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Sublethal and hormesis effects of beta-cypermethrin on the biology, life table parameters and reproductive potential of soybean aphid *Aphis glycines*

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Abstract Beta-cypermethrin has long been recommended as an effective pesticide to control the soybean aphid, *Aphis glycines* Matsumura, a serious pest in soybean crops. Besides acute toxicity, it leads to changes in life history traits of *A. glycines*, notably its reproductive potential. This study has assessed the effects of five sublethal concentrations (0.625, 1.25, 2.5, 5 and 10 μg/L) of beta-cypermethrin on different life history traits of *A. glycines*. Exposure to these concentrations caused shorter oviposition period and reduced adult longevity. The strongest stimulatory effect on aphid reproduction was achieved when exposed to a higher sublethal beta-cypermethrin concentration (5 μg/L). Net reproduction rate (R_0), intrinsic rate of increase (r_m) and finite rate of increase (λ) were significantly higher than that of the control, increasing by 20.58, 4.89 and 2.06%, respectively. We found no significant difference in mean generation time (T) between the treatment of 5 μg/L beta-cypermethrin and the control. However, when the concentration increased to 10 μg/L, the reproduction behavior was restrained and the mean generation time (T) was shortened, resulting in significant decrease in R_0 and T by 16.58 and 3.83%, respectively. In conclusion, a sublethal concentration (5 μg/L) of beta-cypermethrin triggered the strongest hormesis on *A.glycines*, thus providing valuable knowledge on the sublethal effects of this insecticide on soybean aphids. Hormesis may be one of the mechanisms underlying pest resurgences, and better knowledge would enable a more effective use of insecticides in Integrated Pest Management programs.

Keywords Sublethal concentration · Biological traits · Demographic parameter · Integrated Pest Management · Pest resurgence

Introduction

Sublethal effects are defined as physiological and/or behavioral effects on individuals that survive exposure to a toxic compound at sublethal doses (Desneux et al. 2007). These subtle effects can be negative on behavioral and physiological traits of arthropods, including longevity, development rate, fecundity, sex ratio, feeding activity, food searching and oviposition (Desneux et al. 2004; He et al. 2013; Chen et al. 2015; Fekri et al. 2016; Yao et al. 2015; Rix et al. 2016). Such modifications may have significant influence on the demography of exposed populations (Stark and Banks 2003; Desneux et al. 2007). Moreover, it has been reported that in a growing number of arthropod species, pesticide-induced hormesis may account for pest resurgence (Cordeiro et al. 2013; Guedes et al. 2016).

Life table parameters are effective indexes that can be used to assess the overall sublethal effects at the population level (Stark and Banks 2003; Biondi et al. 2013).

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The survival, development and reproduction of the insect individuals exposed to increasing concentrations of a toxicant can be observed and recorded over their life span. Net reproductive rate (R_0: the population growth rate per generation with regard to the number of female offspring produced per female), intrinsic rate of increase (r_m: the ability of a population to increase logarithmically in an unlimited environment), finite rate of increase (λ: the factor by which a population multiplies) and mean generation time (T: the average interval separating births from one generation to the next) are four main indexes calculated in life table experiments (Carey 1993). The intrinsic rate of increase (r_m) is a key parameter, and represents the ability of a population increasing logarithmically. It has been proposed as a more effective parameter to predict the development of population in an unlimited environment (Birch 2007). In addition to assessment of individual-level effects of pesticides, studying the impact on demographic parameters e.g. the intrinsic rate of increase, is proposed as the more reliable assessment on the toxic effect of insecticides (Forbes and Calow 1999, Stark and Banks 2003, Desneux et al. 2006a; 2007).

