Functional Response of Aphidoletes aphidimyza *Rondani (Diptera: Cecidomyiidae) to* Aphis gossypii *Glover (Hemiptera: Aphididae): Effects of Vermicompost and Host Plant Cultivar*

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Functional Response of *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) to *Aphis gossypii* Glover (Hemiptera: Aphididae): Effects of Vermicompost and Host Plant Cultivar

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Keywords

Cucumber, melon aphid, predatory gall midge, prey density, trichome, vermicompost, prey density

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Abstract

Interactions between natural enemies and herbivores may be affected by application of fertilizers and different cultivars. We investigated the functional response of the predatory gall midge, *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) larvae to the nymphs of the melon aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae), reared on two commonly grown cucumber cultivars in Iran (Khasib and Karim) treated with different vermicompost/soil ratios (0:100, 10:90, 20:80, and 30:70%). Based on logistic regression analysis, *A. aphidimyza* revealed a type II functional response to the aphid in all treatments. Attack rates and handling times of *A. aphidimyza* larvae on different vermicompost/soil ratios ranged from 0.076 to 0.140 h^{-1} and 0.969 to 1.164 h on Khasib and from 0.092 to 0.123 h^{-1} and 0.905 to 1.229 h on Karim, respectively. Furthermore, increasing the density of the melon aphid on both cultivars amended with vermicompost/soil ratios resulted in increased prey consumption by the predator. Density of trichomes increased when plants received higher concentrations of vermicompost. So, trichomes may be responsible for different attack rates and handling times of *A. aphidimyza* on both cultivars.

Introduction

The predatory gall midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) is one of the most important biological control agents of aphids. This predator either exists naturally on aphid-infested plants (Minarro *et al* 2005) or is used in greenhouses for aphid control (Meadow *et al* 1985). Larvae of *A. aphidimyza* are the voracious stage to suck out the aphids' body contents after paralyzing them by injecting a toxin into their leg joints (Perdikis *et al* 2008). It has been reported that *A. aphidimyza* attacks more than 80 aphid species (Yukawa *et al* 1998), including the melon aphid *Aphis gossypii* Glover (Hemiptera: Aphididae) (Bennison 1992, Hosseini *et al* 2010). *Aphis gossypii* is a polyphagous and cosmopolitan species that is widely distributed in tropical, subtropical, and temperate regions of the world (Satar *et al* 1999). It is a serious pest of a wide range of plants, such as several cucurbitaceous crops, cotton, potato, and ornamental plants in both field and greenhouse production (Deguince *et al* 1994, Blackman & Eastop 2000). It feeds on the underside of the leaves, sucking phloem sap from the plant, which causes both direct damage, by making foliar chlorosis and leaf curling, and indirect damage, by transmission of several plant viruses (Blackman & Eastop 2000).

One of the primary methods for assessing the efficiency of a predator against a prey is to understand the relationship between prey density and predator consumption, which is defined as functional response (Solomon 1949). The functional response is an important characteristic of predator-prey dynamics, understanding of which can help improving

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the effectiveness of biological control of the target pest (Jeschke *et al* 2004). Several biotic and abiotic factors have been reported that influence the functional response of predators (Parajulee *et al* 1994, Kalyebi *et al* 2005, Ding-Xu *et al* 2007, Hassanpour *et al* 2011), one of which is bottom-up factors (Mahdian *et al* 2007). In general, efficiency of natural enemies may be affected by host plants both directly (morphological features) and indirectly (chemical characteristics) (Price *et al* 1980, Sabelis *et al* 1999).

Top-down regulation of herbivore populations may be affected by plant cultivars. Due to various physical and chemical characteristics, different cultivars of a plant species may influence prey as well as predator fitness. Significant impacts of host plant cultivars on growth, development, reproduction, body size, and foraging behavior of natural enemies have been well-documented (De Kogel *et al* 1999, Gao *et al* 2008, Sarfraz *et al* 2008). Furthermore, there have been numerous studies demonstrating that nutrient addition can mediate the strength of top-down forces by influencing plant quality (Forkner & Hunter 2000, Denno *et al* 2002). For example, according to Fox *et al* (1990), fertilized *Brassica oleracea* plants infested by *Plutella xylostella* L. were preferred by the parasitoid *Diadegma insulare* (Cresson) than unfertilized plants. Similarly, fertilization of *Brassica napus* plants positively affected the performance of *A. aphidimyza* on *Lipaphis erysimi* Kalt. (Fallahpour *et al* 2015). Intensified efficiency of a few natural enemies has been detected by addition of organic fertilizers to the growth medium, as well. For instance, it has been reported a better settling of predators in crops fertilized with cow manure than with synthetic fertilizers (Duchovskiene *et al* 2012), as well as a high parasitism rates of parasitoids in either compost (Ponti *et al* 2007) or vermicompost (Suryawana & Reyes 2007) fertilized plants.

