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Temperature effects on the hormetic response of *Myzus persicae* after sublethal exposure to insecticides

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Abstract

Studies on insecticide-induced stimulatory effects in pest insects have become of utmost importance due to their potential implications in pest management. Temperature influences the physiology and biology of ectothermic organisms like pest insects. It can also affect the toxicity and relative efficacy of insecticides that are used in agricultural fields. However, the impact of temperature on the insect stimulatory responses after exposure to mild insecticide-induced stresses has frequently been overlooked. Here, we investigated how different temperature levels (15; 20; 25; 28 °C) can modulate the toxicity of two synthetic insecticides chlorpyrifos (organophosphate) and deltamethrin pyrethroid; and subsequently how temperature impacts the survival and reproduction of the green peach aphid *Myzus persicae* exposed to sublethal concentrations of the two insecticides. Our findings indicated temperature-dependent effects of the two chemicals on mortality, longevity, and the number of nymphs produced by the aphids after lethal and sublethal exposures. In fact, besides the high toxicity induced by temperature at lower concentrations, the change's magnitude and occurrence of stimulatory responses varied between temperatures and depended on the sublethal concentrations faced by the aphid females. Temperature increase from 15 to 28 °C increased chlorpyrifos and deltamethrin toxicity 4 and fivefold. Sublethal exposure of aphids extended the longevities for individuals treated with chlorpyrifos at 15 (all sublethal concentrations) and 25 °C (LC₁₅ and LC₂₀) and with deltamethrin at 20 (LC₁) and 28 °C (LC₂₀). Additionally, the total number of nymphs produced during the females' lifespan was increased after sublethal exposure to chlorpyrifos at 15 °C (LC₁, LC₅, and LC₂₀) and at 20 °C (LC₁₀) and to deltamethrin at 20 °C (LC₁), 25 °C (LC₅ and LC₁₀) and 28 °C (LC₁, LC₅, and LC₂₀). Our results reinforce the importance of a shift from studies focusing on the stimulatory effects of single stresses to studies investigating the effects of stressors' combinations on insect hormetic response.

Keywords Hormesis, Temperature stress, Pesticides stress, Fecundity, Longevity, Aphids

Background

The use of insecticides is still a cornerstone strategy in pest insect control. Insecticides present a large number of chemical classes with various modes of action covering different target sites in relation to the biology and physiology of insects (Simon 2011; Gupta et al. 2019). To reduce crop damage caused by pest insects, an optimal amount of insecticides needs to be applied (Gupta et al. 2019; Tudi et al. 2021). However, various abiotic and

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biotic processes can alter the concentrations of insecticides before reaching their physiological target (s) within the insect body (Bantz et al. 2018; Müller 2018; Tudi et al. 2021). Misapplication, drift, and degradation under environmental conditions can alter insecticides' coverage and efficacy (Cutler 2013; Müller 2018; Cutler et al. 2022; Guedes et al. 2022). Therefore, insects do experience sublethal exposure to these products. Such sublethal exposures do not induce apparent mortality in the population, but potentially cause positive physiological or behavioral effects; termed hormetic effects; in surviving individuals (Desneux et al. 2007; Deng et al. 2016; Ullah et al. 2019; Cutler et al. 2022; Agathokleous et al. 2023; Agathokleous et al. 2023).

Hormesis has been observed in a multitude of organisms. It is a biphasic adaptive response characterized by stimulation at low doses and inhibitory effects at high doses of stressors like insecticides (Calabrese and Baldwin 2003; Agathokleous, et al. 2022; Cutler et al. 2022; Guedes et al. 2022; Rix et al. 2022). Hormesis can cause various responses in numerous key biological, metabolic, molecular, cognitive, functional, and immune processes (Calabrese and Baldwin 2003; Cutler 2013; Duke 2014; Rix and Cutler 2022; Rix, et al. 2022), which can include short-term (improved performance and increased mating success) and/or long-term (increased longevity and performance in subsequent generations) changes (Berry III and López-Martínez 2020). Moreover, hormetic effects are not only limited to chemical stressors but include bioinsecticides and plant based pesticides (Haddi et al. 2015; Haddi et al. 2016; Haddi et al. 2020; Pineda et al. 2023). They also can manifest after temperature, radiation, and food restriction stresses (Feinendegen 2005; Mironidis and Savopoulou-Soultani 2010; Calabrese and Blain 2011; Cutler 2013; Berry III and López-Martínez 2020; Agathokleous et al. 2022).

Insects are ectothermic organisms that are highly susceptible to abiotic changes in the environment (Neven 2000; Colinet, et al. 2015; Horn 2019). Temperature has an important role in regulating physiological functions; such as respiration, immunity, metabolism, growth, and reproduction; in these organisms (Neven 2000; González-Tokman, Córdoba-Aguilar et al. 2020). Besides the temperature influencing the population dynamics of ectothermic organisms, it can also affect the toxicity and relative efficacy of insecticides that are used in agricultural fields (Johnson 1990; Noyes et al. 2009). In this sense, abiotic factors become important, since, temperature influences the physiological processes of insects involved in the detoxification and excretion of chemical compounds (Hooper et al. 2013; Dong et al. 2022; Iltis et al. 2022). The influence of temperature on toxicity can be positive

or negative depending on the mode of action of the insecticide and the insect species in question, as well as the route of exposure. Thus, the toxicity of products can increase/decrease with varying temperatures (Wang and Shen 2007; Deng et al. 2016; Ricupero et al. 2020; Swelam, et al. 2022; Ahmad et al. 2023). Moreover, climate change-related temperature variations have been reported to induce phenotypic adjustments in some insect populations (Rodrigues and Beldade 2020; Skendžić et al. 2021). From an applied perspective, climate change may have the potential to alter the benefits/costs balance of pesticides use in the agricultural context, and in this regard, in the literature, there is little detailed knowledge about the thermal modulation of pesticides side effects on pests (Rodrigues and Beldade 2020; Skendžić et al. 2021). Most toxicological studies have frequently focused on the effects of insecticides in insect biology without taking into consideration how thermal regimes shape these effects. Furthermore, there is a knowledge gap on how sublethal effects act on the biological characteristics of individuals exposed to insecticides under temperature variations and how temperatures can affect the stimulatory response of insects after sublethal exposure to stressors.

