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Sublethal Effects of Cyantraniliprole and Imidacloprid on Feeding Behavior and Life Table Parameters of *Myzus persicae* (Hemiptera: Aphididae)

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Abstract

The green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), is an agricultural pest that seriously infests many crops worldwide. This study used electrical penetration graphs (EPGs) and life table parameters to estimate the sublethal effects of cyantraniliprole and imidacloprid on the feeding behavior and hormesis of *M. persicae*. The sublethal concentrations (LC_{30}) of cyantraniliprole and imidacloprid against adult *M. persicae* were 4.933 and 0.541 mg L^{-1}, respectively. The feeding data obtained from EPG analysis indicated that the count probes and number of short probes (<3 min) were significantly increased when aphids were exposed to LC_{30} of imidacloprid-treated plants. In addition, the phloem-feeding behavior of *M. persicae* was significantly impaired on fed tobacco plants treated with cyantraniliprole and imidacloprid at LC_{30}. Analysis of life table parameters indicated that the growth and reproduction of F_1 generation aphids were significantly affected when initial adults were exposed to LC_{30} of cyantraniliprole and imidacloprid. The nymphal period, female longevity, total preoviposition period, and mean generation time were significantly prolonged when initial adults were exposed to LC_{30} of imidacloprid. By comparison, these parameters were prolonged but not significantly in the cyantraniliprole treatment. The fecundity and gross reproductive rate were significantly increased in the treated groups. Similarly, the net reproductive rate was greater in the treated group than the control group. Our results indicate that treatment with LC_{30} of imidacloprid and cyantraniliprole would lead to a hormetic response of *M. persicae*, with higher likelihood of occurrence when initial adults were exposed to LC_{30} of cyantraniliprole.

Key words: sublethal effect, *Myzus persicae*, cyantraniliprole, feeding behavior, life table

The green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), is an agricultural pest that severely affects various crops in many temperate regions worldwide (Van Emden and Harrington 2007). *Myzus persicae* causes direct damage by feeding on the vascular bundles of plants and transmits more than 100 plant viruses (Blackman and Eastop 2000). Tobacco is an important economically crop in China. Large areas of tobacco farms are infested by aphids, particularly *M. persicae*, which transmits viral diseases, leading to huge yield losses every year. Insecticides are the first barrier of defense in the management of aphids. Since the early 1990s, neonicotinoid insecticides, such as imidacloprid, have been used as one of the main insecticides to control green peach aphids (Elbert et al. 2008). Neonicotinoids act on nicotinic acetylcholine receptor sites, thereby preventing signal transduction, resulting in a lasting impairment of the nervous system and final death of aphids (Millar and Denholm 2007).

Recent field studies have reported that cyantraniliprole possesses excellent effect in controlling *M. persicae* populations in pepper and cabbage (Kuhar and Doughty 2010, Palumbo 2011, Walgenbach and Schoof 2011). Cyantraniliprole is a second-generation anthranilic diamide, which acts in insects by stimulating ryanodine receptors that regulate calcium release from intracellular stores in the sarcoplasmic reticulum, resulting in a depletion of those stores, gradual muscle contraction, and paralysis (Insecticide Resistance Action Committee [IRAC] 2007, Sattelle et al. 2008, Jeanguenat 2013). Cyantraniliprole has xylem-mobile activity and is easily taken up by plant roots; it also has translaminar activity after foliar applications (Caballero et al. 2013, Cameron et al. 2013, Barry et al. 2015). In addition, cyantraniliprole has not been cross-resisted by any of the known insecticide mechanisms present in *M. persicae* or *Aphis gossypii* (Foster et al. 2012).

Sublethal effects are defined as physiological and/or behavioral effects on individuals that survive exposure to a toxic compound at low or sublethal concentrations or doses (Desneux et al. 2007). Under field conditions, insecticides would be degraded by abiotic factors over time (Desneux et al. 2005, Biondi et al. 2012), and then

M. persicae would be exposed to sublethal concentrations of pesticides. In addition to direct mortality by representative poisoning effects, insecticides may interfere with the feeding behavior and life table parameters, such as nymph developmental period, adult longevity, and fecundity (Civolani et al. 2014, Jacobson and Kennedy 2014, Koo et al. 2015, Mustafa et al. 2015).

Electrical penetration graphs (EPGs) are an effective tool to assess the effects of insecticides on the feeding behavior of piercing-sucking insect pests, including aphids, whiteflies, psyllids, and thrips (Cho et al. 2011, Butler et al. 2012, Jacobson and Kennedy 2013, Serikawa et al. 2013, Civolani et al. 2014). When an aphid feeds on phloem, the aphid's stylet penetrates between the epidermal and mesophyll cells overlying the vascular tissues of the phloem until a suitable nutritional site is found (Sauge et al. 2002). Thus, aphids can determine whether a plant is suitable for feeding after several probing attempts. Koo et al. (2015) found that exposure to LC_{30} of flonicamid and imidacloprid significantly affects the duration of phloem ingestion of cotton aphids. Life table studies offer a comprehensive description of population dynamics and help illuminate multiple sublethal effects of pesticides on insects (Jones and Parrella 1984, Hamedi et al. 2010, Tang et al. 2015).

