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Exploring Hormesis and Its Impact on Insect Populations

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ABSTRACT

The present study aimed to investigate hormesis and its effect on insect populations. Hormesis is an adaptive response in which low doses of chemicals have a stimulating effect on living organisms. This mechanism suggests that mild stressors can improve the host defense system, while higher concentrations of the same stressors can be harmful or fatal. Insects are often exposed to various stressors, including chemicals, heat, and nutrient deficiencies, frequently at low levels. The hormetic effects on insects are now well-established, and this phenomenon can be harnessed to better manage insect populations, ecological structures, and performance in agricultural environments. Insects, present in nearly all terrestrial and aquatic ecosystems, are constantly exposed to a range of synthetic pesticides and both non-chemical and chemical stressors. These factors lead to dynamic non-biological and biological processes related to pest control, that vary over time and space in the field. Understanding and considering hormesis is crucial in pest management. To accurately assess the effects of insecticides on hormesis, field-based studies, and experiments are necessary to apply these findings to broader ecosystems. Despite the importance of hormesis, limited research has been conducted on insect toxicology in this context. Future studies should delve deeper into the evaluation of physiological, morphological, behavioral, molecular, and demographic markers to better understand how insects cope with hormesis.

Keywords: Insects, Pest management, Hormesis, Agricultural ecosystems

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Introduction

Humans employ various strategies to manage and eliminate plant pests, aiming to protect agricultural products from potential damage. This is crucial, given the significant time and effort involved in food production and the growing global population that places pressure on food supply systems. The most common approach to pest control is using pesticides. According to the US Environmental Protection Agency, a pesticide is any substance or mixture to destroy, prevent, or manage pests [1, 2].

Over the past seven decades, chemical pesticides have predominantly been used for pest (insect) control, especially in agriculture and forestry. This has led to insect populations being exposed to large quantities of pesticides, primarily through respiratory and digestive pathways [3-5]. The effectiveness of insecticides is influenced by a variety of factors, but the dose remains the key determinant. The pesticide dosage that insects are exposed to can vary greatly depending on location and time. For instance, farmers typically aim to apply pesticides evenly across their crops, but environmental factors like wind can cause drift, resulting in uneven pesticide distribution.

Additionally, pesticide evaporation, especially during hot and dry conditions, can reduce the effectiveness of the pesticide by decreasing the amount that remains on the plants. Spray penetration through the plant canopy also varies, with different levels of pesticide absorption occurring on the lower and upper parts of the plant. Environmental conditions such as temperature, humidity, soil composition, and light exposure all play a role in altering the pesticide's toxicity over time. For instance, the rate of photodegradation of an insecticide changes with varying light intensity [6, 7]. Systemic insecticides applied either to the soil or directly to crops can also decompose within the plant, leading to a reduction in toxicity. The concentration of systemic insecticides can fluctuate over time within the same plant, affecting both new and older foliage [8, 9]. Consequently, many abiotic and biotic processes in pest control are influenced by spatial and temporal changes in the field.

While the traditional models for studying pest responses have been based on threshold or non-threshold linear approaches, modern research now recognizes the biphasic response model. This model explains the stimulating effects of low doses and the inhibitory effects of high doses and is widely acknowledged as a general biological phenomenon [3-5].

Despite its significance in pest management, the hormesis phenomenon has not received adequate attention from toxicologists, especially in terms of its potential applications in pest control and its ability to enhance models for initial research. This article aims to explore the hormetic effects of various factors on insects, as documented in prior studies.

Hormesis is a phenomenon in which exposure to low doses of harmful substances or stressors results in positive, beneficial effects for organisms, a concept that has become integral to the study of toxicology and ecology. Over time, the concept of hormesis has evolved, and various terminologies have been introduced to describe its effects, including “hormesis” itself, which is derived from Greek, meaning a swift movement or desire, typically referring to biological responses to low doses of toxins or stressors [10].

