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RESEARCH

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Sublethal concentrations of thiamethoxam induce transgenerational hormesis in cotton aphid, *Aphis gossypii* Glover

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Abstract

In agroecosystems, insects have to compete with chemical insecticides, which are frequently present at sublethal concentrations. The exposure of insects to these modest stresses is now well-established to generate hormesis effects, which has implications for controlling insect pests. In this study, we assessed the sublethal effects of thiamethoxam on the biological parameters of *Aphis gossypii* Glover (Hemiptera: Aphididae), adults (F_0) and subsequent transgenerational impacts, i.e., on the progeny (F_1 generation), using an age stage, two-sex life table analysis. Results showed that thiamethoxam exhibited high toxicity against adult *A. gossypii* with the LC_{50} of 0.313 mg L^{-1} after 48 h exposure. The LC_5 and LC_{10} of thiamethoxam considerably reduced the adult cotton aphids (F_0) longevity and fecundity, while the reproductive days were reduced only at LC_{10}. The pre-adult stage was decreased, while the adult longevity, total longevity, and fecundity were significantly extended in F_1 aphids after exposure of F_0 aphids to the sublethal concentrations of thiamethoxam. Moreover, the key demographic parameters such as intrinsic rate of increase, finite rate of increase and reproductive days were significantly increased, while mean generation time and total prereproductive were significantly reduced in the progeny. No significant effects were observed on the net reproductive rate. Taken together, these results showed that the sublethal concentrations of thiamethoxam affect the directly exposed aphids (F_0) while causing transgenerational hormetic effects on the F_1 generation of *A. gossypii*. In conclusion, our research showed that thiamethoxam has both sublethal and transgenerational effects on cotton aphids; it could be effective in IPM programs targeting this key pest.

Keywords Sublethal effects, Insecticide toxicity, Hormetic effects, Demographic parameters, Thiamethoxam

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Introduction

The cotton aphid or melon aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae), is one of the most economically important sap-sucking insect pests worldwide. It causes serious economic damage through direct feeding and indirectly via virus transmission and contamination of honeydew (Hullé et al. 2020). Although several methods have been developed and used to control agricultural pests (Ragsdale et al. 2011; Jactel et al. 2019; Zhang et al. 2021; Monticelli et al. 2022; Verheggen et al. 2022), the control of *A. gossypii* in China has largely depended on chemical control. Thiamethoxam is a second-generation neonicotinoid insecticide widely used to control sap-sucking insect pests (Ullah et al. 2020; Zhang et al. 2022). This insecticide binds to nicotinic acetylcholine receptors (nAChRs) in the nervous system, producing nerve stimulation, paralysis, and insect death (Tomizawa & Casida. 2005).

In agroecosystems, insects are exposed to sublethal concentrations due to misapplication or degradation of chemical insecticides due to biotic or abiotic factors (Desneux et al. 2005, 2007). After degradation, the residues of pesticides cause sublethal effects on the exposed arthropods as well as induce resistance development (Ullah et al. 2019c; Gul et al. 2021; Pires Paula et al. 2021). Sublethal effects are defined as the physiological or behavioral effects on individuals that survived following exposure to the sublethal or lethal dose/concentrations of pesticides (Desneux et al. 2007). The sublethal effects directly affect the life-history parameters of survived insects and their descendants (Ullah et al. 2019a, 2020; Jia et al. 2022; Shi et al. 2022). However, several factors, such as dose/concentration, affect these sublethal effects of insecticides on the exposed insects (Cutler 2013; Decourtye et al. 2013). The dose/concentrations of insecticides could boost the exposed individuals' metabolic activities, ultimately stimulating insect growth parameters (Rix & Cutler. 2022; Wang et al. 2022). Stimulation at low dose/concentrations and inhibition at higher dose/concentrations are termed hormesis phenomena (Cutler et al. 2022). Therefore, sublethal effects are crucial for checking the overall effects of any insecticides on target or non-target pests (Guedes et al. 2016). Besides lethal effects, insecticides have sublethal effects on the directly exposed arthropod's physiological and behavioral traits, such as lifespan, developmental period, fertility, and feeding activity (Ullah et al. 2019b; Aeinehchi et al. 2021; Hafeez et al. 2022). These sublethal effects can be transgenerational, affecting offspring and ultimately changing the communities and ecological services (Lu et al. 2012; Abd Allah et al. 2019). Ullah et al. (2019a, b) evaluated hormesis effects in *A. gossypii* after exposure to low lethal and sublethal concentrations of imidacloprid and acetamiprid (Ullah et al. 2019a, 2019b). Reproductive hormesis was also reported in *A. gossypii* following treatment with flonicamid, pirimicarb, and nitenpyram (Koo et al. 2015; Wang et al. 2017). Furthermore, the sublethal concentrations of imidacloprid, flupyradifurone, and precocene cause similar hormetic effects in *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) (Tang et al. 2019; Yu et al. 2010; Ayyanath et al. 2015).

Life table analysis is a valuable tool for studying how biotic and abiotic factors influence the life history data of pests at population level (Chi et al. 2020; 2023). Up to now, the age-stage, two-sex analysis has been widely employed to examine the lethal, sublethal, transgenerational, and hormesis effects of insecticides on insect pests (Liu et al. 2022; Gul et al. 2023; Ju et al. 2023).

Therefore, our objectives were to investigate the sublethal effects of thiamethoxam on the biological characteristics of *A. gossypii* adults referred to as the F_0 generation and to explore its subsequent transgenerational effects on the progeny F_1 generation by utilizing the age-stage, two-sex life table analysis approach. The results showed that the fecundity, longevity, and reproductive days of the parental generation (F_1) of *A. gossypii* significantly decreased at the LC_5 and LC_{10} of thiamethoxam. Moreover, the sublethal concentrations of thiamethoxam significantly increased the longevity, fecundity, and key demographic parameters such as intrinsic rate of increase, finite rate of increase and reproductive days of F_1 generation. Overall, this study showed the sublethal and transgenerational effects of thiamethoxam on cotton aphids that could be effective in IPM programs targeting this key pest.

Material and methods

Experimental insect and insecticide

The cotton aphid, *Aphis gossypii* population used in this research was collected from cotton fields in the Xinjiang Uygur Autonomous Region of China in 1999. The laboratory has successfully maintained the individuals for a period exceeding 15 years, with the regular inclusion of newly obtained individuals from the field every 2 years. Throughout this period, the susceptible population of *A. gossypii* has been kept without any insecticide exposure since their initial collection. The cotton plant, *Gossypium hirsutum* (L.), was used to raise *A. gossypii*. All experiments were conducted in a climatic chamber under controlled environmental conditions (22 ± 1 °C, 70 ± 10% R.H., 16:8 L:D).

Bioassays

The toxicity of thiamethoxam against *A. gossypii* was employed using a leaf-dipping technique. Thiamethoxam was diluted into six concentrations from the associated stock solution (highest concentration) to assess the toxicity. The cotton leaves were dissected into round discs with a diameter of 20 mm using a sharpened steel punch. Cotton leaf discs were dipped in the thiamethoxam concentrations or distilled water (control) for 15 s (Ma et al. 2022). The treated leaf discs were set on disposable PE gloves and air-dried at room temperature. All treated leaf discs were put upside down on 2% (w/v) agar substrates in 12-well cell culture plates. The apterous adult cotton aphids were gently put on leaf discs using a camel hair brush, and the plates were coated with Chinese art paper (Xuan paper) to keep them from escaping. The treatment was repeated three times for each concentration, with at least 30 aphids used in each replicate. The mortality was checked at 48 h after exposure to thiamethoxam. The aphids were considered dead if not moving when pushed gently with a soft brush. The LC_5 and LC_{10} values were calculated using PoloPlus 2.00 (LeOra Software Inc., Berkeley, CA).

