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Influence of Genetically Manipulated *Brassica* Genotypes on Parasitism Capacity of *Diadegma semiclausum* Parasitizing *Plutella xylostella*

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ABSTRACT

Plant quality in herbivores' diet may affect the performance of both herbivore and its parasitoids. In the present research, parasitism capacity of *Diadegma semiclausum* (Hellen) on *Plutella xylostella* (L.) reared on different genetically manipulated *Brassica* plants including the canola's progenitor (*Brassica rapa* L.), two cultivated canola cultivars (Cultivar-Opera and Cultivar-RGS$_{003}$), one hybrid (Hybrid-Hyula$_{401}$), one gamma mutated (Mutant-RGS$_{003}$), and one transgenic (Transgenic-PF) genotype was determined. All experiments were carried out in a growth chamber at 25±1°C, 65±5% RH, and a photoperiod of 16:8 (L: D) hour. The value of the net parasitism rate (C_0) of *D. semiclausum* was 14.94, 20.12, 14.95, 12.20, 13.94, and 12.55 hosts on *B. rapa*, Cultivar-Opera, Cultivar-RGS$_{003}$, Hybrid-Hyula$_{401}$, Mutant-RGS$_{003}$, and Transgenic-PF, respectively. The transformation rate from host population to parasitoid offspring (Q_p) on all genotypes was close to 1 ($C_0 \cong R_0$). Moreover, the value of the finite parasitism rate (ω) was 0.271, 0.285, 0.277, 0.202, 0.205, and 0.202 host parasitoid^{-1} day^{-1} on the above-mentioned genotypes, respectively. The finite parasitism rate considers the finite rate of increase, the stable age-stage distribution, and the age-stage specific parasitism rate; therefore, this parameter could be used to assess the efficiency of a parasitoid. In conclusion, *D. semiclausum* had higher parasitism capacity on canola's progenitor and the cultivated genotypes which were more suitable for parasitoid's host based on secondary metabolites concentration.

Keywords: Diamondback moth, Finite parasitism rate, Manipulated canola, Plant chemistry, Two-sex parasitism.

INTRODUCTION

The Diamondback Moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) is considered as one of the most important global pests of crucifer crops for several decades. In the recent decade, *P. xylostella* has caused major problems on *Brassica* crops in different parts of the world (Golizadeh *et al*., 2009), mostly due to the increase in levels of resistance to different classes of insecticides even to *Bacillus thuringiensis* formulations (Shelton *et al*., 1993, Soufbaf *et al*., 2010a, b). Therefore, it is crucial to apply a new management tool for its control. Previous studies showed that biological control agents play a major role in regulating the population of this pest (Golizadeh, *et al*., 2008; Sarfraz *et al*., 2009; Soufbaf *et al*., 2012).

Diadegma semiclausum (Hellen) (Hymenoptera: Ichneumonidae), which is a solitary and host-specific larval endoparasitoid, is known as an important biological control agent of *P. xylostella* (Sarfraz *et al*., 2005). This parasitoid shows

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an excellent search capacity and has been studied as a potential biological control agent in integrated management programs for the diamondback moth (Harcourt, 1960).

Life table parameters are powerful tools for analyzing and understanding the impact of an external factor (e.g., host plant quality and temperature) on the growth, survival rate, reproduction, and increasing rate of a biocontrol agent population (Taghizadeh *et al*., 2008; Pakyari *et al*. 2011). Our previous studies revealed profound effect of genetically manipulated canola genotypes on life table parameters of *P. xylostella* (Nikooei *et al*., 2015) and its parasitoid *D. semiclausum* (unpublished data). Some life table parameters such as the intrinsic rate of increase (*r*) are suitable indices for describing and comparing growth potentials of populations. Since the intrinsic rate of increase cannot alone interpret the parasitism/predation potentials of parasitoids/predators, a standard parameter is needed for description of the capacity of a parasitoid/predator in biological control programs (Chi *et al*., 2011).

