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ORIGINAL PAPER

A functional response evaluation of pre-infestation with *Bemisia tabaci* cryptic species MEAM1 on predation by *Propylea japonica* of *Myzus persicae* on host plant tomatoes

Fan Yang[1] · Xiao-Ling Tan[2] · Fang-Hua Liu[3] · Su Wang[4] · Ju-Lian Chen[2] · Tu-Yong Yi[1]

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Abstract Herbivore feeding on host plants may induce defense responses of the plant which influence other herbivores and interacting species in the vicinity, such as natural enemies. The present work evaluated the impact of pre-infestation with the tobacco whitefly *Bemisia tabaci* cryptic species MEAM 1, on the predation ability of the ladybird *Propylea japonica,* to the green peach aphid *Myzus persicae,* on tomato plants. The results show that *B. tabaci* pre-infestation density, duration, and leaf position, can impact prey consumed by *P. japonica* under various aphid densities. The aphids consumed by *P. japonica* in each treatment were fit using the Holling type II functional response equation. The predatory efficiency (a/T_h) of *P. japonica* was the highest in the treatment with 60 aphids and 48-h infestation directly on damaged leaves. The predatory efficiencies of *P. japonica* decreased with a reduction of pre-infestation density and duration. We also observed that pre-infestation on young and undamaged leaves increased predation by *P. japonica*.

Keywords Induced defense · Infestation density · Infestation duration · Systemic defense · Functional response

Introduction

Ensuring food security involves ‘protection of crops and host plants, targeting herbivores, and biological control agents’ according to principles established for effective agro-ecosystems (Altieri 1999). Previous research has focused on the interactions within communities in the context of ecology (Cohen et al. 2003; Cottenie 2005). Herbivore-induced plant defensive responses have been shown to inhibit the colonization by competing herbivores (Denno et al. 2000). While laboratory tests have shown that natural enemies can also be attracted by herbivore-induced plant volatiles (HIPVs) emitted by damaged plants (Price 1986). It appears that HIPVs facilitate the process and success of prey search and targeting by both predators and parasitoids (Agelopoulos and Keller 1994; Gurr and Kvedaras 2010). Recently, more research has focused on the

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✉ Tu-Yong Yi
tuyong_yi123@163.com

Fan Yang
264549585@qq.com

Xiao-Ling Tan
tanxiaoling2010@163.com

Fang-Hua Liu
liufanghua5@163.com

Su Wang
anthocoridae@163.com

Ju-Lian Chen
jlchen@ippcaas.cn

[1] College of Plant Protection, Hunan Agricultural University, Changsha, Hunan, China

[2] State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, China

[3] State Key Laboratory of Integrated management of Pest Insects and Rodents, Institute of Zoology, University of the Chinese Academy of Sciences, Beijing, China

[4] Institute of Plant and Environment Protection, Beijing Academy of Agriculture and Forestry Sciences, 100097 Beijing, China

ecological interactions among herbivore, pest, and predators promoted by HIPVs, and their potential value in practical pest management (Dicke and Baldwin 2010).

The green peach aphid *Myzus persicae* (Sulzer) and the tobacco whitefly *Bemisia tabaci* (Gennadius) are two of the most severe phytophagous pests of various greenhouse vegetables worldwide (Emden et al. 1969; Inbar and Gerling 2008; Kogan 1998). Although *B. tabaci* is an invasive species and appeared several decades ago in China, it shares a niche with many native herbivores, such as aphids, thrips, and spider mites (Chu et al. 2004). *M. persicae* and *B. tabaci* share many characteristics, including host plant preference (usually the same plant families) and oviposition substrates (Byrne and Bellows 1991; Emden et al. 1969). Previous work has shown that the presence of *B. tabaci* on tobacco leaves may hamper the locating behavior and colonization by *M. persicae* (Xue et al. 2010). Our previous work also showed that damage of tomato plants by *M. persicae* had negative effects on the preference of *B. tabaci* (Tan et al. 2014). Further, the position of damage to the plant and duration of herbivory in prior infestation can have various impacts on the subsequent pests and natural enemies (Howe and Jander 2008; Tan and Liu 2014).