Previous studies indicated that the effects of exposure to sublethal concentrations of insecticides on feeding behavior or life table parameters seem to be highly dependent on the type of insecticide and the exposed insect species (Cho et al. 2011). Cyantraniliprole is a potential insecticide to manage aphids, and imidacloprid is a common insecticide used to control aphids. The sublethal effects of cyantraniliprole and imidacloprid on *M. persicae* have not been systematically studied and compared. This study aimed to determine the effects of tobacco treated with LC_{30} of cyantraniliprole and imidacloprid on the feeding behavior of *M. persicae*. In addition, the LC_{30} of cyantraniliprole and imidacloprid on developmental period of nymphs, adult longevity, and fecundity of *M. persicae* were also determined. Results of this study provide basis for controlling aphids in the field.

Materials and Methods

Insects and Test Plants

The susceptible laboratory population of green peach aphid (*M. persicae*) used in this study was initially collected from a tobacco farm in Chongqing, China (Site: 29°59', N, 106°54' E). The aphids were maintained in our laboratory at College of Plant Protection Southwest University, Chongqing, China, without exposure to any insecticides since September 2014. *Myzus persicae* was reared on tobacco seedlings and maintained at 25 ± 1°C and 70 ± 5% relative humidity (RH), with a photoperiod of 16:8 (L:D) h.

Insecticide efficacy and EPG feeding behavior assays were conducted on tobacco leaves and four true-leaf stage tobacco plants, respectively. For the insecticide efficacy experiments, leaves from tobacco plants at the six-leaf stage were detached and used to evaluate aphid mortality. All plants were kept in a growth chamber under controlled conditions of 25 ± 1°C and a photoperiod of 16:8 (L:D) h.

Insecticides

Cyantraniliprole (commercial formulation 10% SC, DuPont, Delaware, USA) and imidacloprid (commercial formulation 10% WP, Jiangsu Changqing Agrochemical Co., Ltd., Jiangsu, China) were used in all experiments. Serial dilutions were prepared using distilled water. Solutions were used immediately after preparation to minimize any chemical decomposition.

Leaf-Dip Bioassays

The toxicity of the insecticides was evaluated with leaf-dip method (Moores et al. 1996). Different concentrations of cyantraniliprole (1.6, 3.2, 6.4, 12.8, 25.6, and 51.2 mg/L) and imidacloprid (0.13, 0.26, 0.52, 1.04, 2.08, and 4.16 mg/L) were prepared. Tobacco leaf discs (7.5 cm in diameter) were cut out with a stainless steel cork borer. Leaf discs were individually dipped for 30 s into the insecticide solutions, and then placed in the shade to air dry at room temperature until all the droplets evaporated (2 h). The leaf discs were then placed with their abaxial surface downwards onto petri dishes (9 cm in diameter) containing 2% agar to maintain humidity, and each disc was inoculated with 30 adult apterous aphids. For the untreated control, leaf discs were dipped only in distilled water. The petri dishes were kept at 25 ± 1°C, 70 ± 5% RH, and 16:8 (L:D) h photoperiod in a growth chamber, and their mortalities were evaluated under a stereomicroscope at 48 h posttreatment. Aphids that did not move at all when their legs were probed with a fine paintbrush were scored as dead. The bioassays were repeated for three times for each concentration of each insecticide. The mortalities of all the control groups were lower than 2%. LC_{30} and LC_{50} values were calculated by using probit analysis.

Electrical Recording of *M. persicae* Feeding Behavior

For the EPG feeding behavior experiments, tobacco seedlings were sprayed until run-off (adaxial and abaxial leaf sides) with the insecticide solutions or distilled water using a hand sprayer. Test plants were air-dried for 2 h prior to the experiments. The experiments were conducted inside a Faraday cage to avoid electrical noises in the laboratory (25 ± 1°C, 70 ± 5% RH), and all aphids and plants were used only once. Adult wingless aphids were connected individually via their dorsum to gold wire (2−3 cm in length and 15 µm in diameter) using silver conductive paint glue and connected to the input probe of the EPG. Another copper electrode (10 cm in length and 2 mm in diameter) was inserted into the base material of each potted plant. Aphids were starved for approximately 1 h between the time of wiring and the beginning of EPG monitoring. Then, the aphids were placed on the adaxial side of the youngest fully expanded leaf of four true-leaf stage tobacco seedlings, and EPGs were recorded for 6 h. A completely randomized design was used for these experiments. One Giga-4 DC-EPG system with a 1 GΩ of input resistance (EPG Systems) was used to record the probing and feeding activities of aphids. A USB digital converter was used to transfer the EPG signals to a laptop PC.

EPGs were recorded and analyzed using Stylet+ Software. EPG variables were processed using the EPG-Excel Data Workbook developed by Sarria et al. (2009). The waveforms, previously described for *M. persicae* and correlated with the probing activity, were characterized as: 1) non-probing (waveform np, indicating no stylet contact with the plant tissue); 2) pathway phase (waveforms C, F, and pd, representing intercellular stylet pathway, stylet penetration difficulties mechanics, and intracellular feeding, respectively); 3) xylem ingestion (waveform G); and 4) phloem activities (waveforms E1 and E2, reflecting salivation into phloem sieve elements and passive phloem ingestion, respectively).

