

Suitability of Five Tomato Cultivars for *Tuta absoluta* (Lepidoptera: Gelechiidae): Resistance Is Associated with a High Density of Glandular Trichomes

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ABSTRACT

The Tomato Leaf Miner (TLM), *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), is a cosmopolitan tomato pest that has driven a renewed reliance on pesticides in tomato production, negatively affecting biological control of other pests and creating environmental and health hazards. We tested five locally important Iranian tomato cultivars (TD, Karon, Petoprid, Matin, and 8320) for constitutive resistance to TLM by comparing its biological performance and life table parameters under standardized laboratory conditions (27.5±1°C, 65±5% RH, 16 L:8 D hours photoperiod). Survival and developmental rates of immature stages varied significantly among cultivars, as did female fecundity and main parameters of the life table. Karon was most susceptible, affording 90% juvenile TLM survival, the fastest development, and the highest female fecundity, with cultivar 8320 not significantly different in these regards. By contrast, Matin ranked most resistant; i.e. only 59% of larvae survived, and female fecundity was almost halved. TD was the next most resistant, being not significantly different from Matin in these metrics. The intrinsic rates of increase (*r*), in descending order, were Karon (0.178), 8320 (0.169), TD (0.146), Petoprid (0.138), and Matin (0.111). Matin and TD had the highest densities of glandular trichomes on adaxial leaf surfaces. These findings indicate that the Matin, Petoprid and TD are more resistant than the other cultivars and have potential as one component of an IPM strategy to manage *T. absoluta*.

Keywords: Antibiosis, Host plant resistance, Life tables, *Lycopersicon esculentum*, Tomato leaf miner.

INTRODUCTION

The Tomato Leaf Miner (TLM), *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), is native to South America (Desneux *et al.*, 2010; Guedes *et al.*, 2019), but has become a major invasive pest of tomatoes worldwide. Although potato, pepper, eggplant and many solanaceous weeds can serve as host plants, tomato is a preferred host and may sustain 80-100% yield loss under

heavy infestation (Desneux *et al.*, 2010; Desneux *et al.*, 2011). Over the past 10 years, tomato-producing regions of the world infested with TLM have increased from 3% to 60%; and although three major regions, namely, the USA, China, and Mexico, remain unaffected, they are at high risk of invasion (Biondi *et al.*, 2018). Chemical insecticides are frequently required to prevent yield loss when tomatoes are infested with TLM, and reliance on insecticides has led to the evolution of TLM resistance to various insecticide groups

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(Roditakis *et al.*, 2018; Guedes *et al.*, 2019). Environmental pollution, non-target effects on natural enemies, and the emergence of secondary pests are among the various undesirable side effects of reliance on chemical pesticides. Identification of resistant cultivars, with antibiotic traits toward TLM, could contribute to an ecologically-based pest management program that would be compatible with biological control, while simultaneously reducing reliance on harmful insecticides.

Herbivorous insects face various plant defense mechanisms when they consume plant tissues to obtain essential nutrients, and manipulation of host plant resistance traits can be an important component of an integrated pest management strategy (Price, 1986; Schoonhoven *et al.*, 2005). The population growth of *T. absoluta* has been compared among tomato cultivars and other solanaceous plants in order to identify TLM-resistant traits in cultivars suited to particular localities (Gharekhani and Salek-Ebrahimi, 2014; Ghaderi *et al.*, 2017; Rostami *et al.*, 2017; Younes *et al.*, 2019). Resistance to TLM may be due to antibiotic traits that are constitutively expressed in the uninfested plant, or by physiological responses induced by TLM-infestation (Han *et al.*, 2019). The glandular trichomes of tomato plants not only cause a physical barrier against pest but also produce specific defensive compounds that can provide some resistance to TLM via antibiotic effects on oviposition, larval development, and immature survival (Sohrabi *et al.*, 2016, 2017). In certain tomato cultivars, TLM infestation can elicit the production and release of herbivore-induced plant volatiles that attract TLM natural enemies such as predatory mirid bugs (De Backer *et al.*, 2015; Naselli *et al.*, 2017). Thus, identification of constitutive TLM-resistance traits, fortuitously present in a selection of commercially important local cultivars, can be a valuable preliminary step in developing an integrated program for TLM management.

