American Journal of Agriculture and Forestry
2024, Vol. 12, No. 5, pp. 366-372
https://doi.org/10.11648/j.ajaf.20241205.16

SciencePG
Science Publishing Group

Research Article

Research on Resistance Monitoring, Risk Assessment, and Mechanisms of *Megalurothrips usitatus*

Gong Rui[1, 2], Huang Lifei[1], Cao Xuemei[1], Wang Huanting[1, 3], Liu Hongquan[2], Yang Lang[1, *]

[1]Guangxi Key Laboratory of Biology for Crop Diseases and Insect Pests/Key Laboratory of Green Prevention and Control on Fruits and Vegetables in South China Ministry of Agriculture and Rural Affairs/Plant Protection Research Institution, Guangxi Academy of Agricultural Sciences, Nanning, China

[2]School of Marine Sciences and Biotechnology, Guangxi Minzu University, Nanning, China

[3]Guangxi College of Agriculture, Guangxi University, Nanning, China

Abstract

Megalurothrips usitatus, also known as common thrips or cowpea thrips, is a widely distributed and highly destructive pest, primarily infesting legume crops. Due to its short generation cycle, high reproductive capacity, and concealed lifestyle, the effectiveness of chemical pesticide control has been continuously diminishing with the modernization of agricultural production and the extensive use of pesticides. *Megalurothrips usitatus* has gradually developed resistance to various commonly used pesticides, with resistance levels increasing year by year, thus exacerbating the difficulty of pest management and causing significant economic losses to agricultural production. Scholars, both domestically and internationally, have conducted in-depth research using methods from morphology, molecular biology, and ecology, showing that there are three main causes of pest resistance: enhanced detoxification enzymes, reduced sensitivity at target sites, and decreased cuticle penetration. These findings provide a wealth of theoretical support for resistance monitoring and management. The resistance of *Megalurothrips usitatus* to multiple pesticides is not only a local issue but also affects global agricultural sustainability. Research on the monitoring, risk assessment, and mechanisms of resistance in *Megalurothrips usitatus* contributes to prolonging the effective use of pesticides, improving control outcomes, and enhancing both the yield and quality of cowpea crops. These studies also provide a scientific basis for developing more effective control strategies and ensuring sustainable agricultural development.

Keywords

Megalurothrips usitatus, Resistance Monitoring, Risk Assessment, Resistance Mechanism

1. Research Background and Significance

Megalurothrips usitatus (Bagnall), commonly known as bean flower thrips or cowpea thrips, is a primary pest that significantly impacts cowpea crops, leading to substantial reductions in both yield and quality. The prevailing method for controlling cowpea thrips is the application of chemical pesticides. However, due to the pest's short generational cycle,

[*]Corresponding author: yang2001lang@163.com (Yang Lang)

Received: 8 September 2024; **Accepted:** 29 September 2024; **Published:** 29 October 2024

high reproductive capacity, concealed lifestyle, and the annual increase in resistance, the efficacy of chemical pesticides has been steadily diminishing. Consequently, resistance in *M. usitatus* has become increasingly pronounced [1, 2]. Currently, cowpea thrips exhibit varying degrees of resistance to multiple chemical pesticides, with significant regional differences in resistance levels [3]. Monitoring the resistance of cowpea thrips is essential to prolong the efficacy of pesticides and to prevent the rapid development of resistance caused by overuse. Conducting risk assessments can help determine the most effective pesticides for specific regions, thereby optimizing pest control outcomes. Furthermore, an in-depth investigation into the resistance mechanisms of cowpea thrips can provide a scientific basis for developing more effective control strategies, reducing reliance on chemical pesticides, enhancing cowpea yield and quality, and contributing to the sustainable development of agricultural production.

2. Overview of the Present Research Situation

2.1. Introduction to Thrips

Thrips, collectively known as Tysanoptera insects, primarily belong to the family Thripidae, which is mainly phytophagous, although a few species exhibit predatory behavior. By the time they are discovered, the population size is often substantial enough to cause significant damage, complicating prevention and control efforts.