In studies focusing on insects, a variety of terms such as Hormesis, Hormoligosis, and Pesticide-mediated homeostatic modulation are commonly used. Hormesis describes a scenario where the effects of a substance differ at high and low doses, with the low dose promoting positive responses and the high dose causing harmful effects. Essentially, hormesis refers to a biphasic response, where an organism or cell reacts positively to small amounts of a stressor, but negatively to higher amounts under certain conditions, such as chemical exposure or metabolic stress. This pattern of stimulation at low doses and inhibition at higher doses is widely recognized in toxicological studies [3-5].

Initially, the phenomenon of hormesis was identified in research related to growth regulators, such as herbicides or pharmaceuticals. However, further investigations revealed that hormesis could also be observed in natural plant chemicals and the biochemical interactions within plant cells. The effects of hormesis have been observed in a wide range of organisms, from single-celled organisms to complex multicellular life forms, and are tied to numerous biological processes, including growth, immune response, metabolism, and cognitive functions [11, 12].

Recent research has highlighted that hormesis occurs not only due to chemical stressors like pesticides and heavy metals but also in response to environmental stressors like mild radiation or temperature fluctuations. For example, studies have shown that low levels of cadmium can improve reproductive rates in snails, while high doses of the same element are lethal [13-18]. Similarly, selenium, an essential nutrient for human health, can enhance various bodily functions at low levels but becomes toxic and even fatal in high amounts. Hormesis, therefore, is not restricted to chemical stressors but can extend to various mild environmental stressors [19].

The terms “Hormoligant” and “Hormoligosis” were coined by 33. Luckey in the context of agricultural research, particularly during the First International Conference on Antibiotics in Agriculture [20]. Luckey defined hormesis as a process in which small doses of any form of stressor—whether physical, social, psychological, or chemical—may initially irritate an organism, but higher doses can be detrimental. This definition emphasizes the classic hormetic pattern of low-dose stimulation and high-dose inhibition. Hormoligosis refers to a scenario where a small but significant amount of a stressor enables an organism to better cope with subsequent environmental challenges. Understanding how different stressors interact and contribute to hormesis is important, as this insight can help predict how organisms will respond to mixtures of stressors in their environment. Given that nearly all stressors can trigger hormesis, the phenomenon is now viewed as a type of “mixed hormesis,” a broad category that encompasses various types of stress interactions [3-5].

Cohen [21] introduced the concept of homeostatic modulation by pesticides, challenging the conventional use of the term hormesis. He argued that hormesis is not applicable when stimulatory effects are observed in pest arthropods that are neither targeted nor controlled by a pesticide. Specifically, Cohen distinguished acaricides (which target ticks) from insecticides (which affect various arthropods, including insects). He provided examples where exposure to insecticides such as carbaryl, DDT, pyrethroids, or imidacloprid resulted in increased tick reproduction. These chemicals are not designed to control ticks and are typically not classified as acaricides. However, in environments where both insects and ticks coexist, the use of these insecticides sometimes leads to a rise in tick populations. Cohen believed that such stimulatory effects, especially when observed at higher pesticide doses that are typically not harmful to arthropods (such as enhanced reproduction in two-spotted spider mites), should not be labeled as hormesis. Instead, he proposed the term “modulation of pesticide-mediated homeostatic response,” which encompasses both stimulatory and hormetic effects of pesticides on non-target pests.

While the term modulation of pesticide-mediated homeostasis might sound distinct, it does not present a fundamentally different mechanism from hormesis. This is a concept based on semantics and remains biologically intertwined with hormesis. Additionally, the term “Hormoligosis” holds historical significance in insect toxicology, referring to insecticide-induced irritation in insects. This term could be seen as separate from hormesis, as it suggests that an organism must first endure sub-optimal conditions before any biological stimulation occurs from low doses of an insecticide or stressor. Ultimately, this situation aligns with the idea of mixed hormesis [3-5].