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) is a phytophagous insect that feeds on soybean phloem and causes significant damage to soybean, *Glycine max* (L.). The main injuries of the plants caused by the *A. glycines* are leaf curling, premature plant development, stunted growth, fewer pod set and smaller seed size (Wang et al. 1996; Beckendorf et al. 2008). In addition, this pest can transmit numerous plant viruses, including soybean mosaic virus, bean yellow mosaic virus, tobacco vein mottling virus and tobacco etch virus (Hill et al. 2001), which can decrease seed quality and cause yield losses (Ragsdale et al. 2011; Damsteegt et al. 2011). *Aphis glycines* is native to Asia but was detected in North America in 2000, thereafter spreading to 30 states in the US and 3 provinces in Canada by 2009; and became a major pest on soybean crops in North America (Ragsdale et al. 2011). Given the potential for economically significant damage, several control strategies have been experimented and employed against this pest. Although environmentally-friendly control tactics, such as the use of resistant plant varieties (Li et al. 2004; Mensah et al. 2005) and the use of generalist and specialized natural enemies for biological control (Desneux et al. 2006b; 2009; 2012; Miao et al. 2007; Lundgren et al. 2009) have been promoted through biological control programs, chemical control measures still play a basic and important role in Integrated Pest Management (IPM) programs against this pest (Ragsdale et al. 2011).

Beta-cypermethrin belongs to the pyrethroid family. It has a broad insecticide spectrum and a wide application in the control of pests (Gao et al. 2008). In addition, sublethal effects of beta-cypermerthrin have been recently reported for various insect pests. For example, the pupation rate, emergence rate and oviposition period of *Plutella xylostella* exposed to sublethal concentration (LC_{10}) of beta-cypermethrin were significantly decreased. However, fecundity of treated *P. xylostella* significantly increased (Han et al. 2011). Moreover, sublethal concentrations of beta-cypermethrin (LC_{10} and LC_{15}) reduced longevity and fecundity of *Acyrthosiphon pisum* adults (Wang et al. 2014).

Pests may be exposed to sublethal concentrations of pesticides, due to pesticide degradation in fields after initial applications, as well as varying distribution at the time of applications (Desneux et al. 2005). Such an exposure may prompt unintended effects on pests, such as hormesis, and may lead to pest outbreaks (Guedes et al. 2016). Hormesis is a dose-response relationship for a single endpoint whose characteristic is the reversed response between low and high dose of a stressor (Kendig et al. 2010). Research on such sublethal effects of pesticides on pests is important for optimizing pesticide-based IPM (Planes et al. 2013; Guedes et al. 2016). However, potential sublethal effects of beta-cypermethrin on the demographic parameters of *A. glycines* are still unknown. In this study, we assessed the effects of five sublethal concentrations of beta-cypermethrin on various biological traits and demographic parameters of *A. glycines* using a TWOSEX-MSChart computer program (Chi 2012). The results of the present study may be helpful for optimizing IPM programs on soybean aphids.

Materials and methods

Study insects

The laboratory colony of *A. glycines* was established from apterous individuals that were collected from a soybean field in Langfang Experimental Station (Hebei province, China) in June 2007. The colony was maintained by continuous supply of insecticide-free soybean seedlings that grew on vermiculite in climate chambers, at 25 ± 2 °C, 60 ± 10 % RH (relative humidity), L: D (light:dark) = 17:7. New soybean seedlings were provided weekly to the colony and aphids were transferred by replacing infested seedlings with insect-free ones (Qu et al. 2015).

Insecticide and acute toxicity assessment

Analytical grade beta-cypermethrin (95%) was purchased from Jiangsu Pesticide Research Institute Co., Ltd (China). Bioassays were conducted using an insect-dipping method according to the Agricultural Industry standard of the People's Republic of China (NY/T 1154.6-2006).

Preliminary experiments were carried out to determine the scope of concentrations to be tested and then six concentrations of beta-cypermethrin (1000, 100, 50, 10, 1 and 0.1 μg/L) were used in the bioassays. Leaf discs (15-mm diameter) were cut from fully expanded insecticide-free soybean leaves, and then placed upside down onto 2% agar into a 12-well tissue-culture plate. Twenty aphids per replicate were dipped into insecticide solution for 10 s, and then introduced into a well that was confined using a filter paper strip (Hangzhou, China) and there were four replicates per tested concentration. Control aphids were dipped into a solution of distilled water containing 0.005% (v/v) Triton X-100 (a non-ionic surfactant) and 0.1% acetone, which is equal to the concentration of acetone in the dipping solution at the highest concentration tested. The mortality was assessed 24 h post-treatment of exposure; aphids that did not move legs when touched with a fine brush, i.e., no reflex movement, were considered dead (Moores et al. 1996). All the experimental arenas were maintained in climate chambers under the same conditions as above. The concentration-mortality (Abbott 1925) regression line, LC_5 and LC_{15} were calculated to obtain the concentrations for subsequent experiments.

