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Temperature dependent functional response of *Diaeretiella rapae* (Hymenoptera: Aphidiidae) to the cabbage aphid, *Brevicoryne brassicae* (Hemiptera: Aphididae)

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Abstract. *Diaeretiella rapae* MacIntosh (Hymenoptera: Aphidiidae) is one of the most common and successful parasitoids of the cabbage aphid. The functional response of *D. rapae* towards cabbage aphids was examined in laboratory studies at three constant temperatures, 17°C, 25°C and 30°C. *D. rapae* exhibited a type II functional response at all three temperatures. The search rates were uninfluenced by temperature whereas handling times differed significantly between 17°C and 25°C, and between 17°C and 30°C, but not between 25°C and 30°C. This study is a first-step in the evaluation of the effectiveness of *D. rapae* as a biocontrol agent of *Brevicoryne brassicae* at different temperatures.

INTRODUCTION

The cabbage aphid, *Brevicoryne brassicae* (Linneaus) (Hemiptera: Aphididae) is a serious cosmopolitan pest, attacking many cruciferous crops, such as broccoli, canola, cabbage, cauliflower and mustard (Blackman & Eastop, 2000; Capinera, 2001; Modarres Najafabadi et al., 2005; Desneux et al., 2006). This pest can cause direct damage by inducing plant deformations (Oatman & Planter, 1969) and by stunting or killing young plants (Bonnemaison, 1965; Ellis et al., 1998; Ulusoy & Bayhan, 2006). In addition, it can also induce indirect damage by transmitting more than 20 different viruses including yellow mosaic virus, cucumber mosaic virus, onion yellow dwarf virus and cabbage black ring spot (Ellis et al., 1998; Blackman & Eastop, 2000).

Considering the difficulties associated with aphid control there is one environmentally safe control method, which is to use natural enemies, especially parasitoids. *Diaeretiella rapae* MacIntosh (Hymenoptera: Aphidiidae) is reported to be an important and promising endoparasitoid of more than 60 aphid species, including the cabbage aphid (Hagvar & Hofsvang, 1991), green peach aphid [*Myzus persicae* (Sulzer)] (Stark & Acheampong, 2007) and Russian wheat aphid [*Diuraphis noxia* (Mordvilko)] (Stary, 1999; Rakhshani et al., 2008).

Evaluation of the changes that occur in the characteristics and efficiency of candidate biocontrol agents with changes in environmental factors is crucial for their successful use in biocontrol programs. The response of a natural enemy to increasing host density (functional response) is important for the outcome of parasitoid-based biocontrol programs (Berryman, 2004) and together with the numerical response an indispensable element in their biological characterization (Cedola et al., 2001, Gilioli et al., 2005) and an important determinant of their effectiveness as biological control agents (Houck & Strauss, 1985; Jost & Ellner, 2000). Different factors may influence their functional responses, including host plant surface traits (Coll & Ridgway, 1995; Messina & Hanks, 1998; Madadi et al., 2007), host species (Mansfield & Mills, 2004), natural enemy life stages (Seko & Miura, 2008), host age (King, 1994; Ode & Strand, 1995) and spatial complexity (Madadi et al., 2011). However, the functional response of poikilothermic organisms like parasitoids, are greatly affected by temperature (Cave & Gaylor, 1989; Flinn, 1991; Enkegaard, 1994; Bazzocchi & Burgio, 2001; Jones et al., 2003; Kalyebi et al., 2005; Shojaei et al., 2006; Moezipour et al., 2008; Tazerouni et al., 2012).

The functional response of *D. rapae* to the cabbage aphid has been studied (e.g. Fathipour et al., 2006) but no one has considered the effect of temperature. Consequently, the aim of this study was to determine the influence of temperature on the searching efficiency and handling time of *D. rapae* attacking cabbage aphid nymphs.

MATERIAL AND METHODS

Insect rearing

Cabbage aphids and *D. rapae* were originally collected from infested ornamental cabbage, *Brassica oleracea* L. (var. *acephala*), on the Zanjan University campus in October 2010 and subsequently kept in separate cultures on *B. oleracea* in net covered cages (40 × 40 × 40 cm) at 24 ± 2°C, 45 ± 5% R.H. and a photoperiod of 16L : 8D in the Insect Ecology and Biocontrol Laboratory, the Research Institute of Physiology and Biotechnology, Zanjan University.