The significance of studying hormesis in insects has become increasingly important, especially as research has traditionally focused on lethality as the primary endpoint, often overlooking sublethal effects. This trend is shifting with the growing recognition of pesticide-induced hormesis, though much of the progress remains passive, stemming mainly from agricultural pest management and crop yield concerns. In pest control, attention is now being directed not only at the impact of pesticides on pest species but also on the unintended effects on natural enemies, including pollinators [22].

The present study aims to investigate hormesis and its effect on insect populations.

Results and Discussion

The importance of studying hormesis in insects

Historically, toxicological studies on insect pests and beneficial insects have concentrated on lethal effects, with an emphasis on high doses, such as LD50/LC50 values, mirroring toxicological research in other fields. While the harmful effects of low-dose pesticide exposure have been recognized, especially in terms of lethality, less attention has been paid to sublethal impacts, such as fertility, behavior, longevity, and other biological processes. These effects, which result from pesticide-induced hormesis, are now gaining more focus. Extensive research into physiology, molecular biology, insect biochemistry, toxicology, behavior, genetics, and reproduction provides a solid foundation for understanding dose-response relationships. With many insect genomes fully or partially sequenced [23] and an increasing understanding of insect gene functions, there are substantial opportunities for studying the mechanisms of hormesis in insects as model organisms [3-5].

After applying certain insecticides, sometimes the population of insects or mites may increase at a faster rate than when no pesticide is used. This phenomenon, known as pest resurgence, can occur in the target pest species or even in secondary pests that were initially less of a concern [24]. For instance, a study demonstrated that low-lethal doses of limonene (LD20) extended the lifespan of Mediterranean fruit flies deprived of protein, and while females were exposed to sub-lethal doses of limonene, their fertility increased [25].

Evidence for hormesis in insects

Evidence supporting the phenomenon of hormesis in insects has been growing steadily. Sun [26] observed that while high doses of rotenone were detrimental to female aphids, lower doses of the same chemical led to increased reproduction in the treated aphids compared to the control group. Similarly, studies have shown that dieldrin, at lethal doses, extended the lifespan of *Drosophila* [27] and enhanced the weight and fertility of houseflies [28]. Early research on houseflies revealed that exposure to lethal insecticide concentrations could stimulate reproduction in these pests [29, 30].

In another study, Kuenen [31] discovered that weevils fed wheat contaminated with lethal levels of DEET produced about 20 percent more offspring than untreated weevils. Furthermore, other studies have reported that DEET could stimulate egg-laying in beneficial insect species, such as predators [32]. Luckey [33] conducted 1 of the 1st studies to demonstrate low-dose stimulation, showing that exposure to lethal concentrations of fourteen different insecticides led to an increase in the weight of house crickets.

Research by Chelliah *et al*. [34] indicated that the use of insecticides could enhance both the reproductive output and longevity of the citrus brown shield weevil, although the specific response varied depending on the dose and the active ingredient. Further studies have highlighted the stimulatory effects of insecticides on reproduction and growth in aphid species. For instance, Qu *et al*. [35] observed that larvae feeding on poplar leaves treated with organophosphorus and carbamate insecticides survived longer and developed into heavier pupae, with increased protein and calcium content compared to untreated larvae.

Throughout the 1990s and beyond, numerous studies have documented biological stimulation caused by low doses of insecticides in a wide range of insect species, including bees, collembolan beetles, thrips, woodlice, as well as various species of beetles, flies, and butterflies. Cohen [21] also discussed the stimulatory effects of pesticides on ticks, noting that in many cases, the biological stimulation from low doses of insecticides is not formally recognized as hormesis.

This highlights that not all insect toxicologists fully comprehend the concept of hormesis, despite it being an emerging focus of research [3-5]. Hormesis has been observed in a wide range of insect species across various taxonomic groups, including those with gradual, incomplete, and complete metamorphosis, suggesting that it is a widespread phenomenon in insects [3-5].