Herbivore-induced plant responses on both herbivores themselves and subsequent predators have been well studied. The two-spotted spider mite *Tetranychus urticae* (Koch), and the European spider mite *Panonychus ulmi* (Koch), upon damaging eggplant, attract the predatory ladybird *Stethorus gilvifrons* (Mulsant) (Gencer et al. 2009). Our previous study also showed that two whitefly-specific parasitoids *Encarsia formosa* (Gahan) and *E. sophia* (Girault Dodd), and a predatory bug *Orius sauteri* (Poppius), preferred to parasitize or prey on *B. tabaci* on tomato plants that had been previously damaged by *M. persicae* (Tan and Liu 2014).

At present, we focused on the ladybird *Propylea japonica* (Thunberg), which has been widely used to suppress the outbreak of various herbivore pests, including aphids and spider mites (Hodek and Honek 1996; Hodek et al. 2012). We established a study system involving a primary target aphid *M. persicae*, a coexisting whitefly *B. tabaci,* and a tomato host plant, to evaluate if pre-infestation with *B. tabaci* impacts the predation by *P. japonica* on *M. persicae*. We tested prey consumption by *P. japonica* on different densities of *M. persicae* to examine functional responses, using the Holling II model which have proven informative in other coccinellid species (Lin et al. 2006; Liu and Stansly 2002; Mandour et al. 2006). Particularly, we compared pre-infestation densities, exposure duration, and position of pre-infested leaves. Our results improve the knowledge foundation in use of *P. japonica* for biological control of aphids, whiteflies, spider mites, and other pests.

Materials and methods

Plants and insects

Tomato *Solanum lycopersicum* L. (var. Baofen-F1, 2008, Changfeng Institute of Vegetables, Lintong, Xi'an, Shaanxi, China) was used as the host plant. Tomato was cultured in plastic trays (50.0 × 25.0 × 15.0 cm), eight plants per tray. Seedlings, 4–5 cm in height, were transplanted into plastic pots (20 cm in depth and 15 cm in diameter) and were placed in clean cages (60 × 60 × 60 cm; plastic frame, screened with 120 mesh nylon yarn net). Plants used in all experiments were approximately 30 cm in height with 5–7 true and fully expanded leaves. The experiments were conducted in walk-in chambers at 25 ± 2 °C, 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h with artificial lighting at 3500 lx by an automatic environmental regulation system (L-100, Sun-Tech, Beijing, China).

Two herbivores, *M. persicae* and *B. tabaci* MEAM 1 (cryptic species), were collected on tomato plants from a greenhouse in the NOYA® Organic Vegetable Corporation Production Base, Beijing, China. The identity MEAM 1 of *B. tabaci* was confirmed using mitochondrial DNA analysis as described by Chu et al. (2004). The voucher specimens have been deposited in the Insect Collection, State Key Laboratory of Crop Stress Biology for Arid Areas, Northwest A & F University, Yangling, Shaanxi, China. The aphids and whiteflies were maintained on tomato plants in ventilated culturing cages (40 × 40 × 50 cm with 100 mesh plastic fabric net).

The ladybird *P. japonica* was collected from an experimental field at Wangjiayuan Biodiversity Research Station (Beijing, China). The sampled live insects (150 pairs) were transported to the Laboratory of Natural Enemy Research, Institute of Plant & Environment Protection, Beijing Academy of Agriculture and Forestry Sciences. Thirty pairs of ladybirds were reared on a microencapsulated artificial diet in cages (Tan et al. 2014).

Pre-infestation treatments of *B. tabaci*

We treated the host tomato plants by pre-infestation with *B. tabaci,* under three different densities (20, 40 and 60 whiteflies), for different exposure times (12, 24 or 48 h), and on select leaves. We observed the predation by *P. japonica* of *M. persicae,* both on pre-infested leaves and those above and below. Firstly, *B. tabaci* adults of a given density (20, 40 or 60) were introduced on the focal leaf (3rd main leaf from the bottom of the plant) and sealed by a custom-made net cage (40 mesh plastic fabric net) with exposure for a given period (12, 24 or 48 h). For various pre-infestation densities, we introduced the whiteflies on the select leaf, for 24-h exposure. For various exposure durations, we introduced 40 whiteflies on the select leaf. For different leaf tests, we introduced 40 whiteflies and exposure for 24 h also on the select leaf. Then, we removed the net cage and all *B. tabaci* adults and nymphs by shaking the plants. The eggs of whitefly were all carefully removed using needle under a micro-stereoscope (ZEISS V20, ZEISS, Germany). Both these pre-damaged plants and undamaged ones were used in subsequent experiments.