2.2. *Megalurothrips usitatus*

2.2.1. Main Characteristics of *Megalurothrips usitatus*

Huang Weikang provided a comprehensive summary of the research progress on cowpea thrips, offering valuable references for their morphological characteristics and identification [4]. Cowpea thrips are primarily identified based on female morphology: female adults measure approximately 1.6 mm in body length, with a brown to dark brown coloration. The antennae are bead-like, slightly extending forward, and brown in color. Certain body parts, such as the tarsus, most of the foreleg tibia, and the distal ends of the middle and hind tibiae, exhibit a distinct yellow coloration. The narrow wings are fringed with slender tassel-like hairs. The forewings are colorless at the base and near the apex, while the middle and distal sections are brown. The head is slightly wider than it is long, with nearly parallel cheeks. The anterior bristle of the pronotum is well developed, with three pairs of posterior bristles, the longest being the central pair. The number of hairs on the anterior vein of the forewings ranges from 11 to 14, arranged at equal intervals. There are two hairs at the distal end of the anterior vein and 11 to 14 hairs on the posterior vein. The abdomen lacks auxiliary bristles. The middle pair of posterior bristles on the seventh tergite is located anterior to the posterior margin. The posterior margin comb on the eighth tergite is incomplete, present only on the sides and absent in the middle.

2.2.2. Damage Characteristics of *Megalurothrips usitatus*

The damage caused by cowpea thrips has been escalating over time. Previously, cowpea thrips were primarily harmful in spring and summer, but recent studies indicate that their period of activity has extended to include autumn as well. Research indicates that cowpea thrips mainly affect tobacco and navel oranges in Yunnan, and cowpeas in Hainan and Guangxi [4]. Cowpea, a staple vegetable in China and an important “vegetable basket” product, is highly susceptible to thrips throughout its growth cycle [5]. Adult and nymph cowpea thrips possess file-sucking mouthparts, which pierce the plant epidermis to suck plant sap, severely disrupting the plant's physiological functions. This leads to leaf shrinkage and stunted growth during the seedling stage. After flowering, cowpea thrips rapidly invade the flower core, causing it to rot and die, significantly reducing the quality of the cowpeas [6]. *M. usitatus* predominantly reproduces through parthenogenesis, with limited instances of bisexual reproduction. They exhibit strong oviposition capability, with serious infestations occurring in summer and autumn, and have developed substantial resistance to chemical pesticides [4]. In February 2023, the Ministry of Agriculture conducted a training course on cowpea medication supervision and inspection in Haikou City, Hainan Province, which included quality supervision and sampling inspections of cowpeas in Hainan, Guangdong, and Guangxi. The frequent occurrence of cowpea diseases and pests poses significant control challenges, requiring stringent standards for chemical pesticide use. The selection of appropriate chemical agents is crucial for effective prevention and control of cowpea diseases and pests, directly impacting product quality.

2.3. The Concept and Causes of Drug Resistance

2.3.1. The Concept of Drug Resistance

Drug resistance can be categorized into two types: innate resistance and acquired resistance. Innate resistance refers to the natural ability of certain pests to withstand pesticides due to their genetic makeup. Acquired resistance, on the other hand, is the ability of pests to develop tolerance to doses of pesticides that would typically be lethal to the majority of a normal population [7]. In the context of agricultural production, many forms of resistance are evolved through genetic changes [8].

2.3.2. Causes of Pest Resistance

Pest resistance can be attributed to the principle of “survival of the fittest". Pests exposed to insecticides in agricultural settings can develop resistance due to the improper application of these control agents [9, 10]. When the same pesticide is applied repeatedly in the same area over an extended period, pests with stronger resistance survive and reproduce. This leads to a gradual increase in detoxification metabolic enzymes within their bodies, a decrease in target site sensitivity [11], and a reduction in epidermal penetration rates. As a result, the resistance of these pests is strengthened over successive generations. Over time, this process leads to the emergence of new pest populations with enhanced resistance.

The enhancement of detoxification metabolic enzymes, also known as metabolic resistance, is a crucial mechanism by which pests develop resistance to insecticides [12, 13]. When insecticides are introduced into the bodies of pests, only a small fraction of the active ingredients reach their targets. The majority are excreted after being processed by detoxification metabolic enzymes, such as cytochrome P450 multifunctional oxidase, carboxylesterase, glutathione-S transferase, acetylcholinesterase, and ABC transporters [14]. The increased metabolic capacity of these detoxification enzymes can significantly reduce the amount of insecticide that reaches the intended target sites, thereby enhancing the resistance of pests to these chemicals [15]. Moreover, these detoxification metabolic enzymes do not operate in isolation; they are interconnected and function synergistically to bolster the metabolic resistance of insects [16-19].