Life tables summarize population demographic parameters and can be useful for quantitative assessment of interactions

between herbivorous arthropods and their host plants (Maia *et al.*, 2014). We constructed life tables for TLM when reared on five commercial Iranian tomato cultivars (TD, Karon, Petoprid, Matin and 8320), selected because they are the most commonly grown cultivars in Bushehr Province, Iran. We hypothesized that cultivars would vary in their suitability for TLM immature survival, development, and population growth. The objective was to characterize variation in susceptibility to TLM and identify potential resistance traits that might be usefully exploited in an integrated pest management strategy for *T. absoluta* in Bushehr Province.

MATERIALS AND METHODS

Host Plants

Seeds of five common tomato cultivars (TD, Karon, Petoprid, Matin and 8320) were planted in seedling trays (30×60 cm) containing peat moss and perlite in greenhouse under controlled environmental conditions (25±3°C, 55±10% RH and 16 L:8 D hours photoperiod). Upon expansion of the first true leaves, seedlings were transplanted into plastic pots (30 cm diam) containing a sandy loam soil without any fertilizer. Initially 60 tomato pots were prepared for each cultivar and they were charged during the experiment if necessary. Leaves of tomato cultivars were used in the experiments, four weeks after transfer to the plastic pots.

Insect Colony

About 200 pairs of TLM adults were collected from tomato fields in the Borazjan region of Iran (GPS coordinates 29° 13' 14" N, 51° 14' 32" E) in November, 2019. The insects were held in metal-framed cages (120×100×80 cm) covered with fine gauze, 15-20 pairs of insects per cage, in a climate-controlled greenhouse set to 25±3°C,

55±10% RH and a 16 L:8 D hour photoperiod. To remove the effects of previous host, separate colonies of TLM were established in two cages for each of the five cultivars and reared for two generations before use in experiments.

Life Table Experiments

Twenty TLM adult pairs (< 5 days-old) were transferred to each of five ventilated plastic boxes (30×20×15 cm). Each box contained 10 excised young shoots (≈20 cm) of tomato for oviposition, their turgor maintained by balls of wet cotton on the cut ends. After 24 hours, adults were removed and boxes were placed in a climate-controlled growth chamber set to 27.5±1°C, 65±5% RH and a 16 L:8 D hour photoperiod. To determine the incubation period, 70 eggs of TLM were selected at random and monitored daily. Upon hatching, first instar larvae were each isolated in a small ventilated plastic box (10×7×5 cm) with a fresh leaf of related tomato cultivars. Leaf petioles were placed in a wet ball of cotton and fresh leaves were provided every other day. Larvae were observed daily for survival until they emerged as adults. To measure reproduction, pairs of emerged adults, each reared on the same cultivar, were established in small ventilated plastic boxes (10×7×5 cm) containing leaves of the same tomato cultivar, plus a cotton ball soaked in a 10% honey solution. All insects were checked daily and the number of eggs laid, oviposition period, and adult longevity was recorded for each female until she died. The data obtained were used to calculate life table parameters including net Reproductive rate (R_0), intrinsic rate of increase (r_m), finite rate of increase (λ), mean generation Time (T) and population Doubling Time (DT) based on the formulae of Carey (2001).

Assay of Leaf Trichome Density

We counted the density of type VI glandular trichome on the leaf surface of

each tomato cultivar (Bergau *et al.*, 2015; Sohrabi *et al.*, 2016, 2017), using five fully expanded leaves cut from the upper third of five tomato plants of each cultivar. The terminal leaflet was separated and its trichomes were counted on each of three one-cm² squares on both the adaxial and abaxial surfaces using a stereomicroscope (40X).

Statistical Analyses

Homogeneity of variance and normal distribution of data were confirmed using Levene's and Kolmogorov-Smirnov tests, respectively. All development and population growth parameters were subjected to one-way analysis of variance and means were separated using Foisger's LSD test when samples sizes were equal, and Bonferroni test when they were not ($\alpha=0.05$ in both cases) (SPSS, 2011). Pseudo-values of the life table parameters were estimated by the Jackknife method (Maia *et al.*, 2014) using R software (R CoreTeam, 2017).