Predatory evaluations of *P. japonica* on *M. persicae* in variously treated tomato plants

To determine the functional response of *P. japonic*a to *M. persicae* on the host plants which were pre-infested with whiteflies according to the treatments above, one 5-day-old *P. japonica* male or female adult was randomly selected from the lab population for each predation evaluation. The ladybird was starved for 12 h and then introduced with 10 third-instar nymphs of *M. persicae* into a plastic Petri dish on a leaf, either pre-infested or above/below. All the insects were sealed by net cages as above. The plants carrying insects were placed in an environmental chamber (MH-351, Sanyo, Osaka, Japan). The number of aphids consumed by ladybird adults was checked 24 h after treatment. Then we repeated these steps with various prey densities (20, 40, 60, 80, 120, 160 or 200 aphid nymphs), for each pre-infestation treatment. In addition, as blank control, we observed the prey consumption of ladybirds in different aphid densities on the host plants which were not pre-infested by whitefly. Tests for all treatments and aphid densities were replicated 20 times.

Statistical analysis

The software SPSS 18.0 was used for data analysis (Allen and Bennett 2010). Prey consumption data of *P. japonica* at different aphid densities of each *B. tabaci* pre-infestation treatment were compared using a mixed, two-way factorial ANOVA. We fitted the predation functional response equation Holling II (Holling 1959) as

$$N_{\mathrm{a}} = a'TN\big/\left(1 + a'^{T_{\mathrm{h}}}N\right), \qquad (1)$$

where T is the experimental duration (1 day); a is the instant attack rate; T_{h} is the handing time to each aphid by *P. japonica*; N is the prey asphid density; and N_{a} is the amount of aphid consumed by *P. japonica* within 1 sd. Plus, we calculated the theoretical maximum prey consumption of *P. japonica* as $N_{\mathrm{a\ max}} = 1/T_{\mathrm{h}}$. All the parameters were calculated by software Matlab 3.2 (Hanselman and Littlefield 1997).

Results

In each *B. tabac*i pre-infestation treatment, the daily prey consumption by *P. japonica* showed a corresponding increase with *M. persicae* density, whether without pre-infestation (Fig. 1), with different pre-infestation densities (Fig. 2), exposure times (Fig. 3), and leaf positions (Fig. 4). The results also showed that these three factors also significantly affect ladybird predation (Table 1). Further, we found cross-influences of whitefly pre-infestation and aphid density to the predation by *P. japonica* (Table 1).

The variation in aphid consumption by *P. japonica* with an increase of prey density showed good fit to the Holling II functional response model in all *B. tabac*i pre-infestation treatments. As shown in Table 2, the instant attacking rate "*a*" and the theoretical maximum aphid consumption by *P. japonica* increased with a corresponding increase in the density of *B. tabac*i. The aphid handling time "T_{h}" and the net attack frequency "a/T_{h}" by *P. japonica* also showed a corresponding decrease. Furthermore, we observed that a, a/T_{h}, and the theoretical maximum aphid consumption by *P. japonica* increased with prolonging of whitefly exposure, although not apparent in T_{h}. All functional response parameters were highest when *P. japonica* predation occurred directly on the leaves pre-infested by *B. tabac*i. Additionally, the T_{h} of ladybirds was greater on the leaves above than those below the pre-infested leaf. Among all treatments, we found the highest T_{h} and lowest a, a/T_{h}, and theoretical maximum aphid consumption of *P. japonica* when they fed on the aphids on the host plants without pre-infestation with whitefly (Table 2).