Vermicompost, as a nutrient-rich and microbiologically active organic fertilizer, is the final product of the biological breakdown of organic matter by earthworms. It not only improves the physical structure and water holding capacity of the soil but also, by having a high nutrient ratio and microbial activity, enhances seed germination, plant growth, and crop yield (Atiyeh *et al* 2001, Arancon *et al* 2008). Recently, there has been much interest in the potential of vermicompost for controlling pest populations. For example, establishment of pest populations such as two-spotted spider mite (*Tetranychus urticae* Koch), mealy bug (*Pseudococcus* sp.), green peach aphid (*Myzus persicae* Sulzer) (Arancon *et al* 2007), cucumber beetle (*Acalymna vittatum* Fabr.), tobacco hornworm (*Manduca sexta* L.) (Edwards *et al* 2010), and melon aphid (Razmjou *et al* 2012) was negatively affected by addition of vermicompost to the growth medium. However, there are few reports on the effect of vermicompost on the third trophic level, especially on the predatory characteristics of biological control agents (Suryawana & Reyes 2007). Therefore, the aim of the present study was to evaluate the effect of two cucumber cultivars and four vermicompost levels on the biocontrol potential of *A. aphidimyza* on *A. gossypii* populations through the study of its functional response, which can improve our understanding of predator-prey interactions between *A. aphidimyza* and *A. gossypii*.

Material and Methods

Plants and insects

Two commonly cultivated greenhouse cucumber (*Cucumis sativus*) cultivars in Iran, Karim (obtained from Gavrish seeds, Russia) and Khasib (from RijkZwaan, The Netherlands), were used in the experiment. The cultivars were chosen because of their different morphological structures (i.e., trichomes) (Basij *et al* 2011). The seeds were sown and grown in 20-cm-diameter plastic pots containing different vermicompost/soil (V:S) ratios (0:100, 10:90, 20:80, and 30:70%). Vermicompost (produced from cattle manure) was obtained from Anooshe Aaraab Co., Ltd., Tehran, Iran. Plants were maintained in a greenhouse at 24±4°C, relative humidity of 60±10%, and a natural photoperiod.

The colony of *A. gossypii* was initiated with apterous females collected from infested cucumber greenhouses in the suburb of Ardabil, Iran. Aphids were separately reared on each V:S concentration on the mentioned cultivars for three generations before experiments. A culture of *A. aphidimyza* was started with pupae supplied by the Ferdowsi University of Mashhad, Mashhad, Iran. The predatory gall midge was separately reared on each cucumber cultivar in transparent plastic cages (45×30×45 cm) that were treated with various concentrations of vermicompost. Top panel of each rearing cage was covered by a fine-mesh net for ventilation and a sleeve opening (15 cm diameter) centered in the front panel for better handling of flies inside the cage. Rearing cages contained five- or six-leaf stage potted cucumber plants highly infested with *A. gossypii*. Aphid-infested plants of each cultivar were offered into the cages every 2 weeks. All insect cultures were maintained in a controlled environment room at 25±2°C, 65±5% RH and 16L:8D photoperiod.

Experimental procedure

The functional response experiments were carried out with 36-h-old larvae of *A. aphidimyza* on the mixed stages (second and third instars) of *A. gossypii*. The experimental units were plastic Petri dishes (6 cm diameter) with a hole (2 cm diameter) in the lid, which was covered by fine-mesh net for ventilation and bottom lined with a wet filter paper to prevent cucumber leaves from desiccation. In each Petri dish, one leaf disc (4 cm diameter) was centered upside down on the wet filter paper. The leaf belonged to either cucumber cultivar and had received one of the different V:S concentrations. Eight different densities (2, 4, 6, 8, 12, 16, 24, and 32) of *A. gossypii* nymphs were gently transferred with a finebrush on the leaf disc and allowed to settle for about 2 h. Then, one 8-h starved *A. aphidimyza* larva was introduced in each Petri dish. Petri dishes were sealed with parafilm around the edge to prevent insects from escaping. After 16 h, predators were removed from experimental units and the number of killed preys was recorded. Each prey density was replicated 10 times for each cucumber cultivar and V:S ratios. Experiments were carried out in a Binder KBWF-720 climate chamber at 25±2°C, 65±5% RH, and 16:8 h (L:D). Consumed preys were not replaced during the experiments.

In order to investigate the possible effect of vermicompost on plant morphological features, numbers of trichomes on the leaves of both cucumber cultivars grown in the tested vermicompost/soil ratios were counted. Fully expanded leaves (with about 10 cm width) from the middle of each plant were selected and the number of trichomes crossing a 2-mm line counted under a stereomicroscope (Olympus SZX16). Measurements were taken on the underside of 10 leaves from each treatment between the midvein and the leaf margin (Dalin & Björkman 2003, Björkman & Ahrné 2005).

Statistical analysis

Logistic regression analysis (SAS/STAT, CATMOD procedure) was used to determine the type of functional response (SAS Institute 2001) for the proportion of prey consumed (N_e) as a function of the initial prey density (N_0) (Trexler & Travis 1993) as follows:

$$\frac{N_e}{N_0} = \frac{\exp(P_0 + P_1N_0 + P_2{N_0}^2 + P_3{N_0}^3)}{1 + \exp(P_0 + P_1N_0 + P_2{N_0}^2 + P_3{N_0}^3)} \quad (1)$$

where P_0, P_1, P_2, and P_3 are the constant, linear, quadratic, and cubic coefficients, respectively. The sign of the linear coefficient (P_1) estimated by the logistic regression was used to determine the type of the functional response. A significantly negative P_1 indicates a type II functional response, whereas a significant positive sign shows a type III functional response (Juliano 2001). Because the values estimated for the linear coefficient in the original cubic model were not significant (p value>0.05) at all cases, reduced logistic regression model was used by omitting the cubic term until all remained coefficients were significant. After determining the type of the functional response, the parameters of attack rate (a) and handling time (T_h) of the predator were estimated by fitting the data with nonlinear least square regression procedure (PROC NLIN, SAS Institute 2001) to random predator equation (Royama 1971, Rogers 1972). For the type II functional response, the following model was used to fit the data:

$$N_e = N_0\{1 - \exp[a(T_hN_e - T)]\} \quad (2)$$

where N_e is the number of prey consumed, N_0 is the initial prey density, a is the attack rate, T_h is the handling time per prey, and T is the total time of exposure (in this case T=16 h). Once a and T_h were estimated for the original data (m_t), differences in a and T_h parameters were tested for significance and the variance was estimated by the Jackknife method (Meyer *et al* 1986, Ganjisaffar & Perring 2015). The Jackknife pseudo-values (m_j) of the n samples were calculated with the Eqs. 3 and 4:

$$m_{ja} = \text{n. } m_{ta} - (n-1)m_{ia} \quad (3)$$

$$m_{jTh} = \text{n. } m_{tTh} - (n-1)m_{iTh} \quad (4)$$

The mean Jackknife pseudo-values for a and T_h for each treatment were subjected to analysis of variance (ANOVA). Tukey's test was employed to compare means at $p<0.05$ (SPSS 2007).

For each cucumber cultivar and V:S concentration, the predation rate of *A. ahidimyza* larvae was averaged for each density of *A. gossypii* and results were subjected to analysis of variance (one-way ANOVA) followed by a Tukey's test at $p<0.05$ (SPSS 2007). Data of the density of trichomes on the leaves of a cultivar amended with different vermicompost concentrations were analyzed by one-way ANOVA and the corresponding ratios between two cultivars were analyzed using independent sample t test.

Results

Parameter estimates for logistic regression of proportion of prey eaten (N_e/N_0) by *A. aphidimyza* larvae as a function of initial prey density (N_0) on two cucumber cultivars amended with different vermicompost concentrations are presented in Table 1. The linear coefficients of reduced logistic regression model in all cases were significantly negative ($p<0.05$), indicating that the percentage of consumed *A. gossypii* declined as prey density increased (i.e., functional response type II) (Fig 1).

The coefficients of attack rate (a) and handling time (T_h) of *A. aphidimyza* were both affected by the vermicompost composition used (Table 2). Attack rates of the predator on vermicompost/soil ratios ranged from 0.076 to 0.140 h^{-1} on Khasib and 0.092 to 0.123 h^{-1} on Karim, respectively. Handling times of *A. aphidimyza* larvae on different ratios varied from 0.969 to 1.164 h on Khasib and 0.905 to 1.229 h on Karim, respectively.

Table 1 Maximum likelihood estimates from logistic regression of the proportion of *Aphis gossypii* nymphs preyed by *Aphidoletes aphidimyza* larvae as a function of initial prey density on different vemicompost-amended cucumber cultivars.

Vermicompost/soil ratio		Khasib				Karim			
	Parameters	Estimate	SE	χ^2	*p* value	Estimate	SE	χ^2	*p* value
0:100	Constant	1.3549	0.2868	22.32	<0.0001	1.5775	0.2978	28.06	<0.0001
	Linear	−0.1313	0.0339	14.95	0.0001	−0.1216	0.0346	12.35	0.0004
	Quadratic	0.00218	0.000853	6.56	0.0104	0.00183	0.000862	4.51	0.0336
10:90	Constant	2.0329	0.3213	40.02	<0.0001	1.4951	0.2955	25.60	<0.0001
	Linear	−0.1422	0.0365	15.17	<0.0001	−0.1120	0.0345	10.56	0.0012
	Quadratic	0.00189	0.000900	4.43	0.0353	0.00151	0.000860	3.09	0.0789
20:80	Constant	2.2102	0.5362	16.99	<0.0001	1.6425	0.3025	29.49	<0.0001
	Linear	−0.2844	0.1106	6.62	0.0101	−0.1191	0.0351	11.50	0.0007
	Quadratic	0.0118	0.00658	3.21	0.0732	0.00140	0.000877	2.56	0.1093
30:70	Constant	1.8673	0.3108	36.09	<0.0001	2.1448	0.5443	15.53	<0.0001
	Linear	−0.1406	0.0357	15.49	<0.0001	−0.2259	0.1119	4.07	0.0436
	Quadratic	0.00198	0.000886	4.98	0.0257	0.00790	0.00665	1.41	0.2344

In both cucumber cultivars and for a same prey density, there was no significant difference between consumption rates of *A. aphidimyza* on *A. gossypii* reared on different V:S ratios (Table 3). Within each soil ratios of vermicompost and each tested cucumber cultivars, prey consumption of the predator significantly increased with prey density, reaching maximum values when 32 aphids were provided (Table 3).

Different vermicompost:soil ratios significantly affected the density of trichomes on the leaves of both cucumber cultivars (F=6.065, df=3,39, p=0.02 for Khasib; F=12.616, df=3,39, p<0.001 for Karim). The mean number of trichomes increases with the percentage of vermicompost in soil for both cultivars. Khasib trichomes mean ranged from 2.50± 0.17 for the V:S ratio 0:100 to 3.90±0.23 for the ratio 30:70. Karim showed a mean from 3.40±0.31 trichomes for the ratio 0:100 to 5.90±0.38 for the ratio 30:70. Furthermore, Karim had significantly more trichomes than Khasib for the same V:S ratio, except for the ratio 10:90, for which the difference was not significant (Fig 2).