RESULTS

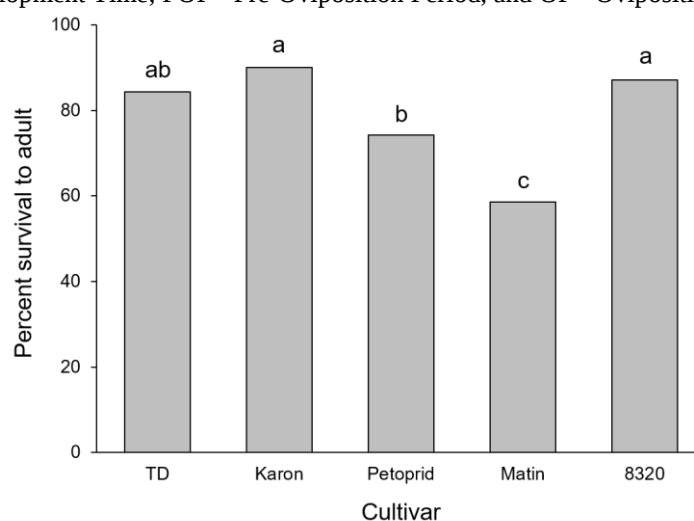
Life History

Immature survival was highest on Karon and cultivar 8320, and lowest on Matin, with other cultivars intermediate (Chi-square, $\alpha=0.05$, Figure 1). The duration of various immature stages and total development time varied with tomato cultivar (Table 1). Development was fastest on Karon and slowest on Matin, with other cultivars intermediate. The preoviposition period was unaffected by cultivar ($F=1.69$; $df=4,158$; $P=0.158$), and means did not separate, although the oviposition period did show significant variation (Bonferroni test, $\alpha=0.05$). The fecundity varied among cultivars ($F=6.53$; $df=4,109$; $P<0.001$) and was highest on Karon and cv. 8320, and lowest on TD and Matin, with Petoprid being

**Table 1.** Mean ($\pm$ SE) duration (in days) of immature stages, preoviposition and oviposition periods of *Tuta absoluta* when reared on five tomato cultivars.^a

Cultivar	Egg	Larva	Pupa	Total DT	POP	OP
TD	4.0 $\pm$ 0.02 a	8.4 $\pm$ 0.12 c	7.8 $\pm$ 0.18 a	20.3 $\pm$ 0.18 b	1.0 $\pm$ 0.18 a	6.7 $\pm$ 0.40 a
Karon	2.5 $\pm$ 0.06 c	9.0 $\pm$ 0.17 bc	7.3 $\pm$ 0.18 abc	18.9 $\pm$ 0.28 c	0.9 $\pm$ 0.18 a	9.4 $\pm$ 0.84 a
Petoprid	3.6 $\pm$ 0.49 b	9.7 $\pm$ 0.24 ab	7.1 $\pm$ 0.16 bc	20.5 $\pm$ 0.26 b	1.5 $\pm$ 0.36 a	7.5 $\pm$ 0.75 a
Matin	3.9 $\pm$ 0.32 a	10.2 $\pm$ 0.22 a	7.6 $\pm$ 0.22 ab	21.6 $\pm$ 0.31 a	1.8 $\pm$ 0.72 a	6.8 $\pm$ 0.90 a
8320	3.4 $\pm$ 0.50 b	9.3 $\pm$ 0.13 b	6.9 $\pm$ 0.16 c	19.6 $\pm$ 0.24 bc	0.8 $\pm$ 0.15 a	8.9 $\pm$ 0.83 a
<i>F</i>	126.46	13.90	4.53	15.01	1.688	2.610
<i>df</i>	4,345	4,286	4,251	4,251	4,109	4,109
<i>P</i>	< 0.001	< 0.001	0.002	< 0.001	0.158	0.039

^a Means bearing the same letter are not significantly different within columns (Bonferroni, $\alpha = 0.05$). Total DT= Totl Development Time; POP= Pre-Oviposition Period, and OP= Oviposition Period.

**Figure 1.** Juvenile survival of *Tuta absoluta* when reared on five different tomato cultivars. Columns bearing different letters are significantly different (Chi-square, $\alpha = 0.05$).

intermediate (Figure 2). Female longevity was significantly shorter on TD (10.6 $\pm$ 0.5 days), with other cultivars not significantly different from one another (Overall mean= 12.8 $\pm$ 0.5 days; $F = 2.75$; $df = 4,109$; $P = 0.032$).

Life Table Parameters

Tuta absoluta age-specific survival rates (l_x) and fecundities (m_x) were plotted for each cultivar; and revealed high mortality for early instar larvae on Petoprid and Matin (Figure 3). Oviposition peaked about one day post-emergence on all cultivars and peaks were highest on Karon and 8320, and lowest on Matin. Steep drops in female survival occurred on all cultivars beginning

about five days post-emergence. There was also a notable drop in female life expectancy on Matin shortly after emergence (Figure 4).