Research has shown that insects experiencing stressors during different life stages—adults, pupae, larvae, or eggs—often experience stimulating effects that persist across these stages [36]. However, the long-term intergenerational impacts of such exposures remain underexplored. For instance, Deng *et al*. [37] studied the effects of different chlorpyrifos concentrations on both resistant and sensitive Platella xylostella species. The insecticide doses stimulated growth and fertility, and also altered resistance and sensitivity at 25 °C. Furthermore, these treatments increased acetylcholinesterase and glutathione S-transferase activity at this temperature. This demonstrates that hormesis can be triggered by a range of insecticide ingredients, underlining the phenomenon's broad applicability. Despite this, much of the research has focused on insecticide neurotoxins.

The study of hormesis in growth regulators for insects, parasites, or pathogens in agricultural settings has been limited [3-5]. While some studies have highlighted reproductive stimulation, few have examined other factors such as weight, behavioral responses, or physiological changes. Even fewer have explored the molecular, hormonal, or biochemical alterations that occur during insect hormesis [3-5]. For example, Lalouette *et al*. [38] explored the effects of deltamethrin on the sexual behavior and olfactory response in cotton leaf-eating insects, revealing that sublethal doses of deltamethrin could induce hormesis, enhancing the males' response to sex pheromones.

In another study, Caribbean fruit fly pupae were exposed to anoxia, mimicking the conditions they face during tropical rainfall. The results showed that exposure to anoxic stress elevated lipid levels throughout the pupal stage, suggesting that anoxia enhances insect fecundity and growth by promoting lipid storage and improving overall performance [39]. Stress-induced changes were also noted in genes, youth hormones, and vitellogenin in the TIS/TOR signaling pathway, which plays a key role in regulating reproduction, growth, and development.

Rix and Cutler [40] examined the phenotypic and biochemical responses to various stressors, including pesticides, oxidative stress, temperature fluctuations, radiation, crowding, and starvation. Their findings revealed that these stressors often stimulated reproduction, development, survival, growth, and longevity, with molecular and biochemical responses closely linked to the phenotypic changes observed. Reproductive stimulation was particularly notable in treatments close to the control group and those with doses below 25%.

Stimulant concentrations

Meta-analyses have demonstrated that hormetic effects typically peak at concentrations that do not inhibit growth (NOEC). However, in studies on insects, stimulatory effects are sometimes observed at much higher concentrations than the NOEC. Stimulation above control levels is not unusual when insecticides are applied at concentrations around LC25. Additionally, stimulation has also been noted at concentrations as high as LC50. The precise concentrations that induce irritation in insects can vary and sometimes differ from the usual quantitative patterns observed in hormetic responses. In many instances, stimulation has been reported at insecticide concentrations significantly higher than those typically considered ineffective. In studies comparing groups treated with specific insecticide doses, such as LC25, to control groups, it has been found that the responses within treated groups are fairly homogeneous. Even when some individuals show normally high reproductive output, these findings do not significantly affect the overall response of the group.

It is important to remember that while insect reproduction would be stimulated by exposure to insecticides at LC25 concentrations, the same dose will also kill about 25 percent of the population (the susceptible insects), which likely negates the stimulating effects on the overall population. Despite this, the apparent stimulation at concentrations well above the NOEC is a noteworthy deviation from the typical hormonal dose-response patterns and warrants further research [3-5].

Nature of the stressor

Hormesis is understood as an adaptive response mechanism whereby mild stressors can improve an organism's defense mechanisms, while excessive stress at higher levels becomes detrimental or lethal [41]. Insects living in agricultural systems are constantly exposed to a variety of stressors, including temperature extremes, chemicals, and nutrient shortages, many of which are typically encountered at low levels. It is recognized that exposure to such stressors can trigger stimulatory effects in insects, which has significant implications for understanding ecological dynamics, insect management, and agricultural practices. Researchers focused on hormesis in entomology need to explore how this phenomenon affects species interactions, community structures, and ecological functions, particularly in agricultural ecosystems [42].