Discussion

In the current study, the functional response of *A. aphidimyza* to increasing density of *A. gossypii* was found to be type II on both cucumber cultivars grown at different V:S ratios, suggesting that different levels of vermicompost did not affect the predator functional response type in our standard conditions. Aqueel & Leather (2012) reported the same result for *Harmonia axyridis* Pallas upon *Rhopalosiphum padi* L. and *Sitobion avenae* Fab. on wheat plants provided with nitrogen fertilizer. Under laboratory conditions, a large number of insects show a type II functional response (Gotoh *et al* 2004, Rocha & Redaelli 2004, Kakimoto *et al* 2006, Nachappa *et al* 2006, Cabral *et al* 2009), comparable to the results of our study. Furthermore, according to Abrams (1990) specialist predators typically exhibit type II functional response because of few alternative preys, while generalist predators with more alternative food show a type III response. These facts are consistent with the findings of this study, because *A. aphidimyza* is a specialist predator that only preys on aphid species. Similarly, Morse & Croft (1987) and Jalalipour *et al* (2014) reported type II functional response for *A. aphidimyza*. However, Madahi *et al* (2013) reported a type III age-specific functional response for *A. aphidimyza* when feeding upon *A. craccivora* on black-eyed bean leaves. The differences between their results and the present study could be attributed to the different preys and plants used, since the type of functional response of a predator may vary on different prey species (Sarmento *et al* 2007) and host plants (De Clercq *et al* 2000).

In order to determine the intensity of predation on *A. gossypii* nymphs, the coefficients of attack rates and handling times were used. Attack rates and handling times on both cultivars on elevated dosages of vermicompost were higher than those estimated on control. Handling times estimated for 36-h-old larvae of *A. aphidimyza* to consume *A. gossypii* nymphs on control plants (particularly on Karim) in this study are comparable with that estimated by (Madahi *et al* 2013) for 6-day-old larvae of *A. aphidimyza* feeding on *A. craccivora* (0.938 h). However, handling time values estimated by Jalalipour *et al* (2014) for *A. aphidimyza* 4-day-old larvae feeding on *A. craccivora* at different foraging periods are shorter than those estimated in the present study. Spending more time on the aphids reared on plants that

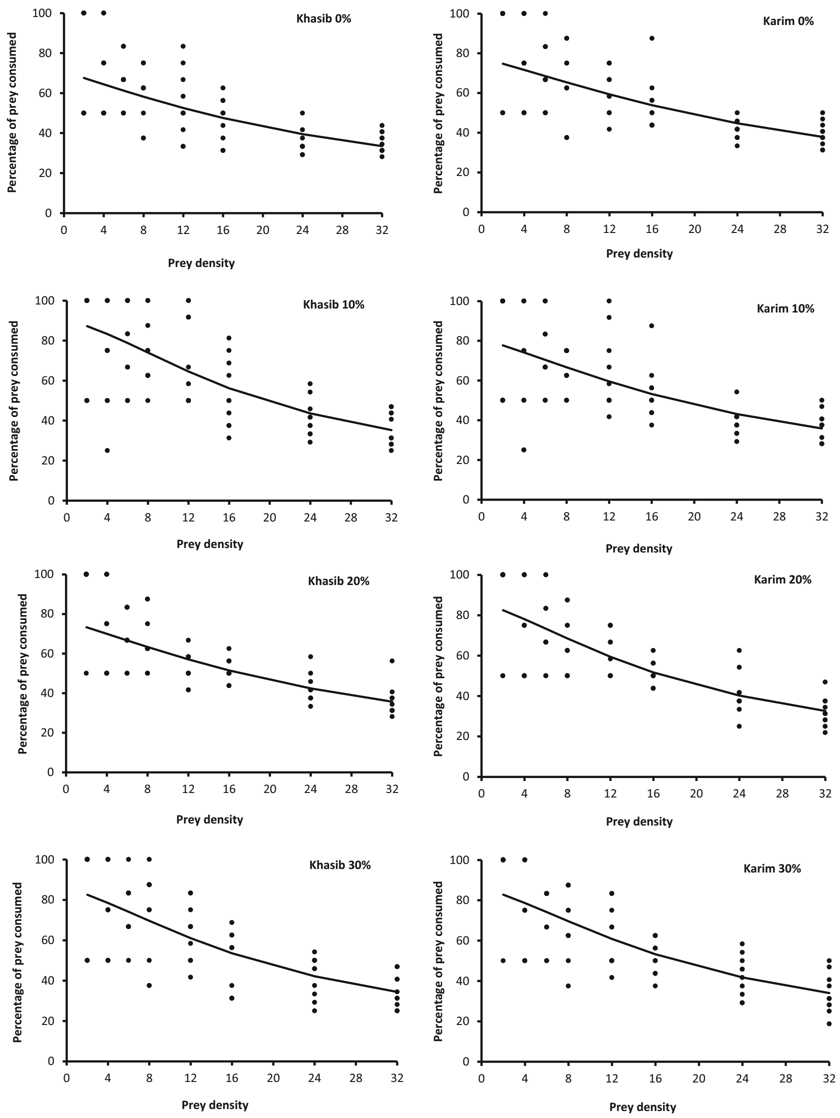

Fig 1 Percentage of predation of *Aphidoletes aphidimyza* larvae to densities of *Aphis gossypii* nymphs on different vermicompost/soil ratios applied to cucumber cultivars. The data points and solid lines represent the percentage of *A. gossypii* killed and the predictions of the best-fitted type II functional response model, respectively.

have received high rates of vermicompost can be explained by the presence of trichomes on the leaf surface, that density of trichomes increased as a function of high percentage of vermicompost in the soil. Similarly, Guang-hui *et al* (2007) demonstrated that application of organic fertilizers to tobacco plant can increase the number of short stalk trichomes on the leaves. High trichome density on the leaf surface may hinder the insects, especially the natural enemies (Southwood 1986). For the case of our study, it seems that the increased trichome density on plants that have received high rates of vermicompost (especially on Karim) may be responsible of changes in the parameters of the functional response. Difference in leaf structure of various cultivars of a plant species may also influence the efficiency of natural enemies. For example, according to Cédola *et al* (2001) differences in hairiness of tomato hybrids negatively affected the functional and numerical response of *Neoseiulus californicus* McGregor. Similarly, searching efficiency of *Trichogramma* wasps on tomato (McGregor *et al* 2002) and foraging behavior of *Stethorus gilvifrons* Mulsant on cucumber (Bayoumy *et al* 2014) were decreased as a result of high trichomes on the leaves.