All demographic population parameters were significantly affected by tomato cultivar (Table 2). The results for net Reproductive rates (R_0), in descending order, were on Karon, 8320, TD, Petoprid, and Matin cultivars, respectively; the same order held for values of intrinsic rate of increase (r) and finite rate of increase (λ). The reverse order held for Generation Time (GT) and population Doubling Time (DT) values; i.e. Matin, Petoprid, TD, 8320 and Karon, confirming Karon and Matin to be the most and the least suitable cultivars for TLM, respectively.

Table 2. Mean ($\pm$ SE) demographic growth parameters of *Tuta absoluta* reared on five tomato cultivars.^a

Cultivar (n)	R_0 ($\varnothing$ Offspring/ $\varnothing$)	r (d^{-1})	λ (d^{-1})	GT (Days)	DT (Days)
TD (24)	37.34 $\pm$ 0.17 c	0.146 $\pm$ 0.0002 c	1.157 $\pm$ 0.0002 c	24.8 $\pm$ 0.02 c	4.8 $\pm$ 0.01 c
Karon (28)	62.15 $\pm$ 0.22 a	0.178 $\pm$ 0.0002 a	1.195 $\pm$ 0.0002 a	23.2 $\pm$ 0.01 e	3.9 $\pm$ 0.00 e
Petoprid (21)	36.32 $\pm$ 0.19 d	0.138 $\pm$ 0.0002 d	1.148 $\pm$ 0.0003 d	26.0 $\pm$ 0.02 b	5.0 $\pm$ 0.01 b
Matin (18)	21.33 $\pm$ 0.18 e	0.111 $\pm$ 0.0004 e	1.118 $\pm$ 0.0004 e	27.5 $\pm$ 0.03 a	6.2 $\pm$ 0.02 a
8320 (27)	59.64 $\pm$ 0.21 b	0.169 $\pm$ 0.0001 b	1.184 $\pm$ 0.0002 b	24.2 $\pm$ 0.02 d	4.1 $\pm$ 0.00 d
<i>F</i>	6918.79	14019.41	14145.17	7319.09	10127.25
<i>df</i>	4,113	4,113	4,113	4,113	4,113
<i>P</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

^a Means bearing the same letter are not significantly different within columns (Bonferroni, $\alpha = 0.05$). GT= Generation Time, and DT= Doubling Time.

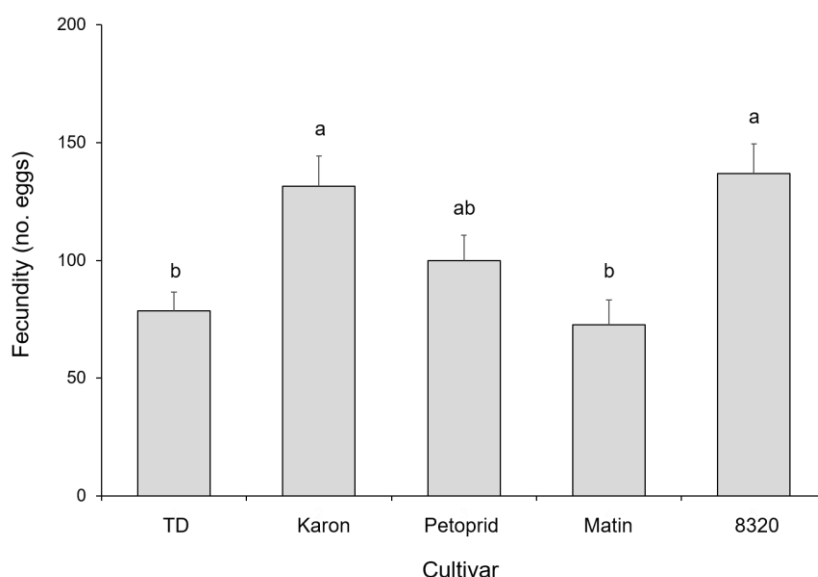


Figure 2. Mean ($\pm$ SE) lifetime fecundity of female *Tuta absoluta* when reared on five different tomato cultivars. Columns bearing different letters are significantly different (ANOVA followed by Bonferroni, $\alpha = 0.05$).