Transgenerational Sublethal Effects on the F_1 Generation of Aphids

The LC_{30} values of two insecticides were obtained from previous bioassays. Solutions with LC_{30} of cyantraniliprole and imidacloprid were prepared using distilled water, and distilled water was used for the control group. Leaf discs were prepared using the method

previously described (see the *Leaf-dip bioassays* section). In total, 180 adult apterous aphids were distributed on six tobacco leaf discs dipped in cyantraniliprole and imidacloprid for the treatment groups. For the control group, 120 aphids were placed equally on four tobacco leaf discs. Mortality after 48 h of exposure was calculated, and any surviving aphids were gently transferred onto petri dishes (9 cm in diameter) containing new tobacco leaf discs without any insecticide.

After 6 h, 120–135 F_1 neonate nymphs were randomly selected from the treatment and control groups and placed individually on leaf discs (3.4 cm in diameter) without any pesticide in six-well cell culture plates containing 2% agar–water medium. The population parameters including the nymph development time of different stages, adult longevity, and the number of progeny produced per female were recorded every 12 h. During the experiments, leaf discs were replaced in each dish every 5 d and the skin and newborn nymphs were removed every 12 h. The experiments were conducted in the growth chamber at 25 ± 1°C and 70 ± 5% RH, with a photoperiod of 16:8 (L:D) h.

Statistical Analysis

Concentration–mortality relationships from the toxicity tests were determined using standard probit analysis in Polo Plus, version 2.0 to determine the LC_{30}. The means, standard errors, and significant differences of life table parameters were calculated with bootstrapping methods (Efron and Tibshirani 1993, Huang and Chi 2013) performed in TWOSEX-MSChart 2015.045 (Chi 2012). The data of basic life table parameters (developmental time and female longevity) and feeding behavior were statistically analyzed using one-way analysis of variance and least significant difference test under the significance level of 0.05 (P-value = 0.05) in SPSS 17.0. We designed the life table parameters with 10,000 bootstrap replications (m = 10000) and calculated the mean. Survival rates, fecundity, and reproductive value curves were built using Origin Pro 9.0.

Results

Toxicity of Cyantraniliprole and Imidacloprid on *M. persicae* Adults

Standard probit analysis of concentration–mortality data showed that after 48 h of exposure to cyantraniliprole and imidacloprid, the LC_{50} values were estimated at 12.726 and 1.691 mg L^{-1}, respectively (Table 1). The LC_{30} values of cyantraniliprole and imidacloprid (i.e., 4.933 and 0.541 mg L^{-1}, respectively) were used for the subsequent assessment of feeding behavior and life table studies.

EPG and Feeding Behavior of *M. persicae*

Table 2 shows that both the LC_{30} of cyantraniliprole and imidacloprid significantly affected the feeding behavior of *M. persicae* compared with the control (water-treated tobacco plants). The count probes and number of short probes (C<3 min) were significantly increased in aphids exposed to LC_{30} imidacloprid-treated plants when compared with those in aphids exposed to LC_{30} cyantraniliprole-treated plants and water-treated plants ($F = 8.15$; df = 2, 57; $P = 0.001$). No significant differences were observed in the sum time of np waves and total duration of C waves among the treatments and control group. However, the mean values of these time parameters were extended after exposure to LC_{30} of cyantraniliprole and imidacloprid. In the plants treated with LC_{30} of cyantraniliprole, the number of pd (intracellular punctures) was reduced, but no significant differences were detected among the groups. The duration of F waves was significantly different in aphids exposed to LC_{30} cyantraniliprole- and imidacloprid-treated plants compared with water-treated plants ($F = 3.90$; df = 2, 57; $P < 0.05$), with a mean duration of (81.35 ± 21.41), (68.35 ± 15.89), and (21.31 ± 7.47) min, respectively. Treatment with LC_{30} of the tested insecticides did not significantly affect xylem ingestion of *M. persicae*, but the duration of G wave on aphids exposed to LC_{30} cyantraniliprole-treated plants and imidacloprid-treated plants was longer than that of the control.

The proportions of individuals that produced E1 and E2 waveforms by aphids feeding on tobacco plants treated with LC_{30} of cyantraniliprole and imidacloprid were lower than that in the control group. The number of E1 and E2 waveforms was not different between aphids feeding on the insecticide-treated and control plants. Moreover, treatment with LC_{30} of the tested insecticides did not significantly affect the time from first probe to first E2 waveform and the total duration of the E1 waveforms produced by aphids, but the time in the treatment groups was shorter than that in the control group. However, *M. persicae* that fed on insecticide-treated tobacco plants showed significant reductions in the number of sustained E2 wave (>10 min; $F = 13.39$; df = 2, 57; $P < 0.001$), total duration of E2 wave ($F = 27.56$; df = 2, 57; $P < 0.001$), duration of first E waveform ($F = 18.51$; df = 2, 57; $P < 0.001$), and duration of the longest E2 wave ($F = 20.00$; df = 2, 40; $P < 0.001$) compared with aphids that fed on plants treated only with water. Interestingly, when aphids fed on tobacco plants treated with LC_{30} cyantraniliprole and imidacloprid, the contribution of E1 to phloem phase (%) was higher than that in the control group ($F = 12.11$; df = 2, 57; $P < 0.001$).