It is generally assumed that the predation is a function of prey size (Holling 1961, Fantinou *et al* 2012). Addition of fertilizers to the soil, as described by Aqueel & Leather (2012), can alter the body size of aphids. Interestingly, by application of vermicompost, the body size of *A. gossypii* was negatively affected. We previously demonstrated that *A. gossypii* yielded the largest aphids in terms of their hind-tibial length (0.332±0.006 mm) on plants grown in the soil without

Table 2 Mean values (±SE) of attack rate (*a*) and handling time of *Aphidoletes aphidimyza* larvae feeding on *Aphis gossypii* reared on different vemicompost-amended cucumber cultivars.

Vermicompost/soil ratio	Khasib		Karim	
	a	T_h	a	T_h
0:100	0.076±0.013[a]	1.004±0.123[a]	0.092±0.015[a]	0.905±0.117[a]
10:90	0.140±0.031[a]	1.164±0.093[a]	0.102±0.018[a]	1.028±0.116[a]
20:80	0.091±0.008[a]	0.969±0.115[a]	0.122±0.017[a]	1.229±0.119[a]
30:70	0.118±0.030[a]	1.139±0.152[a]	0.123±0.016[a]	1.158±0.137[a]

Means in the same column followed by the same superscript letters are not significantly different (p>0.05, Tukey test).

vermicompost and the smallest ones (0.303±0.005 mm) on plants treated with 30% vermicomopst rate (Mottaghinia *et al*, unpublished data). Theoretically, it is expected that much more aphids must be eaten by the predator on high ratios of vermicompost because of their smaller size. But, prey consumptions of *A. aphidimyza* larvae were not affected by different V:S ratios. Causes for the unchanged consumption of predator on these treatments may be attributed to trichomes that interfered with the search success of *A. aphidimyza* and resulted to less consumption of prey. However, the number of *A. gossypii* nymphs attacked by *A. aphidimyza* increased with increasing the availability of prey. Similar to our results, some other researchers reported that prey consumption of predators increased with exposure to high prey densities (Rocha & Redaelli 2004, Cabral *et al* 2009, Fantinou *et al* 2012). At high prey densities, the predator spends less time to find the prey. According to Holling (1959), predation rate increases with the total time, prey density, and/or attack rate. It seems that encounter rate of the larvae of the predatory gall midge increases at higher aphid densities, and consequently, the predator spends less time to find the prey and consumes more aphids than the time when fewer aphids are available (Cabral *et al* 2009).

In summary, our findings emphasize the crucial influence of organic fertilizer and cultivars on the predation potential of *A. aphidimyza*. Cucumber cultivars amended with different vermicompost concentrations affected functional response parameters of the predatory gall midge. The influence may be related to the morphological structure of the plants, especially the increased density of trichomes. However, other morphological and especially chemical features of the plants may have changed by application of vermicompost and influenced the predator (Rao 2002). Based on the results, since higher proportions of *A. gossypii* were consumed by *A. aphidimyza* at lower densities of the aphid, it can be considered as a potential biological control agent for management of *A. gossypii* in both tested cultivars especially at early infestation. These findings may be used to understand the complex interactions between soil composition, plants, prey, and predators. Furthermore, the results would be useful for the development of a better strategy for biological control of the melon aphid using vermicompost

Table 3 Prey consumption (mean±SE) by *Aphidoletes aphidimyza* larvae when feeding on various densities of *Aphis gossypii* reared on different vemicompost-amended cucumber cultivars.

Density	Khasib				Karim			
	[0:100]	[10:90]	[20:80]	[30:70]	[0:100]	[10:90]	[20:80]	[30:70]
2	1.60±0.16[Ag]	1.70±0.15[Af]	1.90±0.10[Af]	1.70±0.15[Af]	1.70±0.15[Af]	1.50±0.17[Af]	1.80±0.13[Af]	1.90±0.10[Ae]
4	2.70±0.26[Afg]	2.90±0.31[Aef]	2.90±0.28[Aef]	3.00±0.26[Aef]	3.00±0.26[Aef]	2.70±0.37[Aef]	2.90±0.28[Aef]	3.10±0.28[Ade]
6	3.90±0.23[Aef]	4.80±0.39[Ade]	4.10±0.23[Ade]	4.50±0.27[Ade]	4.10±0.31[Ade]	4.40±0.34[Ade]	4.40±0.34[Ade]	4.40±0.27[Ad]
8	4.70±0.33[Ade]	5.90±0.43[Acd]	5.30±0.33[Acd]	5.80±0.57[Acd]	5.20±0.44[Ad]	5.30±0.26[Acd]	5.30±0.37[Ad]	5.50±0.43[Acd]
12	6.50±0.64[Acd]	8.50±0.85[Abc]	6.30±0.30[Ac]	7.70±0.54[Abc]	7.40±0.45[Ac]	7.60±0.75[Abc]	7.40±0.43[Ac]	7.40±0.58[Abc]
16	7.50±0.54[Abc]	8.60±0.87[Abc]	8.30±0.30[Ab]	7.90±0.75[Abc]	8.60±0.69[Abc]	8.60±0.70[Ab]	8.20±0.29[Abc]	8.40±0.45[Aab]
24	8.50±0.48[Ab]	9.90±0.71[Aab]	10.20±0.55[Aa]	10.10±0.77[Aab]	10.00±0.36[Ab]	9.30±0.52[Ab]	9.80±0.80[Aab]	10.20±0.77[Aa]
32	11.40±0.52[Aa]	11.70±0.87[Aa]	11.50±0.82[Aa]	11.20±0.84[Aa]	12.60±0.64[Aa]	12.10±0.74[Aa]	10.30±0.73[Aa]	10.80±0.99[Aa]