Accordingly, Chi *et al*. (2011) defined the finite parasitism/predation rate (ω) as a standard parameter linking the finite rate of increase (λ), the stable age-stage distribution (a_{xj}), and the age-stage specific parasitism/predation rate (c_{xj}). The finite parasitism rate considered both the increase rate of parasitoid and the age-stage specific parasitism rate and then it would be capable to describe and compare the parasitism potential of the natural enemies. To compare parasitism/predation capacity among different parasitoids/predators under the same condition or capacity of a parasitoid/predator under different conditions, the finite parasitism/predation rate can be an efficient tool (Yu *et al*., 2013).

It has been demonstrated that plant quality in herbivores' diet may not only affect the performance of the herbivore but also that of its natural enemies (Ode, 2006; Harvey *et al*., 2007; Gols *et al*., 2007; 2008a, b). Here, we selected *Brassica rapa* L. as a canola's progenitor, two cultivated canola cultivars (Cultivar-Opera and Cultivar-RGS_{003}), one hybrid (Hybrid-$Hyula_{401}$), one genetically mutated with gamma radiation (Mutant-RGS_{003}), and one transgenic (Transgenic-PF) genotype which differ dramatically in their degree of manipulation. We previously showed that these genotypes had significant effects on life table parameters and fitness of *D. semiclausum* (unpublished data). Since this parasitoid is an effective biological control agent of *P. xylostella*, the present study was carried out to reveal the effect of these genotypes on parasitism capacity of this parasitoid parasitizing *P. xylostella*.

MATERIALS AND METHODS

Plants

One of the progenitors of canola (*B. rapa*) as a wild genotype and five genotypes of canola including two cultivars (Opera and RGS_{003}), one hybrid ($Hyula_{401}$), one gamma mutated (Mutant-RGS_{003}), and one transgenic (Transgenic-PF) were used in the experiments. The seeds were planted in plastic boxes (90×50×30 cm) containing sandy loam soil, peat, and perlite (1:1:1). Twenty seeds were sown in each box. All plants were grown in a climate-controlled growth chamber at 25±1˚C, 65±5% RH, and a photoperiod of 16:8 (L: D) hour without any fertilizer and pesticides.

Insects

Plutella xylostella moths were originally collected from *Brassica* fields in Tehran province, Iran, during May 2012. Separated colonies of *P. xylostella* were kept on each host plant in ventilated cages (90×80×70 cm). The stock culture was maintained for about two months in the greenhouse. Sub-colonies were established on six plant genotypes separately and maintained in a constant environment at 25±1˚C on the respective host plants for more than three generations before the trials. At least 130 pairs of moths were used to initiate the colony and 20 wild adult males and females, collected from the field, were added to each colony (stock culture and sub-colonies) weekly.

A potted canola plant with one cohort of 200 early-third instar larvae of *P. xylostella* was placed in a Perspex cage (30×30×30 cm) with a muslin sleeve on one side of the cage. Ten pairs of 2-day-old mated *D. semiclausum* were introduced into the cage. The wasps were provided with a diet of 10% honey solution. After 24 hours, the exposed larvae were removed and placed in ventilated plastic containers (20×15×7 cm). Also, fresh canola leaves were added until pupation. *Plutella xylostella* pupa could not form in case of parasitized larva, so the parasitoid pupae were harvested and put in clean plastic containers for adult emergence. The *D. semiclausum* culture was established and maintained in a constant environment at 25±1˚C, and adults of the second generation were used in the experiments.

Parasitism Capacity of *D. semiclausum*

All experiments were carried out in a growth chamber set at 25±1˚C, 60±5% RH, and a photoperiod of 16:8 (L: D) hour. To evaluate parasitism capacity, when the parasitoid adults emerged, they were sexed, paired, and kept in individual containers (6 cm in diameter, 5 cm in height) with a fresh leaf from the respective host plants and 20 third-instar larvae of the diamondback moth. A piece of cotton wool soaked with 20% honey solution was supplied as food to the adults. After 24 hours, the parasitoids were transferred to a new container with another 20 third-instar larvae of the diamondback moth. The daily observations continued until the death of the last individual.