Sublethal concentration assessment

The assessment was carried out using the insect-dipping method, as described above (section *Insecticide and acute toxicity assessment*). Five low concentrations of beta-cypermethrin i.e., 0.625, 1.25, 2.5, 5 (nearly LC_5) and 10 μg/L (nearly LC_{15}) were used during the assays. The mortality rates induced by the five concentrations were compared with those observed in control individuals that were exposed to distilled water containing 0.005% (v/v) Triton X-100 plus 0.001% acetone.

Sublethal effects on biological and demographic parameters

Newly-hatched *A. glycines* nymphs were collected within 24 h after spawning. There were 31, 32, 33, 32, 40, 32 newly-hatched nymphs in control, 0.625, 1.25, 2.5, 5 and 10 μg/L beta-cypermethrin treatment groups, respectively, in the life table experiment. Each individual growing on one insecticide-free soybean seedling was considered as one replicate which was kept in climate chambers, at 25 ± 2 °C, 60 ± 10 % RH, L:D = 17:7. Survival and development of each nymph were recorded every day. On the fifth day after birth, the third instar nymphs in the six groups were exposed to the corresponding concentrations of beta-cypermethrin (0.625, 1.25, 2.5, 5 and 10 μg/L) and control solution, respectively. Survivals and development were recorded daily until the end of the experiment (i.e., when adults died). When the nymphs became adults, oviposition was also checked until adult death. Every 5 days, the soybean seedlings were replaced by new ones for aphid feeding (Qu et al. 2015).

Data analysis

LC_5, LC_{15} and LC_{50} values were calculated using SPSS 20.0 in probit analysis (SPSS Inc, Chicago, USA). Mortality of the apterous adults exposed to beta-cypermethrin was analyzed using SPSS 20.0 in a one-way analysis of variance (ANOVA) followed by a Tukey's HSD test for multiple comparisons to assess the sublethal concentrations of beta-cypermethrin. A two-way ANOVA was processed on the cumulative number of offspring over time exposed to different treatments. Moreover, to compare the differences of cumulative number of offspring among treatments ($P < 0.05$), a Tukey's HSD test was carried out. Raw data from all individuals were analyzed using the TWOSEX-MSChart computer program (Chi 2012) according to the age-stage, two-sex life table theory (Chi 1988). Moreover, survival, development, oviposition and population parameters, their mean values and standard errors were estimated by the bootstrap method involved in the TWOSEX-MSChart computer program. Significant differences ($P < 0.05$) among different treatments were calculated by Tukey's HSD method included in the TWOSEX-MSChart computer program. The curves of survival rates and cumulative number of offspring per female were drawn by Sigmaplot 10.0.

In the two-sex life table theory, the age-stage specific survival rate (S_{xj}) (x = age, j = stage) is the probability that a newly laid egg will survive to age x and stage j. The fecundity value (F_{xj}) is defined as the reproductive rate of an individual in age x and stage j. The life expectancy (E_{xj}) is the time that one individual of age x and stage j is expected to live. The age-specific survival rate (l_x) and the age-specific fecundity (m_x) were also recorded. Among the demographic growth parameters calculated according to Chi and Su (2006) as follows: (i) Net reproductive rate ($R_0 = \sum l_x m_x$), (ii) Intrinsic rate of increase (r_m) can then be estimated with the iterative bisection method from the Euler-Lotka equation, with age indexed from 0 (Goodman 1982) as follows: $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$. (iii) Finite rate of increase ($\lambda = \exp(r_m)$. (iv) Mean generation time (T) is calculated as $T = \ln R_0 / r_m$.