Values in square brackets are vermicompost/soil ratios. Means in the same row and for each cultivar followed by the same superscript uppercase letters are not significantly different (p>0.05, Tukey's test). Means in the same column followed by the same superscript lowercase letters are not significantly different (p>0.05, Tukey's test).

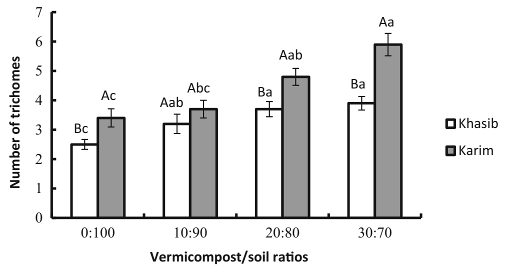

Fig 2 Number of trichomes crossing a 2-mm line on leaves of two cucumber cultivars (Khasib and Karim) grown at different vermicompost/soil ratios. Different lowercase letters indicate significant different means among various vermicompost ratios in a cultivar (Tukey's test). Different uppercase letters represent significant differences within a same vermicompost/soil ratio in the cultivars (independent-samples *t* test).

as a promising alternative to inorganic fertilizers in both field and greenhouse crops. Since functional response studies in simplified conditions (Petri dishes) may have little resemblance of those measured in natural conditions (O'Neil 1989, Kareiva 1990), supplementary studies under field conditions are needed to provide further details of the predator-prey interactions.

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References

Abrams PA (1990) The effects of adaptive behavior on the type-2 functional response. Ecology 71:877–885

Aqueel MA, Leather SR (2012) Nitrogen fertilizer affects the functional response and prey consumption of *Harmonia axyridis* (Coleoptera: Coccinellidae) feeding on cereal aphids. Ann Appl Biol 160:6–15

Arancon NQ, Edwards CA, Yardim EN, Oliver TJ, Byrne RJ, Keeney G (2007) Suppression of two-spotted spider mite (*Tetranychus urticae*), mealy bug (*Pseudococcus* sp) and aphid (*Myzus persicae*) populations and damage by vermicomposts. Crop Prot 26:29–39

Arancon NQ, Edwards CA, Babenko A, Cannon J, Galvis P, Metzger JD (2008) Influences of vermicomposts, produced by earthworms and microorganisms from cattle manure, food waste and paper waste, on the germination, growth and flowering of petunias in the greenhouse. Appl Soil Ecol 39:91–99

Atiyeh RM, Arancon NQ, Edwards CA, Metzger JD (2001) The influence of earthworm-processed pig manure on the growth and productivity of marigolds. Bioresour Technol 81:103–108

Basij M, Askarianzaeh A, Asgari S, Moharramipour S, Rafezi R (2011) Evaluation of resistance of cucumber cultivars to the vegetable leaf miner (*Liriomyza sativae* Blanchard) (Diptera: Agromyzidae) in greenhouse. Chil J Agric Res 71:395–400

Bayoumy MH, Osman MA, Michaud JP (2014) Host plant mediates foraging behavior and mutual interference among adult *Stethorus gilvifrons* (Coleoptera: Coccinellidae) preying on *Tetranychus urticae* (Acari: Tetranychidae). Environ Entomol 43:1309–1318

Bennison JA (1992) Biological control of aphids on cucumbers: use of open rearing systems or "banker plants" to aid establishment of *Aphidius matricareae* and *Aphidoletes aphidimyza*. Meded Faculteit Landbouwwetenschappen Universiteit Gent 57:457–466

Björkman C, Ahrné K (2005) Influence of leaf trichome density on the efficiency of two polyphagous insect predators. Entomol Exp Appl 115: 179–186

Blackman RL, Eastop VF (2000) Aphids on the world's crops: an identification and information guide. Wiley, London, United Kingdom, 467 p

Cabral S, Soares AO, Garcia P (2009) Predation by *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) on *Myzus persicae* Sulzer (Homoptera: Aphididae): Effect of prey density. Biol Control 50:25–29

Cédola CV, Sánchez NE, Liljesthröm GG (2001) Effect of tomato leaf hairiness on functional and numerical response of *Neoseiulus californicus* (Acari: Phytoseiidae). Exp Appl Acarol 25:819–831

Dalin P, Björkman C (2003) Adult beetle grazing induces willow trichome defense against subsequent larval feeding. Oecologia 134:112–118

De Clercq P, Mohaghegh J, Tirry L (2000) Effect of host plant on the functional response of the predator *Podisus nigrispinus* (Heteroptera: Pentatomidae). Biol Control 18:65–70

