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Life Table Parameters and Digestive Enzyme Activities in *Chrysodeixis chalcites* (Esper) (Lepidoptera: Noctuidae) Fed on Some Commercial Cultivars of Tomato

M. MARDANI-TALAEE[1], A. ZIBAEE[2]* and V. RAHIMI[2]

[1]Department of Plant Protection, Faculty of Agricultural Sciences, University of Mohaghghegh-Ardabili, Iran
[2]Department of Plant Protection, Faculty of Agricultural Sciences, University of Guilan, Rasht, Iran

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Effects of six commercial tomato cultivars, Super Strain B, Super crystal, Hed rio grande, SUN 6108 f1, Rio grande UG and Cal.JN3 were determined on digestive physiology and life table parameters of *Chrysodeixis chalcites* (Esper). The highest values of consumed foods were determined in the larvae fed on Rio grande UG and Cal.JN3 while the lowest values were observed on SUN 6108 f1. Statistical difference was found in the pupal weight by the highest value on SUN 6108f1. The highest values of intrinsic rate of increase (r_m) and the net reproductive rate (R_0) were obtained on SUN 6108 f1 but the lowest values were obtained on Cal.JN3. Significant differences were also found in activities of digestive enzymes including specific proteases, α-amylase, glucosidases and TAG-lipase. Our findings showed that the highest and the lowest activities of specific proteases and TAG lipase were obtained on Rio grande UG and SUN 6108 f1, respectively. In addition, activities of the carbohydrases were the highest in the larvae fed on Cal.JN3. The demographical and physiological findings here revealed Cal.JN3 and Rio grande UG as the partially unsuitable cultivars for *C. chalcites* in comparison with other ones which may be recommended in integrated pest management.

Keywords: *Chrysodeixis chalcites*, life table, digestive enzyme, tomato cultivar.

Quality and quantity of host plants are described as presence of components affecting positively or negatively nutritional performance of herbivorous insects (Browne and Raubenheimer, 2003). These parameters depend on chemical compounds in host plants which are divided into four main groups including nitrogen-containing compounds, cyanogenic glycosides (glucosinolates), terpenoids and phenolics although some of them including alkaloids, phenolics, flavonoids and tannins are found occasionally in some families of plants (Schoonhoven et al., 1998). These chemicals, somehow defensive metabolites, are primarily toxic whereas others have anti-feedant and/or repellent properties leading to plant resistance against herbivorous insects. Host plant resistance occurs under three main mechanisms as antixenosis, antibiosis and tolerance by presence of secondary metabolites or morphological properties (Schoonhoven et al., 1998). Plants with antibiosis mechanisms may directly alleviate insect survival, size or weight, longevity and fecun-

* Corresponding author; e-mails: arash.zibaee@gmx.com, arash.zibaee@guilan.ac.ir

dity. Antixenosis refers to morphological properties in host plant caused non-preference for biological activity and tolerance is considered as potential of host plant to compensate feeding invasion of insects. Taken collectively, nutritional regulation of insects indicates a highly complex set of interacting processes to improve survival and reproduction of insects (Simpson and Raubenheimer, 1999).

The tomato looper, *Chrysodeixis chalcites* (Esper) (Lepidoptera: Noctuidae) is a polyphagous insect that attacks different plant species such as vegetables, fruits and ornamental crops in fields and greenhouses (Murillo et al., 2013). Larvae of *C. chalcites* feed on leaves of solanaceous plants leading to considerable damages of vegetative parts especially on tomato (*Lycopersicone sculentum* Miller) around the world (Murillo et al., 2013). Development of efficient strategies to control *C. chalcites* will require knowledge on its nutritional relationships in various host plants. It seems that *C. chalcites* must utilize several digestive enzymes to obtain required nutrients for biological processes like other ones so that their activities might be fluctuated when the larvae fed on various tomato cultivars. Also, a common method to delineate resistant cultivar(s) is the comparison of life table parameters of a given pest on host plants because those are the important indicators of population growth capacity on different host plants (Southwood and Henderson, 2000). Hence, objectives of the current study were to determine the effects of some commercial cultivars of tomato on ecological parameters and activities of digestive enzymes to gain knowledge on ecological and nutritional performance of *C. chalcites* on tomato cultivars.