The decrease in target site sensitivity, also known as increased target resistance, occurs when gene mutations alter the protein structure of the insecticide target in pests. These mutations reduce the expression level of the coding target gene, leading to decreased synthesis of the receptor protein. As a result, the efficacy of the insecticide is diminished, thereby increasing the pest's resistance [20]. For instance, acetylcholinesterase is the target enzyme for organophosphorus and carbamate insecticides. This enzyme rapidly hydrolyzes acetylcholine in the synaptic cleft. When insecticides bind to acetylcholinesterase, they inhibit its ability to hydrolyze acetylcholine. In *Laodelphax striatellus* (Fallén), changes in the expression of nicotinic acetylcholine receptor subunits mediate resistance to cycloxaprid and imidacloprid [21-23]. In studies of pyrethroid-resistant populations of *Anopheles gambiae* and *Anopheles arabicus* in northern Uganda, it was found that the GST4 gene was highly expressed in these mosquitoes. Research indicates that multiple mutation sites in the coding region of the GST4 gene are present in resistant individuals. These mutations enhance the binding ability of the GST4 protein to pyrethroids, thereby conferring strong resistance to these insecticides.

The penetration rate of the cuticle is reduced, meaning the rate at which pesticides penetrate into insects decreases]. This reduction is due to changes in the pest's epidermal structure, which prolongs the time it takes for the insecticide to reach the target site. During this process, pests also utilize the influence of detoxification enzymes to enhance their resistance. By reducing the penetration rate, pests gain more time to release metabolic enzymes, which improves the catabolism of the insecticide and reduces its effect on the target site [24].

2.4. Research on the Resistance Mechanism of *Megalurothrips usitatus*

2.4.1. Molecular Level

The molecular mechanism of insect resistance is the core focus of resistance research. When a pest develops resistance to an insecticide, it is likely to develop resistance to other insecticides with the same structure, type, or mechanism [25-28]. Resistance is also associated with mutations in sodium channels within the pest [29]. Pyrethroid insecticides, known for their high efficiency and low toxicity, are commonly used for pest control. In a study by Yuan et al. [30], the resistance mechanism of cowpea thrips was analyzed in depth. The resistance of the Sanya population to cypermethrin was assessed using cowpea thrips from Hainan. From 2019 to 2021, thrips populations in Haikou, Ledong, and Sanya exhibited high to extremely high levels of resistance to permethrin and fenpropathrin, with an increasing trend observed year by year. On this basis, mutation sites in selected cowpea thrips were detected, revealing the M283R mutation site in all three field-resistant populations. This mutation site was first identified in the Haikou population (HK2019), with mutation frequencies of 3.3%, 3.3%, and 10.0% over three years. Total RNA was extracted from *M. usitatus*, and cDNA was synthesized by constructing a recombinant plasmid. A positive plasmid containing the full-length sodium ion channel was obtained and sequenced. The study found that the M283R mutation site in the sodium channel protein of cowpea thrips appeared in the domain I-S5 of the pyrethroid drug binding region. This finding suggests that resistance is associated with factors such as sodium channel mutations. However, further experiments are needed to verify the degree of association with resistance, providing experimental data to support an in-depth understanding of the overall resistance mechanism of *M. usitatus*.

2.4.2. Physiological Level

In addition to the molecular level, studying the resistance of *M. usitatus* also requires attention to physiological changes. Cytochrome P450 enzymes are closely related to insecticide metabolism and play an essential regulatory role in the metabolism of both endogenous compounds (such as steroids, fatty acids, and hormones) and exogenous compounds (such as pesticides, drugs, environmental pollutants, and plant toxins) [31-33]. NADPH-cytochrome P450 reductase (CPR) and cytochrome P450 (P450) are central components of the P450 enzyme system [34-36]. The detoxification metabolic genes in insects are associated with the emergence and development of insecticide resistance [37, 38]. P450 genes contribute significantly to insect resistance to pesticides, primarily through overexpression, which leads to high levels of metabolic resistance to various pesticides. The role of P450 genes in insect resistance is multifaceted, involving mutations in the coding region, promoter region mutations, changes in cis- and trans-regulatory factors, and gene amplification. These mechanisms collectively contribute to the high level of resistance observed in insects. However, research on the regulation of pest resistance through CPR gene mutations is still in its early stages, and its relationship with insecticide metabolism and resistance has not been systematically studied. Although there have been reports on the relationship between CPR and drug resistance in several insects [39, 40], the specific mechanisms remain to be fully explored. The expression level of the CPR gene and its regulation of drug resistance vary among different pests. The mechanism of CPR-mediated drug resistance is a complex field requiring further investigation, which has potential implications for pesticide development and resistance management.