Parasitism Capacity Analysis

The data obtained from daily parasitism of total cohort were used to calculate the age-stage specific parasitism rate (c_{xj}). The age-stage specific parasitism rate c_{xj} is defined as the number of *P. xylostella* larvae parasitized by a parasitoid of age x and stage j. Because only females can oviposit in their hosts, there is only a single curve of c_{xj} The age-specific parasitism rate (k_x) is the mean number of *P. xylostella* larvae parasitized by *D. semiclausum* at age x and was calculated by the following formula proposed by Chi and Yang (2003):

$$k_x = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \quad (1)$$

Where, β is the number representing the life stage and s_{xj} is the age-stage specific survival rate (where x= Age in days and j= Stage). In addition, the age-specific net parasitism rate (q_x) was calculated as follows:

$$q_x = l_x k_x \quad (2)$$

According to Chi and Yang (2003), the net parasitism rate (C_0) gives the mean number of host parasitized by an average individual parasitoid during its entire life span, and is calculated as:

$$C_0 = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj}\, c_{xj} \quad (3)$$

According to these equations, the total number of parasitized hosts by a cohort of size N is calculated as NC_0. Q_p is the transformation rate from host population to parasitoid offspring. In other words, Q_p is the proportion of the net parasitism rate to the net reproductive rate, and is calculated as:

$$Q_p = \frac{C_0}{R_0} \quad (4)$$

The stable parasitism rate (ψ) is the total parasitism capacity of a stable population, of which the total size is one (Chi *et al.*, 2011), and is calculated as follows:

$$\psi = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} c_{xj} \quad (5)$$

Where, a_{xj} is the proportion of individuals belonging to age x and stage j in a stable age-stage distribution.

Because the parasitoid population will increase at the finite rate λ, the total number of parasitized hosts will be increased at the rate of $\lambda\psi$. The finite parasitism rate ($\lambda\psi = \omega$) describes the parasitism potential of a parasitoid population by combining its growth rate (λ), age-stage parasitism rate (c_{xj}), and stable age-stage structure (a_{xj}) (Chi *et al.*, 2011), and is calculated as follows:

$$\omega = \lambda\psi = \lambda \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj}\, c_{xj} \qquad (6)$$

Considering this, the intrinsic parasitism rate is calculated as $\ln(\omega)$. In other words, the parasitism capacity will increase exponentially ($\omega = e^{intrinsic\ parasitism\ rate}$) (Khanamani *et al.*, 2015).

Parasitism rate data were analyzed using the computer program CONSUME-MSChart as designed by Chi (2013). The means, variances, and standard errors of parasitism parameters were estimated with the bootstrap resampling method and compared using Tukey-Kramer procedure. In the bootstrap procedure, we randomly took a sample of *n* individuals from the cohort with replacement and calculated the $C_{0,i\text{-}boot}$ for this bootstrap sample as:

$$C_{0,i-boot} = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj}\, c_{xj} \qquad (7)$$

Where, the subscript *i-boot* represents the *i*th bootstrap and s_{xj} and c_{xj} are calculated from the *n* individuals selected randomly with replacement. Generally, the data on the same individual are repeatedly selected. We repeated this procedure *m* times (m=10,000) and computed the mean of these *m* bootstraps as:

$$C_{0,B} = \frac{\sum_{i=1}^{m} C_{0,i-boot}}{m} \qquad (8)$$

The variance ($VAR\ C_{0,B}$) and standard error (SE $C_{0,B}$) of these *m* bootstraps were calculated as:

$$VAR\ C_{0,B} = \frac{\sum_{i=1}^{m}(C_{0,i-boot} - C_{0,B})^2}{m-1} \qquad (9)$$

$$SE\ C_{0,B} = \sqrt{VAR\ C_{0,B}} \qquad (10)$$

All graphs were drawn using Microsoft Excel 2010.