Transgenerational Effects of LC_{30} of Cyantraniliprole and Imidacloprid on F_1 Generation Individuals

The development time, longevity, and fecundity of F_1 generation aphids are presented in Table 3. The developmental period of nymphs was not significantly different in the LC_{30} cyantraniliprole treatment, but was significantly delayed by LC_{30} imidacloprid treatment, compared with the control. The female longevity, adult preoviposition period (APOP), and total preoviposition period (TPOP) for the LC_{30} imidacloprid treatment were significantly prolonged compared with those for the control and cyantraniliprole treatment. More offspring were laid by F_1 generation adult aphids than the control adults.

The effects of treatment with LC_{30} of cyantraniliprole and imidacloprid on population parameters of *M. persicae* were evaluated

Table 1. Toxicity of cyantraniliprole and imidacloprid to adult *M. persicae*

Insecticides	N^a	Slope ± SE	LC_{30} (95% CI[b]) mg L^{-1}	LC_{50} (95% CI) mg L^{-1}	χ^2	df
Cyantraniliprole	630	1.274 ± 0.124	4.933 (3.711–6.211)	12.726 (10.312–15.974)	0.632	4
Imidacloprid	630	1.060 ± 0.125	0.541 (0.392–0.704)	1.691 (1.292–2.373)	1.399	4

[a] Total number of aphids used in the experiments.
[b] Confidence interval.

Table 2. Probing and feeding behavior of *Myzus persicae* on cyantraniliprole-, imidacloprid-, and water-treated (control) tobacco plants

Feeding behavior	Control	Cyantraniliprole	Imidacloprid	*P*
Count probes	15.45 ± 1.53a	13.95 ± 1.80a	30.95 ± 5.20b	0.001
	$N^a = 20$	$N = 20$	$N = 20$	
Number of short probes (C<3 min)	9.5 ± 1.35a	6.9 ± 1.15a	21.95 ± 4.49b	0.001
	$PPW^b = 19/20$	PPW = 19/20	PPW = 20/20	
Sum time of np wave (min)	79.58 ± 12.21	86.29 ± 16.78	116.09 ± 11.35	0.141
	$N = 20$	$N = 20$	$N = 20$	
Total duration of C (min)	108.46 ± 10.98	134.18 ± 17.29	145.62 ± 14.22	0.183
	$N = 20$	$N = 20$	$N = 20$	
Number of pd	113.95 ± 12.51	109.75 ± 16.25	131.40 ± 12.28	0.505
	$N = 20$	$N = 20$	$N = 20$	
Number of F	0.50 ± 0.17b	1.80 ± 0.59a	1.55 ± 0.37ab	0.070
	PPW = 7/20	PPW = 12/20	PPW = 14/20	
Duration of F (min)	21.31 ± 7.47b	81.35 ± 21.41a	68.35 ± 15.89a	0.026
	PPW = 7/20	PPW = 12/20	PPW = 14/20	
Number of G	0.50 ± 0.22	0.30 ± 0.16	0.65 ± 0.33	0.615
	PPW = 5/20	PPW = 4/20	PPW = 5/20	
Duration of G (min)	1.77 ± 0.92	8.30 ± 6.42	8.39 ± 3.96	0.477
	PPW = 5/20	PPW = 4/20	PPW = 5/20	
Number of E1	2.90 ± 0.79	4.80 ± 2.21	3.55 ± 1.12	0.664
	PPW = 20/20	PPW = 14/20	PPW = 17/20	
Total duration of E1 (min)	7.98 ± 2.19	19.25 ± 6.83	11.67 ± 3.41	0.217
	PPW = 20/20	PPW = 14/20	PPW = 17/20	
Number of E2	1.90 ± 0.46	4.40 ± 2.16	1.95 ± 1.00	0.360
	PPW = 20/20	PPW = 12/20	PPW = 6/20	
Time from 1st probe to 1st E2 (min)	148.17 ± 20.67	180.01 ± 36.57	223.82 ± 34.11	0.180
	PPW = 20/20	PPW = 12/20	PPW = 6/20	
Number of sustained E2 (>10 min)	1.45 ± 0.18a	0.50 ± 0.20b	0.30 ± 0.11b	<0.001
	PPW = 20/20	PPW = 6/20	PPW = 6/20	
Total duration of E2 (min)	140.91 ± 18.82a	30.63 ± 13.25b	9.88 ± 3.15b	<0.001
	PPW = 20/20	PPW = 12/20	PPW = 6/20	
Duration of 1st E (min)	88.23 ± 17.89a	14.01 ± 5.01b	3.46 ± 0.83b	<0.001
	PPW = 20/20	PPW = 14/20	PPW = 17/20	
Contribution of E1 to phloem phase (%)	9.59 ± 3.05b	37.89 ± 7.59a	56.82 ± 8.54a	<0.001
	PPW = 20/20	PPW = 14/20	PPW = 17/20	
Duration of the longest E2 (min)	128.31 ± 18.68a	17.41 ± 4.58b	13.27 ± 3.16b	<0.001
	PPW = 20/20	PPW = 12/20	PPW = 6/20	

Data in the table are mean ± SE. Means followed by different small letters indicate significant difference ($\alpha = 0.05$).

