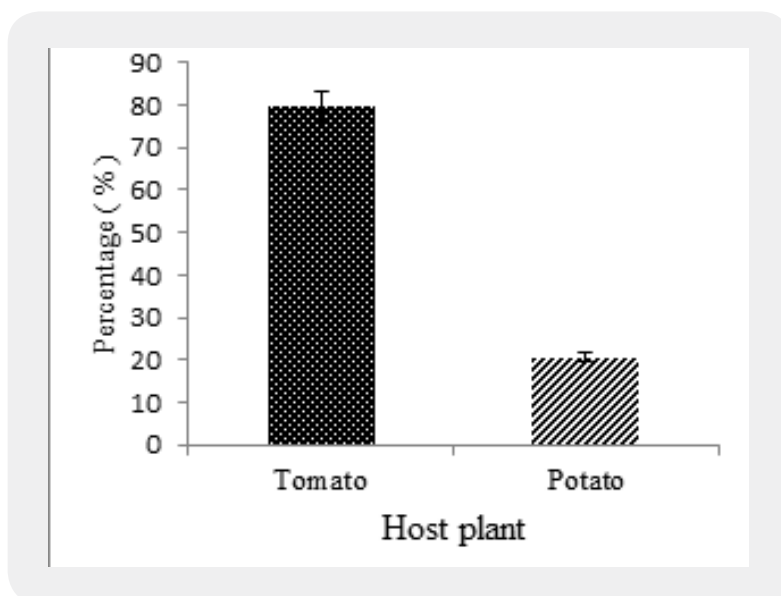


Figure 4: Ovipositional preference (%) of *T. absoluta* towards tomato and potato plants (dual-choice)

Table 2: Ovipositional preference of *T. absoluta* towards tomato and potato plants (dual-choice)

Host plant	No. of eggs (Mean±SE)
Tomato	10.07±0.68a
Potato	2.60±0.49b
t-value	8.82
df	28
P-value	P < 0.0001

-Means followed by the same letter, in the same column, are not significantly different ($P > 0.05$).

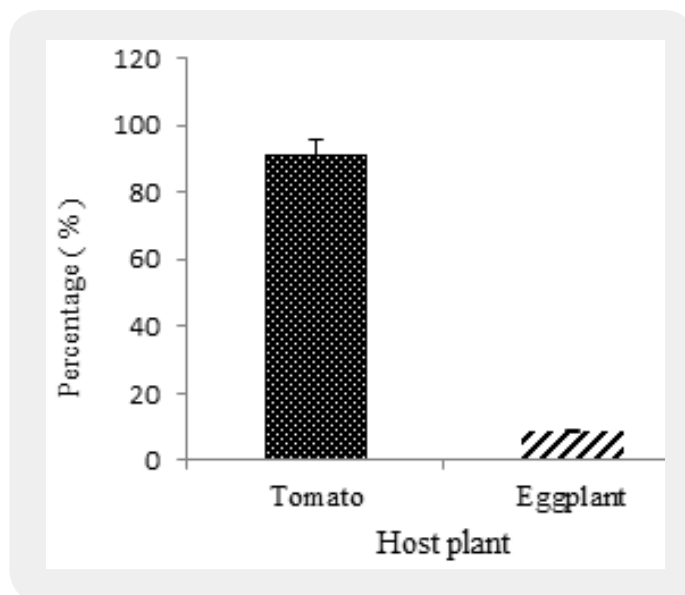


Figure 5: Ovipositional preference (%) of *T. absoluta* towards tomato and eggplant (dual-choice)

Table 3: Ovipositional preference of *T. absoluta* towards tomato and eggplant (dual-choice)

Host plant	No. of eggs (Mean±SE)
Tomato	10.40±0.64a
Eggplant	1.0±0.37b
t-value	12.78
df	28
P-value	P < 0.0001

-Means followed by the same letter, in the same column, are not significantly different (P>0.05).