Results

Acute toxicity of beta-cypermethrin on *A. glycines*

Based on log-probit regression analysis, the regression equation of mortality relative to concentration is $Y = 1.699X + 2.270$ ($\chi^2 = 10.914$, $P = 0.976$). The LC_{50} of beta-cypermethrin on third instar *A. glycines* was 46 µg/L (95% confidence interval: 34–59 µg/L). LC_5 and LC_{15} of beta-cypermethrin on *A. glycines* were 5 µg/L (2–9 µg/L) and 11 µg/L (6–17 µg/L), respectively.

Assessment of sublethal concentrations

The exposure to 0.625, 1.25, 2.5, 5, 10 µg/L beta-cypermethrin and control solution led to 5.76 % (95% confidence interval: 0.83–10.69 %), 7.72% (2.34–13.10 %), 8.97% (6.35–11.59 %), 6.04 % (2.88–9.20 %), 12.1 % (5.51–18.65 %) and 7.74 % (4.09–11.38 %) mortality of aphids, respectively. There was no significant difference in mortality among these exposure concentrations, including control ($F_{5,\ 24} = 1.940$, $P = 0.125$). Therefore, all these beta-cypermethrin concentrations were considered as sublethal ones according to Desneux et al. (2007).

Effects of sublethal concentrations of beta-cypermethrin on demographic parameters of *A. glycines*

Sublethal beta-cypermerthrin concentrations showed little influence on survival rate in the first 8 days after exposure to the insecticide (Fig. 1). However, the survival rate of individuals exposed to 10 µg/L i.e., approximately LC_{15}, declined rapidly on the 14th day after birth, which was 7 days earlier than that of the control. Aphids from the control group survived the longest and the last one survived until the 28th day, while the last aphid of 0.625, 1.25, 2.5, 5 and 10 µg/L beta-cypermethrin treatment groups died on the 27th, 23rd, 27th, 26th and 21st day, respectively.

Effects of sublethal concentrations of beta-cypermethirn on the development duration in young instar, adult longevity and oviposition period of *A. glycines* are reported in Table 1. The 10 µg/L beta-cypermethrin significantly prolonged the development time of aphids in the 4th instar. However, the sublethal concentrations of beta-cypermethrin significantly shortened the adult lifespan and oviposition period of *A. glycines*. In addition, the 10 µg/L beta-cypermethrin had a strongest negative effect on both lifespan and oviposition period of *A. glycines*, which were significantly shorter than those of other sublethal concentrations.

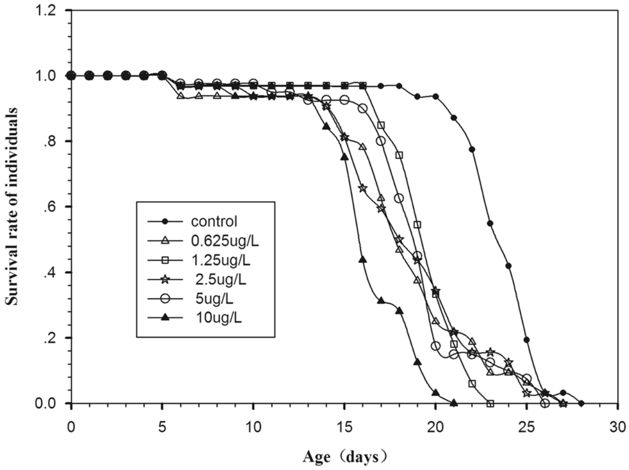

Fig. 1 The survival rate of *A. glycines* exposed to five sublethal concentration of beta-cypermethrin (and water as control)

The result of two-way ANOVA showed that concentration has a significant effect ($F_5 = 17.87$, $P < 0.001$) on the cumulative number of offspring over time. The cumulative numbers of offspring per adult in 0.625, 1.25, 2.5, 5 and 10 µg/L beta-cypermethrin treatment groups and control were (i) 60.27(95 % confidence interval: 57.57–62.97); (ii) 58.28 (56.17–60.39); (iii) 63.16 (59.27–67.06); (iv) 75.41 (72.46–78.36); (v) 52.52 (49.25–55.78) and (vi) 62.97 (60.65–65.29) respectively. The cumulative number of offspring in 5 µg/L beta-cypermethrin treatment group significantly increased but it significantly decreased in 10 µg/L treatment group compared to control and other treatments (Fig. 2).