[a] Total number of aphids recorded per treatment where all insects exhibited the reported waveform.

[b] Proportion of individuals that produced the waveform type.

Table 3. Developmental time, female longevity, APOP, TPOP, total preadult survivorship, and fecundity of F_1 generation of *M. persicae* following 48-h exposure of initial adults to LC_{30} of cyantraniliprole and imidacloprid

Stage	Control		Cyantraniliprole		Imidacloprid	
	n	Developmental time (days)	*n*	Developmental time (days)	*n*	Developmental time (days)
First instar (N1)	132	1.03 ± 0.05b	135	1.17 ± 0.03a	120	1.14 ± 0.03a
Second instar (N2)	132	1.23 ± 0.04a	135	1.17 ± 0.02ab	120	1.09 ± 0.04b
Third instar (N3)	123	1.28 ± 0.03	132	1.22 ± 0.02	89	1.25 ± 0.03
Fourth instar (N4)	121	1.55 ± 0.03	132	1.53 ± 0.01	84	1.58 ± 0.03
Preadult	121	5.02 ± 0.07b	131	5.11 ± 0.04ab	84	5.25 ± 0.06a
Female longevity	121	13.46 ± 0.29b	131	13.84 ± 0.25b	84	16.74 ± 0.50a
APOP	117	0.58 ± 0.02b	131	0.57 ± 0.02b	84	0.70 ± 0.04a
TPOP	117	5.60 ± 0.07b	131	5.68 ± 0.04b	84	5.95 ± 0.09a
Total preadult survivorship (%)		91.67		97.04		70.00
Fecundity(offspring)	117	42.71 ± 1.89b	131	52.29 ± 1.45a	84	54.93 ± 2.28a

Data in the table are mean ± SE. Means followed by different small letters indicate significant difference ($\alpha = 0.05$)

(Table 4). The intrinsic rate of increase (r) and finite rate of increase (λ) increased considerably in the LC_{30} cyantraniliprole treatment, but a significant reduction was found in LC_{30} imidacloprid treatment, compared with the control group. The net reproductive rate (R_0) was significantly increased by LC_{30} cyantraniliprole treatment. The mean generation time (T) was significantly prolonged in the treatment groups, particularly significant in the LC_{30} imidacloprid treatment. Initial adults treated with LC_{30} of cyantraniliprole and

Table 4. Population parameters of F_1 generation of *M. persicae* following 48-h exposure of initial adults to LC_{30} of cyantraniliprole and imidacloprid

Parameters	Original			Bootstrap (mean ± SE)		
	Control	Cyantraniliprole	Imidacloprid	Control	Cyantraniliprole	Imidacloprid
r (d^{-1})	0.4335	0.4542	0.3881	0.4333 ± 0.0068b	0.4542 ± 0.0038a	0.3878 ± 0.0089c
λ (d^{-1})	1.5428	1.5749	1.4741	1.5424 ± 0.0105b	1.5749 ± 0.0060a	1.4738 ± 0.0131c
R_0 (offspring/individual)	37.86	50.75	38.45	37.85 ± 2.0423b	50.75 ± 1.6025a	38.45 ± 2.7740b
T (d)	8.38	8.65	9.40	8.38 ± 0.07c	8.65 ± 0.05b	9.41 ± 0.08a
GRR (offspring/individual)	58.13	63.20	64.10	58.11 ± 1.9592b	63.20 ± 1.5400a	64.12 ± 1.6857a

Data in the table are mean ± SE. Means followed by different small letters indicate significant difference ($\alpha = 0.05$).
r, intrinsic rate of increase; λ, finite rate of increase; R_0, net reproductive rate; T, mean generation time; GRR, gross reproduction rate.
The standard errors of the population parameters were calculated by using the bootstrap procedure (m = 10,000).

imidacloprid showed significantly increased gross reproductive rate (GRR) compared with the control.

Fig. 1 shows the transgenerational effect of LC_{30} of cyantraniliprole and imidacloprid on age–stage survival rate (s_{xj}), which represents the probability of survival of a newly laid nymph in terms of age x and stage j. In our experiments, distinct overlaps among stages were demonstrated for both control and treatment groups. The survivorship of preadult was 97.04% for the cyantraniliprole group, which was higher than that for the imidacloprid group (70.00%) and control group (91.67%).

The age-specific survival rate curve (lx) shows the probability of survival of a newborn nymph at age x (Fig. 2A). The survivorship of the LC_{30} imidacloprid-treated group had the fastest decline in the larval stage and the gentlest fall in the adult stage. However, the LC_{30} cyantraniliprole-treated group had a completely inverse result. In the curve m_x (Fig. 2B), the earliest occurrence of the highest fecundity peak (3.8600 offspring) was observed in the control group at the age of 6.5 d; the highest fecundity peak (4.3664 offspring) of the test populations was observed in the cyantraniliprole treatment at the age of 7.5 d. The maximal $l_x m_x$ values appeared at the age of 8.5, 7.5, and 6.5 d, with a mean number of 2.6333, 4.2370, and 3.4773 offspring for the imidacloprid, cyantraniliprole, and control groups, respectively (Fig. 2C).