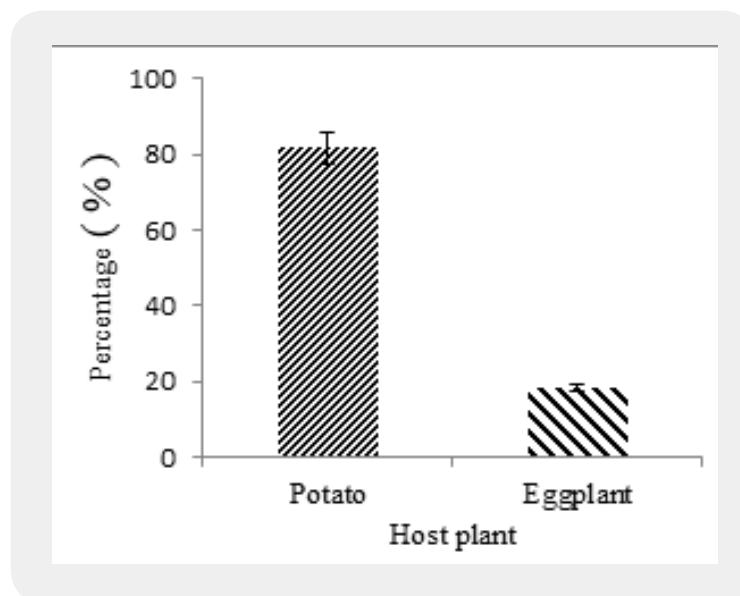


Figure 6: Ovipositional preference (%) of *T. absoluta* towards potato and eggplant (dual-choice)

Table 4: Ovipositional preference of *T. absoluta* towards potato and eggplant (dual-choice)

Host plant	No. of eggs (Mean±SE)
Potato	8.60±0.46a
Eggplant	1.93±0.34b
t-value	11.50
Df	28
P-value	P < 0.0001

-Means followed by the same letter, in the same column, are not significantly different ($P > 0.05$).

Performance Development of *T. absoluta* On the Host Plants

Table (5) shows the duration of different immature stages and total developmental time of *T. absoluta* reared on tomato, potato and eggplant leaves. The incubation periods of eggs ranged from 5.22 ± 0.09 to 5.25 ± 0.09 days. Statistically, no significant difference was found among the three host plants regarding egg durations ($F_{(2,87)} = 0.29$; $P = 0.74$). The differences in the duration periods were obtained considering larvae fed on tomato leaves and those fed on potato or eggplant leaves. The mean duration period of the larvae that fed on tomato leaves was 10.83 ± 0.18 days in comparison with 13.30 ± 0.31 and 13.13 ± 0.33 days in the case of larvae fed on potato and eggplant leaves, respectively. Statistically, significant difference was obtained between the duration of larvae fed on tomato leaves and those fed on potato or eggplant leaves ($F(2,87) = 24.05$; $P < 0.0001$). The same significant differences were obtained considering durations of pupae obtained from larvae fed on tomato, potato or eggplant leaves (Table 5).

The total developmental period of larvae fed on tomato leaves was the minimum (24.45 ± 0.25 days) in comparison with those fed on potato (28.38 ± 0.33 days) or eggplant (28.69 ± 0.30 days). Larvae fed on potato or eggplant leaves developed approximately slower 3-4 days than those fed on tomato. Statistically, significant difference was obtained in comparison the total developmental period of *T. absoluta* larvae fed on tomato and those fed on potato or eggplant ($F_{(2,70)} = 67.3$; $P < 0.0001$)

Table 5: Developmental periods of T. absoluta fed on different host plants

Host plant	Developmental period (Mean± SE) days			
	Pupa	Larva	Egg	Total developmental period
Tomato	5.25±0.99 a	10.83±0.18 a	8.37±0.16 a	24.45±0.25 a
Potato	5.23±0.09a	13.30±0.31 b	9.76±0.16 b	28.38±0.33 b
Eggplant	5.22±0.09 a	13.13±0.33 b	10.34±0.19c	28.69±0.30 b
F (df)	0.29 (2,87)	24.05 (2,87)	36.26 (2,70)	67.3 (2,70)
P-value	0.74	<0.0001	<0.0001	< 0.0001

-Means followed by the same letter, in the same column, are not significantly different ($P > 0.05$).