RESULTS

Age-Stage Specific Parasitism Rate

Age-stage specific parasitism rate (c_{xj}) of *D. semiclausum* on *P. xylostella* reared on different genotypes of canola is plotted in Figure 1. Because only females can oviposit in their hosts, there is only a single curve of c_{xj} in Figure 1. Therefore, for the non-parasitic stages (e.g., egg, larva, pupa and male) their parasitism rates ($c_{x\text{Egg}}$, $c_{x\text{Larva}}$, etc.) were zero. First, age-stage specific parasitism rate (c_{xj}) on all of the plant genotypes increased with increasing age, and then decreased.

Net Parasitism Rate and Transformation Rate

Net parasitism rate (C_0) and transformation rate from host population to parasitoid offspring (Q_p) of *D. semiclausum* on the different genotypes of canola are shown in Table 1. There was a significant difference among the values of net parasitism rate on all plant genotypes. The value of the net parasitism rate (C_0) of *D. semiclausum* ranged from 12.20 to 20.12 hosts on all studied genotypes. The Q_p gives a demographic estimation for the relationship between the parasitism rate and reproductive rate of a parasitoid. The transformation rate from host population to parasitoid offspring of all genotypes was close to 1($C_0 \cong R_0$).

Age-specific Parasitism Rate and Age-specific Net Parasitism Rate

Age-specific parasitism rate (k_x) and age-specific net parasitism rate (q_x) of *D. semiclausum* on the different genotypes of canola are shown in Figure 2. The age-specific parasitism rate is the mean number of *P. xylostella* larvae parasitized by *D. semiclausum* at age *x*. By considering the survivorship, the age-specific net parasitism rate ($q_x = l_x k_x$) is defined as the weighted number of hosts parasitized by a parasitoid of age *x*.

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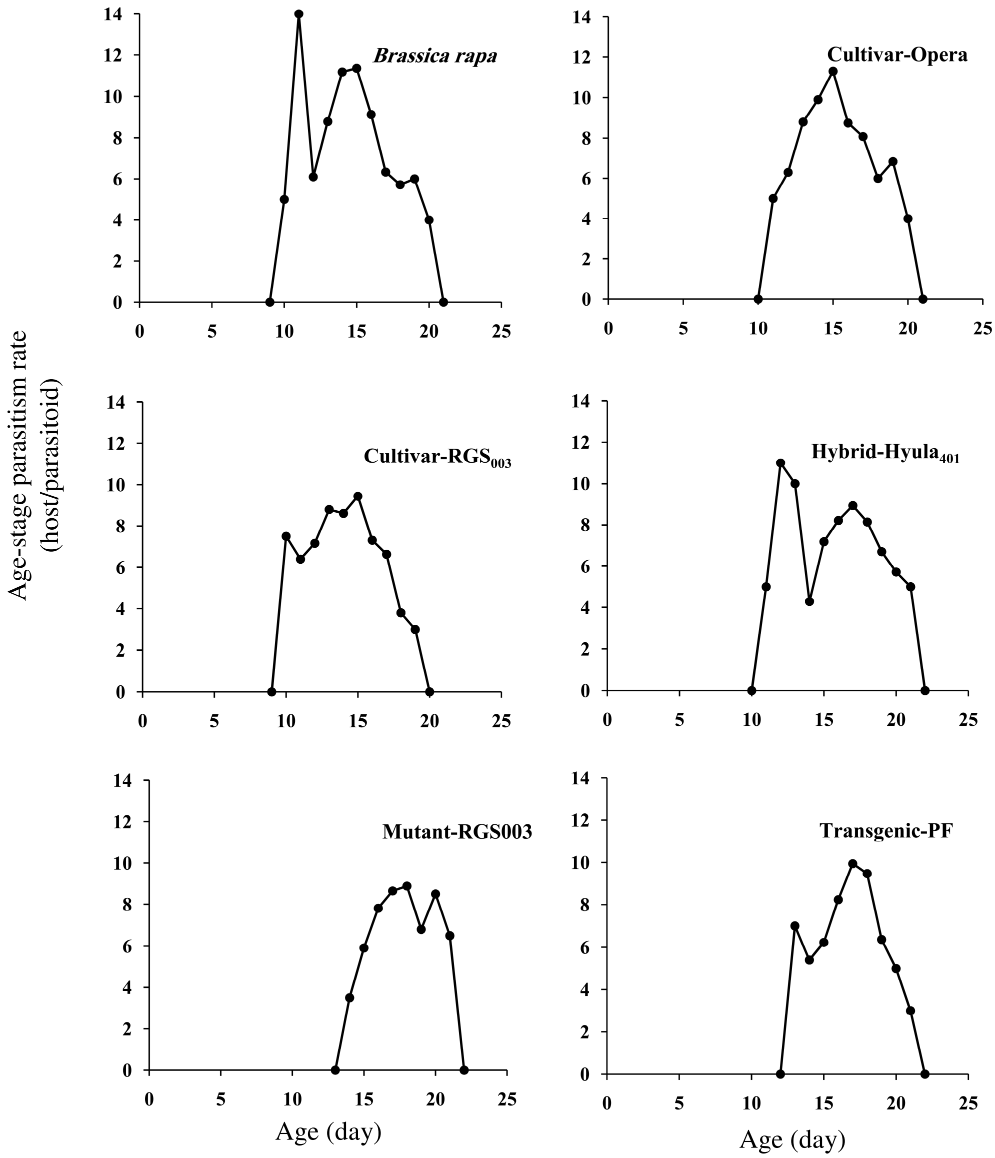