Leaf Trichomes

There were significant differences among tomato cultivars in the numbers of type VI glandular trichomes per cm^2 on both adaxial ($F = 12.44$; $df = 4,10$; $P = 0.001$) and abaxial ($F = 6.25$; $df = 4,10$; $P = 0.009$) leaf surfaces (Figure 5). Cultivar Matin had the highest density of trichomes on both adaxial and abaxial leaf surfaces, with TD expressing similarly high numbers on adaxial surfaces only. Other cultivars did not differ significantly from one another in trichome densities.

DISCUSSION

The present study revealed that these five Iranian tomato cultivars varied significantly in their suitability for *T. absoluta*, as reflected in the observed life history and demographic parameters of the pest. Other studies have found considerable variation in TLM life history across tomato cultivars (Gharekhani and Salek-Ebrahimi, 2014; Ghaderi *et al.*, 2017; Rostami *et al.*, 2017). But, differences in the tomato cultivars, source of initial population of the pest and temperature conditions employed (25.5-27.5°C), and

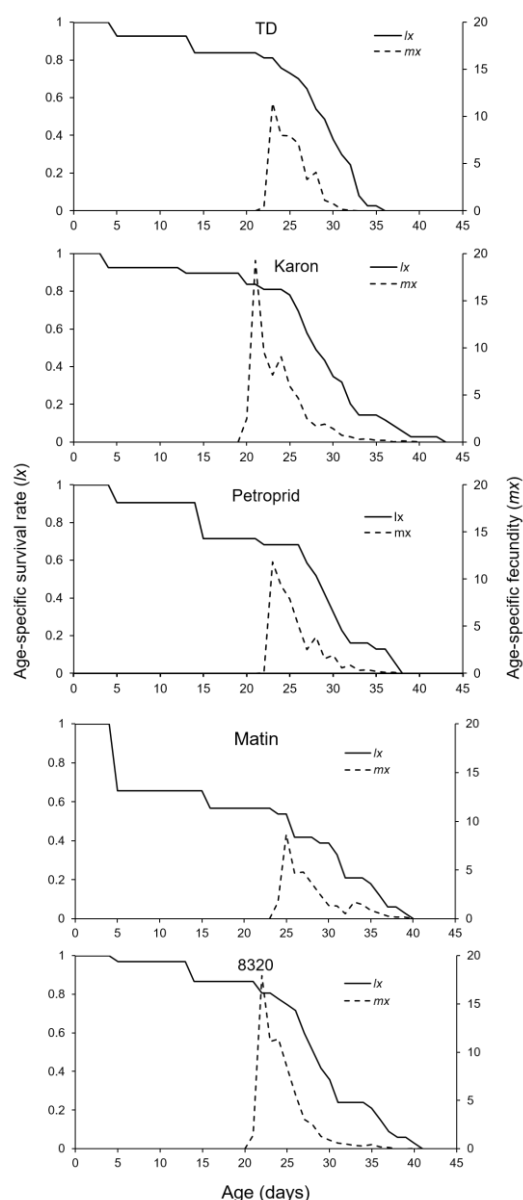


Figure 3. Age-specific survival rates (l_x) and fecundities (m_x) of *Tuta absoluta* when reared on five different tomato cultivars.

possible effects of different growing conditions make it difficult for direct comparison of life table parameters among studies. Also, both Ghaderi *et al.* (2017) and Rostami *et al.* (2017) used two-sex life tables (Chi, 1988), which can lead to different outcomes from a female-only approach if there is an unequal sex ratio (Fathipour and Maleknia, 2016). However, both TD and

Matin maintained lifetime fecundity well below 100, and r -values low enough to compare favorably with the variety 'Cluse', which Gharekhani and Salek-Ebrahimi (2014) categorized as an "unsuitable" host for TLM. Similarly, Ghaderi *et al.* (2017) compared seven tomato cultivars, with none yielding fecundity below 100, although two varieties yielded r -values slightly lower than Matin in our study, and were categorized as "resistant" by the authors. However, these two were tested at a lower temperature, which would be expected to lower reproductive rate and enhance longevity. In contrast, Rostami *et al.* (2017) found no significant differences in primary life table parameters among the three cultivars they tested. We conclude that both TD and Matin can be considered moderately resistant to TLM.