2.4.3. Research on the Relationship Between Insecticide Resistance and Environmental Factors

The effect of environmental factors on the resistance of *M. usitatus* should be carefully considered [41]. Environmental factors such as temperature, humidity, and light can influence the efficacy of pesticide compounds [42]. High temperatures can accelerate the biochemical reactions of insecticides [43]. For instance, the pathogenicity of acephate, methomyl, and imidacloprid to the red and green biotypes of *Myzus persicae* increases with temperatures ranging from 15-25 ℃. However, there are exceptions; for example, the pyrethroid insecticide cypermethrin exhibits higher toxicity to *Thrips alliorum* (Priesner) under low-temperature conditions [44]. The correlation between insecticide toxicity and temperature is linked more to the type of insecticide than to the pest itself. Additionally, secondary substances in host plants can influence pest responses to insecticides. After feeding on host plants, pests may experience activated or inhibited detoxification enzyme activity [45]. For example, the cytochrome P450 gene in *Helicoverpa armigera* is easily induced by phytochemicals [46]. Feeding on cowpea can induce the expression of glutathione S-transferase (GST) in *Spodoptera frugiperda*. Environmental factors play a critical role in the development and emergence of pest resistance. However, these influences are complex and multifaceted, necessitating further study to fully understand their specific mechanisms. A comprehensive understanding of how environmental factors affect pest resistance will enhance our overall knowledge of the resistance mechanisms in *M. usitatus*.

2.5. Management of Drug Resistance

2.5.1. Resistance Monitoring

The monitoring methods for insecticide resistance in general insects encompass molecular biology, ecology, and physiology. Bioassay is a traditional technique for monitoring drug resistance, with its core aspect being the cultivation of sensitive strains [47]. By collecting cowpea thrips populations from natural environments with minimal or no pesticide usage, cultivating sensitive or relatively sensitive strains, and applying bioassay methods, the susceptible toxicity baseline (LD-p), LC50, or LD50 can be determined. The resistance level is then expressed as the ratio of LC50 or LD50 (resistance index). The discriminating dose method is another commonly employed monitoring technique. This method involves continuously treating the field population with a discriminating dose by hybridizing high-level resistant lines with sensitive lines to monitor the frequency changes of resistant individuals. Both methods have their own strengths and limitations. Accurate resistance determination requires repeated experiments and strict control conditions. The resistance monitoring methods must also account for the specific characteristics of the pest. Yuan Linlin *et al*. evaluated the resistance of *M. usitatus* to permethrin and fenpropathrin in Hainan Province from 2019 to 2021. The toxicity of these two pyrethroid insecticides to relatively sensitive strains and nine field populations was assessed. The bioassay method used was an improvement on the TIBS (Thrips Insecticide Bioassay System) method [48]. The leaf-tube membrane method was refined by treating cowpea with different concentrations of the insecticides and then exposing the cowpea thrips adults to the treated plants. The mortality rate of the cowpea thrips was recorded, and the resistance ratio was calculated. The median lethal concentration (LC50, 95% confidence interval) of different pesticides in various populations was determined using Polo Plus 2.00 software. For the indoor relatively sensitive strains, the LC50 of permethrin was 1.4 mg/L, and the LC50 of fenpropathrin was 1.9 mg/L. The results indicated that from 2019 to 2021, the resistance of Haikou, Ledong, and Sanya populations to fenpropathrin and permethrin showed an increasing trend.

2.5.2. Risk Assessment

Understanding the risk assessment methods for general insects is crucial for effective agricultural pest management [49]. The study by Zhang *et al*. [50] presented the results of national agricultural pest resistance monitoring and provided scientific medication suggestions in 2020, offering practical experience and data support for the risk assessment of general insects. The resistance of Frankliniella occidentalis (Pergande) to five varieties of three insecticides was monitored. The results indicated that F. occidentalis exhibited high levels of resistance to spinetoram and emamectin benzoate, with resistance ratios ranging from 195 to 10,095 and 331 to 1,384, respectively. It showed moderate to high levels of resistance to spinosad and chlorfenapyr, with resistance ratios between 34 and 2,552 and 24 and 295, respectively. It exhibited low to medium levels of resistance to thiamethoxam, with a resistance ratio of 5.5 to 37. Compared to 2019, the overall resistance ratios did not change significantly. Comprehensive resistance management suggests the rotation and alternate use of insecticides or pesticide combinations with different mechanisms, such as chlorfenapyr and thiamethoxam, in areas with high resistance levels. Although this study focused on F. occidentalis, it still provides valuable reference data for the risk assessment of *M. usitatus*.