Figure 1. Age-stage parasitism rate (c_{xj}) of *Diadegma semiclausum* on *Plutella xylostella* reared on different *Brassica* genotypes.

Table 1. Parasitism parameters of *Diadegma semiclausum* reared on *Plutella xylostella* on different *Brassica* genotypes under laboratory conditions.[a]

Plant genotypes	C_0 (hosts parasitoid^{-1})	Q_p	ψ (hosts parasitoid^{-1})	ω (hosts parasitoid^{-1} day^{-1})
Brassica rapa	14.945±3.05^{ab}	≅ 1	0.227±0.05^{b}	0.271±0.05^{b}
Cultivar-Opera	20.128±3.54^{a}	≅ 1	0.236±0.03^{a}	0.285±0.04^{a}
Cultivar-RGS$_{003}$	14.951±2.93^{ab}	≅ 1	0.231±0.03^{ab}	0.277±0.05^{ab}
Hybrid-Hyula$_{401}$	12.202±2.61^{b}	≅ 1	0.175±0.03^{c}	0.202±0.03^{c}
Mutant-RGS$_{003}$	13.943±2.81^{ab}	≅ 1	0.177±0.03^{c}	0.205±0.03^{c}
Transgenic-PF	12.556±2.52^{b}	≅ 1	0.175±0.03^{c}	0.202±0.03^{c}

[a] Means with the same letters are not significantly different (α= 0.05) using Tukey-Kramer procedure.