The ability of different chemicals to induce hormesis can vary, even when their molecular structures are similar [43]. Some insecticides may fail to produce any stimulatory effects at low doses, even when the concentrations are below the NOEC. For example, Chelliah *et al*. [34] observed that Nilaparvaa lugens showed reproductive stimulation when exposed to LC50 and LC25 doses of Decamethrin (a synthetic pyrethroid) and Methyl parathion (an organophosphate), respectively. However, no such stimulatory effects were observed when the pest was exposed to similar doses of Perthane (a chlorinated hydrocarbon). Likewise, Neubauer *et al*. [44] reported significant hormetic effects in aphids treated with lethal doses of aldicarb, but no such effects were found with Dimethoate or Ethiofencarb. In a separate study, exposure to an LC30 concentration of endosulfan resulted in faster growth time for Heliocoverpa armigera, while other chemicals such as Spinosad, chlorpyrifos, cypermethrin, and asphalt showed negative effects at the same concentration. This highlights that the dose-response curve is not only influenced by the concentration but also by the mode of action and the chemical structure of the substance. Unlike neurotoxins, the study of hormesis in insects exposed to growth regulators at low doses, particularly when combined with insect pathogens, remains limited [3-5].

Hormesis in populations of insecticide-resistant species

Insecticide resistance is a significant challenge in pest control, particularly for vectors and pest insects [45]. Research suggests that hormesis could contribute to pest resurgence, a phenomenon where pest populations increase after pesticide exposure. This resurgence can lead to more extensive crop damage, necessitating additional pesticide applications, which can exacerbate the impact on non-target organisms, further environmental contamination, and the spread of insecticide resistance. The effects are particularly pronounced in insecticide-resistant pest populations, where exposure to insecticides can push insects into a zone where hormetic responses occur. As a result, these insects may show increased reproductive rates and a higher frequency of resistance alleles. Although the role of insecticide-induced hormesis in resistance evolution and management strategies is recognized, it has not been sufficiently studied [46]. For instance, a study on Nilaparvata lugens, a migratory rice pest, exposed to an LC20 concentration of Nitenpyram for six generations, revealed that hormesis not only improved the pest's biological fitness (such as population size and life table parameters) but also enhanced its resistance to other insecticides like cycloxaprid and imidacloprid [47].

Beneficial insects and hormesis

The production and mass breeding of beneficial insects is a thriving multi-billion-dollar industry. Hormesis offers promising potential in enhancing the biological traits of these insects for human benefit. For instance, hormesis could be leveraged in insect mass rearing to boost their longevity, immune function, and reproductive capacity. Guedes *et al*. [48] found that a low dose of permethrin increased the reproductive output and decreased reproductive time in the predator insect Podisus distinctus. Similar hormetic effects were observed in Suppurius cincticeps, another predatory insect [49]. In a separate study, the parasitoid wasp Encarsia formosa demonstrated hormesis when exposed to an LC10 concentration of Spirotetramat, leading to a quicker location of its host, Bemisia tabaci, and improved efficiency [50]. Furthermore, research by Cutler and Rix [51] showed that bees responded positively to low doses of various chemical stressors, indicating hormesis. Long-term studies are necessary to determine if these hormetic effects can be effectively applied in the economic context of mass-rearing beneficial insects.

Conclusion

Insects are found in nearly every ecosystem, spanning both terrestrial and aquatic environments. Agricultural systems, whether intentionally or unintentionally, are subjected to a variety of synthetic pesticides and other chemical and non-chemical stressors. As a result, the biological and ecological dynamics within pest control programs are subject to change over time and across different environments. Understanding and incorporating the concept of hormesis into pest management strategies is crucial. To fully assess the impact of insecticide-induced hormesis, it is essential to conduct field studies that reflect real-world conditions, ensuring the results can be applied to broader ecosystems. Despite the significance of this phenomenon, research on its toxicological effects in insects has been limited. Future studies should explore hormesis more comprehensively, focusing on molecular, physiological, morphological, behavioral, and demographic indicators of insect responses.

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