De Kogel WJ, Bosco D, van Der Hoek M, Mollema C (1999) Effect of host plant on body size of *Frankliniella occidentalis* (Thysanoptera: Thripidae) and its correlation with reproductive capacity. Eur J Entomol 96:365–368

Deguince JP, Goze E, Leclant F (1994) Incidence of early outbreaks of the aphid *Aphis gossypii* Glover in cotton growing in Cameroon. Int J Pest Manag 40:132–140

Denno RF, Gratton C, Peterson MA, Langellotto GA, Finke DL, Huberty AF (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. Ecology 83:1443–1458

Ding-Xu L, Juan T, Zuo-Rui S (2007) Functional response of the predator *Scolothrips takahashii* to hawthorn spider mite, *Tetranychus viennensis*: effect of age and temperature. BioControl 52:41–61

Duchovskiene L, Surviliene E, Valiuškaite A, Karkleliene R (2012) Effects of organic and conventional fertilization on the occurrence of *Brevicoryne brassicae* L. and its natural enemies in white cabbage. Acta Agr Scand B-S P 62:16–22

Edwards CA, Arancon NQ, Vasko-Bennett M, Askar A, Keeney G (2010) Effect of aqueous extracts from vermicomposts on attacks by cucumber beetles (*Acalymna vittatum*) (Fabr.) on cucumbers and tobacco hornworm (*Manduca sexta*) (L.) on tomatoes. Pedobiologia 53:141–148

Fallahpour F, Ghorbani R, Nassiri Mahallati M, Hosseini M (2015) Interaction of different nitrogen fertilization regimes of canola with mustard aphid (*Lipaphis erysimi* Kalt.) and the predatory gall midge (*Aphidoletes aphidimyza* Rondani). Biol Control Pests Plant Dis 4:1–12 (Abstract in English)

Fantinou AA, Baxevani A, Drizou F, Labropoulos P, Perdikis D, Papadoulis G (2012) Consumption rate, functional response and preference of the predaceous mite *Iphiseius degenerans* to *Tetranychus urticae* and *Eutetranychus orientalis*. Exp Appl Acarol 58:133–144

Forkner RE, Hunter MD (2000) What goes up must come down? Nutrient addition and predation pressure on oak herbivores. Ecology 81:1588–1600

Fox LR, Letourneau DK, Eisenbach J, Nouhuys SV (1990) Parasitism rates and sex ratios of a parasitoid wasp: effects of herbivore and plant quality. Oecologia 83:414–419

Ganjisaffar F, Perring TM (2015) Prey stage preference and functional response of the predatory mite *Galendromus flumenis* to *Oligonychus pratensis*. Biol Control 82:40–45

Gao F, Zhu SR, Sun YC, Du L, Parajulee M, Kang L, Ge F (2008) Interactive effects of elevated CO2 and cotton cultivar on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Propylaea japonica*. Environ Entomol 37:29–37

Gotoh T, Nozawa M, Yanaguchi K (2004) Prey consumption and functional response of three acarophagous species to eggs of the two-spotted spider mite in the laboratory. Appl Entomol Zool 39:97–105

Guang-hui K, Zhao-li X, Wei W, Tian-fu L (2007) Effect of fertilizer on glandular trichome density and exudates accumulation in middle leaf of "Honhuadajinyuan". Acta Tabacaria Sin 4:41–44

Hassanpour M, Mohaghegh J, Iranipour S, Nouri-Ganbalani G, Enkegaard A (2011) Functional response of *Chrysoperla carnea* (Neuroptera: Chrysopidae) to *Helicoverpa armigera* (Lepidoptera: Noctuidae): effect of prey and predator stages. Insect Sci 18:217–224

Holling CS (1959) Some characteristics of simple types of predation and parasitism. Can Entomol 91:385–398

Holling CS (1961) Principles of insect predation. Annu Rev Entomol 6: 163–182

Hosseini M, Ashouri A, Enkegaard A, Weisser WW, Goldansaz SH, Nassiri Mahallati M, Sarraf Moayeri HR (2010) Plant quality effects on intraguild predation between *Orius laevigatus* and *Aphidoletes aphidimyza*. Entomol Exp Appl 135:208–216

Jalalipour R, Sahragard A, Karimi-Malati A (2014) Effect of different foraging periods on the functional response of *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae) at different densities of *Aphis craccivora*. J Crop Prot 3:283–293

Jeschke JM, Kopp M, Tollrian R (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biol Rev 79:337–349

Juliano SA (2001) Non-linear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Chapman and Hall, New York, pp 178–196

Kakimoto K, Inoue H, Hinomoto N, Noda T, Hirano K, Kashio T, Kusigemati K, Okajima S (2006) Potential of *Haplothrips brevitubus* (Karny) (Thysanoptera: Phlaeothripidae) as a predator of mulberry thrips *Pseudodendrothrips mori* (Niwa) (Thysanoptera: Thripidae). Biol Control 37:314–319

Kalyebi A, Overholt WA, Schulthess F, Mueke JM, Hassan SA, Sithanantham S (2005) Functional response of six indigenous trichogrammatid egg parasitoids (Hymenoptera: Trichogrammatidae) in Kenya: influence of temperature and relative humidity. Biol Control 32:164–171

Kareiva P (1990) The special dimension in pest-enemy interaction. In: Mackauer M, Ehler LE, Roland J (eds) Critical issues in biological control. Intercept, Anover, Hants, pp 213–227

Madahi Kh,Sahragard A, Hossieni R (2013) Larval age-specific searching efficiency of *Aphidoletes aphidimyza* (Dip.: Cecidomyiidae) preying on different densities of *Aphis craccivora* (Hem.:Aphididae). J Entomol Soc Iran 33:33–43

