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Understanding Insect Responses to Sublethal Insecticide Exposure

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ABSTRACT

The effects of insecticides are biphasic as it produces high-dose inhibition and low-dose stimulation against several insects. Moreover, these effects are often discussed in terms of lethal and acute toxicity, but the impact of sublethal doses (low dose) on insect-pests is often overlooked. The exposure to sublethal dose of insecticides cause changes in physiology, biology, demography and behaviour of insect-pests and contribute to the adaptation in the environment making the challenge of managing them difficult. In this review, sublethal effects of insecticides on insects (both harmful and beneficial) associated with the agricultural crops have been summarized.

INTRODUCTION

Insecticides play a crucial role in managing insect-pests that threaten crop yield and food security. Unfortunately, the extensive use of insecticides resulted in insecticidal resistance development, a resurgence of insect-pests, residues of insecticides, chronic toxicity or diffuse environmental pollution and declining biodiversity (Lalouette *et al*. 2015). However, lethal doses of insecticides are degraded by biotic and abiotic processes to sublethal or lower doses (Bartling *et al*. 2024). Although the exposure to low doses of insecticides occurs more often, the lethal effects of pesticides received more recognitions but the sublethal effects of insecticides on insect species at the individual, population and community level have not been studied more (Tosi *et al*. 2022)

The predominantly used insecticides for crop protection as well as in public and human health protection are of contact, vapor and stomach mode of action, which are available in the market individually or in combination with other insecticides that produce lethal, sublethal and combined toxicity. Tosi *et al*. (2022) found a major knowledge gap on lethal, sublethal and combined toxicity of pesticides on multiple bee species (*Bombus, Osmia, Megachile, Melipona, Partamona* and *Scaptotrigona*) and found that it has been not investigated for 71% of individual substances (n = 377 pesticides) and 99% of their combinations. This meta-analysis demonstrates how much we do not know about the sublethal and combined effects that pesticides have on bees.

Over the last decade, there has been increasing awareness about the negative effects of insecticides on non-target species, especially pollinators like bees (Hymenoptera), increased insecticide resistance and focus on development of new molecules that are environmentally safe even at a very low dose have gain importance. When a query "sublethal effects of insecticides on insects" searched in a PubMed database [PubMed (nih.gov)] it has received nearly two thousand responses (Fig. 1). Moreover, the number of publications about studies in Hymenoptera and Diptera insect order were 59% of the total. Therefore, there is need to more work on insects belonging to other orders regarding how insecticides, even at sublethal doses can affect insects' physiology and behaviour.

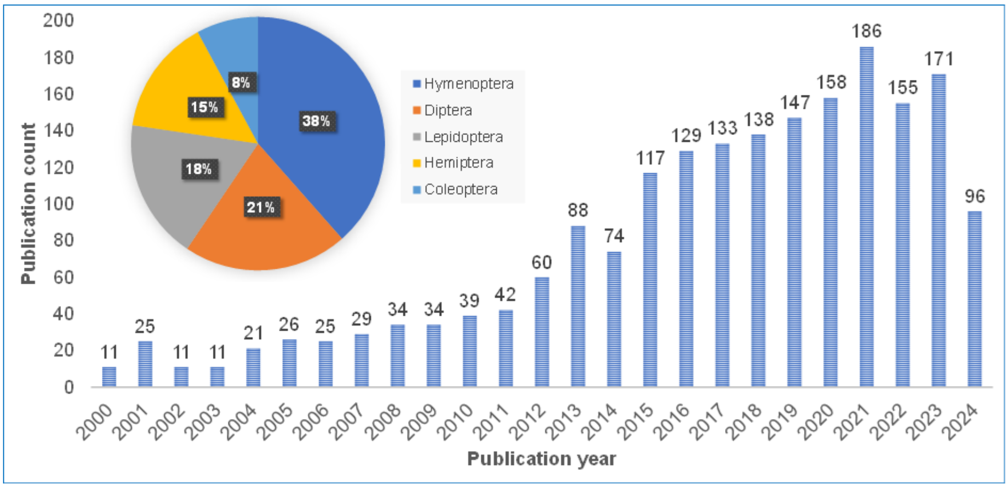

Fig. 1: Annual publication counts (histogram) and research subjects of publications (pie graph) on sublethal effects of insecticides in the past 25 years (2000-2024) [PubMed (nih.gov)]

What is a sublethal effect?