Functional response experiments

Mummified cabbage aphids were collected from the colony and placed individually in small vials (approx. 4 ml). After 24 h, newly emerged parasitoids were removed and placed in plexiglas cylindrical cages (15 × 35 cm) and fed a 10% honey solution. Twenty four hours later mated females were recovered and kept individually in similar small vials for 2–3 h before using them in the experiments.

The experimental arena consisted of a cabbage leaf placed in a Petri dish (9 cm diameter) with two droplets of honey and a piece of wet cotton wool added as food and a source of water. Two, 4, 6, 8, 16, 24, 40 or 50 second instar nymphs of *B. brassicae* were placed randomly on the leaf. The number of replicates was 15 except for the density 8 nymphs per leaf at 17°C and 50 at 30°C, for which there were 14 replicates. One female *D. rapae* was added to each arena, which was then placed in a growth chamber at 17, 25 or 30°C, 65 ± 5% R.H. and a photoperiod of 16L : 8D. After 24 h the parasitoids were removed and the arenas were kept in the same conditions for a further 2 weeks after which the numbers of mummified aphids were recorded. The present study thus only examines the influence of temperature on the functional response in terms of the parasitization activity of the adult parasitoids. All replicates at each temperature were conducted simultaneously over a 3-week period.

Statistical analysis

The overall effect of temperature on the rate of parasitization of *B. brassicae* by *D. rapae* was analysed by comparing the number of mummified aphids recorded at the different temperatures (one-way ANOVA or Kruskal-Wallis test, SAS Institute Inc. 2004).

Subsequently, the type of functional response and the parameters characterizing it were estimated for each temperature (Juliano, 2001). Logistic regressions of the proportions of aphids parasitized at different host densities were used to determine the type of functional response (Trexler et al., 1988; Trexler & Travis, 1993) using the quadratic model:

$$(1)\quad \frac{N_e}{N_0} = \frac{\exp(P_0+P_1N_0+P_2N_0^2)}{1+\exp(P_0+P_1N_0+P_2N_0^2)}$$

where N_e is the number of parasitized aphids, N_0 is the host density and P_0, P_1 and P_2 are the parameters to be estimated. Significant negative values of P_1 indicate a type II functional response, whereas positive significant values indicate a type III functional response (Juliano, 2001).

Non-linear least-square regression (NLIN procedure, SAS Institute Inc., 2004) of the number of mummified aphids recorded at different host densities was used for estimating searching rates and handling times (Juliano & Williams, 1987; Juliano, 2001) based on either the Random Parasitoid Equation (Rogers, 1972) (Equation 2), or if that failed to provide an adequate fit or meaningful parameter estimates, Holling's Disc Equation (Holling, 1961) (Equation 3).

$$(2)\ \text{Roger's model}\quad N_e = N_0\left\{1-\exp\left[-\frac{aT}{1+aT_hN_0}\right]\right\}$$

$$(3)\ \text{Holling's Disc Equation}\quad N_e = \frac{aN_0T}{(1+aN_0T_h)}$$

Where a is the search rate, T the total available time (here 24 h) and T_h the handling time (Juliano & Williams, 1987; Juliano, 2001). The individual parameters for each pair of temperatures were compared using *t*-tests (SAS/STAT, NLMIXED, SAS Institute Inc., 2004).

TABLE 1. Mean (± SE) number *Brevicoryne brassicae* nymphs parasitized by *Diaeretiella rapae* at different temperatures.

Density	17°C	25°C	30°C
2	1.44 ± 0.16 A	1.56 ± 0.13 A	1.50 ± 0.13 A
4	2.56 ± 0.25 A	3.06 ± 0.27 A	2.88 ± 0.26 A
6	4.07 ± 0.36 A	4.50 ± 0.42 A	4.27 ± 0.42 A
8	5.14 ± 0.41 A	5.94 ± 0.32 A	5.88 ± 0.42 A
16	6.81 ± 0.67 A	8.19 ± 0.56 A	7.87 ± 0.54 A
24	7.73 ± 0.82 A	10.44 ± 0.7 B	9.94 ± 0.7 AB
40	10.4 ± 0.89 A	14.13 ± 1.22 B	13.13 ± 1.03 AB
50	10.93 ± 0.88 A	15.8 ± 1.17 B	13.64 ± 1.2 AB

Different letters in a row (A, B) indicate significant differences between different temperatures, P < 0.05.