Discussion

In addition to direct mortality induced by insecticides, survivors exposed to these products may experience behavioral and/or physiological alterations (Desneux et al. 2007). In our study, we assessed the sublethal effects of cyantraniliprole (a new insecticide) and imidacloprid (a conventional insecticide) on the feeding behavior and life table parameters of *M. persicae*.

In the present EPG study, the count probes and number of short probes (C<3 min) were significantly increased after exposure to LC_{30} imidacloprid compared with the cyantraniliprole treatment and control. This finding may be closely related to the characteristics of the tested insecticides, i.e., imidacloprid induces phobotaxis and cyantraniliprole could palsy insects. The total duration of C wave and duration of F waves produced by aphids feeding on tobacco plants treated with LC_{30} of cyantraniliprole and imidacloprid were longer than those of the control. Thus, aphids need more time to search for suitable nutritional sites when exposed to LC_{30} of cyantraniliprole and imidacloprid. The durations of G wave in the insecticide treatment were longer than that of the control. The ingestion of xylem sap is associated with the water balance of an insect (Powell et al. 1995). Our result indicates that aphids may need to ingest more xylem sap to maintain water balance when feeding on tobacco plants treated with LC_{30} of cyantraniliprole and imidacloprid. The feeding data obtained from EPG analysis indicated that the phloem-feeding behavior of *M. persicae* fed with tobacco plants treated with LC_{30} of cyantraniliprole and imidacloprid had changed significantly. Imidacloprid at low concentrations has antifeedant effects, as determined by honeydew excretion and feeding behavior studies (Nauen et al. 1998, He et al. 2013). Likewise, feeding of plants treated with cyantraniliprole showed a reduction in the amount of honeydew produced by *Bemisia tabaci* adults (Cameron et al. 2014). Our result demonstrated that LC_{30} of cyantraniliprole and imidacloprid could suppress the phloem ingestion of aphids feeding on the treated tobacco.

Moreover, the number of pd (intracellular stylet punctures) was reduced after exposure to LC_{30} of cyantraniliprole. EPG analysis showed two of the pd subphases, i.e., II-1 and II-3, with salivation and ingestion events by experimental evidence from inoculation and acquisition of nonpersistent viruses, respectively (Spiller et al. 1990, Martin et al. 1997, Powell 2005). The process lasts for a matter of seconds; although cyantraniliprole reduced the number of intracellular punctures, the result would not be expected to reduce transmission of nonpersistently transmitted viruses (Jacobson and Kennedy 2014). However, cyantraniliprole acts in insects by reducing intracellular calcium concentration, resulting in muscle contraction and paralysis. Thus, mobility of insects was slowed after exposure to cyantraniliprole, and the intercellular penetration was reduced. A previous study suggested that cyantraniliprole has a quick immobilizing effect and induces movement of apterae from treated plants to other plants, resulting in reduced virus transmission (Foster et al. 2012).

Persistent aphid-borne viruses are acquired from and inoculated into plants by aphids performing passive phloem ingestion (E2 waveform) and salivation into phloem sieve elements (E1 waveform). Imidacloprid is effective in reducing the incidence of persistent viruses by producing rapid feeding cessation of insect vectors (Mowry and Ophus 2002, Mowry 2005, Royer et al. 2005). For example, a reduction in feeding time and percentage of individuals that fed on phloem sap is believed to be responsible for reduced transmission of barley yellow dwarf virus, a phloem-borne virus, by *Schizaphis graminum* (Costa et al. 2011). In our study, proportion of individuals that produced E1 waveform and E2 waveform, number of sustained E2 wave (>10 min), total duration of E2 wave, duration of first E waveform, and duration of the longest E2 wave showed significant reductions in aphids feeding on the insecticide-treated plants. Thus, the probability of transmitting persistent aphid-borne viruses was reduced with the application of cyantraniliprole and imidacloprid at LC_{30} on tobacco. However, both the