According to Desneux *et al*. (2007), it is defined as the one that does not cause the death of the individual, rather it produces a physiological, biological, demographical or behavioural change in an individual or population that survives upon the exposure to a substance at a lethal or sublethal dose.

Factors affecting sublethal effects

The precise sublethal effects depend on insect species, age and sex; spatial and temporal environmental context; type and dose of active ingredients; application methods of insecticides as well as insect exposure route (Bartling *et al*. 2024), which are briefly described here under.

1) **Insect:** The characteristics of the insect itself can affect how it responds to sublethal insecticide exposure.
    a) **Species:** Different insect species have varying susceptibilities to insecticides which can influence their survival, behaviour and reproduction after exposure to a sublethal dose.

b) **Age**: Younger or older insects may have different tolerance levels to insecticides e.g. Juvenile stages of insects are more vulnerable than adult stages.

c) **Sex:** Male and female insects could respond differently to insecticides due to biological and physiological differences among both the sexes.

2) **Environmental context:** The specific conditions of the insect's environment that can modify the effects of sublethal exposure.

a) **Spatial:** It is nothing but the geographical location or habitat where the insect lives. Factors such as temperature, humidity or vegetation type existing in that location could alter the impact of insecticides.

b) **Temporal:** It is a time-related factors such as the season or time of day when exposure occurs. e.g. Insects may be more active during certain periods, making them more or less vulnerable to insecticide exposure.

3) **Insecticides**: The properties and application of the insecticides themselves play a crucial role in determining sublethal effects.

a) **Type of insecticides and its dose:** Different insecticides have different chemical properties and dose. e.g. Higher doses might cause acute toxicity, while lower doses may lead to sublethal effects.

b) **Application methods:** Whether the insecticide is applied as a spray, bait, powder or granules affects how insects come into contact with it and resulting sublethal impacts.

4) **Exposure route:** It refers to how the insect comes into the contact with insecticide.

a) **Oral:** Insects may ingest the insecticide through feeding. This route could affect internal organs and behaviours such as feeding and digestion. Feeding and collecting nectar and pollen from insecticide-treated plants can expose bee and their colony to insecticides.

b) **Contact:** Insects may absorb the insecticide through their body surface after coming into contact with a treated surface. This route could impact mobility, reproduction or development. The contact with thiamethoxam-contaminated honeydew significantly increased mortality of parasitic wasps, *Anagyrus pseudococci* (64%) and hover fly, *Sphaerophoria rueppellii* (73%) [Agudo, 2021].

Types of sublethal effects

There are four types of sublethal effects of insecticides to insects (Fig. 2) which include physiological, biological, demographical and behavioural effects (Bantz *et al*. 2018; Bartling *et al*. 2024).