Sublethal effects of thiamethoxam on life-history traits of the F_0 generation

Three hundred apterous adult cotton aphids were introduced on fresh cotton plants. After 24 h, all adults were removed, and the newborn nymphs were retained until they developed into apterous adult aphids. This procedure ensured all aphids were the same age (and growth stage) at the initial exposure stage to the insecticide. These adult aphids were subsequently used in the experiment as the F_0 generation. Thiamethoxam was diluted to the LC_5 and LC_{10} with distilled water. Cotton leaf discs (20 mm) were immersed for 15 s in thiamethoxam concentrations (LC_5 and LC_{10}) or distilled water (control). Each treated leaf disc was put on a plastic sheet to air dry at room temperature. The dried leaf discs were put on agar again in the 12-well cell-culture plates. The apterous adults were subsequently placed onto the cotton leaf discs and coated with filter paper to avoid escape. The cell plates were placed in the incubator. After 48 h, 40 alive aphids were individually transferred from each group (LC_5, LC_{10}, and control) onto new 20 mm cotton leaf discs without any insecticide. Throughout the experiment, fresh cotton leaf discs free of insecticide were substituted every 2–3 days. The survival, development, and fecundity were monitored every day. The newly born nymphs were counted daily and removed until the adult aphids reached the end of their life span.

Transgenerational effects of thiamethoxam on biological parameters of the progeny generation

Biological parameters were obtained by using same method described in the previous section from F_1 generation, whose parents were sprayed LC_5 and LC_{10} of thiamethoxam and control group. According to the preceding description, these aphids were individually kept on cotton leaf discs without insecticide. This process was carried out on 40 newly born F_1 progeny for the thiamethoxam treatments and the control. The life table parameters, including fecundity, development, and survival rate of the F_1 aphids, were monitored daily. Daily counts and removals of the newborn nymphs ensured that only adult aphids were left. The fresh cotton leaf discs free of insecticide were replaced every 2–3 days until the adult died. During the experiment, the developmental time, the adult stage's life duration, and the daily fecundity of each aphid were observed.

Life table and statistical analysis

The life table data of thiamethoxam-treated parental aphids (F_0) and their offspring (F_1) were evaluated using the age-stage, two-sex life table technique (Chi 1988; Chi et al. 2020, 2022b). The TWOSEX-MS Chart computer program (Chi et al. 2022a; Chi 2023a) was used to calculate the parameters such as the age-stage specific survival rate (s_{xj}), the age-specific survival rate (l_x), the age-stage reproductive value (v_{xj}), as well as life history traits such as reproductive days, development time, male and female longevity, the adult pre-reproductive period (APOP), the total pre-reproductive period (TPOP), fecundity (F) (eggs/female), the intrinsic rate of increase (r), the finite rate of increase (λ), the net reproductive rate (R_0), the mean generation time (T). To compute the differences and SEs, 100,000 bootstrap replicates were performed (Efron & Tibshirani 1993; Huang & Chi 2012; Akca et al. 2015; Akköprü et al. 2015). At a 5% significant level, the paired bootstrap test was used to evaluate the differences in demographic parameters between the thiamethoxam-exposed groups and the control group based on the confidence interval of the difference (Wei et al. 2020).

Population projection

The population projections for the control group and the cohorts treated with LC_5 and LC_{10} of thiamethoxam were determined using the TIMING-MSChart program (Chi 2023b) following the methodology outlined by Chi (1990). In each cohort (control, LC5, and LC10), the initial aphid population consisted of ten newborn nymphs. These populations were projected over a period of 60 days under the assumption of no suppression by biotic or abiotic factors. To estimate the uncertainty of projection 100,000 bootstrap iterations were performed, and the resulting net reproductive rate (R_0) values were sorted to determine the 2.5th and 97.5th percentiles, corresponding to the 2,500th and 97,500th sorted bootstrap samples. Subsequently, the bootstrap life table samples associated with the R_0 values at the 2.5th and 97.5th percentiles were utilized to project the population for an additional 60 days. These results highlighted the variability and uncertainty inherent in the projected populations by illustrating confidence intervals (Huang et al. 2018).

Results

Toxicity of thiamethoxam on *Aphis gossypii*

The toxicity of thiamethoxam against adult cotton aphids was investigated using leaf-dip bioassay procedure. Results showed that thiamethoxam was highly toxic against adult *A. gossypii* after 48 h exposure with the LC_{50} value of 0.313 mg L^{-1} with confidence interval of 0.262–0.371 mg L^{-1} (Table 1). The LC_5 and LC_{10} values of thiamethoxam against adult cotton aphids were 0.057 mg L^{-1} with confidence interval of 0.037–0.078 mg L^{-1} and 0.083 mg L^{-1} with confidence interval of 0.058–0.108 mg L^{-1} (Table 1). The sublethal concentrations (LC_5 and LC_{10}) were selected to investigate the direct effects of thiamethoxam on parental aphids and indirect effects (transgenerational) on the biological and demographic parameters of progeny generation *A. gossypii*.

Impact of LC_5 and LC_{10} of thiamethoxam on parental *Aphis gossypii* (F_0)

The longevity and fecundity of *A. gossypii* adults were considerably impacted by the LC_5 and LC_{10} of thiamethoxam (Table 2). The longevity of *A. gossypii* decreased extensively after exposure to the LC_5 and LC_{10} of thiamethoxam, compared to the control ($P<0.05$). The *A. gossypii* treated with LC_5 and LC_{10} had a decreased fecundity compared to the untreated control ($P<0.05$). The LC_{10} individuals treated with thiamethoxam had the lowest number of reproductive days than the LC_5 and control group (Table 2, $P<0.05$).

Developmental duration and adult longevity of F_1 *Aphis gossypii*

The transgenerational sublethal effects on F_1 *A. gossypii* whose parents (F_0) were exposed to the LC_5 and LC_{10} of thiamethoxam are presented in Table 3. Results indicated a substantial reduction in the developmental period of the 1st instar when treated with thiamethoxam at LC_5 and LC_{10} concentrations, as compared to the control group (Table 3, (*P < 0.05*). The developmental duration of 3rd instar *A. gossypii* was statistically shortened ($P<0.05$) at LC_5 concentration, while no effects were observed for the LC_{10} group compared to the control. The duration of 2nd and 4th instar aphids was not

Table 1 Toxicity of thiamethoxam against adult *Aphis gossypii* after 48 h exposure

Treatments	Slope ± SE[a]	LC_5 mg/l (95% CL)[b]	LC_{10} mg/l (95% CL)[b]	LC_{50} mg/l (95% CL)[b]	χ2 (*df*)[c]	*P*-value
Thiamethoxam	2.223 ± 0.206	0.057 (0.037–0.078)	0.083 (0.058–0.108)	0.313 (0.262–0.371)	9.416 (16)	0.895

[a] Standard error

[b] 95% confidence intervals

[c] Chi-square value (χ2) and degrees of freedom (*df*) calculated by PoloPlus 2.0