Effect of Host Plants On the Age-Specific Survival

The survival rate (l_x) of *T. absoluta* reared on tomato, potato or eggplant leaves is shown in figure (7) and table (6). The survival of the egg stage was 100 % for *T. absoluta* fed on tomato, potato or eggplant. The highest survival rate of immature stages was obtained with larvae fed on tomato leaves (86.7 %) while survival rates of 83.4 % and 80.1 % were obtained for larvae fed on potato and eggplant leaves, respectively. Age-specific mortality revealed that 13.3 %, 13.3 % and 16.6 % mortality was obtained for larvae fed on tomato, potato and eggplant, respectively. On the other hand, age-stage mortality of pupae of resulting from larvae fed on potato or eggplant was 3.3 % while no pupal mortality (0 %) was obtained for pupae resulting from larvae fed on tomato.

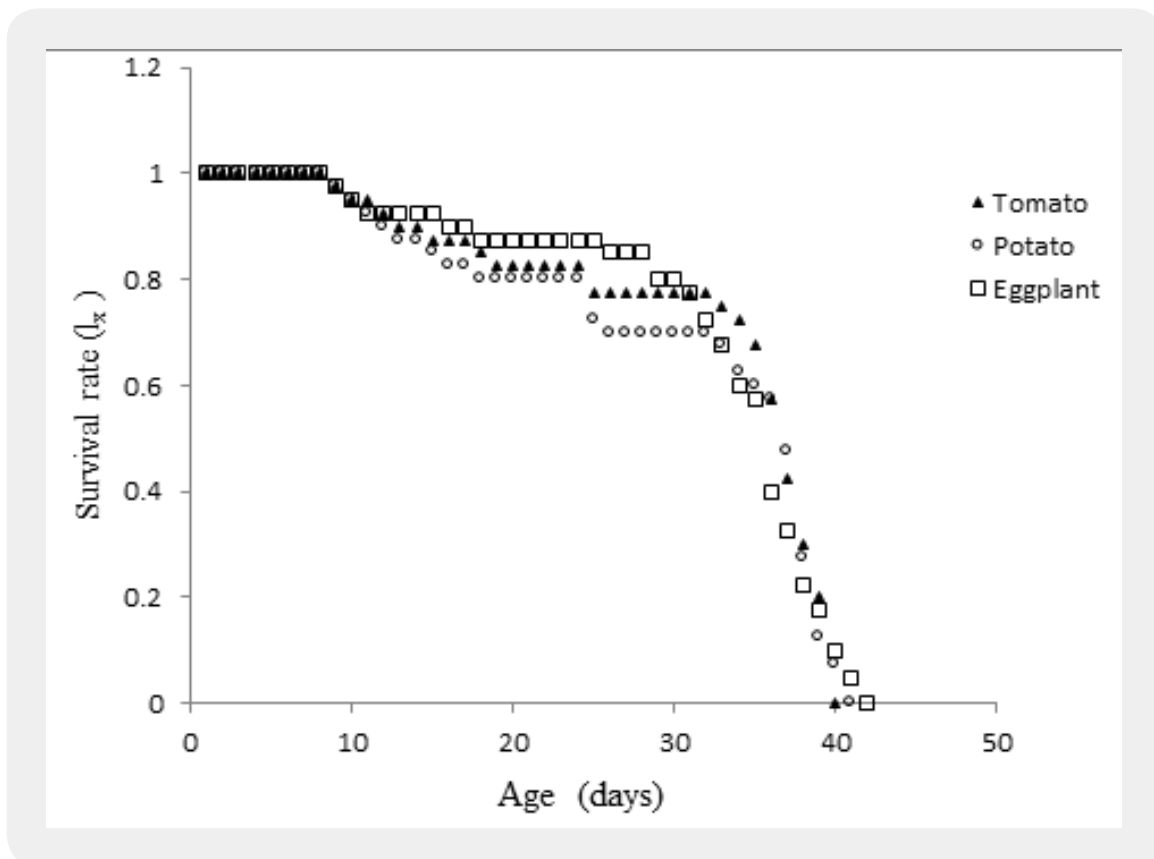


Figure 7: Effect of host plants on the age-specific survivorship (l_x) of *T. absoluta*

Table 6: Age-specific mortality of T. absoluta fed on different host plants

Age stage (x)	Host plant	Number alive at begging of x(l _x)	Number dying during (x)	% mortality (100q _x)	% cumulative surviving (100r _x)
Egg	Tomato	30	0	0	100
	Potato	30	0	0	100
	Eggplant	30	0	0	100
Larva	Tomato	30	4	13.3	86.7
	Potato	30	4	13.3	86.7
	Eggplant	30	5	16.6	83.4
Pupa	Tomato	26	0	0	86.7
	Potato	26	1	3.3	83.4
	Eggplant	25	1	3.3	80.1
Adult	Tomato	26			86.7
	Potato	25			83.4
	Eggplant	24			80.1

x = developmental stage; l_x = number entering stage; 100q_x = percent apparent mortality; 100r_x = percent cumulative surviving.

Effect of Host Plants On the Adult Longevity