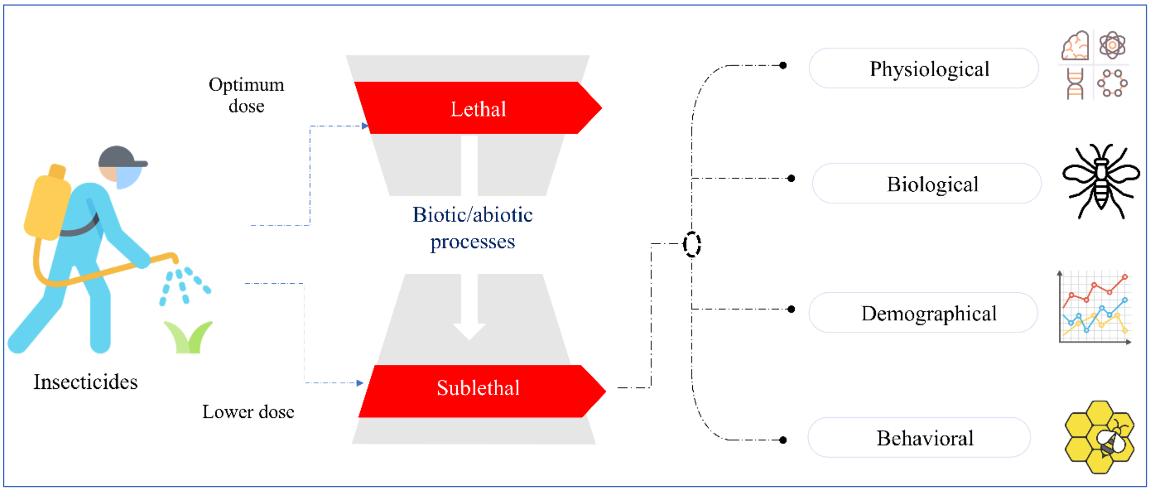

Fig. 2: Sublethal effects of insecticides on insects

1. Physiological sublethal effects

It includes modifications in insect biochemistry such as changes in enzyme activity, hypothermia (response to cold stress) and alterations in oxidative metabolism; insect immunity which includes changes in the number of haemocytes (immune cells in invertebrates), encapsulation (a defense mechanism against pathogens) and hydrogen peroxide (H_2O_2) production. Cellular-level sublethal effects include necrosis, vacuolization (formation of vacuoles within cells), accumulation of reactive oxygen species (ROS) and protein expression, production of enzymes that help in detoxifying the insecticide. Moreover, it leads to transcriptional changes in gene expression through microRNAs (critical in regulating protein production by targeting mRNAs) and mRNA (messenger RNAs) splicing (different forms of proteins from the same gene). Further, epigenetic changes by DNA methylation (a process that adds a methyl group to DNA) and histone modification (changes to the proteins that DNA wraps around). The cellular modifications affect heritable molecular information, which leads to changes in cellular targets of the insecticide and reduces its effectiveness (Bantz *et al*. 2018). Ultimately, it allows insect to adapt presence of the insecticide in its environment. Also, the epigenetic changes can be passed down to future generations and influence population dynamics across generations. Moreover, it causes changes in growth and development like modification in wing development and altered body mass.

Changes in enzymatic activity and immune system

Insects can detoxify insecticides through various enzymatic activities. The key enzymes such as cytochrome P450 monooxygenases (detoxify xenobiotics, source of ROS), esterase (hydrolyze ester bonds), glutathione S-transferases (conjugate toxic substances with glutathione, making the toxins more water-soluble and easier to excrete) and phosphatases (dephosphorylation) work together to break down insecticides, enhancing the insect's metabolism to counteract the toxins. As a result, insects may develop target site insensitivity, reduced penetration of insecticides and nerve insensitivity, which makes them less vulnerable to the chemicals. This enzymatic defence allows insects to adapt and survive sublethal doses of insecticides, which reflects their ability to resist toxic substances.

Potato plants treated with imidacloprid @ 0.25 µg/L resulted in 36-44% increased *P450-CYP6CY3* gene expression in 7 days old green peach aphids, *Myzus persicae* (Sulzer) and 54% increased expression of *E4-esterase* gene and 96% increased expression of *Hsp60* gene in 21 days old *M. persicae* (Rix *et al*. 2016). So, it could be predicted that the exposure of *M. persicae* to a low-imidacloprid dose (0.25 µg/L) will increase the expression of detoxification enzymes. LC_{40} of imidacloprid (6.31 mg/L) significantly increased (28.57%) acetylcholinesterase (AChE) activity in kudzu bug, *Megacopta cribraria* (Fabricius) nymphs developing on soybean plants whereas, the AchE activity of *M. cribraria* significantly decreased by 34.19% and 55.48% when exposed to the LC_{10} (32.36 mg/L) and LC_{40} (89.13 mg/L) of acephate, respectively as compared with the control. The difference in AChE activity is due to different modes of action of insecticides (Miao *et al*. 2016). The negative impact of various organophosphates and neonicotinoids insecticides on insect immunity leads to increased vulnerability to various biotic and abiotic stressors.

