Persian J. Acarol., 14(4): 140403.

Review Article https://biotaxa.org/pja https://doi.org/10.22073/pja.v14i4.87081

Breaking acaricide resistance: Sustainable strategies for phytophagyous mite control with natural and advanced solutions

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Received:
01 April, 2025
Accepted:
29 May, 2025
Published:
15 October, 2025
Subject Editor:
E. Torabi

ABSTRACT

The phytophagous mite viz., *Tetranychus urticae* Koch has increasingly developed resistance against 558 acaricides worldwide and threatens crop yield in key agricultural regions, affecting economically important crops such as tomato, strawberry, and citrus which leads to more reliance on chemical control. Hence, global acaricide usage records high levels in mite management. This resistance arises from various mechanisms, including genetic mutations, reduced acaricide uptake, and enhanced detoxification. Such resistance reduces the effectiveness of chemical control and necessitates alternative strategies. This review summarizes current resistant management strategies for phytophagous mites, focusing on both conventional and innovative approaches. Integrated Pest Management (IPM) strategies emphasize the importance of integrating chemical, biological, and cultural control methods to slow down the development of resistance. Secondary metabolites produced by microorganisms, plants, and fungi offer promising natural solutions for controlling mite populations, with a broad spectrum of action. These compounds help to delay resistance by reducing reliance on chemical treatments while maintaining effective mite control. Also, natural biological control agents, such as insect predators, predatory mites, bacteria, fungi, and viruses have shown good potential for pest control. Additionally, plant-derived compounds provide an eco-friendly alternative, with multi-target effects on mite physiology. Advanced strategies, such as oligonucleotide acaricides, CRISPR/Cas9 technology, and RNA interference, have demonstrated promising results in laboratory studies for combating acaricide resistance, although their practical success and widespread application in field conditions remain under investigation. These strategies offer concrete opportunities to significantly reduce chemical pesticide reliance, effectively mitigate acaricide resistance, and enhance the sustainability and resilience of global crop production systems, thereby contributing to safer and more environmentally responsible agricultural practices.

KEYWORDS

Acaricide resistance management, CRISPR/Cas9, Oligonucleotide acaricide, phytophagous mites, RNA interference, secondary metabolites.

CITE: Sathiya Priya, S., Sumathi, E., Renukadevi, P., Murugan, M., Kumar, K.K. & Thamarai Selvi, S.P. (2025) Breaking acaricide resistance: Sustainable strategies for phytophagous mite control with natural and advanced solutions. *Persian Journal of Acarology*, 14(4): 140403.
https://doi.org/10.22073/pja.v14i4.87081

INTRODUCTION

Mites belong to the class Arachnida within the Chelicerata subphylum and Arthropoda phylum which represents the second-largest group of arthropods, following insects. Chelicerates first originated from the ancestral root of the Arthropoda phylum and subsequently diversified into various branches, including horseshoe crabs, scorpions, ticks, spiders and mites (Friedrich and Tautz 1995; Boore *et al.*

1995). Approximately 40,000 mite species have been documented and about 0.5 to 1 million more species remain undiscovered (Niu *et al.* 2018). In terms of their range of habitation, mites are as widespread as insects (Jeppson *et al.* 1975) and notably, mite pests represent a major limiting factor in agricultural and horticultural produce, as well as for stored products.

Phytophagous mites primarily belong to the families Eriophyidae, Tenuipalpidae, Tarsonemidae and Tetranychidae (Devi *et al.* 2019). Eriophyidae includes gall mites (which form galls) and vagrant species (living freely on plant surfaces) (Lindquist and Amrine 1996). Some eriophyid mites cause economic damage to orchards, vineyards (*Aculus cornutus, Aceria mangiferae*) and greenhouses (*Aculops lycopersici*) (Messelink 2014; Devi *et al.* 2019). Tenuipalpidae, predominantly found in tropical and subtropical areas, encompasses 1100 identified species across 38 genera (Beard *et al.* 2012). Notably, *Tenuipalpus* and *Brevipalpus* stand out as the primary genera affecting crops. Within *Brevipalpus*, species like *B. phoenicis*, *B. californicus*, and *B. obovatus* pose a threat to 928 plant species in 139 families (Childers *et al.* 2003). Tarsonemidae consists of 530 species within 40 genera, including plant parasites like *Polyphagotarsonemus latus* (chilli), *Phytonemus pallidus* (cyclamen), *Steneotarsonemus ananas* (pineapple), *S. bancrofti* (sugarcane) and *S. spinki* (rice) (Devi *et al.* 2019). Tetranychidae, the predominant family of mites that feed on plants, poses a threat to ornamental plants, greenhouse crops, and trees. Out of 1,250 identified mite species, around 100 are recognized as economically important pests (Migeon *et al.* 2014). *Tetranychus urticae* Koch, *T. kanzawai* Kishida, *T. pacificus* McGregor, *Panonychus ulmi* (Koch), *P. citri* (McGregor), *Oligonychus coffeae* (Nietner), *O. punicae* (Hirst), and *Eutetranychus orientalis* (Klein) are considered as major pests in Tetranychidae.

Despite advancements in integrated pest management (IPM), many farmers remain dependent on acaricides for mite control, but continuous use of acaricides has induced resistance in polyhouse and open field conditions. The first occurrence of resistance in mites to synthetic insecticides was reported in the 20th century when organophosphates could not eliminate mites worldwide (Cranham 1985). Due to their widespread and extensive application, various species have developed resistance to a broad spectrum of acaricides globally (Katsavou *et al.* 2020; Agwunobi *et al.* 2021). Acaricide resistance significantly prolonged the developmental period compared to the susceptible laboratory population (Das *et al.* 2022). In most cases, the primary detoxification enzymes like glutathione-S-transferases (Enayati *et al.* 2005), P450 monooxygenases (Gilbert *et al.* 2005), and esterases (Oakeshott *et al.* 2010) undergo either quantitative or qualitative alterations, leading to the insecticide being either sequestered or metabolized before reaching its intended target site. Sequencing of the *T. urticae* genome, the first complete chelicerate genome, has expanded the arthropod genomes beyond Pancrustacea and provided insights into resistance-related genes and detoxification mechanisms. The gene families responsible for detoxification, digestion and transport of xenobiotics are discovered in the complete genome of *T. urticae* which is vital in resistance (Grbić *et al.* 2011). Aside from this, understanding the mechanisms underlying acaricide resistance is crucial for managing mite infestations or breaking the resistance.