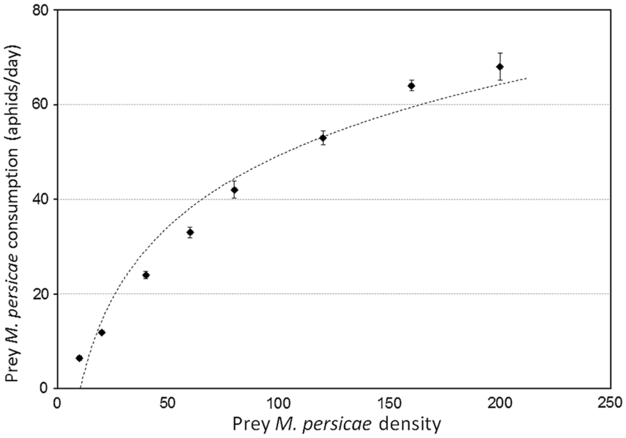

Fig. 1 Daily prey *Myzus persicae* consumption and fitted response curve of *Propylea japonica* on the host tomato without pre-infestation of *Bemisia tabaci*. Points and error bars are mean ± SE

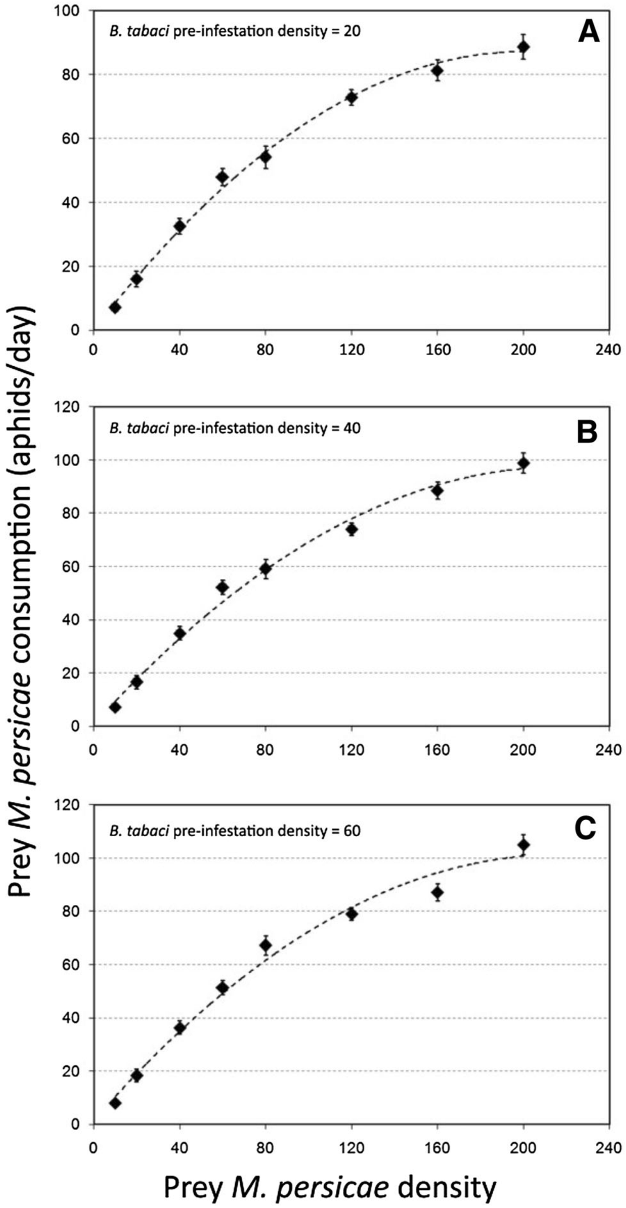

Fig. 2 Daily prey *Myzus persicae* consumption and fitted response curve of *Propylea japonica* in different *Bemisia tabaci* pre-infestation density treatments. **a**, **b**, **c** represent treatments of *Bemisia tabaci* pre-infestation density of 20, 40, and 60 on the target leaf, respectively. Points and error bars are mean ± SE