Materials and Methods

Plant and insect sources

Larvae of *C. chalcites* were collected from tomato fields of Ardabil, north-west of Iran. The larvae were reared on a local tomato cultivar for three generations in the greenhouse conditions to have a homogeneous population. Then, larvae were reared on six commercial cultivars of tomato including Super Strain B, Super crystal, Hed rio grande, SUN 6108 f1, Rio grande UG and Cal.JN3 cultivars provided from Agricultural Research Station of university of Mohaghegh Ardabili, Iran. Experiments were conducted in a growth chamber with 25 ± 2 °C of temperature, 65 ± 5% of relative humidity and a photoperiod of 16:8 L:D hours.

Feeding responses of C. chalcites *to tomato cultivars*

A gravimetric method described by Waldbauer (1968) was used to evaluate effects of tomato cultivars on larval and pupal weights as well as amount of consumed food. To obtain percentage of dry weights of larvae and pupa, 20 extra specimens were weighed, oven-dried (48 h at 60 °C) and subsequently reweighed. Also, method of Tuomi et al. (1981) and Koricheva and Haukioja (1992) was used to calculate the index of plant 1 quality (IPQ) for each host-plant (IPQ = pupal weight (mg) / frass dry weight (mg)).

Life table parameters

A pair of female and male moths were reared on each tomato cultivar and separately introduced into an plastic oviposition container (10 cm diameter, 15 cm depth), which was sealed at the top with a fine mesh net for ventilation in a growth chamber (25 ± 2 °C, 65 ± 5% RH and 16:8 (L: D) h). Each container was supplied by a 10% honey solution for moth feeding. The experiment was conducted in a completely randomized design for each cultivar with 15 replications. The number of eggs laid and adult longevity were recorded daily until death of the last adult. The egg laying containers were equipped by window screen as oviposition substrate to prevent eggs being laid on the container wall. Eggs laid from each adult pair within the same day were monitored to determine incubation period. During hatching, these eggs were checked daily and the number of newly hatched larvae was recorded.

The raw life table data were analyzed using the age-stage and two-sex life table approach. The intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0) and the mean generation time (T) were estimated by the following equations. The intrinsic rate of increase was calculated with the bisection method from the Euler-Lotka equation as follows (Chi and Liu, 1985; Chi, 1988):

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$$

The means, variances and standard errors of the population parameters were estimated by bootstrap technique (Efron and Tibshirani, 1993) which is also included in the two sex-ms-chart program.

Assay of digestive enzyme activity

Sample preparation

Larvae fed on each cultivar were randomly selected and dissected in ice cold distilled water. The midguts were removed from body and homogenized in distilled water by a handling glass pestle. Homogenate samples were centrifuged at 13000 rpm for 10 min at 4 °C. Finally, supernatants were pooled and stored at −20 °C for subsequent experiments (Mardani-Talaee et al., 2014).

Determination of the activity of specific proteases

Serine proteinases

Trypsin-, chymotrypsin- and elastase-like activities (as three subclasses of serine proteinases) were assayed using 1 mM of BApNA (Na-benzoyl-DL-arginine-*p*-nitroanilide), 1 mMSAAPPpNA (*N*-succinyl-alanine-alanine-proline-phenylalanine-*p*-nitroanilide), and 1 mMSAAApNA (*N*-succinyl-alanine-alanine-alanine-*p*-nitroanilide) as substrates, respectively. The reaction mixture consisted 50 μL of universal buffer (20 mM, pH 8), 20 μL of each substrate and 10 μL of enzyme solution. The reaction mixture was incubated at 30 °C for 10 min prior to be read at 405 nm (Mardani-Talaee et al., 2014).