The escalating problem of acaricide resistance among phytophagous mites highlights the urgent need for sustainable and innovative management strategies. It is essential to develop approaches that not only enhance control efficiency but also prioritize environmental safety. This review synthesizes the current status of acaricide resistance in phytophagous mite species and critically evaluates management strategies designed to mitigate this growing challenge. The integration of secondary metabolites derived from macrobial and microbial agents demonstrates a promising alternative, offering multi-targeted modes of action that reduce the likelihood of resistance development. Furthermore, advances in genetic technologies such as CRISPR/Cas9 and RNA interference (RNAi) demonstrate great potential for precise and targeted mite control. However, their application in both open-field and polyhouse (greenhouse) conditions remains limited and requires further validation. Future research should aim to assess the effectiveness of these innovative tools under real-world conditions across diverse agricultural environments, thereby supporting the development of holistic, eco-friendly frameworks for sustainable mite management.

Status of acaricide resistance problem in phytophagous mites

The Arthropod Pesticide Resistance Database (ARPD) has reported 551 resistant cases of *T. urticae* to 96 compounds globally, including some novel acaricide molecules like fenazaquin, propargite, spiromesifen, fenpropathrin, diafenthiuron, organophosphates, pyrethroids and chlorfenapyr in around 263 sites (Mota-Sanchez and Wise 2021). Due to its diminutive size, rapid reproduction rate, short life cycle, high egg-laying capacity, and unique reproductive strategy of arrhenotokous parthenogenesis, which is a form of parthenogenesis in which unfertilized eggs develop into haploid males while fertilized eggs develop into diploid females, this species can easily develop resistance to acaricides (Gulati 2014). Some authors have extensively documented various molecular-level resistance mechanisms in *T. urticae* in their recent studies (Van Leeuwen *et al.* 2008; Khajehali *et al.* 2010; Kwon *et al.* 2010a; De Rouck *et al.* 2023). Table 1 summarizes documented resistance cases across phytophagous mite species (Mota-Sanchez and Wise 2021).

Table 1. Reports of acaricide resistance cases in phytophagous mites.

Species	Taxonomy (Family)	Common name	No. of resistance cases	No. of active ingredients
Aculops lycopersici	Eriophyidae	Tomato rust mite	1	1
Aculops pelekaasi	Eriophyidae	Pink citrus rust mite	1	1
Aculus cornutus	Eriophyidae	Peach silver mite	3	3
Aculus fockeui	Eriophyidae	Plum rust mite	1	1
Aculus schlechtendali	Eriophyidae	Apple rust mite	1	1
Phyllocoptruta oleivora	Eriophyidae	Citrus rust mite	3	3
Brevipalpus chilensis	Tenupalpidae	False grape/red mite	3	3
Brevipalpus phoencis	Tenupalpidae	Passionvine mite	1	1
Panonychus ulmi	Tetranychidae	European red mite	203	48
Panonychus citri	Tetranychidae	Citrus red mite	106	29
Tetranychus atlanticus	Tetranychidae	Strawberry spider mite	7	5
***Tetranychus urticae* red form**[a]	Tetranychidae	Carmine spider mite	37	19
Tetranychus kanzawai	Tetranychidae	Tea red spider mite	12	12
Acarus siro	Tetranychidae	Grain mite	5	3
Tetranychus urticae	Tetranychidae	Two-spotted spider mite	558	96
Rhizoglyphus echinopus	Tetranychidae	Bulb mite	6	5
Rhizoglyphus robini	Tetranychidae	Bulb mite	23	22
Tetranychus mcdanieli	Tetranychidae	Mcdaniel spider mite	19	13
Tetranychus turkestani	Tetranychidae	Strawberry spider mite	5	5
Tetranychus viennensis	Tetranychidae	Hawthorn spider mite	7	7

[a] Currently acknowledged as *T. urticae* red form.

Bibliographic analysis of global research landscape on acaricide resistance in phytophagous mites

As most resistance cases are reported in the Tetranychidae family, this review conducted a comprehensive analysis by leveraging bibliometric data to map the global research landscape on acaricide resistance. The data were systematically extracted from the SCOPUS database (https://www.scopus.com) covering the period from 2000 to 2024, to create a detailed network of published studies worldwide utilizing the keywords "Tetranychidae" AND "Acaricide resistance" AND Management. Using various bibliometric indices such as keywords, countries, and leading journals, the analysis was performed and visualized with VOSviewer software (v1.6.20, Leiden University, The Netherlands). A co-occurrence analysis was conducted with keywords as the unit of analysis. A total of 1,808 documents were retrieved from Scopus, and a minimum keyword co-occurrence threshold of 10 was applied, resulting in 875 keywords meeting the criteria from an initial pool of 28,376. Figure 1a presents the cluster analysis derived

from the co-occurrence network of keywords extracted from the SCOPUS database. The analysis reveals five distinct clusters. Cluster 1 (red, 227 keywords) focuses on the acaricidal properties of plant extracts and their impact on the biology of phytophagous mites, while Cluster 2 (green, 152 keywords) highlights key acaricides with reported resistance and the main resistance mechanisms, including detoxification enzymes and target site mutations. Cluster 3 (blue, 72 keywords) primarily addresses the molecular mechanisms and management strategies for acaricide resistance in phytophagous mites. Cluster 4 (yellow, 45 keywords) focuses on the factors influencing resistance, while Cluster 5 (violet, 6 keywords) explores acaricides that show resistance in organisms other than mites. The network analysis illustrates the global spread of articles on acaricide resistance in phytophagous mites, highlighting the connections between countries and offering a broad view of current research in this area (Fig. 1b). This analysis further emphasizes the significant contributions from countries such as China, the United States, Brazil, South Korea, and India in advancing research on acaricide resistance. These nations are represented by large nodes and frequent connections, highlighting their significant involvement in this field.