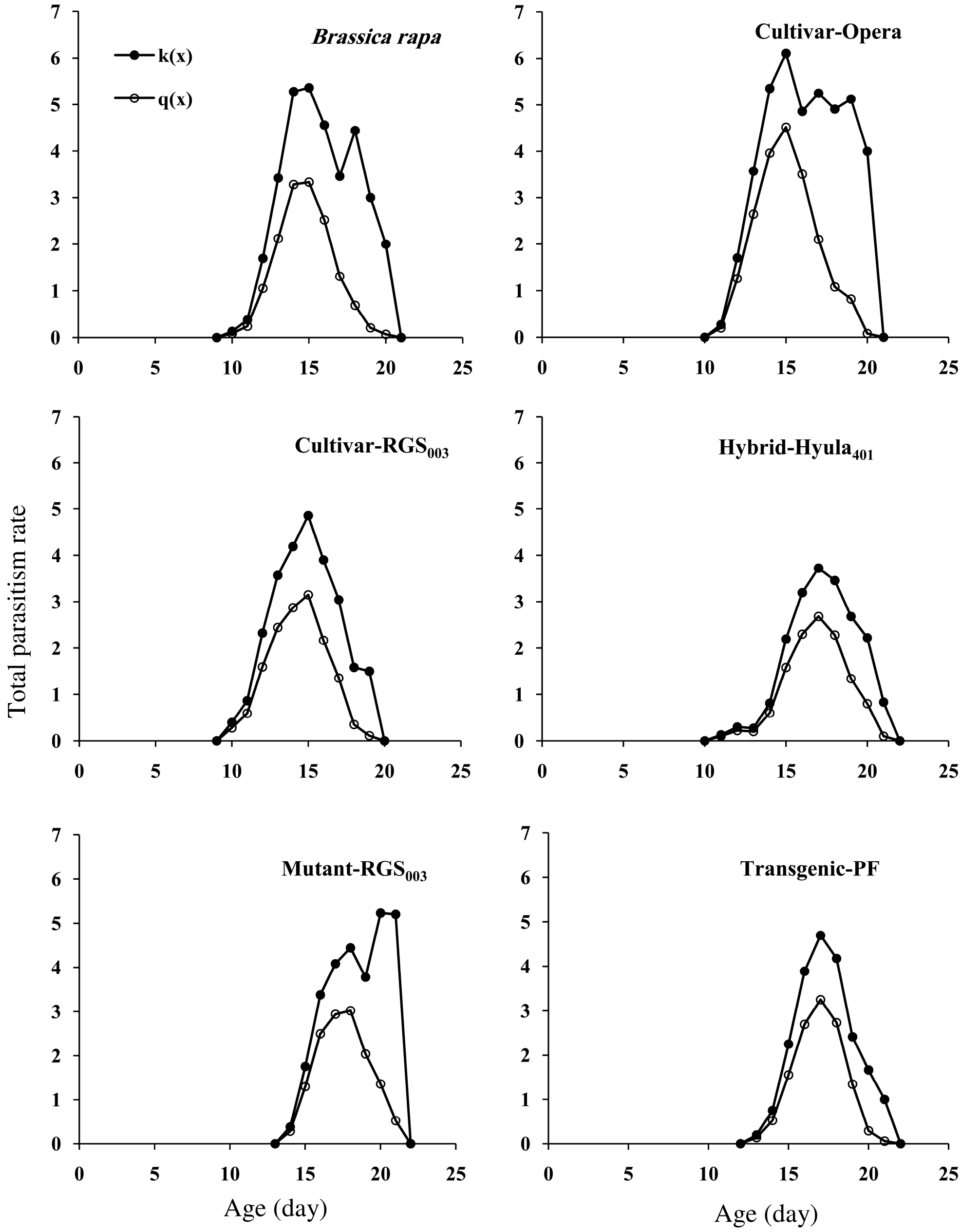

Figure 2. Age-specific parasitism rate (k_x) and age-specific net parasitism rate (q_x) of *Diadegma semiclausum* on *Plutella xylostella* reared on different *Brassica* genotypes.

Stable and Finite Parasitism Rates

Stable parasitism rate (ψ) and finite parasitism rate (ω) of *D. semiclausum* on different genotypes of canola are shown in Table 1. The value of the stable parasitism rate (ψ) ranged from 0.175 (on Hybrid-Hyula$_{401}$) to 0.236 (on Cultivar-Opera) host/parasitoid. Also, the highest and lowest values of the finite parasitism rate (ω) were observed on Cultivar-Opera and Transgenic-PF, respectively. These results indicated that, if the parasitoid population is stable and the parasitoid number is one, the parasitism capacity of this parasitoid ranged from 0.202 to 0.285 hosts per day.

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DISCUSSION

Plant quality in herbivores' diet may affect the parasitism capacity of their parasitoids. The net parasitism rate (C_0) gives the mean number of hosts parasitized by an average individual during its entire life span. Since only female parasitoids are capable of laying eggs in their host larvae and all c_{xj} of immature stages are zero, we obtained low value of C_0 (ranged from 12.21 to 20.12 hosts) compared with predators (Chi *et al*., 2011; Farhadi *et al*., 2011; Khanamani *et al*., 2014, 2015). The parasitism rate of the parasitoid will be equal to its fecundity when the parasitoid lays only one egg per host and all eggs can develop to the adult stage. If some offspring of a parasitoid kill their hosts but fail to emerge from the larvae, the parasitism rate will differ from the fecundity rate (Ebrahimi *et al*., 2013).