Given the above, this work aimed to investigate how temperature changes modulate the effects of lethal and sublethal exposure to insecticides on the longevity and fecundity of insects. We used a study system composed of the green peach aphid *Myzus persicae* (Sulzer), two synthetic insecticides from the organophosphate and pyrethroid chemical groups, and four temperatures (15, 20, 25, and 28 °C). The green peach aphid is a widely distributed agricultural pest. The green peach aphid is a phytophagous sucking insect, having a size ranging from 2 to 3 mm, and is considered one of the most important pests in numerous crops, both in open field conditions and in protected crops due to the high reproductive capacity. The aphid's reproduction occurs with several generations per year, through thelytokous parthenogenesis with the production of diploid female offspring from unfertilized eggs. Different aphids species showing the ability to survive exposure to low concentrations/doses of a toxic compounds and manifest hormetic responses have been reported in several studies and include *M. persicae* (Rix et al. 2016; Wang et al. 2017; Wang et al. 2017; Sial et al. 2018; Tang et al. 2019; Ullah et al. 2019; Ullah et al. 2020). Organophosphorous and pyrethroids pesticides are among the most widely used synthetic pesticides for controlling insect pests in agriculture, public health, and animal health. Longevity and reproduction-related traits represent two of the most important biological parameters that are studied in pesticide lethal and sublethal effects in pest insects due to their crucial outcomes at the

population level (Cutler et al. 2022; Rix et al. 2022; Rix and Cutler 2022).

Material and methods

Insect, insecticides, and temperatures

The *M. persicae* adult females are from an insecticides susceptible laboratory colony established in 2016 and maintained without exposure to insecticides at the Laboratory of Molecular Entomology and Ecotoxicology (M.E.E.T) at the Entomology Department of the Federal University of Lavras (UFLA). The aphids were reared on entire leaves of the shoo-fly plant *Nicandra physalodes* (L.) Gaert floating on a hydrogel layer in Petri dishes (\varnothing 12 cm) (Silva et al. 2023). The colony is kept in a climate-controlled chamber, with temperature maintained at 20 ± 2 °C, relative humidity at $70 \pm 5\%$, and photophase of 16 h. The age of aphid females' cohorts was standardized, before experiments, by placing about 100 newly born nymphs (less than 48 h) on leaf discs (12 cm diameter) of *N. physalodes* plants and held for about 8 days to ensure that all aphids are the same age (and growth stage) at the beginning of each bioassay.

The insecticides used were commercial formulations of the organophosphate chlorpyrifos (CAPATAZ[®]) and the pyrethroid deltamethrin (DELTAMAX 25 CE). The highest recommended label rates were used to prepare the stock solutions before making the subsequent serial dilutions.

The effects of different temperatures on the aphid's responses to insecticide sublethal exposure were assessed under four temperatures: (i.e.; 15, 20, 25, and 28 °C) and all bioassays were carried out in climate-controlled chambers (BOD, ELETROlab) with relative humidity at $70 \pm 5\%$ and photophase of 16 h.

Effect of temperature on chlorpyrifos and deltamethrin toxicity to aphid's adults

The insecticides' toxicities were evaluated using the foliar immersion method proposed by the Insecticide Resistance Action Committee (IRAC 2011). Concentration–response curves were determined for each insecticide under different temperatures.

Initial preliminary tests were conducted to determine and adjust the range of experimental concentrations, causing mortalities ranging from 0 to 100%, for each insecticide. Then, five to seven concentrations were used to establish the concentration–response curves. Concentrations of the active ingredient (a.i.) ranged from 0.028×10^{-6} to 0.028×10^2 mg/ml for chlorpyrifos and from 0.015×10^{-6} to 0.015×10^2 mg/ml for deltamethrin. The insecticides were diluted with distilled water containing 0.01% (v/v) Tween 20, and for the control, only distilled water containing 0.01% (v/v) Tween 20 was used.

The insecticides' solutions were used immediately after preparation to avoid potential chemical degradation.

Leaf discs (5.6 cm in diameter) of *Brassica oleraceae* var. *acephala* were cut and individually dipped for about 8–10 s in the insecticide and control solutions, and then placed at room temperature to air dry for about 2 h. The leaf discs were placed with the abaxial surface upwards in Petri dishes ($\varnothing = 5.6$ cm) on 1% w/v agar. Five replicates were made for each insecticide concentration, and each replicate was inoculated with 20 adult aphids. After the aphids' introduction, the Petri dishes were sealed with plastic film, with several small holes made to allow gas exchange. Aphid mortality was assessed under a magnifying glass (Zeiss Stemi 2000C–Stereo Microscope 1.5x) after 48 h of exposure. Aphids that did not move when touched with a fine brush were considered dead (Silva et al. 2023).

Effect of temperature on the longevity and fecundity of sublethally exposed female aphids

For sublethal exposure, the concentrations of LC_{10} , LC_{15} , LC_{20} , LC_{25} , LC_{30} of each insecticide under each temperature were tested (Additional file 1: Table S1). Leaf discs (5.6 cm in diameter) of *B. oleraceae* were dipped into the different insecticide concentrations, left to air dry, and placed in Petri dishes as described above. A cohort of 100–150 adult females was casually distributed on the treated leaf discs for each concentration.

After 48 h of exposure, 50 surviving females were individualized and transferred to a new untreated leaf disc in a Petri dish ($\varnothing = 3$ cm). The Petri dishes were sealed with plastic film as described above and kept in climate-controlled chambers under the corresponding temperatures. The untreated leaf discs were replaced every 5 days during the whole period of the experiment.

Each combination of sublethal concentration x temperature consisted of fifty repetitions (individualized females). After exposure, the fecundity (number of newborn nymphs) and mortality of the adult females were recorded daily during their whole lifespan. The newly hatched nymphs were counted and removed from the Petri dishes. Nymphs produced during the 48 h of exposure to the sublethal concentrations were not considered in assessing the final fecundity.

Statistics

The mortality rate of adults was corrected for the natural mortality observed in controls (i.e., leaf discs treated with distilled water containing 0.01% (v/v) Tween 20) prior to analysis. Concentration–mortality curves were estimated by Probit analyses using the PROC PROBIT procedure (SAS Institute, Cary, NC, USA), with a Probit regression method analysis, to obtain 95% confidence intervals.