Differences in TLM suitability among tomato cultivars can result from differences in morphological, physiological, and nutritional traits. Juvenile TLM mortality was highest on Matin, with most mortality occurring in the larval period, and this cultivar, along with TD, also had the highest densities of type VI glandular trichomes on its leaves. These trichomes could physically impede penetration of the leaves by first instar larvae and are known to contain tomato metabolites with anti-herbivore properties (Bergau *et al.*, 2015), primarily methyl-ketones, sesquiterpines, and acyl sugars (Han *et al.*, 2019). For example, Sohrabi *et al.* (2017) reported lower TLM damage on tomato cultivars with more type VI trichomes, which appear to provide a constitutive form of plant defense against folivores such as TLM. Bleeker *et al.* (2012) introduced the biosynthetic pathway of 7-epizingiberene, a sesquiterpene, from a wild relative into cultivated tomato and demonstrated substantially increased resistance to whiteflies and spider mites, largely as a result of greatly reduced fecundity. In case of the influence of tomato nutrient contents on herbivore development, Coqueret *et al.* (2017) revealed that reducing nitrogen content can cause slow TLM larval development. Similarly, Uesugi (2015)

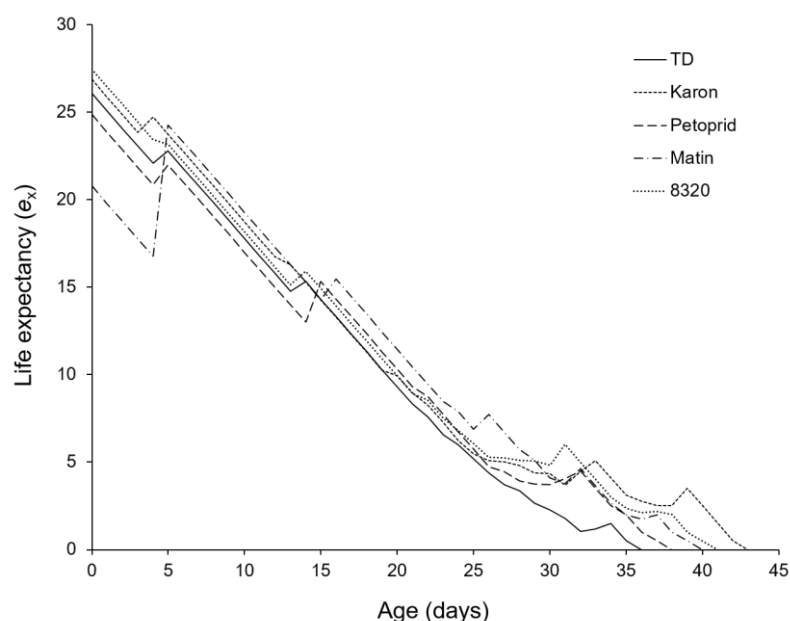


Figure 4. The age-specific life expectancy (e_x) of *Tuta absoluta* on five tomato cultivars.

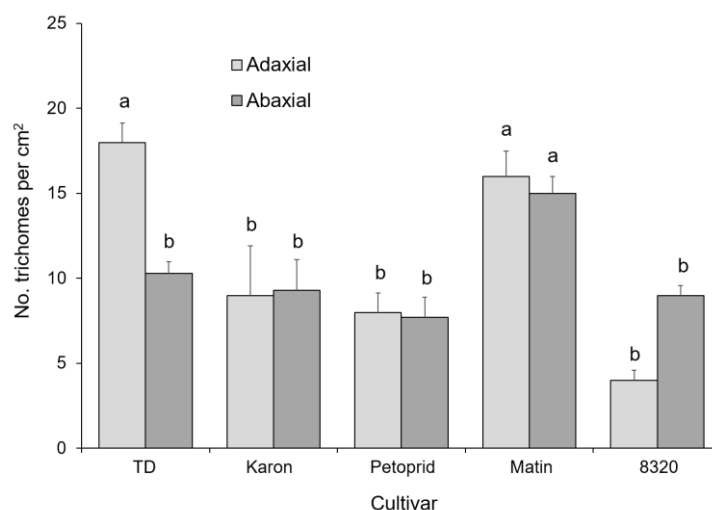


Figure 5. Mean (+SE) numbers of type VI glandular trichomes per unit area on the adaxial and abaxial leaf surfaces of five tomato cultivars. Columns bearing different letters are significantly different from others on the same surface (ANOVA followed by LSD test, $\alpha=0.05$)

showed that host plant with low nitrogen content can increase larval development time and mortality of leafminer fly, *Amauromyza flavifrons* Meigen (Dip.: Agromyzidae).