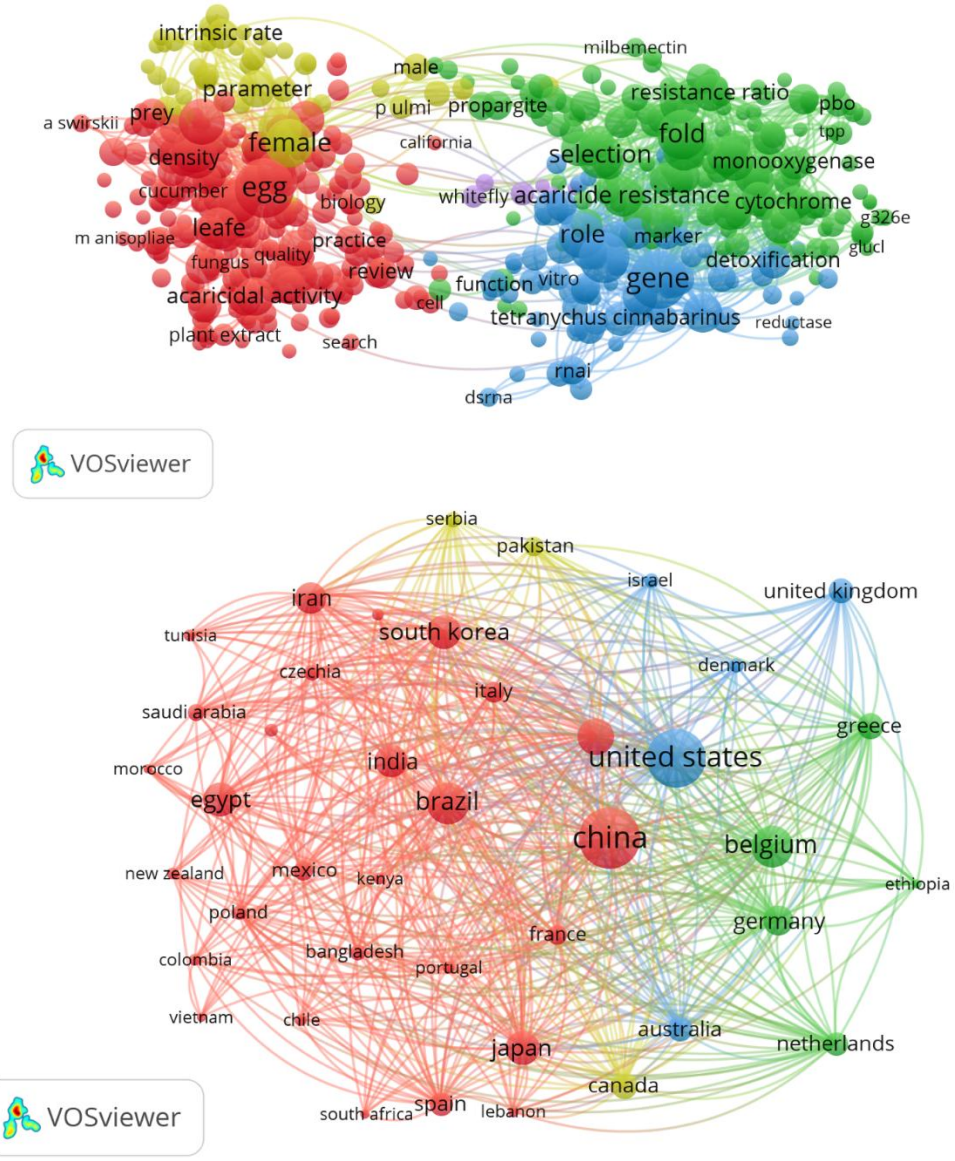

Figure 1. Acaricide resistance research network visualization. Legend: Colors represent major clusters of research themes; nodes represent keywords (the size of the node indicates keyword frequency); links represent relationships between keywords (keywords co-occurring in published articles); colors represent the temporal order of keyword appearance; link thickness indicates the strength of the association between keywords. Data analysis was performed by "VOSviewer version 1.6.20," 2023.

Mechanisms of resistance

Mites can withstand fatal concentrations of acaricides through a variety of resistance mechanisms,

which are broadly categorized into decreased exposure or decreased responsiveness to the pesticides, depending on their biochemical and physiological properties (Taylor and Feyereisen 1996; Roush and Tabashnik 2012). These mechanisms collectively limit the efficacy of the acaricides by either reducing the mite's exposure to the pesticide or by diminishing its ability to respond to the pesticide once it reaches the organism. One of the key mechanisms is behavioral resistance, where mites alter their behavior in response to pesticide exposure. For instance, some mites may stop feeding or move away from treated areas in response to acaricides like mitochondrial electron transport inhibitors (MET-I) *viz*., fenpyroximate, pyridaben, and fenazaquin or mite growth inhibitors (MGIs) *viz*., etoxazole, hexythiazox, and clofentezine, which can act as irritants or repellents. Such behavioral adaptations have been documented through altered dispersal and escape responses, as observed in *Aceria guerreronis* Keifer following chemical exposure (Galvão *et al*. 2012; Lima *et al*. 2013). The behavioral modifications, such as reduced feeding or altered oviposition patterns, can significantly reduce the pesticide's impact on mite populations, especially in resistant strains of *T. urticae* (Adesanya *et al*. 2019).

In addition to behavioral adaptations, penetration resistance plays a crucial role in acaricide resistance. Alterations in the mite's physical characteristics, such as changes in the cuticle, can prevent the pesticide from penetrating the body. Cuticular thickening has traditionally been linked to resistance, but recent studies have also suggested that changes in the cuticular composition may significantly reduce the penetration of toxic substances (Dang *et al*. 2017; Balabanidou *et al*. 2018). A recent transcriptomic analysis revealed that cuticular proteins in *T. urticae* were differentially expressed in acaricide-resistant strains, suggesting that modifications in the cuticle may reduce the penetration of toxic substances (Koirala *et al*. 2024). These modifications in the outer layer of the mite act as a barrier, preventing acaricides from penetrating the mite's internal tissues, thus reducing the effectiveness of the acaricides.