Risk assessment is fundamental for formulating scientific prevention and control strategies. More in-depth research is required for the risk assessment methods of *M. usitatus*. The study by Zhang *et al*. [50] screened chemical agents for the prevention of *M. usitatus*, providing practical application data for its risk assessment. In this study, five commonly used chemical pesticides were tested for their effectiveness against cowpea thrips. The results demonstrated that the compound reagent of 5% emamectin benzoate + 20% acetamiprid had the best control effect on cowpea thrips, with a population decline rate of 78.46% and a corrected control effect of 81.00%. After using 20% acetamiprid, the population decline rate reached 66.20%, and the corrected control effect was 70.17%, though the duration of the control effect was shorter. The effect of 5% imidacloprid was less satisfactory, with a population decline rate of only 46.15% and a corrected control effect of 52.49%, and the duration was short. These reagents have no adverse effects on the growth and development of beans and are high-efficiency, low-toxicity insecticides.

3. Prospect

Insecticide resistance in *M. usitatus* can primarily be attributed to three mechanisms: increased detoxification enzyme activity, reduced sensitivity at target sites [11], and decreased epidermal penetration rates [19]. Future research should focus on a comprehensive investigation of these resistance mechanisms, integrating studies at both the molecular and physiological levels to develop more effective resistance management strategies. It is also crucial to consider the impact of environmental factors on the development of resistance. Future research can address the following aspects: investigating the genetic and molecular bases of resistance, including the identification of specific genes involved in detoxification and target site modifications; examining the physiological and biochemical pathways that contribute to resistance and their interactions with environmental factors; studying the role of environmental conditions, such as climate, soil composition, and agricultural practices, in influencing resistance development and spread.

In-depth research on the resistance mechanisms of *M. usitatus* is crucial. This includes analyzing the interaction between molecular and physiological levels. Emerging gene editing technologies can be utilized to accurately verify potential drug resistance-related genes. Developing new insecticides should be based on a comprehensive understanding of resistance mechanisms to create more innovative and efficient insecticides, improve selectivity, and slow down resistance development. The application of biopesticides and genetic engineering technology also represents a significant future research direction. A comprehensive pest control strategy should integrate biological control, cultural control, and chemical control. Tailored prevention and control programs should be developed according to the specific characteristics of different regions. Environmental impact studies are essential to understand how factors such as climate change, soil quality, and pesticide residues contribute to drug resistance. International cooperation and information sharing are also vital. Strengthening global partnerships and sharing experiences and technological advancements in resistance management can help establish a global pest resistance monitoring and prevention network. This will enable real-time information sharing and enhance pest control efforts worldwide.

Abbreviations

CPR	NADPH-cytochrome P450 Reductase
GST	Glutathione S-Transferase
LC50	Lethal Concentration 50%
LD50	Median Lethal Dose
TIBS	Thrips Insecticide Bioassay System

Funding

This research was supported by grants from Guangxi Natural Science Foundation (No.2023GXNSFAA026464), Guangxi Science and Technology Major Project (No.Guike-AA17204041).

Conflicts of Interest

The authors declare no conflicts of interest.

References

[1] Qiu H Y, Fu B L, Tan K S et al. Monitoring the resistance of field populations of Megalurothrips usitatus to various insecticides in Hainan [J]. China Plant Protection Guide, 2022, 42(11): 67-71. https://doi.org/10.3969/j.issn.1672-6820.2022.11.016

[2] Wang P, Yang S L, Wang Y, et al. Identification and control of Megalurothrips usitatus [J]. China Vegetables, 2023, (12): 109-113. https://doi.org/10.19928/j.cnki.1000-6346.2023.3061

[3] Wu S Y, Xie W, Liu W C et al. Research progress and comprehensive prevention and control measures of cowpea thrips in China [J / OL]. Plant protection, 2023(12): 1-11. https://doi.org/10.16688/j.zwbh.2023043

[4] Huang W K, Kong X Y, Ke Y C, et al. Research progress of Megalurothrips usitatus [J]. China Vegetables, 2018(02): 21-27. https://doi.org/10.19928/j.cnki.1000-6346.2018.02.005

[5] Huang X Y, Cheng Y. SWOT analysis and countermeasures for the development of cowpea industry in Hepu [J]. Changjiang vegetables, 2022(9): 1-3.