Effects of sublethal concentrations of beta-cypermethrin on the demographic parameters of *A. glycines* are reported in Table 1. Net reproduction rate (R_0) of the aphids exposed to 5 µg/L beta-cypermethrin (73.521 ± 2.348) significantly increased while R_0 in 10 µg/L beta-cypermethrin treatment group (50.863 ± 2.214) significantly decreased compared to the control (60.975 ± 2.262) and other sublethal concentration treatments (0.625, 1.25 and 2.5 µg/L), whose R_0 were 56.459 ± 2.846; 56.535 ± 1.985 and 61.184 ± 2.709, respectively. In addition, intrinsic rate of increase (r_m) of *A. glycines* exposed to 5 µg/L beta-cypermethrin (0.429 ± 0.003) was significantly higher than that of the control (0.409 ± 0.006) and other sublethal concentration treatments. Similar results were achieved on finite rate of increase (λ), i.e., the λ of *A. glycines* treated with 5 µg/L beta-cypermethrin (1.536 ± 0.006) was significantly higher than that of the control (1.505 ± 0.008) and other sublethal concentrations. Mean generation time (T) of aphids exposed to 1.25 µg/L (9.742 ± 0.088) and 10 µg/L (9.665 ± 0.095) was significantly shorter than that of the control (10.05 ± 0.099), while the other sublethal concentrations showed no significant differences in T values.

Discussion

In this study, sublethal and stimulatory effects of beta-cypermethrin at sublethal concentrations on *A. glycines* were evaluated. We demonstrated that these concentrations decreased the adult lifespan and reproductive period of *A. glycines*. These results concur with the recent research

Table 1 Effects of sublethal concentrations of beta-cypermethrin on development duration and demographic parameters of *A. glycines*

Concentration (μg/L)	Stages (days)					Oviposition period	Demographic parameters			
	First-instar	Second-instar	Third-instar	Forth-instar	Adult longevity		Net reproductive rate (R_0)	Intrinsic rate of increase (r_m)	Finite rate of increase (λ)	Mean generation time (T)
0.625	2.09 ± 0.05 a	1.91 ± 0.05 a	1.12 ± 0.06 a	1.00 ± 0.00 b	13.10 ± 0.59 b	9.30 ± 0.28 cd	56.459 ± 2.846 b	0.407 ± 0.006 b	1.503 ± 0.009 b	9.899 ± 0.085 ab
1.25	2.12 ± 0.06 a	1.91 ± 0.05 a	1.12 ± 0.06 a	1.00 ± 0.00 b	13.65 ± 0.30 b	9.72 ± 0.23 c	56.535 ± 1.985 b	0.414 ± 0.005 b	1.513 ± 0.007 b	9.742 ± 0.088 bc
2.5	2.13 ± 0.06 a	1.88 ± 0.06 a	1.13 ± 0.06 a	1.00 ± 0.00 b	12.87 ± 0.68 b	9.51 ± 0.36 c	61.184 ± 2.709 b	0.410 ± 0.004 b	1.507 ± 0.008 b	10.03 ± 0.110 a
5	2.08 ± 0.04 a	1.87 ± 0.05 a	1.10 ± 0.05 a	1.00 ± 0.00 b	13.37 ± 0.49 b	10.84 ± 0.27 b	73.521 ± 2.348 a	0.429 ± 0.003 a	1.536 ± 0.006 a	10.02 ± 0.077 a
10	2.09 ± 0.05 a	1.91 ± 0.05 a	1.06 ± 0.04 a	1.03 ± 0.03 a	10.58 ± 0.42 c	8.74 ± 0.34 d	50.863 ± 2.214 c	0.406 ± 0.005 b	1.502 ± 0.007 b	9.665 ± 0.095 c
control	2.10 ± 0.05 a	1.90 ± 0.05 a	1.13 ± 0.06 a	1.00 ± 0.00 b	17.77 ± 0.37 a	13.31 ± 0.33 a	60.975 ± 2.262 b	0.409 ± 0.006 b	1.505 ± 0.008 b	10.05 ± 0.099 a