Changes in cellular activity

In insects at the cellular level in the brain, Kenyon cells of the mushroom bodies are involved in functions like learning, memory and sensory integration; in the gut, epithelial cells which play a critical role in digestion and protein kinases, precursors and receptors are mostly affected by sublethal doses of insecticides. The modifications in these organs can significantly affect the physiological processes *viz*. neural, digestive and cellular signaling in insects. Imidacloprid @ 14.651 ppb ($LC_{50}^{1/100}$) caused nuclear and mitochondrial damage and vacuolization in the midgut cells, increased spacing among the Kenyon cells in the mushroom bodies and increased the expression of proteins like vascular endothelial growth factor receptor, amyloid protein precursor and protein kinase C, whereas decreased the expression of the nicotinic acetylcholine receptor alpha 1 in European honeybee, *Apis mellifera* Linnaeus (Catae *et al.* 2018). These alterations demonstrated that extremely lower dose of imidacloprid could compromise the viability of the midgut epithelium, as well as inhibiting important cognitive processes in individuals and it cause the loss of the bee colony.

Growth and development

Insecticides can also interfere with insects' growth and development. The sublethal effects have serious consequences on the duration of insect life cycle even if the insecticides do not cause immediate death. These impacts are particularly concerning when considering beneficial insects like pollinators (bees) or natural enemies (stink bugs, lacewings and parasitic wasps) of insect-pests. The sublethal doses (LD_{20}) of imidacloprid (0.09 ng/insect) and dinotefuran (0.15 ng/insect) showed significant induction of macropterous adults in both macropterous and brachypterous families of brown plant hopper (BPH), *Nilaparvata lugens* (Stål). However, dinotefuran produced higher rates of macropterous adults than imidacloprid. These results indicated that insecticides at the sublethal doses could affect wing polymorphism in BPH (Bao *et al*. 2009). After being treated with fluxametamide at LD_{10} (0.09 mg/kg) and LD_{30} (0.25 mg/kg) some pupae of rice striped stem borer, *Chilo suppressalis* Walker could not be generated, and the pupal tail was crumpled and darker in color while some adults failed to be eclosed from pupae, manifested as pupal shells that cannot be detached, or the wings were curled (Li *et al*. 2022). The application of a botanical insecticide, Anisom 2.71 mg/L (LC_{30}) recorded lowest larval (309.0±7.5 mg) and pupal weights (133.2±3.9 mg) and highest malformation in adults (75%) of fall armyworm, *Spodoptera frugiperda* (JE Smith) [Pavana *et al.* 2023]. The hind tibia and wings of egg parasitoid, *Trichogramma brassicae* Bezdenko that developed and emerged from cabbage looper, *Trichoplusia ni* (Hübner) eggs treated with sublethal spinosyn (100 ng/mL) were 11.6% and 26.9% larger compared to control, respectively (Smith *et al*. 2024).

2. Biological sublethal effects

The sublethal doses of insecticides can affect an organism's biological traits. It includes the efficiency of parasitism, the number of individuals that successfully emerge from developmental stages and how traits are passed on generations to generations.

The tebufenozide (0.12 g a.i./L) caused the greatest reduction in parasitism capacity of ectoparasitoid, *Tamarixia radiata* (Waterston) in the F_0 (79%) and F_1 (48%) generations. Moreover, azadirachtin (0.03 g a.i./L) and tebufenozide (0.12 g a.i./L) increased longevity with means of 10.2 and 9.6 days, respectively in F_2 generation (Beloti *et al*. 2015). The key life table parameters such as intrinsic and finite rate of increase of progeny (F_1) diamondback moth, *Plutella xylostella* (L.) were significantly decreased whereas mean generation time was significantly prolonged when parents (F_0) treated with LC_{10} (0.06 mg/L) and LC_{30} (0.11 mg/L) of fluxametamide (Gope *et al*. 2022). Chlorantraniliprole 0.11 mg/L (LC_{10}) significantly increased emergence of parasitoid wasp, *Trichogramma japonicum* Ashmead and showed higher parasitism of *C. suppressalis* under field conditions. Results highlighted a positive sublethal effect, a hormesis (a biphasic dose-response, characterized by high-dose inhibition and low-dose stimulation during or following exposure to a toxicant) effect of chlorantraniliprole on parasitism (Wang *et al*. 2022).

3. Demographical sublethal effects

Demographical traits like intrinsic rate of increase (r), finite rate of increase (λ), mean generation time (T) and population size are modified by sublethal doses of insecticides. These modifications result in altered population dynamics and population growth parameters.