T. absoluta adult moths emerged from larvae fed on different host plants showed different life spans as shown in table (7). Both sexes emerged from larvae reared on tomato leaves lived longer than those emerged from larvae reared on potato or eggplant leaves. Life span of females resulting from tomato-fed larvae was 13.78±0.17 days in comparison with 12.29±0.16 days and 11.47±0.21 days for female moths resulting from larvae fed on potato or eggplant, respectively. Statistically, significant difference ($F_{(2,37)} = 42.68$; $P < 0.0001$) was obtained in comparison the life span of females emerged from tomato-fed larvae and those emerged from potato- or eggplant-fed larvae. Males resulting from tomato-fed larvae had longer life span (10.35±0.17 days) in comparison with those emerged from potato (9.43±0.20) days and eggplant-fed larvae (10.13±0.25) days. Statistically, significant difference was obtained considering life span of males resulting from tomato, eggplant and potato-fed larvae, respectively ($F_{(2,33)} = 5.6$; $P = 0.008$).

Table 7: Life span of *T. absoluta* fed on different host plants

Host plant	Life span (days)	
	Males	Females
	Mean ± SE	Mean ± SE
Tomato	10.35±0.17a	13.78±0.17a
Potato	9.43±0.20b	12.29±0.16b
Eggplant	10.13±0.25ab	11.47±0.21c
F (df)	5.6 (2,33)	42.68 (2,37)
P-value	0.008	< 0.0001

-Means followed by the same letter, in the same column, are not significantly different ($P>0.05$).

Correlation of *T. absoluta* Ovipositional Preference and Performance

Ovipositional preference and performance of *T. absoluta* correlated significantly among host plants. Most eggs were laid on tomato, whereas the least on eggplant. Correlation of ovipositional preference with developmental period, survival and female life span is shown in table (8). Significant correlations were obtained between oviposition preference and developmental time ($t = 6.53$; $p = 0.022$), survival ($t = 12.78$; 0.006) and female life span ($t = 5.54$; $p = 0.03$).