The sublethal concentrations were determined using the estimated concentration-mortality curves. The females' survival data were subjected to survival analysis using Kaplan–Meier estimators (log-rank method) with SigmaPlot 12.0 (Systat Software, San Jose, CA, USA). The overall similarity between survival times and median survival times (LT₅₀ values) was tested using the χ^2 log-rank test, and pairwise comparisons between curves were performed using the Holm-Sidak test ($P < 0.05$). Fecundity data (total number of nymphs per female) were analyzed using a generalized linear model (GLM) with sublethal concentrations as the independent variable. The analyses were carried out using the statistical program R (R core team, 2023).

Results

Effect of temperature on chlorpyrifos and deltamethrin toxicity to aphid's adults

The Probit model satisfactorily described the concentration-mortality data (goodness-of-fit tests exhibited low χ^2 -values [< 13] and high P-values [> 0.05]) and indicated significant differences between the LC₅₀s of each insecticide (Table 1). Generally, the temperature-dependent decrease in the concentrations (a.i. mg/ml) needed to kill 50% (LC₅₀s) of the aphid population suggested that toxicity of the two tested insecticides (chlorpyrifos and deltamethrin) increased with temperature's increase.

The toxicity of chlorpyrifos to adults of *M. persicae* increased with temperatures showing respective increases in toxicity ratios of 4 and fivefold between the LC₅₀s of this insecticide at 15 °C, 20 °C, and 25 °C. However, the toxicities of chlorpyrifos were not significantly different between the temperatures 15 °C (LC₅₀=0.0089 mg/ml) and 20 °C (LC₅₀=0.0073 mg/ml) and between the temperatures 25 °C (LC₅₀=0.0018 mg/ml) and 28° (LC₅₀=0.0021 mg/ml) (Table 1). A similar trend was found for deltamethrin presenting

identical lethal effects at the temperatures of 15 °C (LC₅₀=0.0042 mg/ml), 20 °C (LC₅₀=0.0047 mg/ml), and 25 °C (LC₅₀=0.0054 mg/ml) but being significantly more toxic under the temperature of 28 °C (LC₅₀=0.0011 mg/ml) and presenting an increase of fourfold in the toxicity ratio.

Effect of temperature on unexposed aphid's survival and fecundity

Overall, the aphids unexposed to insecticides (pooled controls under each temperature) performed better at lower temperatures compared to higher temperatures (Fig. 1). In fact, at 15 (11.9±0.66 days) and 20 °C (10.9±0.38 days) the females lived significantly ($H=281.3$; $df=3$; $p < 0.001$) longer compared to 25 (6.8±0.23 days) and 28 °C (4.6±0.14 days) (Fig. 1A). Additionally, the average number of nymphs produced during the female's lifespan was significantly ($H=202.8$; $df=3$; $p < 0.001$) higher at 15 (25.7±1.4) and 20 °C (19.7±0.9) compared to 25 (9.6±0.45) and 28 °C (3.4±0.4) (Fig. 1B).

Effect of temperature on aphid's survival after sublethal exposure

Exposure during 48 h of *M. persicae* adults to chlorpyrifos and deltamethrin sublethal concentrations had temperature-dependent significant effects on the longevity of exposed individuals (Figs. 2, 3). Generally, the aphids' longevity decreased with increasing temperatures and concentrations. However, the longevity of sublethally exposed aphids was significantly greater than the longevity of the unexposed ones at 15 °C ($\chi^2=91.630$, $df=6$, $p < 0.001$; Fig. 2A) for all sublethal concentrations and at 25 °C ($\chi^2=25.632$, $df=6$, $p < 0.001$; Fig. 2E) for LC₁₅ and LC₂₀ concentrations of chlorpyrifos.

Regarding deltamethrin, such significant positive effects of exposure to sublethal concentrations were

Table 1 Relative toxicity of organophosphate and pyrethroid (i.e., chlorpyrifos and deltamethrin) to individuals of *Myzus persicae*

Insecticides	Temperatures	N	LC ₅₀ (95% CI)	χ^2	P	TR
Chlorpyrifos	15 °C	700	8.6 (6.7–10.5) ^a	12.97	0.15	5.05
	20 °C	700	7.0 (6.5–7.6) ^a	7.06	0.13	4.11
	25 °C	600	1.7 (1.3–2.2) ^b	5.55	0.23	–
	28 °C	800	2.0 (1.7–2.6) ^b	10.84	0.09	1.17
Deltamethrin	15 °C	800	4.2 (3.7–4.7) ^a	7.38	0.19	3.81
	20 °C	600	4.6 (4.0–5.2) ^a	6.16	0.18	4.18
	25 °C	700	5.3 (4.7–5.8) ^a	4.49	0.10	4.81
	28 °C	600	1.1 (1.0–1.3) ^b	5.21	0.26	–

N: number of individuals tested. LC₅₀ (95%): lethal concentration to cause mortality in 50% of individuals (10⁻³.mg active ingredient /ml). CI: confidence intervals. Different lower case letters indicate statistical differences between the lethal concentrations. χ^2 : Chi-square for Goodness-of-fit to the probit model. P: Probability associated with the chi-square statistic. TR = toxicity ratio, calculated by dividing the LC₅₀s of the different temperatures by the lowest LC₅₀

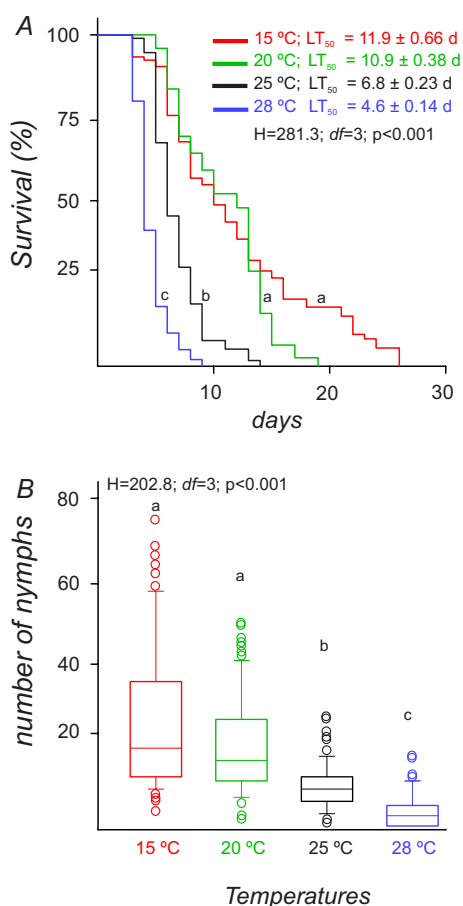


Fig. 1 Survival **A** and fecundity **B** of unexposed female adults of *Myzus persicae* under four temperature regimes (15, 20, 25 and 28 °C). Different lowercase letters indicate significant statistical differences ($p < 0.05$)