Data (mean ± SE) were analyzed using Twosex-MSChart and followed by Tukey test. Within a column, different letters indicate significant differences ($P < 0.05$)

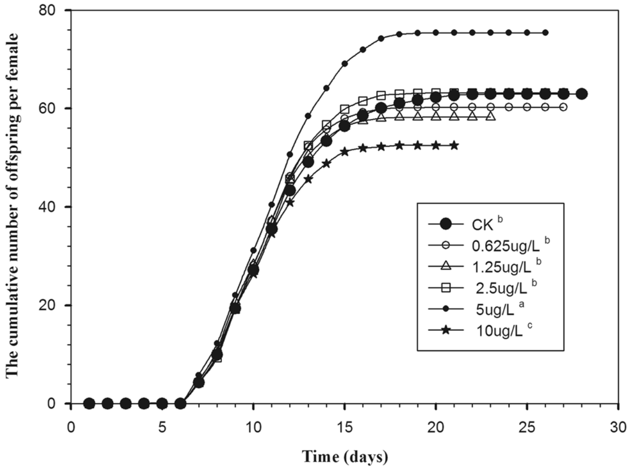

Fig. 2 The cumulative number of offspring per *A. glycines* adult exposed to sublethal concentrations of beta-cypermethrin. The cumulative number of offspring per adult was analyzed using two-way ANOVA over the time among different treatments and followed by Turkey HSD test to compare the difference among different treatments. The curves of cumulative number of offspring with different letters indicated significant difference at $P < 0.05$ level

showing that low concentrations of beta-cypermethrin reduced oviposition period and adult male longevity in *P. xylostella* (Song et al. 2013). Similar findings have been reported for other pyrethroid insecticides e.g. *P. xylostella* adult longevity significantly decreased by 36% when larval stages were treated with LC_1 of permethrin and fenvalerate (Kumar and Chapman 1984). Sublethal concentration of Cyhalothrin (LC_{20}) shortened the adult lifespan of *Adelphocoris suturalis* and prolonged their hatching periods (Li et al. 2008). In addition, both repellent and antifeedant activities were detected on larvae of *P. xylostella* exposed to sublethal concentrations of pyrethroid. Therefore, pyrethroids probably reduced insect fitness by lowering its feeding activity, thus negatively affecting uptake of nutriments.

In our study, a significantly stimulatory effect on fecundity was obtained when the aphids were exposed to 5 μg/L beta-cypermethrin (LC_5), the exposed adults producing more offspring than in the control group; therefore pesticide-induced hormesis may occur in *A. glycines* when exposed to beta-cypermethrin in soybean fields. Similar hormesis has been reported in *P. xylostella* which laid more eggs when exposed to sublethal doses of the pyterthroid fenvalerate (Sota et al. 1998; Fujiwara et al. 2002). Such stimulatory effect on fecundity may also occur in case of natural enemies; the cumulative numbers of offspring increased by 49.64% (compared to the control) after ladybird beetles were exposed to a sublethal concentration of beta-cypermethrin (LC_5) (Xiao et al. 2016). The possible physiological mechanisms of stimulatory effects on reproduction were closely related to the insect hormone and change in the transcription level of vitellogenin. The levels of juvenile hormone III in adult aphids which fed on leaves treated with sublethal concentrations of imidacloprid showed a similar trend to that of fecundity (Yu et al. 2010).