[6] Hunter W B, Ullman D E. Precibarial and cibarial chemosensilla in the western flower thrips, Frankliniella occidentalis (Pergande) (Thysanoptera: Thripidae) [J]. International Journal of Insect Morphology & Embryology, 1994, 23(2): 69-83. https://doi.org/10.1016/0020-7322(94)90001-9

[7] He Y P, Shen J L. Genetic origin and molecular mechanism of pest resistance evolution [J]. Chinese Journal of Applied Entomology, 2008, 45(2): 175-181. https://doi.org/10.3969/j.issn.0452-8255.2008.02.002

[8] Wang Q L, Xia J H. Drug resistance of agricultural pests and its control [J]. Plant protection, 2004, 30(6): 15-18. https://doi.org/10.3969/j.issn.0529-1542.2004.06.003

[9] Hawkins N J, Bass C, Dixon A, et al. The evolutionary origins of pesticide resistance [J]. Biological Reviews, 2019, 94(1): 135-155. https://doi.org/10.1111/brv.12440

[10] Gould F, Brown Z S, Kuzma J. Wicked evolution: Can we address the sociobiological dilemma of pesticide resistance? [J]. Science, 2018, 360(6390): 728-732. https://doi.org/10.1126/science. aar3780

[11] Soderlund D M, Knipple D C. The molecular biology of knockdown resistance to pyrethroid insecticides [J]. Insect biochemistry and molecular biology, 2003, 33(6): 563-577. https://doi.org/10.1016/S0965-1748(03)00023-7

[12] Hemingway J. The molecular basis of two contrasting metabolic mechanisms of insecticide resistance [J]. Insect biochemistry and molecular biology, 2000, 30(11): 1009-1015. https://doi.org/10.1016/S0965-1748(00)00079-5

[13] Xu L, Sun Y, Liu B S, et al. Research progress on the molecular mechanism of resistance of C. suppressalis to diamide insecticides [J]. Chinese Journal of Pesticide Science, 2023, 25(2): 257-266. https://doi.org/10.16801/j.issn.1008-7303.2022.0088

[14] Sayyed A H, Wright D J. Genetics and evidence for an esterase-associated mechanism of resistance to indoxacarb in a field population of diamondback moth (Lepidoptera: Plutellidae) [J]. Pest Management Science: formerly Pesticide Science, 2006, 62(11): 1045-1051. https://doi.org/10.1002/ps.1270

[15] Khan S, Uddin M N, Rizwan M, et al. Mechanism of Insecticide Resistance in Insects/Pests [J]. Polish Journal of Environmental Studies, 2020, 29(3). https://doi.org/10.15244/pjoes/108513

[16] Cao G, Lu Q, Zhang L, et al. Toxicity of chlorantraniliprole to Cry1Ac-susceptible and resistant strains of Helicoverpa armigera [J]. Pesticide Biochemistry and Physiology, 2010, 98(1): 99-103. https://doi.org/10.1016/j.pestbp.2010.05.006

[17] Claudianos C, Russell R J, Oakeshott J G. The same amino acid substitution in orthologous esterases confers organophosphate resistance on the house fly and a blowfly [J]. Insect biochemistry and molecular biology, 1999, 29(8): 675-686. https://doi.org/10.1016/S0965-1748(99)00035-1

[18] Lee SE, Purification and characterisation of a carboxylesterase from a chlorpyrifos methyl resistant strain of Oryzaephilus surinamensis (Coleoptera: Silvanidae) [J]. Australian Journal of Entomology, 2011, 50: 187-194. https://doi.org/10.1111/j.1440-6055.2010.00799.x

[19] Liu Z W, Han Z J, Zhang L C. Cross-resistance and biochemical mechanisms of resistance to methamidophos in N. lugens. [J]. Acta Entomologica Sinica, 2002, (4): 447-452. https://doi.org/10.16380/j.kcxb.2002.04.006

[20] Zhang H Y, Chen X, Zhang H Q, et al. The resistance status of stored grain pests to phosphine and its comprehensive management strategy [J]. Science and Technology of Cereals, Oils and Foods, 2024, 32(1): 161-167. https://doi.org/10.16210/j.cnki.1007-7561.2024.01.021