Metabolic resistance is another critical mechanism by which mites can neutralize acaricides. This involves the upregulation of various detoxification enzymes, which break down toxic substances before they can reach their target sites (Van Leeuwen *et al*. 2010). Key enzymes involved in metabolic resistance include cytochrome P450 monooxygenases, glutathione S-transferases (GSTs), and carboxyl esterases (CEs). P450 enzymes, particularly from the CYP392 family, have been shown to play a significant role in detoxifying acaricides like abamectin, fenbutatin oxide, pyflubumide, and spirodiclofen in *T. urticae* (Riga *et al*. 2014; Khalighi *et al*. 2016). Esterases also contribute substantially by hydrolyzing ester bonds in certain acaricides, leading to detoxification, and have been mostly associated with resistance to organophosphates and pyrethroids (Van Leeuwen et al. 2010). GSTs, especially the delta and epsilon classes, and CEs, such as TuCCE27, TuCCE55, and CCE04SR-VP, contribute to resistance mainly by catalyzing the conjugation of glutathione to pesticide molecules, thereby modifying and detoxifying them, while carboxyl esterases hydrolyze ester bonds to reduce toxicity, collectively decreasing the mite's exposure to harmful compounds (Pavlidi *et al*. 2017; Wei *et al*. 2016; Vontas *et al*. 2001). These detoxification enzyme genes are often expressed at basal levels but can be significantly upregulated upon acaricide exposure, enhancing the mite's ability to metabolize and survive chemical treatments; this inducible overexpression contributes to enhanced resistance against a broad spectrum of acaricides (Dermauw *et al*. 2013).

Target-site resistance involves mutations in the genes encoding the proteins that acaricides are designed to target. These mutations alter the structure of target proteins, disrupting the ability of acaricides to bind effectively and thereby rendering them less effective or even ineffective. For example, mutations in acetylcholinesterase (AChE) contribute to resistance against organophosphate pesticides, while voltage-gated sodium channel (VGSC) mutations are linked to resistance against pyrethroids in *T. urticae* (Tsagkarakou *et al*. 2009; Kwon *et al*. 2010b). Similarly, mutations in GluCl genes contribute to resistance to abamectin in *T. urticae*, and mutations in mitochondrial complexes, such as complex I (H110R, A112V) and complex II (I260T/V, H258Y/L), have been linked to resistance against METI-I and METI-II acaricides like tebufenpyrad and pyridaben (Khalighi *et al*. 2016; Bajda *et al*. 2017).

Furthermore, mutations in octopamine receptors, such as T8P and L22S in the α-adrenergic-like genes, have been implicated in resistance to amitraz in *Rhipicephalus microplus* (Acari: Ixodidae) (Chen *et al*. 2007; Baron *et al*. 2015), and mutations in acetyl-CoA carboxylase (ACCase), like the A1079T substitution,

are associated with resistance to spirodiclofen in *T. urticae* (Wybouw *et al.* 2019). ACCase is a crucial enzyme in fatty acid biosynthesis, plays an essential role in energy storage and membrane formation in mites. Because of its vital metabolic function, ACCase is targeted by certain acaricides, and mutations in this enzyme can confer resistance by reducing the binding affinity of the chemical (Gressel 2011; Zhu *et al.* 2016). These target site alterations directly impair the interaction between acaricides and their binding sites, contributing to resistance.

In addition to genetic mutations in the target sites, other resistance mechanisms, such as the overexpression of UDP-glycosyltransferases (UGTs), also play an essential role. UGTs, acquired by mites via lateral gene transfer from bacteria, are involved in the detoxification of pesticides like abamectin and spirodiclofen (Papapostolou *et al.* 2021; Xue *et al.* 2020). Their overexpression has been linked to resistance across multiple acaricide classes, with specific UGTs like UGT201D3 and UGT28 identified as key contributors in *T. urticae* and *P. citri* (Ahn *et al.* 2014; Papapostolou *et al.* 2021). Although cytochrome P450s and carboxylesterases are often more prominently associated with metabolic resistance, UGTs provide a complementary detoxification pathway by conjugating glycosyl groups to lipophilic toxic molecules, thereby increasing their solubility and facilitating excretion from the mite's system (Lairson *et al.* 2008; Nagare *et al.* 2021; Wang *et al.* 2020).

Overall, the development of acaricide resistance in mites is driven by a combination of behavioral, physiological, penetration and genetic adaptations. These mechanisms reduce pesticides efficacy by limiting the mite's exposure to the pesticide, increasing the breakdown of toxic substances, or altering the target sites, making it imperative to understand and manage these resistance strategies for effective pest control in agricultural settings (Feyereisen *et al.* 2015; Adesanya *et al.* 2021). These mechanisms were further elaborated in De Rouck *et al.* (2023), providing an in-depth exploration of the complex resistance dynamics in acaricide-resistant mite populations.

Acaricide resistance management strategies in phytophagous mites

General resistance management strategies

Resistance management in Acari depends on the strategic application of acaricides which includes regular monitoring, rotation, and combination of acaricides. Monitoring acaricide resistance has become a crucial component in delaying resistance evolution (Kramer and Nauen 2011). The timely identification of resistance, followed by the removal and substitution of the treatment, helps preserve the susceptible population (Abbas *et al.* 2014). Frequent use of acaricides poses a significant risk for the emergence of resistance. For instance, the probability of amitraz resistance was notably elevated in central Queensland, particularly when the number of applications exceeded five (Jonsson *et al.* 2000). Similarly, another study on *Rhipicephalus microplus* showed resistance after exposure to deltamethrin, with a resistance factor (RF) of 9.2 after five generations, escalating to a very high level (RF = 756) after 11 generations (Thullner *et al.* 2007).

Employing a rotation strategy with acaricides that possess varied modes of action mitigates the risk of developing resistance to any particular group of acaricides. Rotating deltamethrin with coumaphos proves effective in delaying the development of strong resistance to deltamethrin (Thullner *et al.* 2007). Although acaricide rotation is a widely recommended strategy for resistance management, relying on it alone may not ensure comprehensive control (Thind and Ford 2007), and its practical implementation is often hindered by increased operational costs, limited access to diverse active ingredients, and the absence of clear guidelines on optimal rotation intervals (Maggi *et al.* 2011).