Table 8: Correlation of *T. absoluta*-ovipositional preference with its performance towards the three host plants (tomato, potato and eggplant)

Parameters	t	R	p-value
Developmental period	6.53	- 0.997	0.022
Survival	12.78	0.988	0.006
Female life span	5.54	0.977	0.03
Male life span	2.86	0.574	0.11

Discussion

Many plants belonging to family Solanaceae have been cited as host-plants for *T. absoluta* [14], however studies regarding their suitability to insects are lacking. According to the present investigation, *T. absoluta* is developed almost on tomato and at the same time it could develop and grow, but with lower rate, on potato and eggplant. The availability of alternative host plants is an important factor that allows the sustainability of the pest in the absence of the primary host (tomato). This capacity must be carefully considered with integrated control strategies. Our study showed that tomato is a more suitable host-plant than potato or eggplant.

The ovipositional choice of female *T. absoluta* was host plant species-dependent. According to Awmack and Leather (2002) [15] and Gripenberg *et al.* (2010) [16] lepidopteran larval survivability depends on the females' oviposition choice because most of them are unable to move to an alternative food source. Ovipositional preference experiments showed that *T. absoluta* more preferred tomato plant than potato and eggplant. Also, potato was more preferred by the female than eggplant. The study of Proffit *et al.* (2011) [17] indicated that the attraction and oviposition of female *T. absoluta* are mediated by the volatile signature of their host plant. Also, they elucidated that tomato leaf odors mainly include volatile terpenoid compounds which elicit in mated females upwind orientation flight followed by landing as well as egg-laying. In the current study, previous feeding experience of the larvae did not influence host acceptance (adult oviposition), because tomato-, potato- and eggplant- reared larvae could not affect the ovipositional preference of the female which preferred tomato's plant. This finding may agree with that of Capparos Megido *et al.* (2014) [18] as they reported that during oviposition, females are exposed to a variety of cues, including plant volatiles, contact chemicals, and visual signals, which help in determining the characteristics of the plant. Consequently, the host plant experience, have little effect on the adult ovipositional preference. Oviposition on a suitable host in response to plant cues is of major importance for an insect to maximize its fitness [19].

In our study the less developmental time and high survival rate of *T. absoluta* fed on tomato compared to those fed on potato or eggplant seem likely to be attributed to high nutritional quality of tomato. Slansky (1993) [20] concluded that quality and quantity of food consumed by herbivore insects affect the growth, survival and fecundity of individuals and hence their population improvement.

Although marginally statistical differences between tomato and the two other plants (potato and eggplant) were observed, *T. absoluta* successively developed on potato and eggplant. Preference and performance parameters obtained from cohorts of *T. absoluta* reared on tomato, potato and eggplant under laboratory conditions are useful for the assessment of biotic potential of this pest. Sanchez and Pereyra (1995) reported that demographic parameters obtained from cohorts reared on different host plants under laboratory conditions are useful for assessment of the biotic potential of an insect facing a new food and for the evaluation of the host-plant quality.

Plant species differ greatly in suitability as hosts for specific insects when assessed in terms of survival, development and reproductive rate. Shorter developmental time along with greater total reproduction of insects on a host indicate greater suitability of a host plant [21]. High survival rates, short development times and high fecundity rated (number of eggs per female) of herbivorous insects are all related to a suitable food quality [14,22].

The present study demonstrated the relationship between adult oviposition preference and offspring performance. It is obvious that *T. absoluta* female prefers to oviposit on tomato that suitable for survival and development of its offspring compared to potato and eggplant. Tomato plants can be used as trap plants on field edges of potato or eggplant in developing IPM strategies for the control of *T. absoluta*.

Authors' contribution

AY and NZMZ conceived and designed the research. HAA and RF conducted the experiments. AY and RF analyzed the data and wrote the manuscript. AY and NZMZ made critical reviewed and approved the final version. All authors reviewed and approved the final manuscript.

Acknowledgment

The authors would like to thank Prof. Dr. Sayed Shaurub; the head of the Entomology Department, Faculty of Science, Cairo University. His help and guidance had the greatest impact in completing this work.

Conflict of Interest

The authors declare that they have no conflict of interest.

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