Table 2 Sublethal effects of thiamethoxam LC_5 and LC_{10} on adult longevity, fecundity, and reproductive days of the F_0 generation of *Aphis gossypii*

Parameters	Control Mean ± SE	Thiamethoxam (LC_5) Mean ± SE	Thiamethoxam (LC_{10}) Mean ± SE
Adult Longevity (days)	23.41 ± 0.34 a	21.21 ± 0.27 b	17.03 ± 0.50 c
Fecundity (nymphs/female)	33.21 ± 0.48 a	28.82 ± 0.70 b	23.49 ± 1.03 c
Reproductive days (days)	20.44 ± 0.34 a	19.55 ± 0.31 a	15.97 ± 0.40 b

Standard errors were estimated by using the bootstrap technique with 100,000 resampling. Difference was compared using the paired bootstrap test ($P<0.05$). The means within a row followed by a different lowercase letters indicate significant differences among the treatments

Table 3 Duration (days) of different developmental stages of *Aphis gossypii* F_1 generation, originated from parents (F_0) treated with LC_5 and LC_{10} of thiamethoxam

Stage	*n*	Control Mean ± SE	*n*	Thiamethoxam (LC_5) Mean ± SE	*n*	Thiamethoxam (LC_{10}) Mean ± SE
First-instar nymph	40	2.20 ± 0.09 a	40	1.85 ± 0.08 b	40	1.88 ± 0.07 b
Second-instar nymph	39	1.62 ± 0.09 a	39	1.41 ± 0.08 a	40	1.43 ± 0.08 a
Third-instar nymph	38	1.50 ± 0.09 a	37	1.22 ± 0.07 b	38	1.34 ± 0.08 ab
Fourth-instar nymph	37	1.22 ± 0.07 a	36	1.14 ± 0.06 a	37	1.16 ± 0.06 a
Pre-adult	37	6.54 ± 0.08 a	36	5.64 ± 0.08 b	37	5.81 ± 0.06 b
Adult (Female)	37	24.11 ± 0.30 b	36	27.42 ± 0.29 a	37	26.81 ± 0.37 a
Total longevity (Female)	37	30.65 ± 0.31 b	36	33.06 ± 0.29 a	37	32.62 ± 0.40 a

Standard errors were estimated by using the bootstrap technique with 100,000 resampling. Difference was compared using the paired bootstrap test ($P<0.05$). The means within a row followed by a different lowercase letters indicate significant differences among the treatments affected at both concentrations ($P<0.05$). Consequently, when the parental aphids were exposed to the LC_5 and LC_{10} of thiamethoxam, the pre-adult period of F_1 *A. gossypii* was dramatically reduced compared to the control group ($P<0.05$). Conversely, thiamethoxam considerably improved ($P<0.05$) the adult longevity and total longevity of F_1 aphids at the LC_5 and LC_{10} compared to the control group (Table 3).

Reproduction and life table parameters of F_1 *Aphis gossypii*

The reproductive and life table parameter effects of thiamethoxam on F_1 aphids, whose parental generation was subjected to LC_5 and LC_{10} concentrations (Table 4). These values displayed the transgenerational effect of the insecticide. Results demonstrated that the net reproductive rate (R_0) and adult prereproductive period (APRP) of F_1 aphids at the LC_5 and LC_{10} concentrations have no significant difference ($P<0.05$) compared to the control. The intrinsic rate of increase (r) and the finite rate of increase (λ) were significantly increased ($P<0.05$) in the F_1 generation at both LC_5 and LC_{10} concentrations. Similarly, compared to control, the fecundity (F) and reproductive days (RP_d) of F_1 individuals were increased ($P<0.05$) at both concentrations. However, the mean generation time (T) and total prereproductive period (TPRP) were substantially reduced ($P<0.05$) at both the LC_5 and LC_{10} of thiamethoxam as compared to the control group (Table 4).

The s_{xj} represented the probability of a freshly born *A. gossypii* nymph surviving to age x and stage j (Fig. 1). The differences in the developing and adult stages of *A. gossypii* resulted in several overlaps between the LC_5, LC_{10}, and control groups. The l_x, m_x, and $l_x m_x$ curves for the LC_5, LC_{10}, and control groups are shown in Fig. 2. The sublethal concentrations of thiamethoxam stimulated the l_x, m_x, and $l_x m_x$ parameters of *A. gossypii* compared to the control. The e_{xj} indicates the predicted duration of an individual aphid of age x and stage j after age x (Fig. 3). The curves show that, in comparison to control, the F_1 generation of *A. gossypii* is likely to survive longer in the LC_5 and LC_{10} treatments of thiamethoxam. The v_{xj} curves illustrate the population's adherence to potential offspring from age x to stage j (Fig. 4). The LC_5 and LC_{10} treatments of thiamethoxam had elevated v_{xj} values compared to the control.

Population projection

The population projections and their corresponding percentiles (2.5th and 97.5th) for the progeny generation (F1) of *A. gossypii*, whose parental generation was subjected to LC_5 and LC_{10} concentrations of thiamethoxam for a 60-day period, are plotted in Fig. 5. Notably, the lowest total population size of *A. gossypii* was observed in the cohort derived from the untreated control group, comprising approximately 6.9 million individuals. Conversely, population projections for the F1 progeny exposed to LC_5 and LC_{10} concentrations of thiamethoxam yielded nearly 24 million and 23 million individuals, respectively, thereby indicating clear hormesis effects in comparison to the control population. Significantly, the total population sizes of *A. gossypii* treated with LC_5 and LC_{10} concentrations of thiamethoxam were markedly higher than those of the untreated control group after a 60-day period (Fig. 5).

Discussion

In the present work, we examined the transgenerational and sublethal effects of thiamethoxam (LC_5 and LC_{10}) on two successive generations (F_0 and F_1) of *A. gossypii*. Following a 48-h treatment period, the results revealed that thiamethoxam leaned more toxic to *A. gossypii*, with an

Table 4 Reproduction and life table parameters of *Aphis gossypii* F_1 generation, originated from parents (F_0) treated with LC_5 and LC_{10} of thiamethoxam

Parameters[a]	Control Mean ± SE	Thiamethoxam (LC_5) Mean ± SE	Thiamethoxam (LC_{10}) Mean ± SE
R_0 (offspring/individual)	32.03 ± 1.62 a	36.20 ± 2.00 a	35.80 ± 1.83 a
r (day^{-1})	0.2394 ± 0.0047 b	0.2606 ± 0.0065 a	0.2591 ± 0.0053 a
λ (day^{-1})	1.2705 ± 0.0059 b	1.2977 ± 0.0085 a	1.2958 ± 0.0068 a
T (days)	14.48 ± 0.16 a	13.77 ± 0.22 b	13.81 ± 0.15 b
F (nymphs/female)	34.62 ± 0.79 b	40.22 ± 0.64 a	38.70 ± 0.93 a
RP_d (days)	22.05 ± 0.41 b	24.31 ± 0.32 a	24.32 ± 0.47 a
APRP (days)	0.11 ± 0.05 a	0.25 ± 0.08 a	0.22 ± 0.08 a
TPRP (days)	6.65 ± 0.10 a	5.89 ± 0.12 b	6.03 ± 0.10 b

Standard errors were estimated by using the bootstrap technique with 100,000 resampling. Difference was compared using the paired bootstrap test ($P<0.05$). The means within a row followed by a different lowercase letters indicate significant differences among the treatments