observed at 20 °C for the concentration LC₁ ($\chi^2 = 29.547$; $df = 6$; $p < 0.001$; Fig. 2D) and at 28 °C for the concentration LC₂₀ ($\chi^2 = 34.056$; $df = 6$; $p < 0.001$; Fig. 2H).

Furthermore, when the median lethal times (LT_{50s}) were plotted against the sublethal concentrations (LCs), characteristic bell-shaped curves were obtained for chlorpyrifos at 15 °C; 25 °C (Fig. 3A, E) and for deltamethrin at 20 °C; 28 °C (Fig. 3D, H).

Effect of temperature on aphid's fecundity after sublethal exposure

Concerning the fecundity of females, exposure to the sublethal concentrations LC₁ (32.4 ± 3.1), LC₅ (32.9 ± 2.4), and LC₂₀ (32.9 ± 2.2) of chlorpyrifos significantly ($H = 8.607$; $df = 6$; $P < 0.001$) increased the total number of produced nymphs during the females' lifespan compared to the control (27.97 ± 2.3) at 15 °C temperature (Fig. 4A). At 20 °C, a similar significant ($H = 50.959$; $df = 6$; $P < 0.001$) increase in the number of produced

nymphs was observed only for females that were exposed to LC₁₀ (25.0 ± 1.7) compared to the control (15.4 ± 0.9) (Fig. 4C). On the other hand, no such stimulatory effects were found at 25 °C (between 11.1 ± 0.6 and 15.0 ± 0.9) and 28 °C (between 0.1 ± 0.02 and 3.6 ± 0.5) temperatures for aphids females exposed to any of the sublethal concentrations (Fig. 4E, G).

In deltamethrin-treated aphids, the increase in female fecundity occurred under the 20 °C and 25 °C temperatures (Fig. 4D, and F). Thus, fecundity was significantly ($H = 57.071$; $df = 6$; $P < 0.001$) increased when females were exposed to LC₁ (29.2 ± 1.6) at 20 °C temperature (Fig. 4D), to LC₅ (9.2 ± 0.6) and LC₁₀ (9.5 ± 0.7) ($H = 133.048$; $df = 6$; $P < 0.001$) at 25 °C (Fig. 4F).

More interestingly, although an overall and drastic reduction of produced nymphs occurred at 28 °C, the females exposed to the sublethal concentrations LC₁ (4.8 ± 0.5), LC₅ (4.7 ± 0.5), and LC₂₀ (4.4 ± 0.4) of deltamethrin still presented significantly greater fecundity ($H = 31.165$; $df = 6$; $P < 0.001$) compared to control females (3.1 ± 0.4) (Fig. 4G).

As shown for survival, biphasic-shaped curves were obtained when the average number of produced nymphs per female aphid were related to the sublethal concentrations used for chlorpyrifos at 15 °C; 20 °C (Fig. 5A, C) and for deltamethrin at 25 °C; 28 °C (Fig. 5F, H).

Discussion

Our findings indicated that under constant temperatures, the green peach aphids colony used here showed its optimal survival and fecundity between 15 and 20 °C. This temperature range is lower than the 25–26 °C range previously reported as optimal temperatures for green peach aphids (Davis et al. 2006). Such differences could be linked to the aphid biotypes. Variations in the longevity and fecundity responses to temperature changes were previously reported in insect populations from different climate zones, including aphid species (Dampc et al. 2021), and were related to different genetic backgrounds (Mołóń et al. 2020). Additionally, temperatures around 28 °C or above were found to be detrimental (Davis et al. 2006; Dampc et al. 2021; Khurshid et al. 2022). Insect growth occurs under optimal temperature ranges and when exposed to extreme temperatures, the development and reproduction rates are negatively affected due to reduced respiration, increased water loss, and accumulation of oxidative stress products like the reactive oxygen species (ROS) (Dampc et al. 2021).

Sublethal effects of agrochemicals on life traits (e.g., fecundity, longevity, and behavior) are commonly observed in agricultural pests after exposure to low concentrations of insecticides (Cutler 2013; Cutler et al. 2022; Guedes et al. 2022; Agathokleous et al. 2023;