Another approach to delay resistance development is combining acaricides (Kočišová and Plachý 2008). A combination of carbamates, synthetic pyrethroids, and chitin synthesis inhibitors was found to be effective against *T. urticae*, *P. citri*, and *A. guerreronis*, demonstrating the potential of integrated chemical strategies for managing different Acari pests (Abbas *et al.* 2014). The effectiveness of such mixtures depends on the nature of their interaction. For example, the combination of abamectin and chlorfenapyr has shown synergistic effects against *T. urticae*, resulting in enhanced toxicity compared to individual applications (Badawy *et al.* 2022). In contrast, certain combinations, such as spinosad and abamectin, have exhibited antagonistic effects, leading to reduced efficacy (Ismail *et al.* 2007). Certain acaricide

combinations have demonstrated additive effects in controlling *T. urticae*. For example, the mixture of fenpyroximate and pyridaben exhibited additive toxicity against *T. urticae*, improving efficacy without significantly increasing non-target effects (Kim and Yoo 2002; Ahn *et al.* 2004). However, for this strategy to be effective, the chemicals used must be compatible and exhibit equivalent persistence concerning the target species.

Secondary metabolites for mite management

Secondary metabolites produced by bacteria, fungi, and plants, including naturally derived microbial, biochemical, and macrobial agents, serve as effective agents for managing pests, weeds, and plant pathogens (Šunjka and Mechora 2022; Shang *et al.* 2024) (Fig. 2).

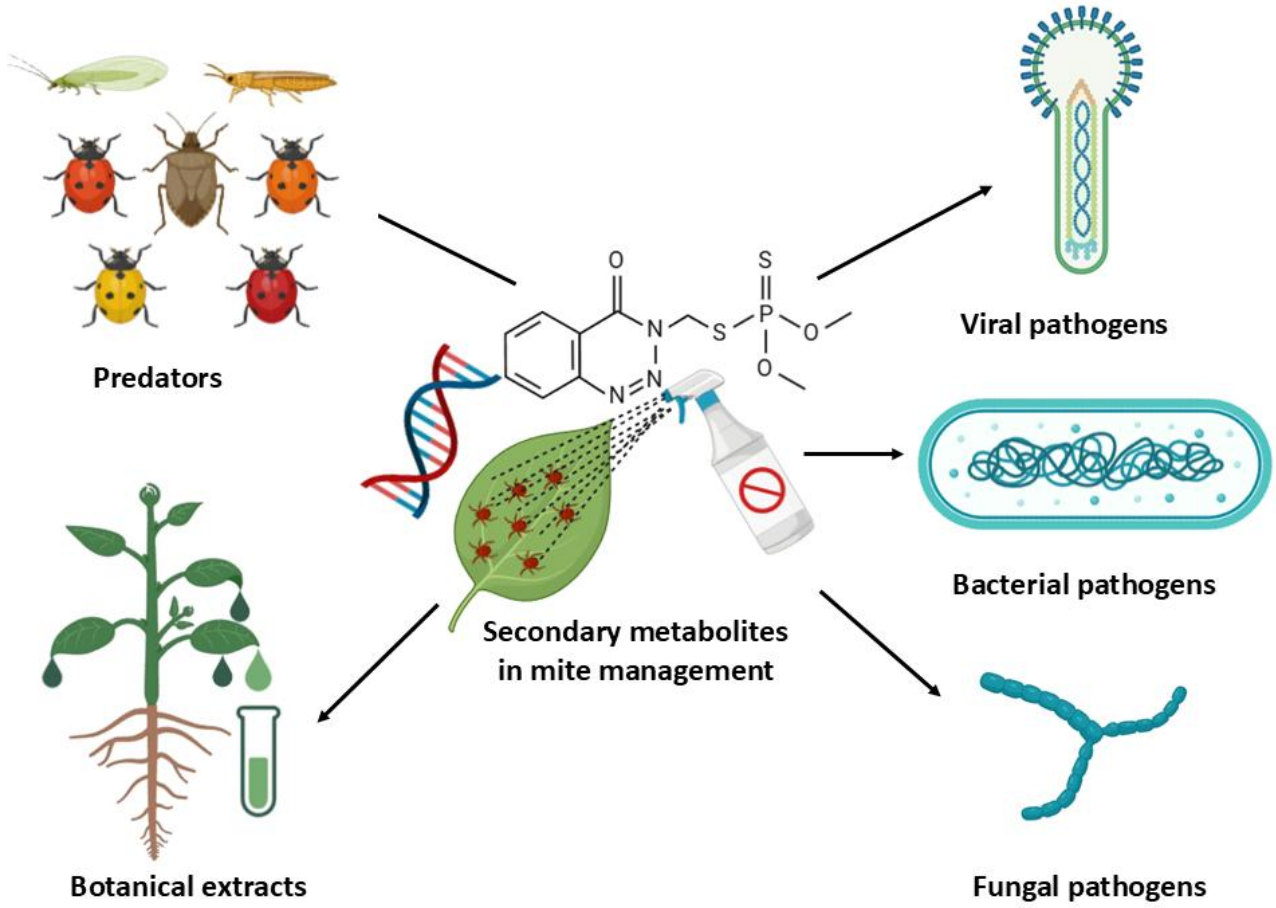

Figure 2. Overview of secondary metabolite-based strategies for mite management.

Microbial agents

Bacterial pathogens for mite control

Bacillus thuringiensis (Bt) insecticidal toxins are extensively used to safeguard crops such as cotton, maize, rice, and wheat from pests belonging to the Coleoptera and Lepidoptera orders. *Bt* toxin genes have also been incorporated into plants to enhance their resistance to insect pests (Aswathi *et al.* 2024). However, the application of these toxins can exert strong selective pressure on pest populations, potentially accelerating the development of resistance in the pests. Research has shown that *B. thuringiensis* var. *tenebrionis* wettable powders have limited efficacy against adult female two-spotted spider mite (*T. urticae*) at tested concentrations of 0.1X, 0.5X, and 1.0X, the recommended application rate (Chapman and Hoy 1991). On the other hand, in earlier studies, the β-exotoxin component of *B. thuringiensis* was found to cause significant mortality in mites such as *P. citri, T. pacificus*, and *T. urticae* (Krieg 1968; Hall *et al.* 1971; Hoy and Ouyang 1987). Additionally, two-spotted spider mite, *T. urticae* (also known as the carmine spider mite) was observed to show a reduced host preference for Bt maize compared to non-Bt maize, indicating a possible repellency or altered feeding behavior rather than direct toxic effects (Sarwar

et al. 2013). In contrast, crude *Bt kurstaki* formulations caused significant mortality in *Eutetranychus orientalis* under controlled laboratory conditions, leading to a notable reduction in population density (Veloorvalappil Narayanan *et al.* 2018). These studies underscore the diverse responses of mite species to Bt-based products. These variations in response may be attributed to differences in species-specific susceptibility, Bt strain or toxin type, formulation quality, application method, and environmental conditions during exposure.