[a] R_0 net reproductive rate, r intrinsic rate of increase; λ finite rate of increase; T mean generation time; F fecundity; RP_d reproductive days; *APRP* adult prereproductive period; *TPRP* total prereproductive period

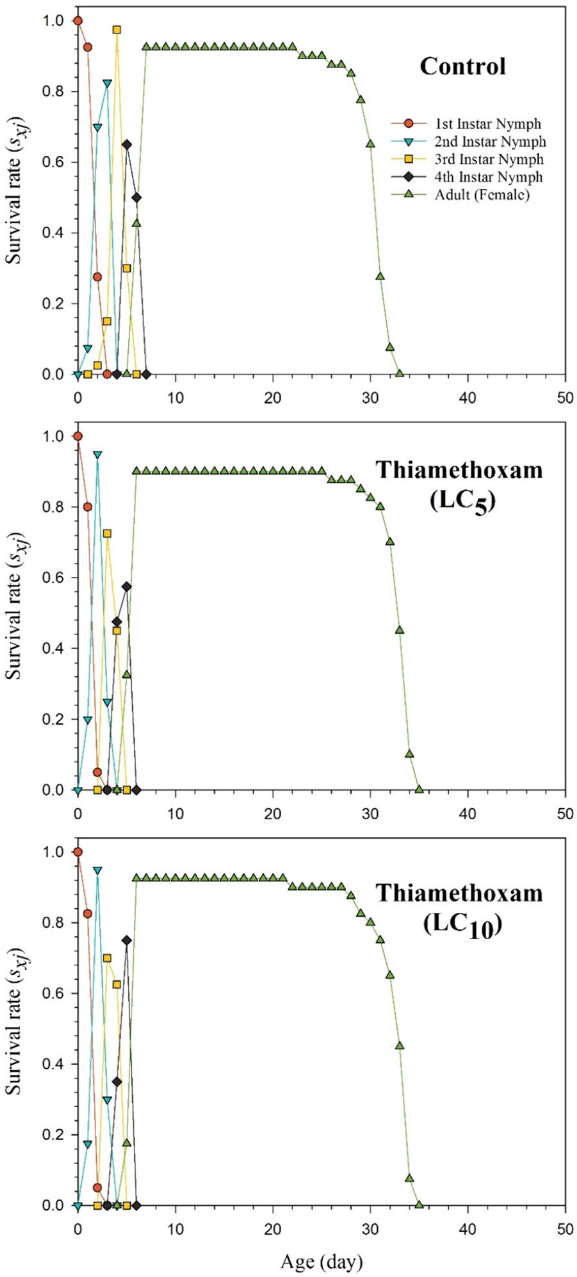

Fig. 1 Age-stage specific survival rate (s_{xj}) of F_1 generation *Aphis gossypii* originated from F_0 individuals treated with the LC_5 and LC_{10} of thiamethoxam

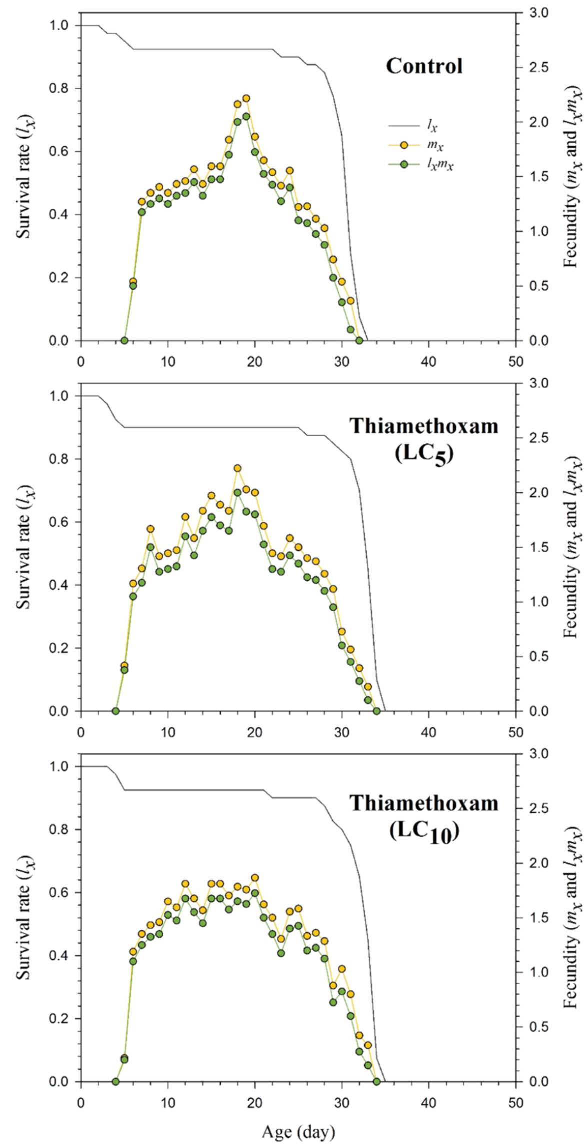

Fig. 2 Age-specific survival rate (l_x), age-specific fecundity (m_x), and the age-specific maternity (l_xm_x) of F_1 generation *Aphis gossypii* originated from F_0 individuals exposed with the LC_5 and LC_{10} of thiamethoxam

LC_{50} of 0.313 mg/l. Aphids exposed to thiamethoxam exhibit transgenerational sublethal/hormesis effects on their biological parameters and lethal toxicity (Ullah et al. 2020). According to these findings, the LC_5 and LC_{10} concentrations may be crucial for managing cotton aphids in field environments.

The current study demonstrates that after exposure to the sublethal concentrations of thiamethoxam for 48 h, the longevity and fecundity of adult *A. gossypii* (F_0) were decreased. Our findings are consistent with (Ma et al. 2022), who reported that treatment with LC_{10} of afidopyropen dramatically decreased the lifespan and fecundity of paternal adult *A. gossypii*. Similarly, decreased fecundity and longevity of the cotton aphid were observed by (Ullah et al. 2019a) following direct exposure to the LC_5 and LC_{15} of imidacloprid. The flupyradifurone was administered to *M. persicae* at sublethal concentrations, and the unfavorable effects, including a shorter lifespan and reduced fertility, were also noted (Tang et al. 2019).