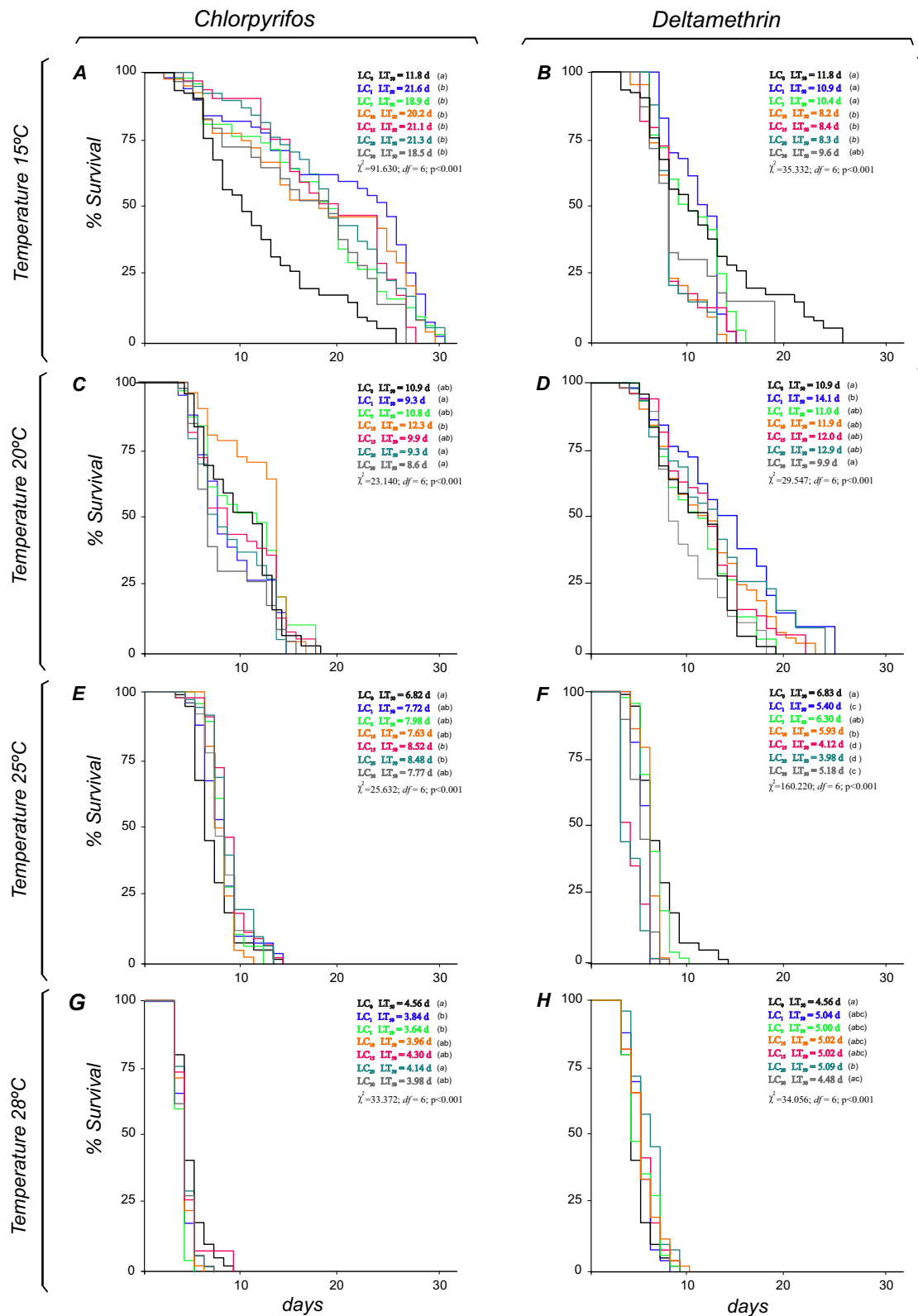


Fig. 2 Effects of sublethal exposure to the organophosphate chlorpyrifos **A, C, E, G** and the pyrethroid deltamethrin **B, D, F, H** on longevity of *Myzus persicae* females at 15 °C **A, B**; 20 °C **C, D**; 25 °C **E, F** and 28 °C **G, H**

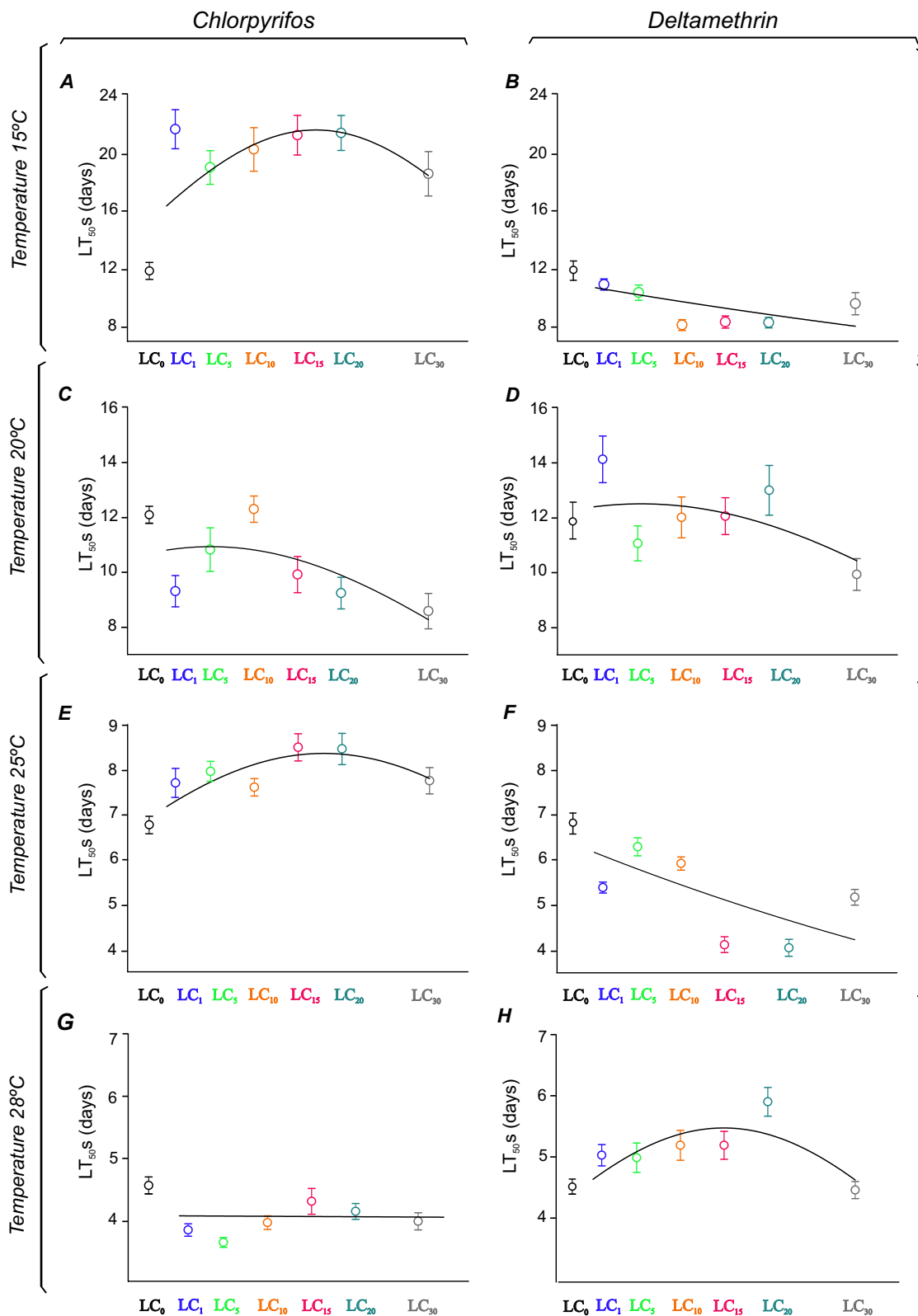


Fig. 3 Mean lethal times (LT_{50s}) of female adults of *Myzus persicae* unexposed (LC_0) and sublethally exposed (LC_1 – LC_{30}) to the organophosphate chlorpyrifos **A, C, E, G** and the pyrethroid deltamethrin **B, D, F, H** at 15 °C **A, B**; 20 °C **C, D**; 25 °C **E, F** and 28 °C **G, H**. Data are expressed as Mean \pm SE. Different lowercase letters indicate significant statistical differences ($p < 0.05$)