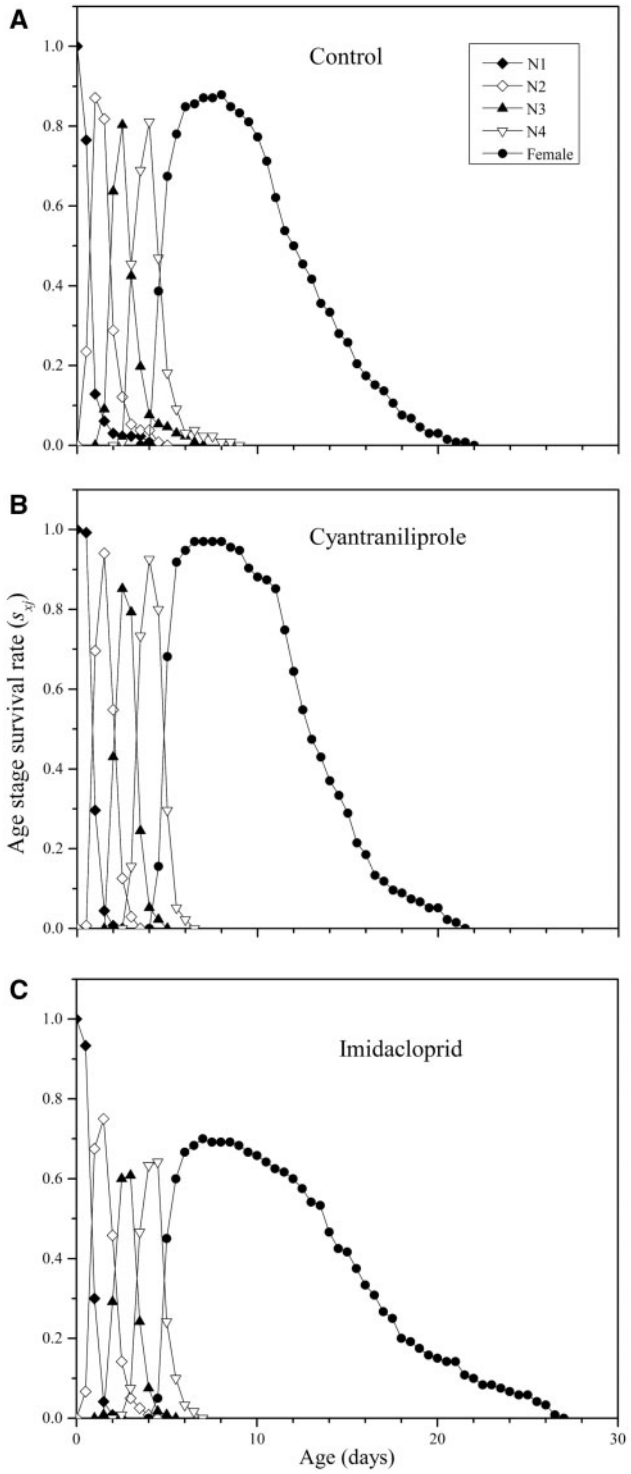

Fig. 1. Age–stage-specific survival rate (s_{xj}) of *M. persicae* F_1 generation following 48-h exposure of initial adults to LC_{30} of cyantraniliprole and imidacloprid

number of E1 wave and the total duration of E1 wave were increased in the treatment groups. In particular, the contribution of E1 to phloem phase (%) was significantly higher in the treatment groups than in the control group. This result may be due to need of aphids to secrete more saliva to cope with toxicant compounds. For example, a grain aphid could secrete saliva to react with a range of phenolic compounds occurring naturally in cereals (Urbanska et al. 1998).

The present study indicated that the nymphal period, female longevity, TPOP, and mean generation time (T) were prolonged but not significantly when initial adults were exposed to LC_{30} of cyantraniliprole. However, these parameters were significantly prolonged when initial adults were exposed to LC_{30} of imidacloprid. Consistent results were obtained when parent generation aphids were stimulated by LC_{25} of sulfoxaflor (Tang et al. 2015). The developmental time of the progeny of mother aphid treated with LC_{25} of imidacloprid was significantly delayed compared with that of the control (Wang et al. 2008). These phenomena may be explained by the finding that F_1 generation requires more time to obtain nutrients, reproduce mass progeny, and cope with the stress caused by the test insecticides (Tang et al. 2015). Moreover, results of the present study showed that the fecundity and GRR were significantly increased in treatment groups. Similarly, the R_0 was greater in the treatment group than in the control group. Similar result has been reported in Cutler et al. (2009), in which the number of F_2 progeny was significantly greater than the untreated control when F_1 *M. persicae* adult was exposed to 0.3 μg L^{-1} imidacloprid. The higher reproduction rates of parent generation in the treatment groups may be closely related to ensure that their progeny population was large enough to compensate for the disrupted homeostasis of *M. persicae* caused by LC_{30} of insecticides (Tang et al. 2015). However, the higher intrinsic rate of increase (r) and finite rate of increase (λ) indicated that LC_{30} of cyantraniliprole may result in rapid outbreak of *M. persicae*.

The survival and stage differentiation of aphids under different conditions are comprehensively described in Fig. 1. Combining with Fig. 2A (l_x), the lower survivorship of progeny in the nymphal stage treated with LC_{30} of imidacloprid and the higher survival rate in the cyantraniliprole treatment may cause maternal effects. The different trends of survival rate may be due to entirely different mechanisms of action of the two insecticides: imidacloprid can rapidly knock down pests, whereas cyantraniliprole induces paralysis to death of insects. The m_x results suggested that the cyantraniliprole treatment had a longer approximate plateau stage. LC_{30} of insecticides can induce resurgence of pest populations by stimulating overcompensation in reproduction through a hormetic response (Morse 1998). Our results indicate that LC_{30} of imidacloprid and cyantraniliprole would lead to a hormetic response in *M. persicae*, and the likelihood of occurrence was greater when initial adults were exposed to LC_{30} of cyantraniliprole.