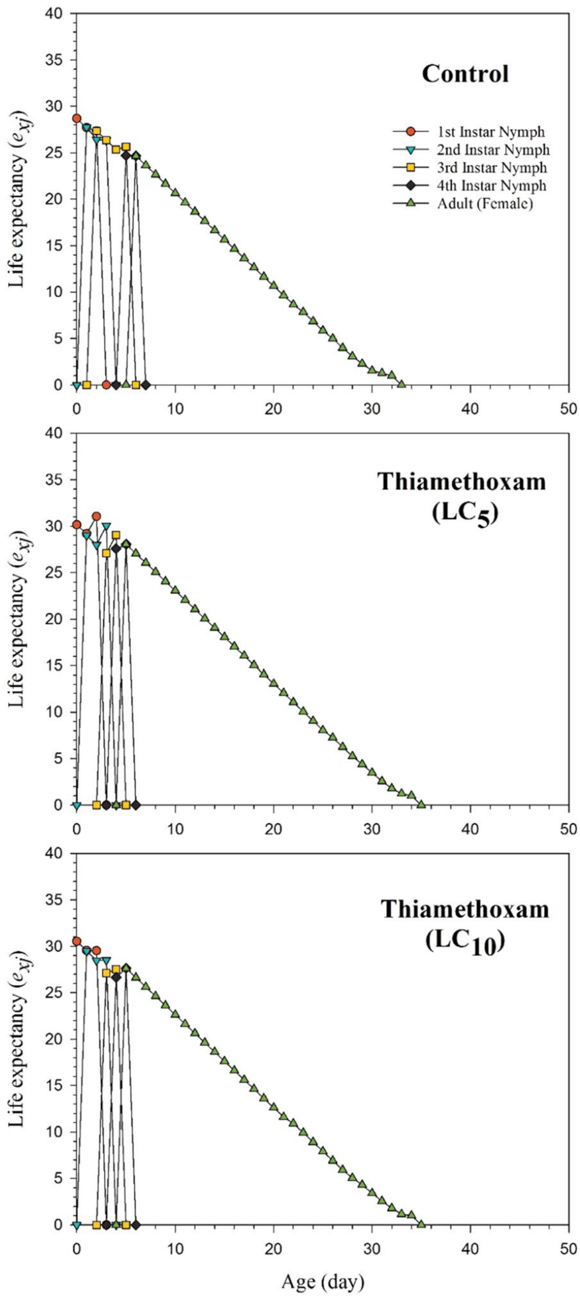

Fig. 3 Age-stage life expectancy (e_{xj}) of progeny generation *Aphis gossypii* (F_1) originated from parental aphids treated with the LC_5 and LC_{10} of thiamethoxam

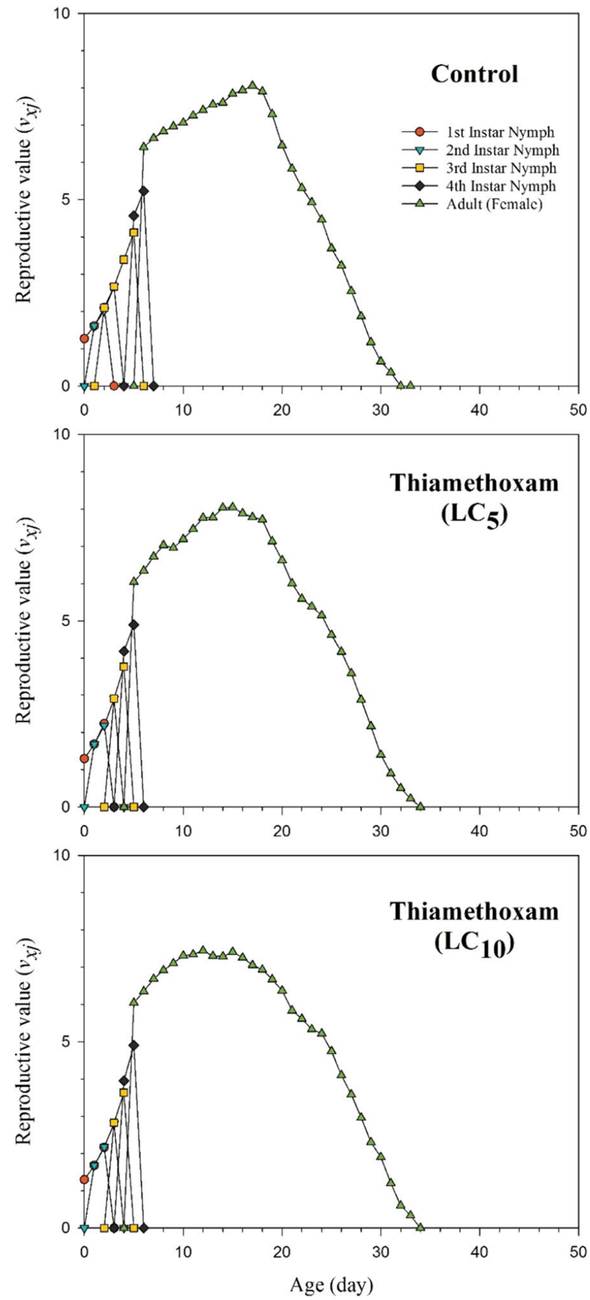

Fig. 4 Age-stage reproductive value (v_{xj}) of progeny generation *Aphis gossypii* (F_1) originated from parental aphids treated with the LC_5 and LC_{10} of thiamethoxam

The greenbug, *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) was exposed to low lethal concentrations of acetamiprid, which drastically decreased its total longevity and fecundity (Vakhide & Safavi. 2014). As a result of sublethal concentrations of cycloxaprid being introduced to parental *A. gossypii*, Cui et al. (2018) also noted a decline in longevity and fertility. These results proved that sublethal concentrations of insecticides significantly affect the adult lifespan and fertility of the surviving aphids in addition to their lethal effects.

The parental aphids (F_0), when exposed to the LC5 and LC10 of thiamethoxam, significantly impacted the developmental phases of F_1 *A. gossypii.* Results showed that the developmental duration of 1st instar of F_1 *A. gossypii*

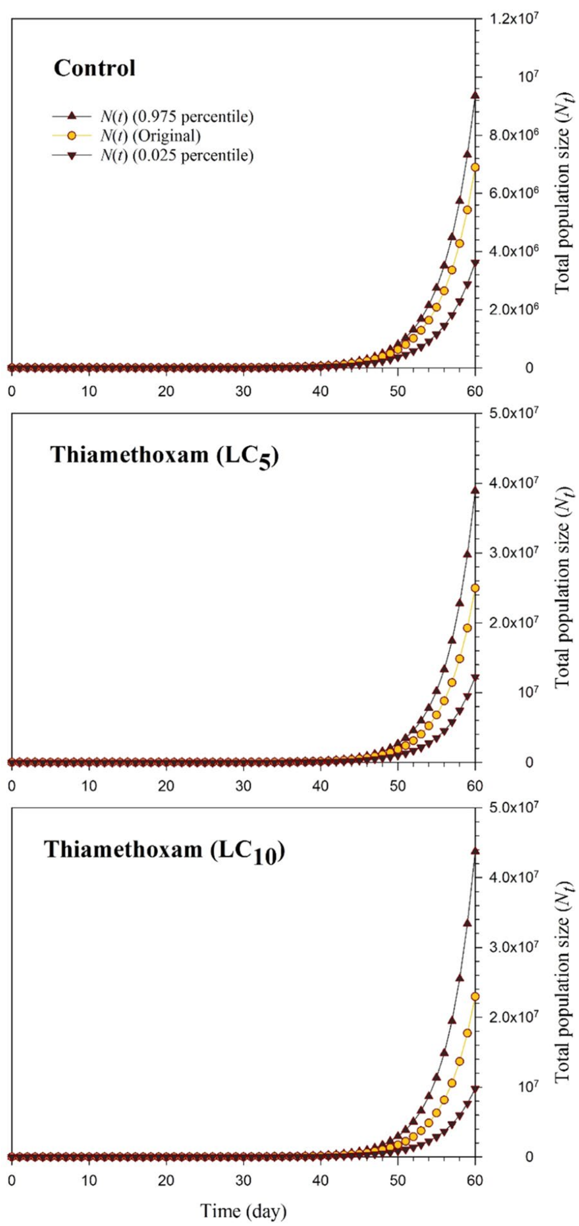

Fig. 5 Projected total population size (N_t) after 60 days for the progeny generation *Aphis gossypii* (F_1) originated from parental aphids treated with the LC_5 and LC_{10} of thiamethoxam and control group using the life table data from the original cohort and the cohorts generated by incorporating the 2.5 and 97.5% percentiles of R_0 (net reproductive rate)

