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Parasitism capacity and searching efficiency of *Diaeretiella rapae* parasitizing *Brevicoryne brassicae* on susceptible and resistant canola cultivars

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ABSTRACT

Different cultivars of aplant species can affect the foraging and efficiency of natural enemies, both directly through physical and biochemical properties or indirectly through the herbivore's diet. In this study, the parasitism capacity and functional response of *Diaeretiella rapae* McIntosh were determined on the cabbage aphid, *Brevicoryne brassicae* (L.) reared on susceptible (Opera) and resistant (Okapi) canola cultivars under laboratory conditions at 25 ± 1 °C, 60 ± 5% RH and a16:8 h L:D photoperiod. The parasitoid exhibited Type II and Type III functional responses on the resistant and susceptible cultivars, respectively. The estimated value of searching efficiency (a) was 0.1637 ± 0.1095 h^{-1} on the resistant cultivar whereas its value was dependent on host density on the susceptible cultivar. The handling times (T_h) on the susceptible and resistant canola cultivars were 0.108 ± 0.040 and 0.320 ± 0.048 h, respectively. The net parasitism rate (C_0) of the parasitoid wasp varied from 128.09 hosts per parasitoid lifetime on the susceptible to 71.01hosts on the resistant canola cultivar. The transformation rate from host population to parasitoid offspring (Qp) was equal to 1 on both cultivars ($C_0 = R_0$). The finite parasitism rate (ω) on the susceptible cultivar (0.819 hosts per parasitoid per day) was significantly higher than that on the resistant one (0.578 hosts per parasitoid per day). In conclusion, canola cultivars affected the performance of *D. rapae* in controlled small-scale laboratory experiments and compared with the susceptible cultivar, the resistant one had anadverseeffect on the efficiency of the parasitoid.

Introduction

The cabbage aphid, *Brevicoryne brassicae* (L.), is one of the most damaging and consistently present pests on cruciferous crops. This pest has a worldwide distribution and causes direct and indirect damage by sucking the sap of plants and transmitting plant viruses (Blackman and Eastop, 2000). *Brevicoryne brassicae* prefers feeding on young plant tissues and this makes it a serious pest of *Brassica* plants. While the most common approach for controlling aphid populations is application of chemical insecticides, the development of resistance by pests to insecticides and the adverse effects of their use on the environment and nontarget organisms have meant that the use of other pest control methods, including resistant cultivars and biological control agents, have received more attention in recent decades (Blande et al., 2008). Aphid parasitoids of the subfamily Aphidiinae are very important control agents for various aphids in many crops (Desneux et al., 2009; Pons et al., 2011; Stara et al., 2011). Among them, *Diaeretiella rapae* MacIntosh (Hymenoptera: Braconidae), a solitary and polyphagous endoparasitoid, is described as the most effective biological control agent of cabbage aphid (Pike et al., 1999; Jankowska and Wiech, 2003).

Before using natural enemies in a biological control program, it is essential to know their efficiency on the crop. There are various criteria for evaluating and selecting biological control agents, including parasitoids (Fathipour et al., 2001; Kalule and Wright, 2002; Askarianzadeh et al., 2008; Desneux and Ramirez-Romero, 2009; Soufbaf et al., 2012; Nikooei et al., 2015a, 2017). The evaluation of natural enemies may entail the study of their demographic parameters and foraging behaviors (Donelly and Phillips, 2001; Fathipour et al., 2006). Functional response, an important behavioral characteristic of parasitoids, is defined as the impact of different densities of a host on the parasitism rate or, for predators, the feeding rate. Searching efficiency (the rate at which a parasitoid searches) and handling time (the time taken for a parasitoid to encounter and parasitize a single host) are two important parameters that can be estimated from analysis of functional response data. Three types of functional response were proposed by Holling (1959). In type I, the number of hosts attacked increases linearly to a

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maximum, then remains constant as host density increases. In type II, the number of hosts attacked increases as host density increases but this increase is not linear and the slope of the curve decreases gradually to reach a constant value. In type III, the number of hosts attacked forms asigmoid curve (S shape) whose slope increases initially and then decreases. The functional response and similar behaviors in natural enemies can be affected not only by the characteristics of the natural enemy and host (King, 1994; Mansfield and Mills, 2004) but also by the variety of the host plant (Coll and Ridgway, 1995; Fathipour et al., 2001), the age of the natural enemy (Asadi et al., 2012; Fathipour et al., 2017, 2018) and the number of generations of a natural enemy (Khanamani et al., 2015). Plant species and cultivar can affect the behavioral characteristics and efficiency of natural enemies through physical and biochemical properties or indirectly by changing the host's dietand hence its quality (herbivores) (Price, 1986). Several studies have been carried out on the functional response of *D. rapae* on different aphid species such as *B. brassicae* (Fathipour et al., 2006; Moayeri et al., 2013), *Diuraphis noxia* (Mordvilko) (Bernal et al., 1994; Lester and Holtzer, 2002; Tazerouni et al., 2012), *Lipaphis erysimi* (Kaltenbach) (Pandey et al., 1984; Abidi et al., 1987) and *Schizaphis graminum* (Rondani) (Dashti et al., 2010). However, since *D. rapae*is perhaps the most important agent for natural control of *B. brassicae* (Pike et al., 1999; Jankowska and Wiech, 2003), it is therefore necessary to pay more attention to it. Here, we selected two canola, *Brassica napus* L., cultivars (Opera and Okapi) as representative of high- and low-quality host plants that differ dramatically in resistance to the cabbage aphid (Karami et al., 2018). We previously showed that Okapi, due to the longer development time of cabbage aphids on it, the lower survival rate of immature aphids, as well as lower fecundity of adult aphids, is the cultivar with the highest known level of resitance to *B. brassicae* (Karami et al., 2018). Conversely, based on the shortest development time and highest values of fecundity and survival of the cabbage aphidon Opera, it was recognized as the most susceptible cultivar to this pest. Since *D. rapae*is an effective biological control agent of the cabbage aphid, the present study was carried out to measure the effect of the susceptible and resistant canola cultivars on the parasitism capacity and the functional response attributes of this parasitoid to varying densities of *B. brassica.*