RESULTS

The effect of temperature on the mean number of cabbage aphid nymphs parasitized by *D. rapae* was apparent only at the higher host densities (Table 1). Temperature, cabbage aphid density and their interaction had a significant effect on the number of nymphs parasitized (GLM 17°C, df = 2, 334, F = 14.89, P < 0.0001; GLM 25°C, df = 7, 334, F = 129.5, P < 0.0001 and GLM 30°C, df = 14, 334, F = 1.84, P = 0.032, respectively) (Table 1).

Temperature did not affect the type of functional response recorded for *D. rapae* as the linear term of the logistic regression in all cases was significantly negative, i.e. the number of cabbage aphids parasitized increased with a decreasing slope, which indicates a type II functional response (Table 2, Fig. 1).

Roger's Random Parasitoid Equation (Rogers, 1972) did not fit the data and the functional response parameters were consequently estimated using Holling's Disc Equation (Holling, 1961) (Table 3). The search rates were not influenced by temperature (t-test, 17°C vs. 25°C, t = –0.152, *P* = 0.879; 17°C vs. 30°C: *t* = –0.243, *P* = 0.809; 25°C vs. 30°C: *t* = –0.098, *P* = 0.922) whereas handling times recorded at 17°C and 25°C and at 17°C and 30°C differed significantly, but not at 25°C and 30°C (17°C vs. 25°C: *t* = 3.876, *P* < 0.001; 17°C vs. 30°C: *t* = 2.762, *P* = 0.006; 25°C vs. 30°C: *t* = –1.138, *P* = 0.256). The maximum attack rates (T/T_h) were 14.54, 24.74 and 20

TABLE 2. Logistic regression analysis of the proportion of *Brevicoryne brassicae* nymphs parasitized by *Diaeretiella rapae* at different host densities at different temperatures.

Temp.	Parameter	Estimate	SE	χ^2 value	Pvalue
17°C	Constant	1.107	0.179	38.32	<.0001
	Linear	–0.095	0.015	41.84	<.0001
	Quadratic	0.001	0.0002	15.48	<.0001
25°C	Constant	1.46	0.185	62.5	<.0001
	Linear	–0.093	0.014	41.06	<.0001
	Quadratic	0.001	0.0002	16.87	<.0001
30°C	Constant	1.347	0.183	54.39	<.0001
	Linear	–0.089	0.0143	37.35	<.0001
	Quadratic	0.0009	0.0002	12.85	0.0003

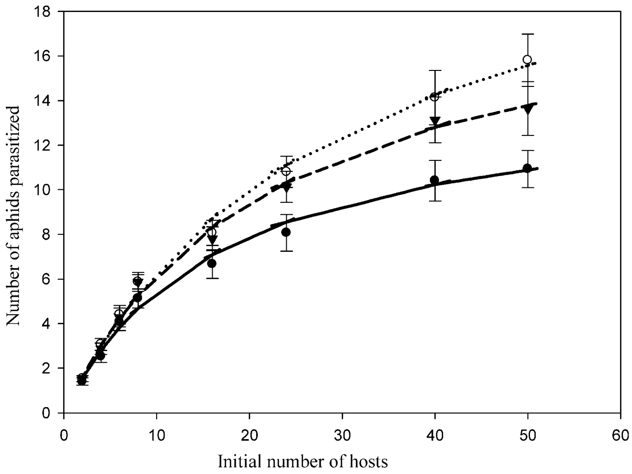

Fig. 1. Functional response of *Diaeretiella rapae* to *Brevicoryne brassicae* nymphs at 17°C (solid line, black circles), 25°C (dotted line, white circles) and 30°C (dashed line, black triangles). The symbols represent average values (with standard errors) and the lines the fitted model.

second instar aphid nymphs per day at 17°C, 25°C and 30°C, respectively.