Exopeptidases

Activities of the two exopeptidases in the midgut of *C. chalcites* were measured using hippuryl-L-arginine and hippuryl-L-phenylalanine for carboxy- and aminopeptidases, respectively. The reaction mixture consisted 50 μL of universal buffer (pH 7), 30 μL of each substrate and 15 μL of enzyme solution. The reaction mixture was incubated at 30 °C for 10 min prior to be read at 340 nm (Mardani-Talee et al., 2014).

α-Amylase assay

The method of Bernfeld (1955) was used to assay α-amylase activity using 1% starch as substrate. Briefly, 10 μL of the enzyme was incubated for 30 min at 35 °C in 50 µL of phosphate buffer (20 mM, pH 7) and 30 µL of 1% starch. The reaction was stopped by adding 100 µL of dinitrosalicylic acid (DNS) and heated in boiling water for 10 min prior to be read at 545 nm. One unit of α-amylase activity was defined as the amount of enzyme required to produce 1 mg maltose per min at 35 °C.

α- and β-glucosidase assay

Activities of α- and β-glucosidases were assayed according to the method of Silva and Terra (1995) with slight modification. Reaction mixture consisted 50 μL of universal buffer (20 mM, pH 7), enzyme extract (15 µL) and substrate (30 µL) (*p*-nitrophenolα-glucopyranoside for α-glucosidase and *p*-nitrophenol β-glucopyranoside for β-glucosidase). The mixture was incubated for 10 min and production of *p*-nitrophenol was measured at wavelength of 405 nm.

Triacylglycrol-lipase assay

Activity of TAG-lipase was carried out using the method of Tsujita et al. (1989). Twenty microliters of midgut extract and 40 µL of *p*-nitrophenyl butyrate (27 mM) as substrate were added to 100 μL of universal buffer (10 mM, pH7), mixed thoroughly and incubated at 37 °C. After 1 min, 100 µL of NaOH (1 M) was added to each tube and absorbance was read at 405 nm. One unit of enzyme will release 1. 0nmol of *p*-nitrophenol per min at pH 7.2 and 37 °C when *p*-nitrophenyl butyrate is used as substrate.

Protein assay

Protein concentrations were assayed according to the method described by Lowry et al. (1951) using a biochemical kit from Biochem Co., Tehran-Iran.

Statistical analysis

All data were tested for normality before statistical analyses. Data were analyzed by one-way analysis of variance (ANOVA) followed by comparison of the means with

Tukey post hoc Honestly Significant Difference (HSD) test at $\alpha = 0.05$ using statistical software SPSS 16.0. Cluster analyses (Ward's method) were carried out based on of activities of digestive enzymes in *C. chalcites* larvae and using statistical software SPSS16.0.

Results

Effects of tomato cultivars on food consumption, larval weight, fecundity and index of plant quality (IPQ)

Feeding of *C. chalcites* larvae on tomato cultivars showed significant changes in food 12 consumptions, weight of larvae, pupae and index of plant quality (IPQ) [F = 52.48, 5.63, 2.62 and 34.21 ;Pr (> F) = 0.000, 0.000, 0.000 and 0.038 (Table 1)]. The highest value of food consumption was observed in the larvae fed on Rio grande UG, Cal. JN3 and Super crystal varieties (Table 1). The highest and the lowest weight gains of larvae were found on Rio grande UG and Cal.JN3, respectively (Table 1). Also, the highest pupal weight of the *C. chalcites* was 264.9 mg in the individuals fed on SUN 6108 f1 as compare with other treatments [(Fig. 1), F = 6.40; Pr24 (> F) = 0.000]. Finally, the highest IPQ value was observed on SUN 6108 f1 and the lowest ones found on Rio grande UG and Cal.JN3 cultivars, respectively (Table 1).