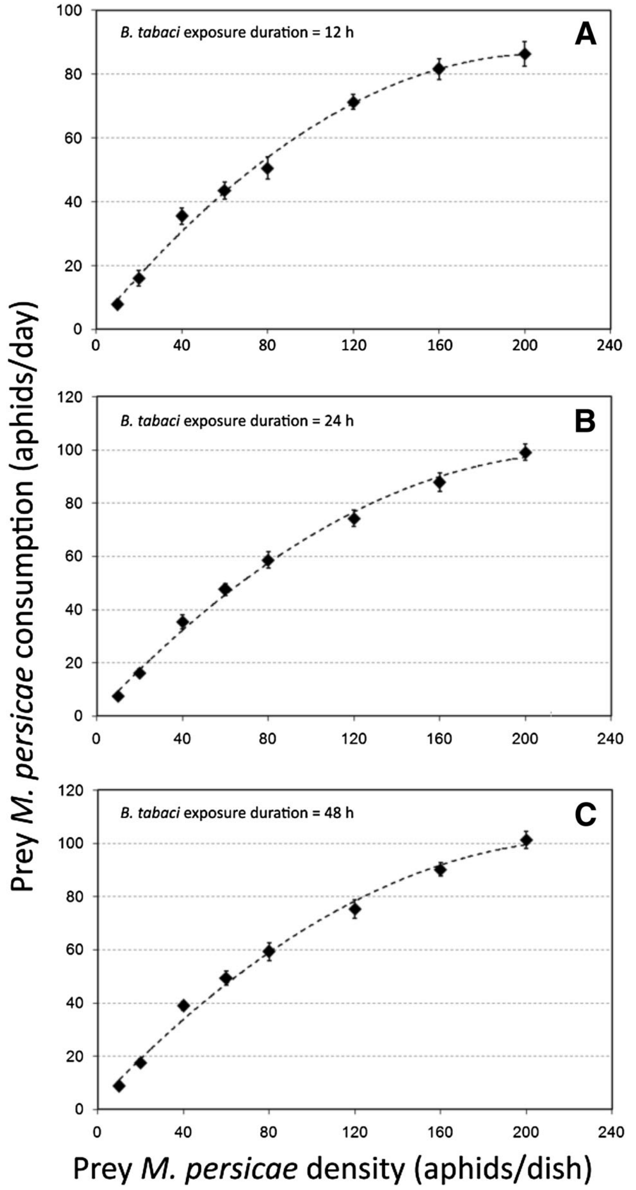

Fig. 3 Daily prey *Myzus persicae* consumption and fitted response curve of *Propylea japonica* in different *Bemisia tabaci* exposure times. **a**, **b**, **c** represent *Bemisia tabaci* exposure time of 12, 24, and 48 h on the target leaf, respectively. Points and error bars in the charts are mean ± SE

Discussion

The present study is the first evaluation of the influence that pre-infestation with a herbivore has on predation by a ladybird on a subsequent herbivore. Our results showed that different *B. tabaci* densities, exposure times, and relative position to pre-infested leaf can affect *M. persicae* consumption by *P. japonica*, jointly with prey density. The implication that using pre-infestation with minor pests might enhance ability of predators in suppressing dominant pests could be worthy of assessment in larger agro-ecosystem settings.

Our results showed that an increase in density of *B. tabaci* or exposure time can increase attack frequency and maximize prey consumption by *P. japonica*. For the herbivores in the primary level of a food chain/web, competition may involve direct conflict: conflict with those sharing the same nutrition resource (host plant), and conflict via the same natural enemy predators (Bonsall and Hassell 1997; Frank 2010; Hassell and Southwood 1978; Pianka and May 1981). Previous work has revealed that *M.*