[21] Wang L, Zhang Y, Han Z, et al. Cross-resistance and possible mechanisms of chlorpyrifos resistance in Laodelphax striatellus (Fallén) [J]. Pest Management Science, 2010, 66(10): 1096-1100. https://doi.org/10.1002/ps.1984

[22] Gao B, Wu J, Huang S, et al. Insecticide resistance in field populations of Laodelphax striatellus Fallén (Homoptera: Delphacidae) in China and its possible mechanisms [J]. International Journal of Pest Management, 2008, 54(1): 13-19. https://doi.org/10.1080/09670870701553303

[23] Yu X, Killiny N. RNA interference of two glutathione S-transferase genes, Diaphorina citri DcGSTe2 and DcGSTd1, increases the susceptibility of Asian citrus psyllid (Hemiptera: Liviidae) to the pesticides fenpropathrin and thiamethoxam [J]. Pest Management Science, 2018, 74(3): 638-647. https://doi.org/10.1002/ps.4747

[24] Zhai Q H. Some Advances in Insect Molecular Biology: Molecular Basis of Insecticide Resistance. [J]. Acta Entomologica Sinica, 1995, (4): 493-501. https://doi.org/10.16380/j.kcxb.1995.04.018

[25] He C S, Xie L F, Xu L, et al. In vitro metabolism and antioxidant activity of S. litura SlGSTO2 against pyrethroid and organophosphorus insecticides [J]. Chinese Journal of Pesticide Science, 2021, 23(6): 1132-1139. https://doi.org/10.16801/j.issn.1008-7303.2021.0148

[26] Zhang Y X, Liu Z W. Pesticide selectivity and pest resistance [J]. Bulletin of National Natural Science Foundation of China, 2020, 34(4): 511-518. https://doi.org/10.16262/j.cnki.1000-8217.2020.04.018

[27] Gong Y H, Wu Q J, Zhang Y J, Xu B Y. Effects of sublethal concentration of spinosad on the activities of detoxification enzymes in F. occidentalis. [J]. Chinese Journal of Pesticide Science, 2009, 11(4): 427-433. https://doi.org/10.3969/j.issn.1008-7303.2009.04.05

[28] Tang Z H, Tao L M. Molecular mechanism of action of novel diamide insecticides on ryanodine receptors. [J]. Acta Entomologica Sinica, 2008, 51(6): 646-651. https://doi.org/10.16380/j.kcxb.2008.06.008

[29] Wu S Y, Duan W B, Li F, et al. Research progress of sodium channels in insects [J]. Acta Entomologica Sinica, 2021, 64(7): 862-874. https://doi.org/10.16380/j.kcxb.2008.06.008

[30] Yuan L L, Pan X L, Lu R C, et al. Monitoring of pyrethroid resistance and mutation detection of sodium channel in cowpea thrips hainanensis [J]. Plant protection, 2023, 49(03): 60-67. https://doi.org/10.16688/j.zwbh.2022062

[31] Pandey A V, Flück C E. NADPH P450 oxidoreductase: structure, function, and pathology of diseases [J]. Pharmacology & therapeutics, 2013, 138(2): 229-254. https://doi.org/10.1016/j.pharmthera.2013.01.010

[32] Wu Y B, Xia P L, Zhang T W, et al. Molecular characterization and expression pattern analysis of cytochrome P450 reductase gene in tobacco beetle [J]. Journal of Environmental Entomology, 2023, 45(1): 124-132. https://doi.org/10.3969/j.issn.1674-0858.2023.01.12

[33] Yin F, Li Z Y, SAMINA SHABBIR, et al. Expression and functional analysis of P450 genes in different chlorantraniliprole-resistant strains of P. xylostella [J]. Scientia Agricultura Sinica, 2022, 55(13): 2562-2571. https://doi.org/10.3864/j.issn.0578-1752.2022.13.007

[34] Qiao X F, Wang K, Peng X et al. Research progress on the role of CPR and P450 genes in insect resistance [J]. Journal of Environmental Entomology, 2023, 45(04): 862-870. https://doi.org/10.3969/j.issn.1674-0858.2023.04.3

[35] Li X, Baudry J, Berenbaum M R, et al. Structural and functional divergence of insect CYP6B proteins: from specialist to generalist cytochrome P450 [J]. Proceedings of the National Academy of Sciences, 2004, 101(9): 2939-2944. https://doi.org/10.1073/pnas.0308691101