Life table parameters

There were significant differences on life table parameters of *C. chalcites* fed on tomato cultivars including net reproductive rate (R_0), intrinsic rate of increase (r_m), finite rate of increase (λ), mean generation time (T) and gross reproduction rate (GRR) parameters [F = 143.758, 573.454, 589.943, 539.001 and 1470.345; Pr (> F) = 0.000, 0.000, 0.000, 0.000 and 0.000 (Table 2)]. The R_0 values of *C. chalcites* fed on six tomato culti-

Table 1

Effects of tomato cultivars on the amounts of consumed food, larval weight, pupal weight and index of plant quality (IPQ)

Cultivate	Consumed food (mg)	Larval weight (mg)	Pupal weight (mg)	Index of plant quality (IPQ)
Cal.JN3	615.0 ± 47 a	248.59 ± 5.11 c	198.3 ± 21.56 b	2.279 ± 0.33 d
Rio grande UG	624.0 ± 24.4 a	265.43 ± 5.3 b	197.12 ± 14.63 b	1.903 ± 0.059 d
SUN 6108 f1	299.43 ± 3.78 c	287.4 ± 6.23 a	264.9.11 ± 63.1 a	22.49 ± 2.62 a
Super crystal	590.26 ± 26.4 a	271.82 ± 3.87 ab	212.22 ± 21.3 ab	13.015 ± 0.963 b
Super strain B	564.87 ± 28.7 ab	260.64 ± 6.95 bc	196.74 ± 12.6 b	8.10 ± 1.10 bc
Hed rio grande	491.2 ± 21.4 b	263.22 ± 8.15 bc	199.47 ± 27.3 b	6.608 ± 0.579 cd

The means followed by different letters in the same columns are significantly different (P < 0.05, Tukeys (HSD))

vars varied from 44.439 to 85.468 female/female/generation, with the lowest and highest values on Cal.JN3 and SUN 6108 f1 cultivars, respectively (Table 2). The r_m varied from 0.087 to 0.115 female/female day^{-1} although the shortest and longest values were observed on Cal.JN3 and SUN 6108 f1, respectively (Table 2). In addition, the lowest (1.092 per day) and the highest (1.123 per day) values of λ were observed on Cal.JN3 and SUN 6108 f1 cultivars, respectively (Table 2). The *T* value was the highest on Hed rio grande (44.620 days) while the lowest value was found on Cal.JN3 (41.613 day) (Table 2). Also, the lowest and highest *GRR* value of *C. chalcites* were observed on Cal.JN3 (117.31 per generation) and SUN 6108 f1 (387.16 per generation), respectively (Table 2).

Effect of various host plants on digestive enzymatic activities

Activities of specific proteases (trypsin, chymotrypsin, elastease, amino- and carboxypeptidases) and carbohydrases showed statistical differences in the larvae of *C. chalcites* fed on different tomato cultivars [F = 1799.38, 397.10, 828.30, 171.34 and 956.03; Pr (> F) = 0.000, 0.000, 0.000, 0.000 and 0.000 (Table 3)]. Results demonstrated that activities of serine proteases, amino- and carboxypeptidase were the highest in the larvae fed on Rio grande UG while the lowest activities were observed in the larvae fed on Super strain B and SUN 6108 f1, respectively (Table 3). The highest activities of α-amylase, α- and ß-glucosidases were observed on Cal.JN3 although the lowest values were found among other cultivars [F = 64.65, 151.81 and 21.32; Pr (> F) = 0.000, 0.000 and 0.000 (Table 4)]. The larvae fed on Rio grande UG showed the highest activity of TAG-lipase while the lowest activity was obtained in the larvae fed on Hed rio grande and SUN 6108 f1, respectively [F = 1950.28; Pr (> F) = 0.000 (Fig. 1)].