On their own, the observed levels of host plant resistance expressed in cultivars Matin, Petoprid, and TD are unlikely to suffice for effective management of TLM in intensive tomato production facilities. However, they

could 'tip the balance' in favor of economically acceptable control when combined with other tactics that exploit either lower or higher trophic levels (Biondi *et al.*, 2018). For example, because leaf nitrogen content is a fundamental requirement for TLM growth and reproduction (Coqueret *et al.*, 2017), fertilization regimes are another variable that can be manipulated to limit TLM population



growth while maintaining plant productivity (Han *et al.*, 2019). Zoophytophagous mirid bugs are commonly augmented as generalist predators in tomato greenhouses where they can contribute to the control of TLM and other pests simultaneously (Molla *et al.*, 2009; De Backer *et al.*, 2014), largely because they lack the aversion many other predators have toward the glandular trichomes of tomato (Bottega *et al.*, 2017). The feasibility of deploying egg parasitoids in combination with hemipteran predators against TLM has also been demonstrated (Mohammadpour *et al.*, 2020), and the possible effects of plant resistance traits on higher trophic level interactions such as intraguild predation are worthy of further exploration.

In conclusion, the 'bottom-up' effects of resistant cultivars are often the foundation of integrated management programs against pests. In the case of TLM, our findings indicate that Matin, Petoprid, and TD cultivars can limit its population growth due to some properties such as high density of type VI glandular trichomes on their leaves. Thus, they have potential as one component of an IPM strategy to manage *T. absoluta*, and can potentially help reduce insecticide use in tomato production.

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مناسب بودن پنج رقم گوجه فرنگی برای *Tuta absoluta* (Lepidoptera: Gelechiidae): مقاومت با بالا بودن تراکم تریکوم‌های غده ای مرتبط است

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چکیده

شب‌پره مینوز برگ گوجه فرنگی با نام علمی *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) یک آفت جهانی گوجه فرنگی بوده که موجب تکیه بیش از حد بر آفتکش‌ها در تولید این محصول شده است و این مساله بر کنترل بیولوژیک سایر آفات و سلامت محیط زیست تاثیر منفی می‌گذارد. ما با مقایسه بیولوژی و پارامترهای دموگرافی این آفت در شرایط آزمایشگاهی ($1 \pm$ 27/5 درجه سلسیوس، رطوبت نسبی 5 ± 65 و دوره روشنایی 16 به 8) میزان مقاومت پنج رقم مهم گوجه فرنگی ایران (تی‌دی، کارون، پتوپراید، متین و 8320) را مورد آزمایش قرار دادیم. نرخ بقا و رشد و نمو مراحل نابالغ آفت و همچنین باروری ماده‌ها و پارامترهای جدول زندگی در بین ارقام به طور معنی داری متفاوت بود. رقم کارون با 90 درصد نرخ بقای دوره نابالغ، کوتاه‌ترین طول دوره رشد و نمو و بالاترین باروری ماده‌ها حساسترین رقم بود؛ رقم 8320 در این پارامترها تفاوت معنی داری با کارون نداشت. در مقابل، متین با نرخ بقای نابالغ 59 درصد و کاهش 50 درصدی باروری ماده‌ها به عنوان مقاوم‌ترین رتبه بندی شد. پس از متین، تی‌دی مقاوم‌ترین رقم بود و در فاکتورهای ذکر شده تفاوت معنی داری با رقم متین نداشت. پارامترهای دموگرافی منعکس کننده عملکرد بیولوژیکی هستند؛ نرخ ذاتی افزایش جمعیت (r) آفت روی ارقام کارون، 8320، تی‌دی، پتوپراید و متین روند کاهشی داشت و به ترتیب 0/178، 0/169، 0/146، 0/138 و 0/111 بر روز حاصل شد. متین و تی‌دی دارای بالاترین تراکم تریکوم‌های غده‌ای در سطح فوقانی برگ بودند. این یافته‌ها نشان می‌دهد که ارقام متین، پتوپراید و تی‌دی نسبت به سایر ارقام مقاوم‌تر بوده و می‌توانند به عنوان یکی از اجزای مدیریت تلفیقی مینوز برگ گوجه‌فرنگی مورد استفاده قرار گیرند.