DISCUSSION

D. rapae showed a type II functional response to increasing densities of cabbage aphid nymphs at all the temperatures tested. Type II functional responses are commonly recorded for parasitoids, especially under controlled conditions in the laboratory (Fernandez-Arhex & Corley, 2003). In fact, more than three quarters of such studies carried out on parasitoids between 1959–2001 report type II functional responses (Fernandez-Arhex & Corley, 2003). This may be due to the generally artificial experimental design in which parasitoids have a fixed time to search for hosts and there is a lack of any spatial complexity within patches (Fernandez-Arhex & Corley, 2003).

A type II functional response of *D. rapae* is reported for the cabbage aphid (Fathipour et al., 2006), Russian wheat aphid (Bernal et al., 1994; Tazerouni et al., 2011, 2012) and green peach aphid (Yu et al., 1993). The rate at which this parasitoid attacks cabbage and green peach aphids is estimated to be 0.033 h^{-1} (Fathipour et al., 2006) and 0.031 h^{-1} (Yu et al., 1993), respectively, which is in accordance with our results, whereas the rate at which it attacks the Russian wheat aphid is higher (0.056 h^{-1} (Bernal et al., 1994) and 0.072 h^{-1} (Tazerouni et al., 2011), respectively). These higher rates of attack might be due to the differences in the sizes of the hosts, as the Russian wheat aphid is smaller than the cabbage aphid (Antolin et al., 2006), and handling time in aphid parasitoids is thought to be inversely related to host size (Hofsvang & Hagvar, 1986).

TABLE 3. Parameter estimates (mean ± SE) and R^2 values of the functional response of *Diaretiella rapae* parasitizing *Brevicoryne brassicae* nymphs estimated using the Disc Equation. Values in square brackets are 95% confidence limits.

Temperatures	a' (h^{-1})	T_h (h)	R^2
17°C	0.036 ± 0.004 [0.027; 0.045]	1.65 ± 0.14 [1.38; 1.93]	0.66
25°C	0.035 ± 0.004 [0.028; 0.042]	0.97 ± 0.095 [0.78; 1.16]	0.77
30°C	0.037 ± 0.004 [0.029; 0.045]	1.2 ± 0.104 [0.99; 1.41]	0.74

Temperature had a significant effect on the number of cabbage aphids parasitized by *D. rapae* only at the higher cabbage aphid densities, which is reflected in the significantly higher handling time recorded at the lowest temperature. No influence of temperature on attack rate was found. The longer handling time recorded at 17°C is most likely a result of an increase in non-searching activities (e.g. resting). A similar temperature-dependent influence on functional response parameters with a decrease in handling time with increase in temperature without significant effects on search rates is recorded for predators, e.g. the predatory mite *Neoseiulus californicus* (McGregor) attacking *Tetranychus urticae* Koch (Ahn et al., 2009). Considering the effect of global warming and climate change, the effect temperature has on the handling time of *D. rapae* indicates that this parasitoid performs best at temperatures around 25°C and it is likely to be less effective at higher temperatures.

Compared with the parasitization of other aphid species by *D. rapae*, such as *D. noxia*, *M. persicae* and *Lipaphis erysimi* (Kaltenbach), the parasitization of cabbage aphids in the present study was slightly higher than that recorded for *D. noxia* (Tazerouni et al., 2012) and lower than for the other two species (Blande et al., 2004). The highest number of aphids parasitized by *D. rapae* in the present study was 15.8 ± 1.17 at the density of 50 at 25°C (Table 1), which is slightly lower than recorded by Fathipour et al. (2006) (17.3 ± 0.87) for the same host-parasitoid system at a similar temperature and host density. This discrepancy may be due to differences in the parasitoid biotypes or size of experimental arena used.

The results of the present research indicate that *D. rapae* can be used as a biocontrol agent of *B. brassicae* and probably other aphid species, such as the green peach aphid, at temperatures ranging between 17 and 30°C. However, for a comprehensive evaluation of the effectiveness of *D. rapae* in controlling cabbage aphids infesting other host plants more natural and field-based studies are needed (Bernal et al., 1994; Montoya et al., 2000). The present results additionally provide a basis for using *D. rapae* for augmentative or conservational biocontrol using the banker plant method (Huang et al., 2011) by developing a system consisting of crop or non-crop plants infested with a specialist crucifer-feeding aphid species as a non-pest alternative prey.

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