Table 2

Life table parameters of *C. chalcites* reared on six different commercial cultivars of tomato under the laboratory conditions

Tomato cultivar	Statistic (Mean±SE)				
	R_0 (offspring)	r_m (day^{-1})	λ (day^{-1})	*GRR* (offspring)	*T* (day)
Calj.JN3	44.439 ± 0.852 e	0.087 ± 0.0008 e	1.092 ± 0.0008 e	117.31 ± 1.784 f	44.621 ± 0.050 a
Rio grande UG	58.387 ± 1.790 d	0.091 ± 0.0120 d	1.094 ± 0.013 d	155.99 ± 3.432 e	43.581 ± 1.272 b
SUN 6108 f1	85.468 ± 1.496 a	0.115 ± 0.0003 a	1.123 ± 0.0003 a	387.16 ± 3.316 a	41.613 ± 0.104 d
Super crystal	68.527 ± 0.847 c	0.099 ± 0.0004 b	1.104 ± 0.0003 b	242.43 ± 2.268 c	42.067 ± 0.046 c
Super strain B	79.096 ± 1.070 b	0.097 ± 0.0004 c	1.102 ± 0.0003 c	220.08 ± 2.490 d	43.254 ± 0.017 b
Hed rio grande	61.524 ± 0.766 cd	0.091 ± 0.0004 d	1.095 ± 0.0004 d	259.36 ± 2.497 b	42.737 ± 0.023 c

The means followed by different letters in the same columns are significantly different (P < 0.05, Tukey (HSD))

Cluster analysis

Dendrogram of growth population parameters and digestive enzymatic activities in *C. chalcites* larvae reared on different tomato cultivars is shown in (Fig. 2). Dendrogram shows two clusters labeled 'A' (consisted of sub-clusters A1 and A2) and 'B'. Different tomato cultivars were grouped in each cluster according to the comparison of growth population parameters and digestive enzymatic activities. Cluster A1 included (Super strain B, Hed rio grande and Super crystal) as an intermediate group, and A2 (Cal.JN3 and Rio grande UG) as a partially unsuitable host. Finally, it shows sub-clusters B (SUN 6108 f1) as suitable hosts for *C. chalcites* larvae (Fig. 2).

Table 3

The effect of six tomato cultivars on specific activities of digestive proteases in the larvae of *C. chalcites*

Tomato cultivar	Statistic (Mean ± SE U/mg protein)				
	Trypsin	Chymotrypsin	Elastease	Amino-peptidases	Carboxy-peptidases
Cal.JN3	4.157 ± 0.011 b	6.629 ± 0.076 c	5.712 ± 0.011 b	0.246 ± 0.015 c	0.149 ± 0.039 b
Rio grande UG	19.635 ± 0.030 a	24.305 ± 0.870 a	24.807 ± 0.638 a	1.682 ± 0.034a	0.723 ± 0.083 a
SUN 6108 f1	1.330 ± 0.080 d	4.351 ± 0.046 d	2.857 ± 0.052 d	0.127 ± 0.006 d	0.115 ± 0.021 b
Super crystal	3.137 ± 0.391 c	7.557 ± 0.055 bc	3.460 ± 0.229 c	0.334 ± 0.014 bc	0.169 ± 0.042 b
Super strain B	1.758 ± 0.025 d	4.799 ± 0.020 d	2.148 ± 0.044 d	0.143 ± 0.002 d	0.137 ± 0.015 b
Hed rio grande	3.483 ± 0.020 c	9.039 ± 0.280 b	4.486 ± 0.049 bc	0.345 ± 0.026 b	0.152 ± 0.017 b

The means followed by different letters in the same columns are significantly different ($P < 0.05$, Tukeys (HSD))

Table 4

Effect of six tomato cultivars on specific activities of digestive carbohydrase enzymes of larvae of *C. chalcites*

Host (cultivar)	Statistic (Mean ± SE U/mg protein)		
	α-Amylase	α-Glucosidase	ß-Glucosidase
Cal.JN3	0.534 ± 0.007 a	0.444 ± 0.018 a	0.462 ± 0.004 a
Rio grande UG	0.213 ± 0.018 c	0.132 ± 0.003 d	0.180 ± 0.006 d
SUN 6108 f1	0.051 ± 0.000 d	0.189 ± 0.005 c	0.388 ± 0.045 b
Super crystal	0.346 ± 0.045 b	0.121 ± 0.009 d	0.305 ± 0.013 b
Super strain B	0.207 ± 0.014 c	0.130 ± 0.001 d	0.209 ± 0.028 c
Hed rio grande	0.163 ± 0.006 c	0.245 ± 0.015 b	0.238 ± 0.015 c