Chi and Yang (2003) used Q_p (the ratio of the net predation rate to the net reproductive rate, $Q_p= C_0/R_0$) to describe the transformation rate from prey population to predator offspring. For a predator, the age-specific predation rate can be defined as the number of prey killed by an individual predator of a specific age, whereas the age-specific fecundity is the offspring produced by an individual female predator of that age. Therefore, the predation rate of a predator usually differs from its fecundity (Chi and Yang, 2003), in other words, $R_0<C_0$. Whereas, most parasitoids successfully emerged from their hosts, thus, their parasitism rate is almost identical to their fecundity ($C_0= R_0$). On the other hand, for most parasitoids, especially those who lay only one egg in their host, Q_p (C_0/R_0) will be 1 or close to 1. The Q_p values of *D. semiclausum* on all tested genotypes were calculated to be 1.0. A similar result (Q_p= 1.0) was reported for *Aphidius gifuensis* (Ashmead) reared on *Myzus persicae* (Sulzer) (Chi and Su, 2006). However, when a female parasitoid lays more than one egg in its host, the Q_p value will be < 1.0. Indeed, a demographic estimation for the relationship between the reproductive rate and parasitism rate of a parasitoid could be obtained by Q_p.

The intrinsic rate of increase (r) is a key demographic parameter to depict the population growth potential of an insect (Safuraie-Parizi *et al*., 2014; Goodarzi *et al*., 2015). In order to precisely evaluate the effect of parasitism/predation in a biological control program, we should both assess the growth potential of the parasitoid/predator and its parasitism/predation potential. The finite parasitism rate (ω) is a standard parameter which combines the finite rate of increase (λ), the age-stage structure, and the age-stage parasitism rate (c_{xj}) of a parasitoid population, and is then qualified to explain and contrast the parasitism potential of natural enemies used in biological control programs (Chi *et al*., 2011; Farhadi, *et al*., 2011).

In the present study, the finite parasitism rate (ω) was affected by different genotypes of canola and ranged from 0.202 to 0.285 host parasitoid^{-1} day^{-1}. The low c_{xj} and very low proportion of parasitoid individuals in SASD resulted in a low value of the finite parasitism rate. On the basis of parasitism parameters, the results indicated that *D. semiclausum* had a similar response on Hybrid-Hyula$_{401}$, Mutant-RGS$_{003}$, and Transgenic-PF genotypes followed by canola's progenitor (*B. rapa*) and the cultivated genotypes (Cultivar-Opera and Cultivar-RGS$_{003}$). Our results showed that ω, ψ and C_0 values were higher on *B. rapa*, Cultivar-Opera, and Cultivar-RGS$_{003}$ than the others. Generally, parasitism of *D. semiclausum* was better on canola's progenitor (*B. rapa*) and the cultivated genotypes (Cultivar-Opera and Cultivar-RGS$_{003}$). A possible explanation for differences in the parasitism parameters may be due to plant chemistry. It is hypothesized that the changes in chemistry of the plants will affect the life history and performance of insects associated with them. Several studies have reported that secondary metabolites in host diets affect the survival rate, growth, development, and body weight

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of their parasitoids (Campbell and Duffey, 1979; Barbosa *et al*., 1991; Sznajder and Harvey, 2003; Harvey *et al*., 2007). We previously measured the levels of secondary metabolites (glucosinolates) in these genotypes (Nikooei *et al*., 2015). Glucosinolates (GS) concentration was higher in canola's progenitor (*B. rapa*) and the cultivated genotypes (Cultivar-Opera and Cultivar-RGS_{003}) and lower on Hybrid-$Hyula_{401}$, Mutant-RGS_{003}, and Transgenic-PF. In addition, the results of our previous study (unpublished data) showed that the life table parameters of *D. semiclausum* was significantly affected by these genotypes. A better performance of the parasitoid was observed on the genotypes which contained higher level of GS.