Materials and methods

Plant cultivation

Our previous study, evaluating ten canola cultivars, indicated that Okapi was the least suitable for the development and reproduction of the cabbage aphid, whereas Opera was the most suitable cultivar (Karami et al., 2018). Seeds of Opera and Okapi were obtained from the Seed and Plant Improvement Research Institute in Karaj, Iran. The seeds were sown in 20 cm diameter plastic pots filled with field soil and grown under greenhouse conditions at 25 ± 5 °C, 60 ± 10% RH and a 16: 8 h L: D photoperiod without any additional fertilizer or pesticide application. Excised fully expanded young leaves of the canola cultivars were used for experiments when plants were five weeks old.

Insect culture

Brevicoryne brassicae and *D. rapae* used in the trials were collected from a cabbage field at the Faculty of Agriculture, Tarbiat Modares University, Tehran. The aphid colony was maintained on potted cabbage (Snow-March cultivar) under laboratory conditions. All experiments and the rearing of the aphid and parasitoid were carried out at 25 ± 1 °C, 60 ± 5% RH and a 16:8 h L:D photoperiod. To allow aphids to adapt to new host plant varieties before experiments, cabbage aphids were reared on each cultivar for two generations in a growth chamber at the above-mentioned conditions before being used in the main experiments. The laboratory colony of the parasitoid was reared on cabbage aphids fed on cabbage. For this purpose, a potted cabbage plant infested by cabbage aphids was placed in a perspex cage (50 × 50 × 80 cm) with a muslin sleeve on one side of the cage. Then ten pairs of 2-day-old mated parasitoids were released into the cage. Before the start of the trials, the offspring of the parasitoid were separately reared forone generation (in the parasitism capacity experiments) or two generations (in the functional response experiments) on cabbage aphid fed on the susceptible and resistant canola cultivars.

Functional response experiments

The experimental arena consisted of clear plastic containers (5 × 12 × 14 cm) with a micromesh screen on the lids for ventilation and the bottom covered with wet tissue paper and a canola leaf, with its petiole wrapped in a piece of moist cotton to provide humidity and keep the leaf fresh, placed upside down within it. Distilled water and a paper strip coated with a thin layer of honey were placed in containers as food for the parasitoid. Nymphs of *B. brassicae* in the stage preferred by the parasitoid (2nd to 4th instars) were randomly placed on the susceptible and resistant canola cultivars leaves inside the containers at densities of 2, 4, 8, 16, 32, 64 and 128 per canola leaf. One mated female parasitoid (maximum 24 h old) was introduced into each container at the start of the experiment. Each host density was replicated eight times. After 24 h, the parasitoid from each dish was removed and the aphids in the dish were kept in the growth chamber until mummification of parasitized aphids.

Functional response analysis

Model selection and hypothesis testing are the two principal steps that underlie the statistical analysis of functional response data (Juliano, 2001). First, we graphed the correlation between the proportion of aphids parasitized versus the initial aphid density using logistic regression. In type II response, the proportion of hosts parasitized declines monotonically with host density while in the type III response, it is positively density-dependent over some region of host density (De Clercq et al., 2000). The negative or positive sign of the linear coefficient estimated by the logistic regression can be used to distinguish the shape of the functional response curve (type II or type III, respectively).

Second, a nonlinear regression was used to estimate the searching efficiency (a) and handling time (T_h) parameters using the least square method with the Doesn't Use Derivatives (DUD) initialization. The DUD method allows the calculation of a confidence interval for each parameter. The random parasitoid equation (Royama, 1971; Rogers, 1972) (Eq. (1)) was used to estimate these parameters. For a type III functional response, if the confidence interval of the parameter c includes zero, it means that this parameter is not significantly different from zero, and must be removed from the model. Finally, the reduced model (Eq. (3)) was used, in which the parameter c was removed. The mentioned equations are as follows:

$$N_a = N_0\,[1 – \exp\,(a\,(T_h\,N_a – T))] \quad (1)$$

$$a = (\mathrm{d} + \mathrm{b}\,N_0)/(1 + \mathrm{c}\,N_0)\ \text{(Full model)} \quad (2)$$

$$a = \mathrm{d} + \mathrm{b}\,N_0\ \mathrm{c} = 0\ \text{(Reduced model)} \quad (3)$$

where N_a is the number of parasitized hosts, N_0 is the initial host density, T is the total time available for the parasitoid (here 24 h), a is searching efficiency, T_h is the handling time, b, c and d are constant values.

Parasitism capacity experiments

The experimental arena for this experiement was the same as used for the functional response experiment. To obtain adult parasitoids to start the experiments, 100 individuals (the number was determined