The means followed by different letters in the same columns are significantly different ($P<0.05$, Tukeys (HSD))

Discussion

Nutrients and secondary compounds of ingested foods do have significantly positive or negative effects on growth, survival, and potential fecundity of herbivorous insects via digestive physiology alteration (Mendiola-Olaya et al., 2000; Silva et al., 2009). Amount of consumed food and growth of lepidopteran larvae directly correlate with quality of nutrient input from host plants (Mendiola-Olaya et al., 2000; Silva et al., 2009). In the current study, it found considerable variability in both quality and quantity of different tomato cultivars because significant reductions were observed in values of larval weight

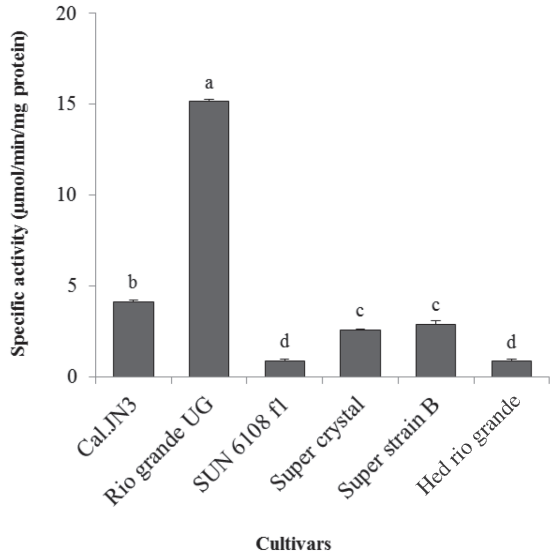

Fig. 1. Comparison of the activities of TAG lipase of *C. chalcites* larvae reared on different tomato cultivars. Error bars indicate SE; different letters indicate significant differences ($P < 0.05$, Tukeys (HSD))

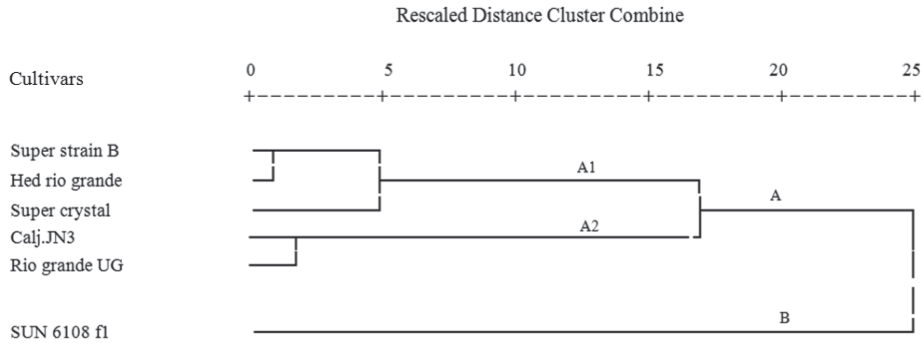

Fig. 2. Dendrogram of six various cultivars of tomato based on growth population parameters and digestive enzymatic activities of *C. chalcites* (Ward's method). High quality figures are available on line