Mahdian K, Tirry L, De Clercq P (2007) Functional response of *Picromerus bidens*: effects of host plant. J Appl Entomol 131:160–164

McGregor RR, Prasad RP, Henderson DE (2002) Searching behaviour of *Trichogramma* wasps (Hymenoptera: Trichogrammatidae) on tomato and pepper leaves. J Entomol Soc B C 99:93–98

Meadow RH, Kelly WC, Shelton AM (1985) Evaluation of *Aphidoletes aphidimyza* (Dip.: Cecidomyiidae) for control of *Myzus persicae* (Hom.: Aphididae) in greenhouse and field experiments in the United States. Entomophaga 30:385–392

Meyer JS, Ingersol CG, McDonald LL, Boyce MS (1986) Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. Ecology 67:1156–1166

Minarro M, Hemptinne J-L, Dapena E (2005) Colonization of apple orchards by predators of *Dysaphis plantaginea*: sequential arrival, response to prey abundance and consequences for biological control. BioControl 50:403–414

Morse JG, Croft BA (1987) Biological control of *Aphis pomi* (Hom.: Aphididae) of *Aphidoletes aphidimyza* (Dip.: Cecidomyiidae); a predator prey model. Entomophaga 32:339–356

Nachappa P, Braman SK, Guillebeau LP, All JN (2006) Functional response of the tiger beetle *Megacephala carolinacarolina* (Coleoptera: Carabidae) on twolined spittlebug (Hemiptera: Cercopidae) and fall armyworm (Lepidoptera: Noctuidae). J Econ Entomol 99:1583–1589

O'Neil RJ (1989) Comparison of laboratory and field measurements of the functional response of *Podisus maculiventris* (Heteroptera: Pentatomidae). J Kans Entomol Soc 62:148–155

Parajulee MN, Phillips TW, Hogg DB (1994) Functional response of *Lyctocoris campestris* (F.) adults: effects of predator sex, prey species, and experimental habitat. Biol Control 4:80–86

Perdikis D, Kapaxidi E, Papadoulis G (2008) Biological control of insect and mite pests in greenhouse solanaceous crop. Eur J Plant Sci Biotech 2:125–144

Ponti L, Altieri MA, Gutierrez AP (2007) Effects of crop diversification levels and fertilization regimes on abundance of *Brevicoryne brassicae* (L.) and its parasitization by *Diaeretiella rapae* (M'Intosh) in broccoli. Agr Forest Entomol 9:209–214

Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annu Rev Ecol Syst 11:41–65

Rao KR (2002) Induce host plant resistance in the management of sucking insect pest of groundnut. Ann Plant Prot Sci 10:45–50

Razmjou J, Vorburger C, Mohammadi M, Hassanpour M (2012) Influence of vermicompost and cucumber cultivar on population growth of *Aphis gossypii* Glover. J Appl Entomol 136:568–575

Rocha L, Redaelli LR (2004) Functional response of *Cosmoclopius nigroannulatus* (Hem.: Reduviidae) to different densities of *Spartocera dentiventris* (Hem.: Coreidae) nymphae. Braz J Biol 64:309–316

Rogers DJ (1972) Random search and insect population models. J Animal Ecol 41:369–383

Royama T (1971) A comparative study of models for predation and parasitism. Res Popul Ecol 1:1–91

Sabelis MW, van Baalen M, Bakker FM, Bruin J, Drukker B, Egas M, Janssen ARM, Lesna IK, Pels B, van Rijn PCJ, Scutareanu P (1999) The evolution of direct and indirect plant defense against herbivorous arthropods. In: Olff H, Brown VK, Drent RH (eds) Herbivores: between plants and predators. Oxford Blackwell Science Ltd., Oxford, pp 109–166

Sarfraz M, Dosdall LM, Keddi BA (2008) Host plant genotype of the herbivore *Plutella xylostella* (Lepidoptera: Plutellidae) affects the performance of its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). Biol Control 44:42–51

Sarmento RA, Pallini A, Venzon M, DeSouza O, Molina-Rugama AJ, Oliveira CL (2007) Functional response of the predator *Eriopis connexa* (Coleoptera: Coccinellidae) to different prey types. Braz Arch Biol Technol 50:121–126

SAS Institute (2001) SAS/STAT user's guide. SAS Institute Inc., Cary, NC Inc

Satar S, Kersting U, Uygun N (1999) Development and fecundity of *Aphis gossypii* Glover (Hemiptera: Aphididae) on three Malvaceae hosts. Turk J Agric For 23:637–643

Solomon ME (1949) The natural control of animal populations. J Anim Ecol 18:1–35

Southwood SR (1986) Plant surfaces and insects—an overview. In: Juniper B, Southwood SR (eds) Insects and the plant surface. Arnold, London, pp 1–22

SPSS (2007) SPSS base 16.0 user's guide. SPSS Incorporation, Chicago

Suryawana IBG, Reyes SG (2007) The influence of cultural practice on population of pea leafminer (*Liriomyza huidobrensis*) and its parasitoids in potato. Indones J Agr Sci 7:35–42

Trexler JC, Travis J (1993) Nontraditional regression analysis. Ecology 74: 1629–1637

Yukawa J, Yamaguchi D, Mizota K, Setokuchi O (1998) Distribution and host range of an aphidophagous species of Cecidomyiidae, *Aphidoletes aphidimyza* (Diptera), in Japan. Appl Entomol Zool 33: 185–193