was significantly decreased at both concentrations while reduced only in LC_5 of the 3rd instar of *A. gossypii* compared to the control. The parental generation (F_0), when treated with the LC_5 and LC_{10} of thiamethoxam, the pre-adult stage was considerably shorter in the offspring aphids (F1) compared to the control group. As opposed to the untreated aphids group, thiamethoxam markedly increased the adult longevity and total longevity of F_1 aphids at both concentrations when F0 aphids were treated with LC_5 and LC_{10}. These results showed that after 48 h of exposure, the sublethal concentrations of thiamethoxam positively impacted the development and total lifespan of *A. gossypii*. (Ullah et al. 2019a) observed a reduction in the developmental duration of 4th instar and pre-adult stage of F_1 *A. gossypii* when LC_5 and LC_{15} concentrations of imidacloprid were applied to parental aphids (F_0). The 3rd and 4th instars developmental duration of *M. persicae*, as well as the pre-adult stages, were considerably reduced after 48 h of exposure to the LC_{25} of flupyradifurone (Tang et al. 2019). Thiamethoxam at low lethal concentrations notably shortened the duration of the fourth instar in F_1 *A. gossypii* (Ullah et al. 2020). The developmental time of *A. gossypii* (F_1 generation) was dramatically shortened by sublethal doses of cycloxaprid, according to (Yuan et al. 2017). The adult longevity of the F_1 generation of *A. gossypii* was greatly extended when the parental generation (F_0) was subjected to sublethal and low lethal concentrations of thiamethoxam and imidacloprid (Ullah et al. 2019a, 2020). Tang et al. (2019) concluded that treating the parental aphids (F_0) with the LC_{25} of flupyradifurone greatly increased the longevity of the F_1 and F_2 generations of *M. persicae*. The lifespan of both male and female *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) exhibited a notable increase after being subjected to the LC_{20} concentration of nitenpyram for six consecutive generations (Gong et al. 2022).

In the current research, parental aphids exposed to the LC_5 and LC_{10} of thiamethoxam cause transgenerational hormesis effects in *A. gossypii* compared to untreated aphids. The female fecundity (*F*) and reproductive days (RP_d) were dramatically increased, while the mean generation time (*T*) and total pre-reproductive period (TPRP) were significantly reduced in the offspring generation (F_1). Consequently, the demographic parameters, specifically the intrinsic rate of increase (*r*) and finite rate of increase (λ), were substantially higher in the LC_5 and LC_{10} treatments than in the control. These alterations to the life history traits of *A. gossypii* showed that transgenerational hormetic effects evolved after parental aphids were exposed to the sublethal concentrations of thiamethoxam. *Aphis gossypii* exhibited this hormetic response without apparent fitness trade-offs following exposure to the LC_5 and LC_{10} of thiamethoxam. The occurrence of simultaneous hormetic effects in various traits has been documented in *A. gossypii* when exposed to thiamethoxam, imidacloprid, and acetamiprid (Ullah et al. 2019a, 2019b, 2020) and *M. persicae* when subjected to flupyradifurone, acetamiprid, and imidacloprid (Ayyanath et al. 2013; Sial et al. 2018; Tang et al. 2019). The study conducted by (Gong et al. 2022) investigated the phenomenon of transgenerational hormesis in *N. lugens* following a six-generation exposure to LC_{20} nitenpyram for 96 h. The mean generation time and the pre-adult developmental duration of the *N. lugens* F-Sub6 strain were found to be drastically decreased in the LC_{20} of nitenpyram. In our current research, a similar phenomenon was observed; the pre-adult developmental length and mean generation time (*T*) of cotton aphids significantly declined in the LC_5 and LC_{10} treated groups compared to the control. At 60 days post-exposure, the estimated *A. gossypii* population size in the thiamethoxam-treated groups was higher than in the control group. The results of this study indicate that insects exhibited increased adaptability to insecticide stress following exposure to hormetic concentrations of insecticide, which typically arise after degradation. Agricultural insect pests that are expected to experience numerous and successive low and sublethal stress levels may need to develop their hormesis (Rix et al. 2016; Cutler et al. 2022). Ullah et al. (2020) reported the hormetic effects of thiamethoxam on F_1 individuals of *A. gossypii*, which might be due to the intermittent changes in expression of genes linked to fertility, growth and insecticide detoxification. The increased mRNA transcription level of the vitellogenin gene (*Vg*) might be translated into an increased reproduction of F_1 generation following exposure of parental *A. gossypii* (F_0) to the LC_5 and LC_{15} of acetamiprid (Ullah et al. 2019b). However, future studies are needed to understand the in-depth underlying molecular mechanisms of transgenerational hormetic effects of insecticides on insects. In general, the findings of this study provide solid evidence that the sublethal concentrations of thiamethoxam induce transgenerational hormetic effects on the demographic parameters of *A. gossypii.* The implications of these findings are quite significant in terms of pest management through the use of insecticides.

Conclusion

The fecundity, lifespan, and reproductive days of the parental generation of *A. gossypii* were all considerably decreased following exposure to the sublethal concentrations of thiamethoxam. Furthermore, the LC_5 and LC_{10} of thiamethoxam had transgenerational effects on the subsequent generation (F_1) by altering the key demographic parameters. To the best of our knowledge, this is the first study to investigate the transgenerational hormetic effects of thiamethoxam on the biological parameters of cotton aphids. However, future research should explore the multi-generational hormesis effects of thiamethoxam on *A. gossypii* under field contexts.

Author contributions
Conceptualization, XL, ND, HG and FU; Insect rearing, HG and XN; methodology, HG; analysis, AG and HG; writing—original draft preparation, HG; writing—review and editing, XL, AG, HG, and FU; project administration, XL; funding acquisition, XL. All authors have read the published version of the manuscript.

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Availability of data and materials
All data presented in this study are available in the article.

Declarations

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Not applicable.

Consent for publication
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The authors declare that they have no competing interests.