In addition to *Bt*, several bacteria have proven effective against phytophagous mites. For example, *Pseudomonas aeruginosa* (Family: Pseudomonadaceae) was found to be the most effective, achieving 100% mortality of adult of *T. urticae* at 10^7 cfu/mL via spraying after 72h, while *Bacillus subtilis* and *Lysinibacillus sphaericus* (Family: Bacillaceae) showed lower mortality rates (73.33% and 62.08%, respectively) with spraying compared to dipping, and *P. aeruginosa* reduced the development of subsequent mite stages across all concentrations (Emam 2021). *Streptomyces* (Family: Streptomycetaceae) species, particularly *S. hygroscopicus* subsp. *aureolacrimosus* and *S. avermitilis*, produce potent acaricidal compounds like milbemycin and abamectin. However, it is important to note that laboratory efficacy may not always translate directly to field settings due to environmental factors such as UV degradation and microbial competition. Interestingly, *Bacillus velezensis* W1 has shown acaricidal potential not only under laboratory conditions but also in greenhouse and field applications. This effectiveness is attributed to its production of virulence factors, biofilm-associated genes, and chitin deacetylases, which collectively enhance its pathogenicity against *T. urticae* (Li *et al.* 2019). And other biopesticides, such as Grandevo® DF 2 (*Chromobacterium subtsugae*; Family: Chromobacteriaceae) and Venerate® EP (*Burkholderia* spp.; Family: Burkholderiaceae) caused significant larval mortality of *T. urticae*, though their toxicity to nymphs was comparatively lower (Golec *et al.* 2020). The pathogenicity of these bacteria is linked to their adhesion, facilitating the penetration of enzymes, such as proteases and chitinases, that contribute to rapid mite death. At the same time, *Pseudomonas* strains also produce volatile secondary metabolites that deter mite colonization on leaves (Raaijmakers *et al.* 2002). Among the bacterial agents explored, *Pseudomonas*, *Bacillus*, *Streptomyces*, *Chromobacterium*, and *Burkholderia* show the most promise for mite management due to their demonstrated efficacy and diverse modes of action. With ongoing advancements in microbial formulation technologies and a growing body of efficacy data under semi-field and greenhouse conditions, these bacterial species are at the forefront of next-generation, sustainable acaricidal solutions. Continued research and field validation are essential to optimize their integration into environmentally responsible pest management programs.

Viral pathogens for mite control

Viral pathogens, though less commonly studied than bacterial or fungal agents, represent an emerging frontier in the biological control of mite pests due to their host specificity and potential for self-propagation in the environment. While many viruses are known to be transmitted by mites, particularly eriophyoid mites to plants, causing substantial crop damage, some viruses have also been identified that infect and cause disease in the mites themselves, highlighting their potential as biological control agents (Helle and Sabalis 1985; Lindquist and Oldfield 1996; Poinar and Poinar 1998). Notably, only a limited number of mite species, such as *Panonychus citri* and *P. ulmi*, are susceptible to viruses that function as biological control agents (Gulati 2014). The first report of a mite virus came from Muma in 1955, who described flaccid citrus mites in Florida exuding black resinous material caused by non-occluded, DNA-containing bacilliform virions of the Baculoviridae family, developing within the nuclei of epithelial cells (Muma 1955). Further studies revealed rod-shaped virions in thin sections of citrus red mites (*Panonychus citri*) infected with a viral disease (Reed and Hall 1972). Field applications, involving the introduction of virus-infected immature mites into a peach orchard, resulted in a significant reduction in mite population density, with infected mites often dying with their legs extended, underscoring the potential of viruses as effective agents for mite control (Putman and Herne 1966). While these foundational studies support the potential of viruses in mite control, we acknowledge the limited scope of research in this area and have now included recent literature (e.g., Shi *et al.* 2016; Tokarz *et al.* 2018) to reflect ongoing efforts in viral discovery through metagenomic tools, which may help identify novel entomopathogenic viruses applicable to mite management in the future. However, the practical application of such viral pathogens

is constrained by their narrow host range and susceptibility to environmental factors such as ultraviolet (UV) radiation, which can degrade viral particles and limit their effectiveness under field conditions (Shaw *et al.* 1967; Anggraini *et al.* 2022).

Fungal pathogens for mite control

Fungal pathogens such as *Hirsutella thompsonii* (Family: Ophiocordycipitaceae) and *Neozygites floridana* (Family: Neozygitaceae) play key roles as natural enemies of mites, particularly infecting members of the families Tetranychidae and Eriophyidae (Chandler *et al.* 2000). Entomopathogenic fungi employed for the control of plant-feeding mites include *H. thompsonii* against *T. urticae* and *Phyllocoptruta oleivora* (Aghajanzadeh *et al.* 2006), *N. floridana* against *T. urticae* and *Panonychus ulmi* (Berdinesen 2012), *Neozygites adjarica* against *Oligonychus pratensis* (Banks) and *T. urticae* (Dick and Buschman 1995), *Metarhizium anisopliae* (Chandler *et al.* 2005), *Beauveria bassiana* (Irigaray *et al.* 2003; Gatarayiha *et al.* 2010; Geroh 2011), *Acremonium hansfodii* (Family: Bionectriaceae) against *T. urticae* (Shang *et al.* 2018) and *Cladosporium cladosporioides* (Family: Cladosporiaceae) against *T. urticae* (Saranya *et al.* 2013). Biopesticides derived from *Lecanicillium lecanii* (Family: Cordicipitaceae) and *S. avermitilis* have demonstrated 90–100% adult and 91–99% larval mortality of *T. urticae* under laboratory conditions (Zenkova *et al.* 2020), though their commercial application remains to be fully explored. Beyond their pathogenic effects, *Metarhizium* species also repel *T. urticae* through dry conidia and volatile organic compounds (VOCs). VOCs such as isoamyl alcohol and the more potent 3-octanone exhibit both repellent and acaricidal activity, underscoring their dual role as effective biocontrol agents and semiochemicals in integrated mite management (Hussien *et al.* 2025). While viruses offer high host specificity and potential for self-replication within mite populations (Muma 1955; Putman and Herne 1966), fungal pathogens such as *B. bassiana* and *M. anisopliae* provide broader-spectrum activity against various mite species but generally require high relative humidity for effective infection and sporulation (Chandler *et al.* 2000; Al-Zahrani *et al.* 2023).