Life table is one of the most useful tools in the research of pest population dynamics (Carey 1993). In our study, stimulating effects on population growth are more obvious when the sublethal concentration of beta-cypermethrin increases. The largest stimulatory effect on fecundity was achieved when aphids were exposed to the sublethal concentration of 5 µg/L (LC_5). Net reproductive rate (R_0), intrinsic rate of increase (r_m) and finite rate of increase (λ) of the *A. glycines* population all significantly increased. However, the population growth was inhibited when the sublethal concentration continued to increase to 10 µg/L (LC_{15}). Our results are consistent with previous studies. The soybean population treated with imidacloprid at a concentration of 0.05 mg/L showed enhanced net reproductive rate (R_0). The reversed effect on R_0 was achieved when soybean aphids were exposed to 0.2 mg/L imidacloprid (Qu et al. 2015). Moreover, it has also been found that beta-cypermethrin at a sublethal concentration (LC_5) increased R_0 and r_m of *Harmonia axyridis* population in F1 generation (Xiao et al. 2015, 2016). However, various studies reported contrasted results on different pests and/or different pesticides. The R_0, r_m and λ of the *P. xylostella* population treated with LC_{25} of chlorantraniliprole were remarkably lower than those of the control (Guo et al. 2013). Different effects on demographic parameters may be linked to the action modes of pesticides, exposure doses of pesticides, pest species, and pest feeding ways used in researches.

Hormesis in insects exposed to sublethal concentrations of insecticides has been documented for several taxa and compounds (Tan et al. 2012; Qu et al. 2015; Xiao et al. 2015), especially for pyrethoids (Cutler. 2013). In the present study, we have assessed whether hormesis effects, especially on fecundity traits, may occur in *A. glycines* during and/or after exposure to sublethal concentrations of beta-cypermethrin. Our findings indicated that a high sublethal concentration of beta-cypermethrin (5 µg/L) increased fecundity by 19 % (12–28 %) compared with control. By contrast, beta-cypermethrin at the highest sublethal concentration (10 µg/L) decreased the fecundity by 17 % (8–25%). Our results concur with a previous study on citrus thrips; high malathion residue concentrations initially inhibited fecundity during exposure while this reproductive trait was increased post-exposure (Morse and Zareh 1991). The mechanism(s) underneath insecticide-induced hormesis effect in insects may be linked to conservation laws in mass and energy. The insects have to allocate energy/mass to detoxify insecticides at sublethal doses. Some life-history traits such as development and reproduction are changed as a result of responses to the stimulation (Jager et al. 2013). Pyrethroid (Cordeiro et al. 2013) and neonicotinoid insecticides (Yu et al. 2010) have been reported to cause a hormesis on pests, especially on the reproduction trait. Exposure to sublethal concentrations of imidacloprid could stimulate reproduction on *Myzus persicae* (Cutler et al. 2009; Rix et al. 2016) and *A. glycines* (Qu et al. 2015). In addition, the applications of synthetic pyrethroids induce resurgence of *Aphis gossypii* on cottons (Nandihalli et al. 1992). Recently, deltamethrin-induced hormesis has been linked to red mite outbreaks (Cordeiro et al. 2013). Still, resurgence of a given pest can be also attributed to various biotic and abiotic factors and not necessarily induced by hormesis. For example, non-target harmful effects of pesticides on arthropod natural enemies could be largely responsible (Desneux et al. 2007). Frequent insecticide sprayings could also induce pest population resurgence by increasing the pest resistance and disrupting the biocontrol services provided by arthropod natural enemies in agroecosystems (Lu et al. 2012).

Overall, our results on *A. glycines*, together with the evidence of other insecticides on pests (Fujiwara et al. 2002; Cutler et al. 2009), suggest that insecticide-induced hormesis should be recognized as one of the mechanisms explaining arthropod pest resurgence (Cutler 2013; Guedes et al. 2016). The resistant genotypes can survive after insecticide spray. Thereafter, the stimulatory effect on development and growth of resistant insects, i.e., hormesis, may favor the population growth of these individuals. Therefore, hormesis is an unfavorable phenomenon to insecticide resistance management and may shorten the lifespan of a given insecticidal compound, especially when it is used frequently. Key changes in biochemical endpoints have recently been analyzed during pesticide-induced stimulation (Cutler 2013; Guedes et al. 2016). However, gene expression during the sublethal effects and hormesis has not been fully studied in insect-insecticide models. Thus, further research on the molecular mechanisms of sublethal effects and insecticide-induced hormesis is required.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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