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References
Abd Allah A, Desneux N, Monticelli LS, Fan Y, Shi X, Guedes RN, Gao X. Potential for insecticide-mediated shift in ecological dominance between two competing aphid species. Chemosphere. 2019;226:651–8.
Aeinehchi P, Naseri B, Rafiee Dastjerdi H, Nouri-Ganbalani G, Golizadeh A. Lethal and sublethal effects of thiacloprid on *Schizaphis graminum* (Rondani)(Hemiptera: Aphididae) and its predator *Hippodamia variegata* (Goeze)(Coleoptera: Coccinellidae). Toxin Rev. 2021;40:1261–71.
Akca I, Ayvaz T, Yazici E, Smith CL, Chi H. Demography and population projection of *Aphis fabae* (Hemiptera: Aphididae): with additional comments on life table research criteria. J Econ Entomol. 2015;108:1466–78.
Akköprü EP, Atlıhan R, Okut H, Chi H. Demographic assessment of plant cultivar resistance to insect pests: a case study of the dusky-veined walnut aphid (Hemiptera: Callaphididae) on five walnut cultivars. J Econ Entomol. 2015;108(2):378–87.
Ayyanath M-M, Cutler GC, Scott-Dupree CD, Sibley PK. Transgenerational shifts in reproduction hormesis in green peach aphid exposed to low concentrations of imidacloprid. PLoS ONE. 2013;8:e74532.
Ayyanath M-M, Scott-Dupree CD, Cutler GC. Effect of low doses of precocene on reproduction and gene expression in green peach aphid. Chemosphere. 2015;128:245–51.
Chi H. Life-table analysis incorporating both sexes and variable development rate among individuals. Environ Entomol. 1988;17:26–34.
Chi H. Timing of control based on the stage structure of pest population: a simulation approach. J Econ Entomol. 1990;83:1143–50.
Chi H. TWOSEX-MS Chart: A computer program for the age-stage, two-sex life table analysis. Taichung: National Chung Hsing University; 2023a.
Chi H. TIMING-MS Chart: a computer program for the population projection based on age-stage, two-sex life table. Taichung: National Chung Hsing University; 2023b.
Chi H, You M, Atlıhan R, Smith CL, Kavousi A, Özgökçe MS, Güncan A, Tuan S-J, Fu J-W, Xu Y-Y, Zheng F-Q, Ye B-H, Chu D, Yu Y, Gharekhani G, Saska P, Gotoh T, Schneider MI, Bussaman P, Gökçe A, Liu T-X. Age-Stage, two-sex life table: an introduction to theory, data analysis, and application. Entomologia Generalis. 2020;40:102–23.
Chi H, Güncan A, Kavousi A, Gharakhani G, Atlihan R, Özgökçe MS, Shirazi J, Amir-Maafi M, Maroufpoor M, Taghizadeh R. TWOSEX-MSChart: the

key tool for life table research and education. Entomologia Generalis. 2022a;42:845–9.

Chi H, Kara H, Özgökçe MS, Atlihan R, Güncan A, Rişvanlı MR. Innovative application of set theory, Cartesian product, and multinomial theorem in demographic research. Entomol Gen. 2022b;42:863–74.

Chi H, Kavousi A, Gharakhani G, Atlıhan R, Özgökçe MS, Güncan A, Gökçe A, Smith CL, Benelli G, Guedes RNC, Amir-Maafi M, Shirazi J, Taghizadeh R, Maroufpoor M, Xu YY, Zheng FQ, Ye BH, Chen ZZ, You MS, Fu JW, Li JY, Shi MZ, Hu ZQ, Zheng CY, Luo L, Yuan ZL, Zang LS, Chen YM, Tuan SJ, Lin YY, Wang HH, Gotoh T, Shaef UM, Botto-Mahan C, De Bona S, Bussaman P, Gabre RM, Saska P, Marcela IMI, Ullah F, Desneux N. Advances in theory, data analysis, and application of the age-stage, two-sex life table for demographic research, biological control, and pest management. Entomologia Generalis. 2023;43(4):705–35. https://doi.org/10.1127/entomologia/2023/2048.

Cui L, Yuan H, Wang Q, Wang Q, Rui C. Sublethal effects of the novel cis-nitromethylene neonicotinoid cycloxaprid on the cotton aphid Aphis gossypii Glover (Hemiptera: Aphididae). Scientific Reports. 2018;8(1):8915.

Cutler GC. Insects, insecticides and hormesis: evidence and considerations for study. Dose Response. 2013. https://doi.org/10.2203/dose-response.12-008.Cutler.

Cutler GC, Amichot M, Benelli G, Guedes RNC, Qu Y, Rix RR, Ullah F, Desneux N. Hormesis and insects: effects and interactions in agroecosystems. Sci Total Environ. 2022;825:153899.

Decourtye A, Henry M, Desneux N. Overhaul pesticide testing on bees. Nature. 2013;497:188–188. https://doi.org/10.1038/497188a.

Desneux N, Decourtye A, Delpuech J-M. The sublethal effects of pesticides on beneficial arthropods. Annual Rev Entomol. 2007;52:81–106.

Desneux N, Fauvergue X, Dechaume-Moncharmont F-X, Kerhoas L, Ballanger Y, Kaiser L. *Diaeretiella rapae* limits *Myzus persicae* populations after applications of deltamethrin in oilseed rape. J Econ Entomol. 2005;98:9–17.

Efron B, Tibshirani R. An Introduction to the Bootstrap. New York: CRC Press; 1993. p. 914.

Gul H, Ullah F, Hafeez M, Tariq K, Desneux N, Gao X, Song D. Sublethal concentrations of clothianidin affect fecundity and key demographic parameters of the chive maggot. *Bradysia odoriphaga* - Ecotoxicology. 2021;30:1150–60. https://doi.org/10.1007/s10646-021-02446-x.

Gul H, ul Haq I, Ullah F, Khan S, Yaseen A, Shah SH, Tariq K, Güncan A, Desneux N, Liu X. Impact of sublethal concentrations of flonicamid on key demographic parameters and feeding behavior of *Schizaphis graminum*. Ecotoxicology. 2023;32:756–67.

Gong Y, Cheng S, Desneux N, Gao X, Xiu X, Wang F, Hou M. Transgenerational hormesis effects of nitenpyram on fitness and insecticide tolerance/resistance of *Nilaparvata lugens*. J Pest Sci. 2022. https://doi.org/10.1007/s10340-10022-01494-10344.

Guedes R, Smagghe G, Stark J, Desneux N. Pesticide-induced stress in arthropod pests for optimized integrated pest management programs. Annu Rev Entomol. 2016;61:43–62.

Hafeez M, Ullah F, Khan MM, Wang Z, Gul H, Li X, Huang J, Siddiqui JA, Qasim M, Wang R-L. Comparative low lethal effects of three insecticides on demographical traits and enzyme activity of the *Spodoptera exigua* (Hübner). Environ Sci Pollut Res. 2022. https://doi.org/10.1007/s11356-11022-20182-11355.

Huang YB, Chi H. Age-stage, two-sex life tables of *Bactrocera cucurbitae* (Coquillett)(Diptera: Tephritidae) with a discussion on the problem of applying female age-specific life tables to insect populations. Insect Sci. 2012;19:263–73.

Huang HW, Chi H, Smith CL. Linking demography and consumption of *Henosepilachna vigintioctopunctata* (Coleoptera: Coccinellidae) fed on *Solanum photeinocarpum* (Solanales: Solanaceae): with a new method to project the uncertainty of population growth and consumption. J Econ Entomol.. 2018;111(1):1–9.

Hullé M, Chaubet B, Turpeau E, Simon J. Encyclop'Aphid: a website on aphids and their natural enemies. Entomologia Generalis. 2020;40:97–101. https://doi.org/10.1127/entomologia/2019/0867.

Jactel H, Verheggen F, Thiéry D, Escobar-Gutiérrez AJ, Gachet E, Desneux, N & Group, NW. Alternatives to neonicotinoids. Environ Int. 2019;129:423–9.

Jia ZQ, Zhan EL, Zhang SG, Wang Y, Song PP, Jones AK, Han ZJ, Zhao CQ. Broflanilide prolongs the development of fall armyworm *Spodoptera frugiperda* by regulating biosynthesis of juvenile hormone. Entomologia Generalis. 2022. https://doi.org/10.1127/entomologia/2022/1420.