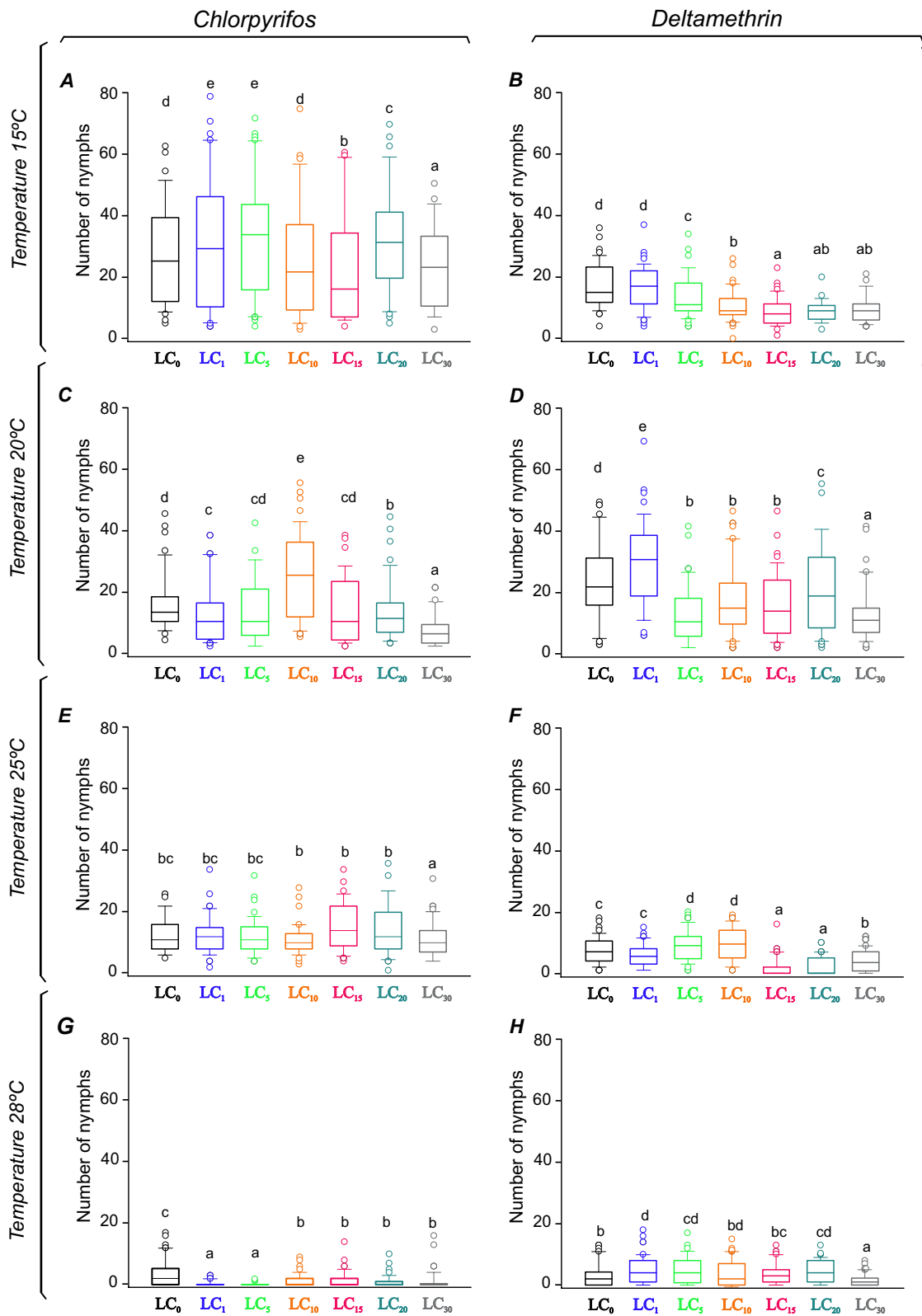


Fig. 4 Effects of sublethal exposure to the organophosphate chlorpyrifos **A, C, E, G** and the pyrethroid deltamethrin **B, D, F, H** on fecundity of *Myzus persicae* females at 15 °C **A, B**; 20 °C **C, D**; 25 °C **E, F** and 28 °C **G, H**. Different lowercase letters indicate significant statistical differences ($p < 0.05$). Horizontal lines inside the boxes indicate the median