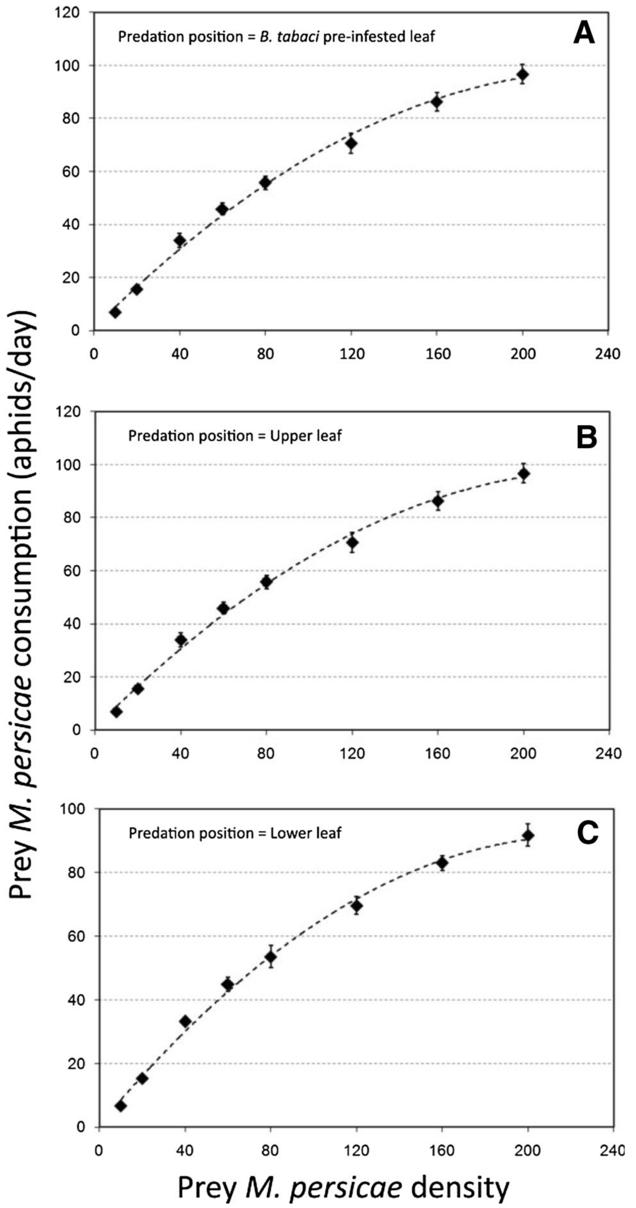

Fig. 4 Daily prey *Myzus persicae* consumption and fitted response curve of *Propylea japonica* in different predation positions on the host plant. **a**, **b**, **c** represent predation positions of *Bemisia tabaci* pre-infested leaf, leaf above, leaf below, respectively. Points and error bars are mean ± SE

Table 1 Factorial multiple-ANOVA of prey consumption of *Propylea japonica* according to various *Bemisia tabaci* pre-infestation treatments and prey *Myzus persicae* densities

Source	*F*	D.f.	*P*
B. tabaci pre-infestation density (BPD)	36.281	2	<0.01
M. persicae density (MD)	13.515	7	<0.01
BPD × MD	7.224	14	<0.01
B. tabaci exposure duration (BED)	62.744	2	<0.01
M. persicae density (MD)	25.17	7	<0.01
BED × MD	8.16	14	<0.01
P. japonica predation position (PPP)	5.411	2	<0.01
M. persicae density (MD)	1429.965	7	<0.01
PPP × MD	0.735	14	0.739

persicae and *B. tabaci*, regardless of which was the first colonizer, inhibits establishment of the successor (Inbar and Gerling 2008). Although the mechanism is not known in detail, the inhibition of successionary herbivores is probably due to plant-induced defenses triggered by the initial herbivore (Ament et al. 2004; Mauricio 2000). In our previous work, we have evaluated various natural enemies, including both predators and parasitoids of *B. tabaci*, and found that aphid-damaged plants can attract natural enemies (Tan and Liu 2014). These results hint at greater complexity to inter-species interactions between herbivore competitors, shared host plants, and natural enemies. Our studies also reveal plant mechanisms regulating competitive herbivores in addition to the impacts of natural enemies, the latter perhaps described as apparent competition (Varley et al. 1974). Our results also showed that the herbivore-induced plant defenses were affected not only by the presence or absence of pre-infestation, but also by the level and type of pre-infestation.

Propylea japonica had the greatest degree of predation when present on the pre-infested leaf itself, while leaves lower down on the plant experienced the least, pointing to systemic responses of tomato plants for regulating herbivore damage. Many laboratory experiments have revealed that herbivore-induced plant reactions appear not only at the site of damage, but include whole-plant immunizing systems (Bezemer and van Dam 2005; Howe and Jander 2008; Schilmiller and Howe 2005). For instance, when herbivore damage in the root generates secondary metabolic (immunological) materials such as jasmonic acid, which are transported throughout plant, which can variously tolerate or repel herbivores (Baldwin 1998; Maurhofer et al. 1994; Stratmann 2003). Further, systemic defensive reactions aggregate more in new leaves and stems than in older tissues (Dicke and Bruin 2001). Work has established that pre-infestation of herbivores may induce the expression of signaling genes which synthesize defensive secondary materials or volatiles, although such genes can be activated in the plant tissues which have not actually been attacked (Dicke and Baldwin 2010). Meanwhile, these systemic reactions can act as an attractant to natural enemies, which is beneficial to the host plant (Dicke and van Poecke 2002; Sabelis et al. 2001; Vet and Dicke 1992). Furthermore, there exists community-level effects, with herbivore-induced plant volatiles triggering direct defensive reactions in neighbor plants (Kost and Heil 2006). Therefore, the influence of herbivore-induced