Higher instantaneous rate of increase (24%) and total reproductive output (almost twice) of aphids, *M. persicae* developing on potato plants was observed when treated with lower dose (0.25 µg/L) of imidacloprid than control plants (Rix *et al*. 2016). It supports the hypothesis that hormesis is likely a manifestation of an adaptive response to a sublethal dose of a stressor. The key demographic parameters such as intrinsic and finite rate of increase of progeny of greenbugs, *Schizaphis graminum* (Rondani) (F_1) were significantly increased when parents (F_0) treated with LC_5 (2.259 mg/L) of thiamethoxam. In addition, it also recorded the highest total population size which was projected to surpass 9.0×10^8 individuals after 50 days of development. Overall, it showed that exposure to thiamethoxam at sublethal dose caused inter-generational hormetic effects on the demographic traits of *S. graminum* (Gul *et al*. 2024). The increased developmental rate might cause pest outbreaks under field and increase the crop damage.

4. Behavioural sublethal effects

It includes modifications in insect mobility, mating, feeding, navigation, orientation and learning behaviour.

Insect mobility

Insect mobility refers to the ability of insects to move, which is essential for various survival functions such as foraging, mating and oviposition. It can be influenced by exposure to sublethal doses of insecticides which affect insect populations and ecosystems. Walking activity of adult workers of Italian honeybee, *A. mellifera* reduced when treated with various botanicals *viz*. garlic extract (0.3 mL/L of water), neem oil (2.0 mL/L), eucalyptus oil (10.0 mL/L) and rotenone (5.0 mL/L). The reduction in walking activities might result in greater contact with pesticide residues and increase their toxic effects (Xavier *et al*. 2015). Several botanical insecticides, which are often touted as safe and environmentally friendly, might generate sublethal effects on honeybees. Therefore, the use of botanicals for managing insect-pests on crops should be exercised with caution.

Mating behaviour

The insect experiences changes in sexual behaviour and reproductive patterns as a result of the exposure to sublethal doses of insecticides, which may affect population dynamics. Cotton leafworm, *Spodoptera littoralis* (Boisd.) males treated with deltamethrin at $LD_{50}^{1/10}$ were much more responsive compared to control and $LD_{50}^{1/100}$ treated males. This faster courtship behaviour could putatively lead to higher reproductive success in treated males. Therefore, the *S. littoralis* males treated with $LD_{50}^{1/10}$ (0.76 ng/insect) of deltamethrin were more (60.5±0.04%) successful for mating than control males (39.5±0.04%) when in a competition with a single female, whereas the LD_{30} treated males showed a lower mating success (30.9 ±0.04%) [Lalouette *et al*. 2015]. Sublethal dose (LD_{30}) of fluxametamide (0.25 mg/kg) inhibited the length and weight (5.47±1.33 mm and 8.81±3.16 mg, respectively) of ovarian tube of adult females of *C. suppressalis* as compared to control (8.74±0.93 mm and 15.50±4.00 mg, respectively). The most direct response of the ovarian development of *C. suppressalis* to fluxametamide was the changes in the size of the ovarian tubes (Li *et al*. 2022). The intergenerational impact of LC_5 (2.259 mg/L) and LC_{10} (3.057 mg/L) of thiamethoxam on the F_1 generation of *S. graminum* showed that the net reproductive rate of F_1 aphids at LC_5 was 1.2 times higher than that of the control. Moreover, the fecundity of F_1 aphids was substantially enhanced only at the LC_5 of thiamethoxam, while the reproductive days were dramatically increased at both concentrations as compared to control (Gul *et al*. 2024). This increased reproduction might cause pest outbreaks under field and thereby increase the crop damage.

Feeding behaviour

The feeding is crucial for their survival and ecological functions, including pollination, nutrient requirement and survival. Exposure to sublethal doses of insecticides can alter feeding behaviours, it impacts their efficiency and roles in ecosystems. *A. mellifera* exposed to agarose cubes incorporated with pyrifluquinazon (PQZ) @ 84 ppm spent significantly less time in the feeding zone as compared to the control. Moreover, after 24 h of exposure to PQZ in honeybees' food, they began avoiding it and by day 4, no bees fed on PQZ-treated food as compared to the control. Hence, this avoiding behaviour of bees exhibited to PQZ in their food could potentially limit the risk of this insecticide in the field (Wilson *et al*. 2019). Total duration of non-probing (Np), intercellular stylet pathway and salivary secretion into sieve element of directly exposed aphids, *S. graminum* (F_0) at LC_5 (2.259 mg/L) and LC_{10} (3.057 mg/L) of thiamethoxam were significantly longer than the control.