Macrobial agents

Predators for mite control

Insect species from the orders Coleoptera, Neuroptera, Hemiptera, Thysanoptera, and Diptera serve as natural predators of mite pests (Gulati 2014). Several predators of phytophagous mites have been identified, including *Scymnus* spp., *Oligota* sp., *Coccinella* sp., *Menochilus* sp., *Chilocorus* sp., *Brumus suturalis*, *Micromus timidus*, *Clanis* spp, and *Adalia* sp. (Coccinellidae), *Chrysoperla carnea* (Chrysopidae), *Scolothrips* sp. and *Holothrips* sp. (Thripidae), and *Anthocoris* sp. (Anthocoridae), all of which have shown effectiveness against mites (Gulati 2014; Jakubowska *et al.* 2022). Among these predators, *Stethorus punctillum* (Coleoptera: Coccinellidae) is a specialist feeder, targeting mite pests such as *T. urticae* and *T. turkestani* (Ugarov & Nikolskii) on cotton (Kapur 1948), *T. urticae* on strawberries and okra (Gulati and Kalra 2006), and *T. macdanieli* (Mac Gregor) and *T. urticae* on red raspberries (Roy *et al.* 1999). The developmental stages of *S. punctillum* feeding on *T. urticae* were studied under laboratory conditions across seasons, revealing that the fourth instar larva exhibited the highest predation rate, consuming up to 135.8 eggs, 126.4 larvae, 96.6 nymphs, and 72.8 adults per day, while the first instar consumed significantly fewer prey (Biswas *et al.* 2007). With high feeding, reproductive capacity, and synchronization with pest populations, this predator can quickly reduce mite infestations. Highly mobile, the beetles search for mites on nearby plants or fly to neighboring plants within minutes of release (Rott and Ponsonby 2000).

In addition to insect predators, certain Acari species, such as *Amblyseius* spp., *Neoseiulus* spp., *Phytoseiulus* spp., *Transeius* spp., and *Typhlodromus* spp. (Phytoseiidae), *Hypoaspis* spp. (Laelapidae), serve as key predators of crop-infesting mites (Lesna *et al.* 2000; Han *et al.* 2003; Opit *et al.* 2004; Greco *et al.* 2005; Jakubowska *et al.* 2022; Jafarian *et al.* 2023; Krasavina and Trapeznikova 2024). Phytoseiid species are the leading group of commercially available mite biocontrol agents, with around 20 species offered worldwide due to their high prey specificity, ease of mass production, rapid reproduction, and compatibility with various cropping systems. Among these, *Amblyseius swirskii* Athias-Henriot, *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus cucumeris* (Oudemans), and *Neoseiulus californicus* (McGregor) are the most significant species (Knapp *et al.* 2018). The combined use of insect and Acari predators demonstrates high efficiency in controlling mite populations. For example, *P. persimilis* and *S. punctillum* have proven effective in

managing *T. urticae* infestations in croton (Adly 2022).

Botanical extracts for mite management

In recent decades, various botanicals including plant extracts and essential oils, which contain compounds such as alkaloids, phenols, quinones, terpenoids, flavonoids, polyacetylenes, and tannins have been isolated from plants, emerging as key sources of biopesticides for crop protection against mite pests (Šunjka and Mechora 2022). This diverse chemical composition not only offers the potential for effective mite control but also creates a multifaceted mode of action that can delay or even prevent the development of resistance (Singh and Saratchandra 2005; Dąbrowski and Seredyńska 2007; Rattan 2010). Extracts derived from aboveground and underground plant parts exhibit potent lethal effects on spider mites (Souto *et al.* 2021). They disrupt sodium channel transport, altering nerve conductivity, while also acting as deterrents or repellents and suppressing egg-laying behavior (Ebadollahi *et al.* 2014; Rincón *et al.* 2019; de Santana *et al.* 2021).

Phytochemicals can be extracted from plants using various techniques, including cold maceration, infusion, Soxhlet extraction, decoction, microwave-assisted methods, percolation, steam or water distillation, accelerated solvent extraction, and ultrasound-assisted extraction. Other advanced strategies include supercritical fluid extraction, pressurized liquid extraction, enzyme-aided extraction, pulsed electric field extraction, and reflux techniques (Azwanida, 2015; Zhang *et al.* 2018; Bitwell *et al.* 2023). These processes are instrumental in isolating active compounds from plant families such as Meliaceae, Rutaceae, Asteraceae, Annonaceae, Lamiaceae, and Canellaceae, which are widely regarded as valuable sources of natural pesticides, supporting sustainable and environmentally friendly pest management practices (Joshi *et al.* 2024). Table 2 provides a comprehensive overview of different plant families, their associated species, the targeted mite families and species, and their documented toxicological effects.

Table 2. Plant families and their toxic effects on target mite species.