Diadegma semiclausum parasitizes *P. xylostella* specially feeding on Brassicaceae plants containing GS. As a specialist herbivore, *P. xylostella* uses GS as feeding stimulant and indicator of host plant suitability (Bartlet *et al*., 1999; Li *et al*., 2000). Therefore, the performance of host could be better on genotypes having higher level of GS (Nikooei *et al*., 2015). Since the performance of a parasitoid is followed by its host, we also found that *D. semiclausum* had higher efficiency on genotypes having higher level of GS (unpublished data). In conclusion, before applying a precise biological control program, it is important to study the interactions among different host plants and biological control agents, considering both growth population potential and parasitism rate of a parasitoid.

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تاثیر ژنوتیپ‌های دستکاری شده ژنتیکی کروسیفر بر ظرفیت پارازیتیسم زنبور پارازیتوئید *Diadegma semiclasum* روی *Plutella xylostella*

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چکیده

کیفیت گیاه در رژیم غذایی گیاهخوار علاوه بر کارایی گیاهخوار ممکن است کارایی پارازیتوئید آن را نیز تحت تاثیر قرار دهد. ظرفیت پارازیتیسم زنبور پارازیتوئید *Diadegma semiclausum* روی بید کلم *Plutella xylostella* پرورش یافته روی ژنوتیپ‌های مختلف دستکاری شده ژنتیکی کروسیفر، شامل جد کلزا *Brssica rapa* L.، دو رقم زراعی کلزا (Opera و RGS_{003})، یک رقم هیبرید ($Hyula_{401}$)، یک ژنوتیپ جهش یافته به وسیله اشعه گاما ($Mutant\text{-}RGS_{003}$) و یک ژنوتیپ تراریخت (Transgenic-PF) مورد ارزیابی قرار گرفت. تمامی آزمایشات در اتاق رشد با شرایط دمایی ۱±۲۵ درجه سلسیوس، رطوبت نسبی ۵±۶۵ درصد و شرایط نوری ۱۶ ساعت روشنایی و ۸ ساعت تاریکی انجام شد. نرخ خالص پارازیتیسم (C_0) زنبور پارازیتوئید *D. semiclausum* روی

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جد کلزا *B. rapa*، رقم زراعی Opera، رقم زراعی RGS_{003}، رقم هیبرید $Hyula_{401}$، ژنوتیپ موتانت RGS_{003} و تراریخت PF به ترتیب برابر ۱۴/۹۴، ۲۰/۱۲، ۱۴/۹۵، ۱۲/۲۰، ۱۳/۹۴ و ۱۲/۵۵ میزبان بود. نرخ تبدیل از جمعیت میزبان به نتاج پارازیتوئید (Q_p)، روی تمامی ژنوتیپ‌ها نزدیک به یک بود ($C_0 \cong R_0$). همچنین، نرخ متناهی پارازیتیسم (ω) روی ژنوتیپ‌های ذکر شده در بالا، به ترتیب برابر با ۰/۲۷۱، ۰/۲۸۵، ۰/۲۷۷، ۰/۲۰۲، ۰/۲۰۵ و ۰/۲۰۲ میزبان/پارازیتوئید/روز برآورد شد. نرخ متناهی پارازیتیسم پارامتری است که نرخ متناهی رشد جمعیت، توزیع سنی - مرحله ای پایدار و نرخ پارازیتیسم ویژه سنی - مرحله‌ای را در بر می‌گیرد، بنابراین این پارامتر می‌تواند برای ارزیابی کارآمدی یک پارازیتوئید مورد استفاده قرار گیرد. در پایان، زنبور پارازیتوئید *D. semiclausum* دارای ظرفیت پارازیتیسم بالاتری روی جد کلزا و ارقام زراعی بود که بر اساس میزان متابولیت‌های ثانویه میزبان‌های گیاهی مناسب‌تری برای بید کلم بودند.

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