Considering the continuous degradation and asymmetrical distribution of insecticides in the field, insect populations are frequently exposed to LC_{30} of insecticides. We used imidacloprid, which is commonly used to control aphids, and cyantraniliprole, which is a potential insecticide to manage aphids. In our experiments, we determined the sublethal effects of cyantraniliprole and imidacloprid on the feeding behavior and life table parameters of *M. persicae* feeding on tobacco. Result showed that the feeding behavior of *M. persicae* was effectively inhibited after spraying LC_{30} of cyantraniliprole and imidacloprid in the foliage of tobacco and, to some extent, suppressed the transmission of aphid-borne viruses. We also studied the sublethal effects of imidacloprid and cyantraniliprole on the life table parameters of F_1 generation aphids in the laboratory. Results showed that pesticide-induced resurgence may occur after exposure of adult aphids to LC_{30} of imidacloprid and, especially, cyantraniliprole. However, evaluation of the influence of pesticides on pest populations for just one life stage is insufficient. The conclusion would have been more persuasive if the life table parameters of F_2

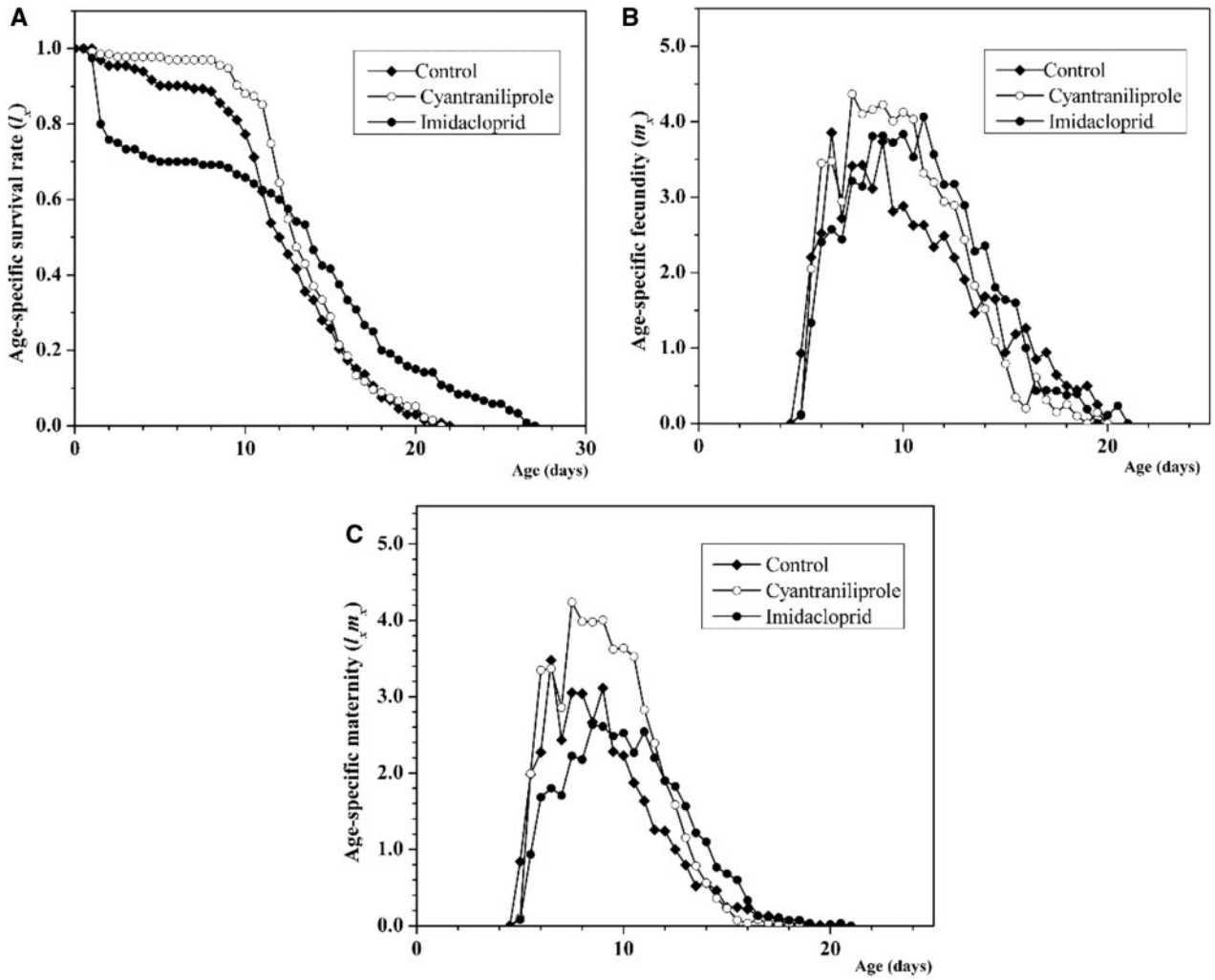

Fig. 2. (**A**) Age-specific survival rate (l_x), (**B**) age-specific fecundity of total population (m_x), and (**C**) age-specific maternity (l_xm_x) of *M. persicae* F_1 generation following 48-h exposure of initial adults to LC_{30} of cyantraniliprole and imidacloprid.

and F_3 generations had been evaluated. In addition, the negative effects of test insecticides on natural enemies (e.g., *Aphidius gifuensis*) should also be studied. Certainly, the effects of the insecticides at LC_{30} on controlling aphid-borne viruses and the population dynamics of *M. persicae* should be investigated under field conditions.

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