and fecundity of *C. chalcites*. On the other hands, larvae of tomato looper reared on the cultivars mainly Cal.JN3 appropriately obtain their nutritional requirements which indicates the ability of an insect to utilize food and increased amount of ingestion and digestion. Although these findings might be attributed to digestibility of food in the mentioned cultivars, even it may be due to lack of anti-feedant materials (Prütz and Dettner, 2005). This could be achievable by calculating IPQ ratio which is an appropriate index showing food quality of various host plants (e.g. tomato cultivars). Here, the highest and the lowest IPQ ratio of *C. chalcites* larvae were obtained on SUN 6108 f1 and on Rio grande UG as well as Cal.JN3, respectively, indicating appropriate and inappropriate qualities of cultivars. The amount of ingested food by insects has a direct relationship with amount of nitrogen in leaves of host plants that affect larval growth (Scriber and Slansky, 1981; Du et al., 2004). Taken collectively, the nutritional components of SUN 6108 f1 can was partially suitable for *C. chalcites*. Also, the larvae reared on it had the lowered values of consumption of nutritionally rich food, because with value of low required food to support their growth and survival. According to our findings, the highest and lowest activities of specific proteases were observed in the larvae fed on Rio grande UG and SUN 6108 f1, respectively. Also, it was demonstrated that activity of carboxypeptidase was the highest on Rio grande UG and no statistical differences was observed among other tomato cultivars. In the current study, it was demonstrated the highest activities of α-amylase and glucosidases (α- and ß-glucosidases) in the larvae of *C. chalcites* fed on Cal.JN3 cultivar. Also, Mardani-Talaee et al. (2014) reported that digestive enzyme activities of *C. chalcites* including specific proteases, α-amylase, glucosidases (α- and ß-glucosidases) increased on dill (*Anethum graveolens* L.) but no statistical differences were obtained between lemon balm (*Melissa officinalis* L.) and corn (*Zea mays* L.). The current study has shown that the digestive enzymes activities were influenced by food plants which were fed during the larval stage. Thus, the relationship between insects and their host plants are regulated via present compounds such as nitrogen compounds, carbohydrates, amino acids and many other compounds (Awmack and Leather, 2002). Developmental time of insects changes due to nutritional requirements that typically reflects in changes of food consumption and feeding behavior (Felton, 1996; Browne and Raubenheimer, 2003).

It was observed that the net reproductive rate (R_0), the intrinsic rate of increase (r_m) and the finite rate of increase (λ) of *C. chalcites* decreased in the larvae fed on cultivar Calj.JN3. The r_m and R_0 are the two key demographic parameters used to compare fitness of populations across diverse climatic and food-related conditions (Liu et al., 2004). It can be concluded that Calj.JN3 cultivar is a less suitable cultivar for *C. chalcites* than the other cultivars. Thus, the ability of insect to fast complete of sensitive immature stages and adult stages correlates with nutritional elements in their host plants. Thus, the partially resistant cultivars causes increasing immature periods and reducing fertility which is useful to application of natural enemy and pesticide (Zalucki and Malcolm, 2002). Also, the highest values of R_0, r_m and λ in reared *C. chalcites* on SUN 6108 f1 cultivar suggesting partially suitable host among used cultivars. The positive relationship between pupal weight and fecundity has been observed in other lepidopteran species (Awmack and Leather, 2002). Quality and quantity of consumed food have indirect effects on pest population dynamics by alterations of adult performance and total fecundity (Morgan et

al., 2001; Liu et al., 2004). Since reared larvae of tomato looper on SUN 6108 f1 had the highest values of pupal weight, and life table parameters, it could be inferred the cultivar as suitable host for *C. chalcites* larvae. These findings are correlated with IPQ value of the cultivar discussed earlier.

Besides earlier findings, we also observed the smaller size of the larvae reared on Rio grande UG and Cal.JN3 may be due to antibiosis properties of the tomato cultivars caused by variation in the contents of secondary metabolites and micro- and macro-elements in the hosts. The lower amount of IPQ value may indicate the point in the larvae fed on Rio grande UG and Cal.JN3 because those must obtain nutritional requirements for growth and development. Also, it can be inferred that Cal.JN3 and Rio grande UG have two levels of allelochemicals and presence of nutrient components. These finding will helpful use to better choose of tomato cultivars in the fields under heavy infestation of *C. chalcites* although more attention should be dedicated to study ecophysiology of the pest under field conditions to achieve the objective.

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