Ju D, Liu Y-X, Liu X, Dewer Y, Mota-Sanchez D, Yang X-Q. Exposure to lambda-cyhalothrin and abamectin drives sublethal and transgenerational effects on the development and reproduction of *Cydia pomonella*. Ecotoxicol Environ Safety. 2023;252:114581.

Koo HN, Lee SW, Yun SH, Kim HK, Kim GH. Feeding response of the cotton aphid, *Aphis gossypii*, to sublethal rates of flonicamid and imidacloprid. Entomol Exp Appl. 2015;154:110–9.

Liu X, Fu Z, Zhu Y, Gao X, Liu T-X, Liang P. Sublethal and transgenerational effects of afidopyropen on biological traits of the green peach aphid *Myzus persicae* (Sluzer). Pestic Biochem Physiol. 2022;180:104981.

Lu Y, Wu K, Jiang Y, Guo Y, Desneux N. Widespread adoption of Bt cotton and insecticide decrease promotes biocontrol services. Nature. 2012;487:362.

Ma K-s, Tang Q-l, Liang P-z, Li J-h, Gao X-w. A sublethal concentration of afidopyropen suppresses the population growth of the cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae). J Integr Agric. 2022;21:2055–64.

Monticelli LS, Desneux N, Biondi A, Mohl E, Heimpel GE. Post-introduction changes of host specificity traits in the aphid parasitoid *Lysiphlebus testaceipes*. Entomologia Generalis. 2022;42:559–69.

Pires Paula D, Lozano RE, Menger JP, Andow DA, Koch RL. Identification of point mutations related to pyrethroid resistance in voltage-gated sodium channel genes in *Aphis glycines*. Entomologia Generalis. 2021;41:243–55.

Ragsdale DW, Landis DA, Brodeur J, Heimpel GE, Desneux N. Ecology and management of the soybean aphid in North America. Annu Rev Entomol. 2011;56:375–99.

Rix RR, Ayyanath MM, Cutler GC. Sublethal concentrations of imidacloprid increase reproduction, alter expression of detoxification genes, and prime *Myzus persicae* for subsequent stress. J Pest Sci. 2016;89:581–9.

Rix RR, Cutler GC. Review of molecular and biochemical responses during stress induced stimulation and hormesis in insects. Sci Total Environ. 2022;827:154085.

Shi D, Luo C, Lv H, Zhang L, Desneux N, You H, Li J, Ullah F, Ma K. Impact of sublethal and low lethal concentrations of flonicamid on key biological traits and population growth associated genes in melon aphid. Crop Prot. 2022;152: 105863.

Sial MU, Zhao Z, Zhang L, Zhang Y, Mao L, Jiang H. Evaluation of Insecticides induced hormesis on the demographic parameters of *Myzus persicae* and expression changes of metabolic resistance detoxification genes. Sci Rep. 2018;8:16601.

Tang Q, Ma K, Chi H, Hou Y, Gao X. Transgenerational hormetic effects of sublethal dose of flupyradifurone on the green peach aphid, *Myzus persicae* (Sulzer)(Hemiptera: Aphididae). PLoS ONE. 2019;14:e0208058.

Tomizawa M, Casida JE. Neonicotinoid insecticide toxicology: mechanisms of selective action. - Annu. Rev Pharmacol Toxicol. 2005;45:247–68.

Ullah F, Gul H, Desneux N, Gao X, Song D. Imidacloprid-induced hormesis effects on demographic traits of the melon aphid. Entomologia Generalis. 2019a;39:325–37. https://doi.org/10.1127/entomologia/2019/0892.

Ullah F, Gul H, Desneux N, Qu Y, Xiao X, Khattak AM, Gao X, Song D. Acetamiprid-induced hormetic effects and vitellogenin gene (*Vg*) expression in the melon aphid. Entomologia Generalis. 2019b;39:259–70. https://doi.org/10.1127/entomologia/2019/0887.

Ullah F, Gul H, Desneux N, Tariq K, Ali A, Gao X, Song D. Clothianidin-induced sublethal effects and expression changes of vitellogenin and ecdysone receptors genes in the melon aphid. Entomologia Generalis. 2019c;39:137–49. https://doi.org/10.1127/entomologia/2019/0865.

Ullah F, Gul H, Tariq K, Desneux N, Gao X, Song D. Thiamethoxam induces transgenerational hormesis effects and alteration of genes expression in *Aphis gossypii*. Pestic Biochem Physiol. 2020;165:104557. https://doi.org/10.1016/j.pestbp.2020.104557.

Vakhide N, Safavi SA. Lethal and sublethal effects of direct exposure to acetamiprid on reproduction and survival of the greenbug, *Schizaphis graminum* (Hemiptera: Aphididae). Arch Phytopathol Plant Prot. 2014;47:339–48.

Verheggen F, Barrès B, Bonafos R, Desneux N, Escobar-Gutiérrez AJ, Gachet E, Laville J, Siegwart M, Thiéry D, Jactel H. Producing sugar beets without neonicotinoids: An evaluation of alternatives for the management of viruses-transmitting aphids. Entomologia Generalis. 2022;42:491–8.

Wang S, Qi Y, Desneux N, Shi X, Biondi A, Gao X. Sublethal and transgenerational effects of short-term and chronic exposures to the neonicotinoid nitenpyram on the cotton aphid *Aphis gossypii*. J Pest Sci. 2017;90:389–96.

Wang X, Tian L, Ricupero M, Harwood JD, Liang Y, Zang L-S, Wang S. Hormesis effects of chlorantraniliprole on a key egg parasitoid used for management of rice lepidopterans. Entomologia Generalis. 2022;42:941–8.

Wei M, Chi H, Guo Y, Li X, Zhao L, Ma R. Demography of *Cacopsylla chinensis* (Hemiptera: Psyllidae) reared on four cultivars of *Pyrus bretschneideri* (Rosales: Rosaceae) and *P. communis* pears with estimations of confidence intervals of specific life table statistics. J Econ Entomol. 2020;113:2343–53.

Yu Y, Shen G, Zhu H, Lu Y. Imidacloprid-induced hormesis on the fecundity and juvenile hormone levels of the green peach aphid *Myzus persicae* (Sulzer). Pestic Biochem Physiol. 2010;98:238–42.

Yuan HB, Li JH, Liu YQ, Cui L, Lu YH, Xu XY, Li Z, Wu KM, Desneux N. Lethal, sublethal and transgenerational effects of the novel chiral neonicotinoid pesticide cycloxaprid on demographic and behavioral traits of *Aphis gossypii* (Hemiptera: Aphididae). Insect Science. 2017;24:743–52.

Zang L-S, Wang S, Zhang F, Desneux N. Biological control with *Trichogramma* in China: history, present status and perspectives. Annu Rev Entomol. 2021;66:463–84.

Zhang A, Zhou W, Wu D, Han L, Zhao K. Effects of multigenerational imidacloprid and thiamethoxam stress on metabolism and physiology of *Aphis glycines* Matsumura (Hemiptera: Aphididae). PLoS ONE. 2022;17:e0271069.

Zhang X, Wang H-C, Du W-M, Zang L-S, Ruan C-C, Zhang J-J, Zou Z, Monticelli LS, Harwood JD, Desneux N. Multi-parasitism: a promising approach to simultaneously produce *Trichogramma chilonis* and *T. dendrolimi* on eggs of *Antheraea pernyi*. Entomologia Generalis. 2021;41:627–36.

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