Interestingly, the total duration of Np was significantly decreased, while the total duration of phloem sap ingestion and concurrent salivation was significantly increased in the progeny generation following exposure of the parental aphids to the LC_5 of thiamethoxam. It showed that the sublethal doses of thiamethoxam affect the feeding behaviour of the directly exposed aphids, while significantly increasing the feeding behaviour of the progeny generation, this validates the hormetic effects of insecticides (Gul *et al*. 2024).

Navigation and orientation behaviour

Insects rely on orientation and navigation to locate food resources, mates and suitable habitats through olfactory and gustatory signals. Also, the time spent for host searching is an important behavioural trait that should be considered when parasitoids are exposed to pesticide residues. The adult female of egg parasitoid, *T. japonicum* after being exposed to LC_{10} of chlorantraniliprole (0.11 mg/L) significantly increased their creeping speed (faster locomotion), showed more frequent changes in the orientation behaviour, significantly fewer interval rest times and spent shorter time for contacting host eggs (Wang *et al*. 2022). It indicated a positive sublethal hormesis effect of chlorantraniliprole on the orientation. After exposure to spirotetramat at LC_{10} (72.79 mg/L), 94.59% of the *Encarsia formosa* Gahan wasps were attracted to the host plant (Common bean: *Phaseolus vulgaris*) volatiles and they crawled the fastest. It indicated that the *E. formosa* exposed to sublethal spirotetramat at LC_{10} were more eager to locate the hosts for their parasitism, which could have been a consequence of the hormesis induced by spirotetramat at a lower concentration (Yang *et al*. 2022).

Learning behaviour

Insects exhibit learning through experience and adapt to their environment by associating stimuli with rewards or dangers. This ability plays an important role in behaviours like foraging, memory, caste determination, predator/parasitoid avoidance and communication. Flupyradifurone (FLU) 0.03 µg/bee/day decreased average olfactory learning by 74% (larval treatment) and 48% (adult treatment) and average memory by 48% (larval treatment) and 22% (adult treatment) in Indian honeybee, *A. cerana* as compared to controls. FLU was thus 1.3 to 2.5-fold more harmful to the olfactory learning and memory of bees exposed as larvae as compared to foragers exposed as adults. These results suggested that larvae were more susceptible to FLU than adults (Tan *et al*. 2017). Therefore, further research should be conducted on the effects of insecticides, expanding beyond its basic effects on honeybee survival and colony strength to consider its impact on their cognition and memory.

CONCLUSION

Insecticides are lethal to insects-pests but improper doses can cause sublethal effects. The sublethal dose of insecticides produces physiological (modifications in expressions of detoxification enzymes, damaged midgut and brain cells of the honeybee, modified wing development in BPH), biological (altered biocontrol activity), demographical (increased intrinsic and finite rate of increase of *S. graminum*) or behavioural (mobility reduction, higher rate of mating success in *S. littoralis*, increased fecundity in *S. graminum*, reduced feeding in *A. mellifera*, hormetic effects on feeding behaviour of *S. graminum*, impaired navigation, orientation and learning behaviour in *T. japonicum,* *E. formosa* and *A. cerana*) sublethal effects on various insect-pests. Therefore, information on sublethal effects is crucial for all insecticidal efficacy trials in the field of agriculture.

Future thrusts

The future research priorities should aim to address challenges in sustainable insect-pest management by focusing on sublethal effects of insecticides. Research in epigenetics to understand how changes at cellular level affect insect-pest populations over generations, which will help in developing strategies to mitigate unintended long-term effects of insecticide use. Moreover, assessing impact of sublethal doses on nutritional stress could help standardize insecticide applications to exploit the weaknesses in physiology. Generally, the current risk assessments often focus on acute toxicity and there is a need to extend guidelines which include sublethal effects, such as physiological alterations, impact on learning and memory of non-target species, that will improve safety and efficacy of insecticides. By advancing knowledge in these areas a more effective, eco-friendly and long-term insect-pest management strategies could be framed.

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