Table 2 The functional response equations and related parameters of *Propylea japonica* to *Myzus persicae* on different tomato plants under various pre-infestation treatments by *Bemisia tabaci*

Pre-infestation treatment	Functional response equations	*r*	*a*	T_h	A/T_h	$N_{a\ max}$ (aphids/day)	Chi-square	*P*
Without pre-infestation (control)	$N_a = 0.694N/(1 + 0.0068N)$	0.954	0.694	0.00992	70.0	101	3.321	0.774
Pre-infestation density								
20	$N_a = 0.717N/(1 + 0.0069N)$	0.971	0.717	0.00973	73.6	102	5.191	0.637
40	$N_a = 0.722N/(1 + 0.0058N)$	0.973	0.722	0.00817	88.4	122	6.213	0.717
60	$N_a = 0.842N/(1 + 0.0059N)$	0.949	0.842	0.00709	118.8	141	6.434	0.798
Exposure duration								
12 h	$N_a = 0.801N/(1 + 0.0056N)$	0.987	0.801	0.0072	111.3	142	5.779	0.566
24 h	$N_a = 0.897N/(1 + 0.0053N)$	0.934	0.897	0.0061	149.5	166	5.963	0.544
48 h	$N_a = 0.946N/(1 + 0.0051N)$	0.946	0.946	0.0053	178.5	188	5.554	0.512
Predation position								
Pre-infested leaf	$N_a = 0.7331N/(1 + 0.005N)$	0.933	0.733	0.0069	106.2	144	6.122	0.526
Upper leaf	$N_a = 0.669N/(1 + 0.0049N)$	0.938	0.669	0.0074	90.4	135	6.161	0.521
Lower leaf	$N_a = 0.634N/(1 + 0.0052N)$	0.929	0.634	0.0082	77.5	122	6.022	0.533

a instant attack rate, T_h handling time, a/T_h net attack frequency, $N_{a\ max}$ theoretical maximum aphid consumption

systemic defense on predation by biological control agents is worthy of more attention for improving pest management effectiveness.

The Holling functional response models, which include type I, II, and III, have been widely used for estimating predator–prey relationships and for evaluating predatory ability on specific prey species (Holling 1966; Rogers 1972). Although classical models have mostly been used in practical measurement of predator ability in pest suppression (De Clercq et al. 2000; Mohaghegh et al. 2001), modified Holling functional response models have been developed for describing some specific ecological situations, such parasitoid–host (Fernández-arhex et al. 2003), mimicry in predator–prey (Holling 1965), and there has been theoretical and formulaic development by mathematicians (Gazori and Hesaaraki 2015). Hassell (1978) developed a modified Holling-type model which was concerned with the unexpected death of prey during observation, probably improving suitability for estimating predation in natural conditions. However, at present, the calculated indexes from the functional response models were primarily required for understanding the influences of pre-infestations. The calculations were not related to specific situations such as unexpected loss or death of prey. Thus, the classic Holling type II model sufficed for providing indexes helping us to explore influences of whitefly pre-infestation to changes in predation strategy of ladybirds. In further work, we will explore the utility of modified Holling models for practical evaluation of predatory ability.

With the development of augmentative biological control, the precision regulation of the interactions among herbivores and predators or parasitoids have been hotspots of research (Huang et al. 2011; Tan et al. 2016). Therefore, increasing understanding of the influences of plant mediation in competition among herbivores may help us to improve pest suppression via more effective predation. More studies are required in the field of quantified regulation of herbivore pre-infestation and its influences on the reproduction and colonization of the predators, in the context of practical biological control.

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