[36] TAO X Y, XUE X Y, HUANG Y P, et al. Gossypol-enhanced P450 gene pool contributes to cotton bollworm tolerance to a pyrethroid insecticide [J]. Molecular Ecology, 2012, 21(17): 4371-4385. https://doi.org/10.1111/j.1365-294X.2012.05548.x

[37] Li X L, Qi Y X, Lu Y Y. Research progress on detoxification metabolic genes of major fruit fly insects [J]. Journal of Plant Protection, 2022, 49(1): 351-365. https://doi.org/10.13802/j.cnki.zwbhxb.2022.2022832

[38] Li X L, Lu Y Y. Effects of biological and environmental factors on the emergence and development of pest resistance [J/OL]. Plant protection: 1-12. https://doi.org/10.16688/j.zwbh.2023366

[39] Bo H, Miaomiao R, Jianfeng F, et al. Xenobiotic transcription factors CncC and maf regulate expression of CYP321A16 and CYP332A1 that mediate chlorpyrifos resistance in Spodoptera exigua [J]. Journal of Hazardous Materials, 2020, 398: 122971. https://doi.org/10.1016/j.jhazmat.2020.122971

[40] Lu K, Cheng Y, Li W, et al. Activation of CncC pathway by ROS burst regulates cytochrome P450 CYP6AB12 responsible for λ-cyhalothrin tolerance in Spodoptera litura [J]. Journal of hazardous materials, 2020, 387: 121698. https://doi.org/10.1016/j.jhazmat.2019.121698

[41] Yan H J, Li W Z, Liang H, Ning Z X, Lu W. Indoor toxicity determination and field efficacy of three neonicotinoid insecticides on Aphis gossypii. [J]. Xinjiang Agricultural Sciences, 2021, 58(8): 1454-1459. https://doi.org/10.6048/j.issn.1001-4330.2021.08.011

[42] Srigiriraju L, Semtner P J, Bloomquist J R. Influence of post-exposure temperature on the toxicity of insecticides to the tobacco-adapted form of the green peach aphid (Hemiptera: Aphididae) [J]. Journal of Entomological Science, 2010, 45(2): 178-187. https://doi.org/10.18474/0749-8004-45.2.178

[43] Satpute N S, Deshmukh S D, Rao N G V, et al. Temperature-dependent variation in toxicity of insecticides against Earias v itella (Lepidoptera: Noctuidae) [J]. Journal of Economic Entomology, 2014, 100(2): 357-360. https://doi.org/10.1093/ jee/100.2.357

[44] Aizawa M, Nakai K, Watanabe T, et al. A simple method of monitoring for cypermethrin resistance in Thrips tabaci (Thysanoptera: Thripidae) using agar-coated glass pipettes [J]. Applied entomology and zoology, 2018, 53(1): 165-170. https://doi.org/10.1007/s13355-017-0541-9

[45] Alyokhin A, Chen Y H. Adaptation to toxic hosts as a factor in the evolution of insecticide resistance [J]. Current opinion in insect science, 2017, 21: 33-38. https://doi.org/10.1016/j.cois.2017.04.006

[46] LI Xianchun, BAUDRY J, BERENBAUM M R, et al. Structural and functional divergence of insect CYP6B proteins: From specialist to generalist cytochrome P450 [J]. Proceedings of the National Academy of Sciences of the United States of America USA, 2004, 101(9): 2939-2944. https://doi.org/10.1073/pnas.0308691101

[47] Tarazona J V, Court-Marques D, Tiramani M, et al. Glyphosate toxicity and carcinogenicity: a review of the scientific basis of the European Union assessment and its differences with IARC [J]. Archives of toxicology, 2017, 91: 2723-2743. https://doi.org/10.1007/s00204-017-1962-5

[48] Wang Z H, Hou W J, Hao C Y, et al. Resistance monitoring of field populations of F. occidentalis in Beijing [J]. Chinese Journal of Applied Entomology, 2011, 48(3): 542-547. https://doi.org/CNKI:SUN:KCZS.0.2011-03-012

[49] Yand Chunhong, QIAO Fengjiao, LU Zhaozhi, et al. Interspecific competitions between Frankliniella intonsa and Frankliniella occidentalis on fresh lentil bean pods and pepper plants [J/OL]. Insects, 2022, 20; 14(1): 1. https://doi.org/10.3390/insects14010001

[50] Zhang S. National agricultural pest resistance monitoring results and scientific medication recommendations in 2020 [J]. China Plant Protection, 2021, 41(02): 71-78. https://doi.org/10.3969/j.issn.1672-6820.2021.02.015