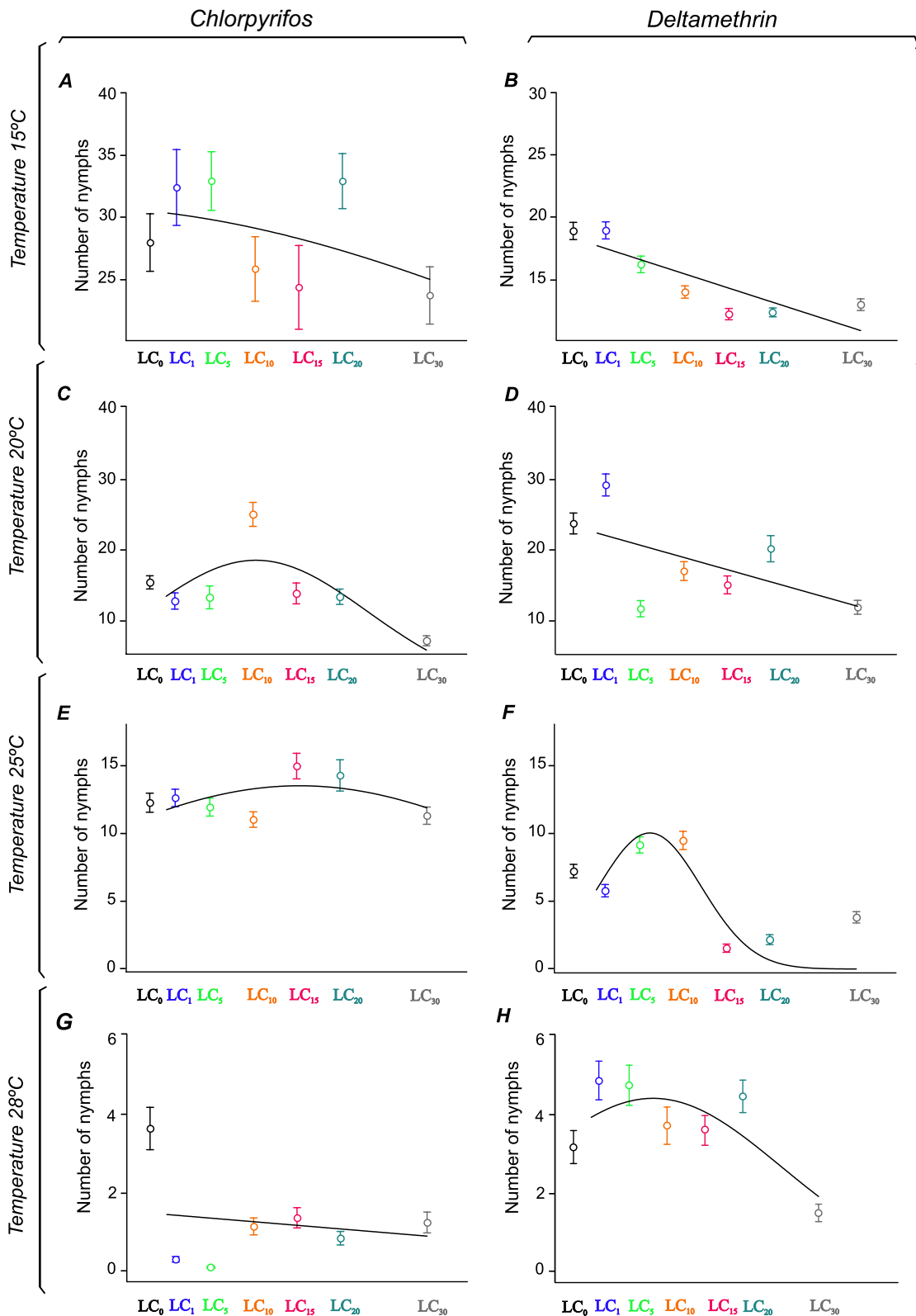


Fig. 5 Average total number of nymphs produced by female adults of *Myzus persicae* unexposed (LC₀) and sublethally exposed (LC₁–LC₃₀) to the organophosphate chlorpyrifos (A, C, E, G and the pyrethroid deltamethrin (B, D, F, H) at 15 °C (A, B), 20 °C (C, D), 25 °C (E, F) and 28 °C (G, H). Data are expressed as Mean ± SE

Agathokleous et al. 2023). Here we demonstrate the temperature-dependent effects of two chemical stressors (chlorpyrifos and deltamethrin) on the longevity and reproduction of the aphid *M. persicae* after both lethal and sublethal exposures.

Our results showed that the toxicities of the two insecticides to the aphids were influenced by temperature levels during exposure. The evaluation of the relationship between insecticide concentrations and their lethality is a very useful tool for comparing the toxicities of chemicals with different active ingredients and formulations. It is known that the toxicity and relative efficacy of insecticides can vary due to several factors, including their modes of action, the chemical structure of their active ingredients and environmental conditions (Musser and Shelton 2005; Mahmoodi et al. 2020). Organophosphates and pyrethroids are neurotoxic insecticides that have generally been considered very effective against insect pests including succivorous like aphids (Haddi et al. 2012; Haddi et al. 2018; Golvankar et al. 2019; Shang et al. 2021). Chlorpyrifos is a synthetic organophosphate acting as an acetylcholinesterase (AChE) inhibitor and deltamethrin is a synthetic pyrethroid that induces toxic responses in the central and peripheral nervous system of insects through modulation of voltage-gated sodium channels.

Furthermore, based on the estimated LC_{50} s, high temperature (28 °C) induced high toxicity at lower concentrations of both chlorpyrifos and deltamethrin. Temperature can impact insecticides' toxicity by affecting their physical and chemical properties, such as molecular stability, tissue penetration, absorption and translocation, biological activity, vaporization and degradation (Johnson 1990; Neven 2000; Noyes et al. 2009; Horn 2019). In this context, organophosphates and pyrethroids have been reported to exhibit positive temperature coefficients with their toxicities increasing with temperatures increases (Li et al. 2006; Mansoor et al. 2015). However, besides different impacts of temperature changes between insecticide classes, there are also differences impacts of temperature changes within insecticide classes and between species (Musser and Shelton 2005). Positive correlation between temperature and toxicity of deltamethrin has been reported in *Plutella xylostella* L. (Lepidoptera: Plutellidae) (Jaleel et al. 2020) while cypermethrin and deltamethrin showed a negative association with temperature in *Musca domestica* L. (Diptera: Muscidae) (Khan and Akram 2014). Moreover, although organophosphate insecticides are generally assumed to have a positive association with temperatures performing well against different insect pest in high temperature conditions (Norment and Chambeas 1970; Saleem et al. 2008; Raj Boina et al. 2009; Glunt et al. 2013), chlorpyrifos was

found to be more toxic to *M. domestica* than profenofos at highest temperature ranges (Khan and Akram 2014).

In addition to direct exposure to chemical insecticides, it is well known that agricultural pests are often exposed to low doses of insecticides in the field due to variable distribution and continuous degradation (Desneux et al. 2007; Duke 2014; Cutler et al. 2022). The uptake of small quantities of insecticides after exposure to these concentrations may contribute to a beneficial and/or stimulatory effects on different biological and reproductive outputs at individual or population levels (Calabrese and Baldwin 2003; Desneux et al. 2007; Schirmmacher 2021; Guedes et al. 2022; Agathokleous et al. 2023; Agathokleous et al. 2023). This positive response is termed hormesis, and is characterized by a biphasic dose–response phenomenon (Cutler 2013; Duke 2014; Cutler et al. 2022). The hormetic response has been described for many biological endpoints, and with a wide range of stressors, including chemical, nutritional and temperature stresses. The study of insecticide-induced hormesis in insects has become extremely important due to its potential implications for pest management.

Previous investigation have reported insecticide-induced hormesis for aphid species, including *M. persicae* (Wang and Shen 2007; Rix et al. 2016; Sial et al. 2018; Tang et al. 2019), *Aphis gossypii* Glover (Chen et al. 2016; Wang et al. 2017), *Aphis craccivora* Koch (Fouad et al. 2022), *Aphis glycines* Matsumura (Qu et al. 2015). However, little is known about the combined effects of sublethal exposure to insecticides with temperature changes on individuals of insect pest and specifically *M. persicae*. The results of the present study showed that exposure to sublethal concentrations of chlorpyrifos and deltamethrin combined with temperature variation, led to significant changes in fecundity and survival in females of *M. persicae*, however, the change's magnitude and occurrence of stimulatory responses depended on the sublethal concentrations faced by the aphid females and varied between temperature regimes.

Few studies have investigated hormesis resulting from multiple stressors (Agathokleous et al. 2022; Guedes et al. 2022) and even fewer have assessed how temperature can modulate the stimulatory responses to pesticides exposure in insects. In this regard, (Yu et al. 2012) tested the combined effects of sublethal doses of the organophosphate triazophos and temperature (high: 34 °C, typical: 26 °C and low: 20 °C) stresses on the protein content of male accessory glands and adult female ovaries and on the fecundity of adult females of *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae). They found that increases in ovary protein after mating and fecundity (the number of egg laid) for triazophos-treated at 20 and 34 °C were greater than those at 26 °C, and concluded

that triazophos treatment enhanced the resistance of adult males or females to temperature stresses (Yu et al. 2012). Furthermore, sublethal doses of chlorpyrifos (lower than $LC_{1}=7.2 \text{ mg l}^{-1}$) significantly stimulated the development and increased the fecundity of *P. xylostella* as well as stimulated the acetylcholinesterase and glutathione S-transferases GSTs activities at 25 °C and/or 38 °C (Deng et al. 2016). In the tortricid moth *Lobesia botrana*, (Iltis et al. 2022) reported significant interaction between low concentrations of a copper-based fungicide and temperature for larval survival and phenoloxidase activity. They suggested that warmer conditions improved the tolerance of moth larvae to copper through temperature-driven hormesis (larval survival) or by shifting the hormesis-related peak of performance toward higher copper concentrations (phenoloxidase activity).

Hormesis is suggested to be an overcompensating adaptive response to homeostasis disruption that aims to repair damage caused by mild exposure to a stressor and that may manifest in different molecular or biochemical processes (Calabrese and Baldwin 2003; Cutler et al. 2022; Erofeeva 2022). In most of reported hormetic cases induced by a single stressor, the underlying molecular and biochemical processes included increased expression of heat shock proteins (temperature tolerance), and increased expression of detoxification genes (pesticide or chemical tolerance and stimulated reproduction) as well as changes in the expression or activity of antioxidants (longevity and reproduction stimulation) (Erofeeva 2022; Rix and Cutler 2022). Furthermore, changes in reproduction related hormones (vitellogenin and juvenile) and genes in the IIS/TOR signaling pathway were linked to growth, development and reproduction cases of hormesis (Rix and Cutler 2022).

Hormesis have been mostly studied under simplified laboratory conditions. In the present study, we used constant temperature instead of the naturally occurring fluctuating temperature regimens. Such simplification of experimental conditions are meant to control the different factors that might interfere with the tested organism responses. However, simplified laboratory conditions do not represent natural environments (Sebastiano et al. 2022) where different sources of stress may co-occur and modulate the individuals and populations response to stressors. How the additive and interactive effects of multiple stressors function on insect performance (at biochemical and molecular levels) to produce hormetic response is yet to be investigated. The complexity deriving from such combination of stressors may explain such knowledge gap (Fan et al. 2021; Agathokleous et al. 2022; Rix et al. 2022). Furthermore, the long-term effects of the combination of insecticides and temperature were not considered here and are worth a closer look.

In our study, we used an insecticide susceptible colony of green peach aphids. The control of *M. persicae* on many crops has relied over many years almost exclusively on the use of chemical insecticides (Bass and Nauen 2023). This intensive use of insecticides has led to selection of populations resistant to several classes of insecticide including organophosphates and pyrethroids. Different biochemical and molecular alterations (e.g., enhanced expression of detoxifying enzymes and target-site mutations) have been described as the underlying mechanisms of resistance in aphids (Bass and Nauen 2023). Such resistance mechanisms may have a strong influence on temperature-dependent and sublethal effects and resistant clones are likely to behave differently after insecticide exposure.

Conclusions

In conclusion, the continuous exposure of pest insects to sublethal concentrations of insecticides under fields' conditions will result in frequent cases of pesticide-mediated hormesis that can lead to alterations in the ecological interactions and function within and between communities. Such alteration are worth studying for their potential implications for crop protection, agroecology, and environmental risk assessment. The knowledge gap on how the interactions of abiotic factor (temperature and insecticides) will be affecting pest population's dynamic under field conditions highlight the urgent need of in situ studies to fully grasp the complexity of such interactions and come up with practical recommendations for the growers and field practitioners.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s43170-024-00213-6>.

Additional file 1: Table S1. Sublethal concentrations of chlorpyrifos and deltamethrin used under varying temperatures.

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Author contributions

KH, APNS: Conceptualization and Design. APNS, CFC, ELAA, VCA: Investigation and acquisition of data. APNS, CFC, ELAA, VCA: Data curation. APNS, KH: analysis and interpretation. APNS: Writing original draft. KH: Writing – review and editing. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations**Ethics approval and consent to participate**

Not applicable.

Consent for publication

All authors agree to publish this article in "CABI Agriculture & Bioscience".

Competing interests

The authors declare that they have no competing interests.

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