Plant family	Plants	Target mite family	Target mite species	Toxicity effect	References
Lamiacaceae	*Salvia officinalis*, *Mentha pulegium*, *Mentha spicata*, *Mentha piperita*, *Viticipremna queenslandica*, *Vitex lignum vitae*, *Scutellaria mollis*, *Premna serratifolia*, *Premna acuminata*, *Pityrodia bartlingii*, *Gmelina leichardtii*, *Clerodendrum traceyi*, *Clerodendrum inerme*, *Ceratanthus longicornis*, *Rosmarinus officinalis*, *Origanum onites*, *Thymbra spicata spicata Lavandula stoechas stoechas, Ocimum sanctum, Pogostemon cablin*, *Salvia fruticose*, *Lavandula angustifolia*, *Thymus vulgaris*, *Plectranthus amboinicus*, *Origanum compactum*	Tetranychidae, Eriophyidae, Tenuipalpidae	*T. urticae*, *Eutetranychus orientalis*, *P. aegypticus*, *Aceria guerreronis*, *Cisaberoptus kenyae*, *Raoiella indica*	Adulticidal, ovicidal and repellent activity	Choi *et al.* 2004; Rasikari *et al.* 2005; Miresmailli *et al.* 2006; Sertkaya *et al.* 2010; Patnaik *et al.* 2010, 2011; Pavela *et al.* 2016; Reddy and Dolma 2018; Elhalawany *et al.* 2019; Allam *et al.* 2020; Ruiz-Jimenez *et al.* 2021; Abo-Shnaf *et al.* 2022; Assouguem *et al.* 2022; Ata *et al.* 2023
Asteraceae	*Xanthium strumarium*, *Artemisia vulgaris*, *Ambrosia maritimal*, *Eupatorium adenophorm*, *Wedelia chinensis*, *Eremanthus goyazensis*, *Tithonia diversifolia*	Tetranychidae, Tenuipalpidae	*T. urticae*, *Panonychus citri*, *Oligonychus coffeae*, *Oligonychus afrasiaticus*, *Brevipalpus phoenicis*	Adulticidal, ovicidal, ovicidal deterrant and repellent activity	El-Sarmah *et al.* 2007, 2009; Afify *et al.* 2011; Fetoh and Al-Shammery 2011; Yanar *et al.* 2011; Baldin *et al.* 2012; Vasanthakumar *et al.* 2012; El-Gepaly *et al.* 2016; Deka *et al.* 2022

Table 2. Continued.

Plant family	Plants	Target mite family	Target mite species	Toxicity effect	References
Fabaceae	*Abrus precatorius, Glycine max*, *Pongamia pinnata*, *Gliricidia maculata*, *Acacia concinna, Prosopis julifora*, *Cassia tora, Cassia alata*	Tetranychidae, Tenuipalpidae, Tarsonemidae	*T. urticae*, *Panonychus ulmi*, *O. coffeae, R. indica*, *Polyphagotarsonemus latus*	Adulticidal, ovicidal, and ovicidal deterrent activity	Dimetry *et al.* 1990; Lancaster *et al.* 2002; Moran *et al.* 2003; Choi *et al.* 2004; El-Sarmah *et al.* 2007; Han *et al.* 2011; Vasanthakumar *et al.* 2012; Gepaly *et al.* 2016; Ebadollahi *et al.* 2017; Suchithra Kumari *et al.* 2018; Krishnan and Sreekumar 2021; Nexticapan-Garcéz *et al.* 2021; Deka *et al.* 2022; Ata *et al.* 2023; Jeevitha *et al.* 2023
Myrtaceae	*Corymbia citriodora*, *Eucalyptus citriodora, Eucalyptus torquate*, *Eucalyptus oleosa*, *Eucalyptus globulus*, *Syzygium cumin*, *Syzygium aromaticum*	Tetranychidae, Tenuipalpidae	*T. urticae*, *E. orientalis*, *Phyllotetranychus aegypticus*, *C. kenyae*, *Tenuipalpus heveae*	Adulticidal, ovicidal activity	Abo-Shnaf *et al.* 2022; Afify *et al.* 2011; Melo *et al.* 2019; Allam *et al.* 2020
Verbenaceae	*Clerodendron infortunatum*, *Lippia sidoides*, *Duranta plumeria*, *Vitex negundo, Lippia origanoides*, *Lippia gracilis*, *Lippia berlandieri*	Tetranychidae, Tarsonemidae, Tenuipalpidae	*T. urticae*, *O. coffeae*, *O. afrasiaticus*, *A. guerreronis*, *R. indica*	Adulticidal, ovicidal, repellent and ovicidal deterrent activity	El-Sarmah *et al.* 2009; Cavalcanti *et al.* 2010; Fetoh *et al.* 2011; Vasanthakumar *et al.* 2012; Mar *et al.* 2018; dos Santos *et al.* 2019; Ruiz-Jimenez *et al.* 2021
Solanaceae	*Capsicum frutescens*, *Capsicum chinense*, *Capsicum baccatum*, *Capsicum annuum*, *Datura stramonium, Solanum nigrum*	Tetranychidae	*T. urticae*	Repellent activity	Antonious *et al.* 2006; Chermenskaya *et al.* 2010; Kumral *et al.* 2010; Yanar *et al.* 2011; Vergel *et al.* 2016
Poaceae	*Cymbopogon winterianus*, *Lolium perenne, Cymbopogon flexuosus*, *Chrysopogon zizanioides*,	Tetranychidae, Eriophyidae	*T. urticae*, *A. guerreronis*	Adulticidal, ovicidal, and repellent activity	Choi *et al.* 2004; Patnaik *et al.* 2010; Patnaik *et al.* 2011; Yanar *et al.* 2011; Reddy *et al.* 2018
Apiaceae	*Carum carvi*, *Conium maculatum*, *Coriandrum sativum, Pimpinella anisum*	Tetranychidae	*T. urticae*, *E.orientalis*	Adulticidal, ovicidal, and repellent activity	Choi *et al.* 2004; Yanar *et al.* 2011; Elhalawany *et al.* 2019; Ata *et al.* 2023
Rutaceae	*Citrus limon*, *Murraya paniculata*, *Aegle marmelos*	Tetranychidae, Eriophyidae	*T. truncatus*, *O. coffeae*, *A. guerreronis*	Adulticidal, ovicidal, and ovicidal deterrent activity	Patnaik *et al.* 2010; Patnaik *et al.* 2011; Hazarika *et al.* 2020; Deka *et al.* 2022; Laya *et al.* 2022

Table 2. Continued.

Plant family	Plants	Target mite family	Target mite species	Toxicity effect	References
Lauraceae	*Laurus nobilis*, *Licaria puchurymajor*, *Cinnamomum camphora*	Tetranychidae	*T. urticae*, *P. aegypticus*	-	Yanar *et al.* 2011; Azevedo *et al.* 2018; Allam *et al.* 2020
Amaranthaceae	*Chenopodium ambrosioides*, *Chenopodium album*, *Kochia scoparia*	Tetranychidae	*T. urticae*, *T. cinnabarinus*, *T. viennensis*	-	Chiasson *et al.* 2004; Shi *et al.* 2006; Yanar *et al.* 2011
Euphorbiaceae	*Jatropha curcas*, *Chrozophora oblongifolia*, *Euphorbia helioscopia*	Tetranychidae, Eriophyidae	*T. urticae*, *Phyllocoptruta oleivora*	-	Syahputraa *et al.* 2013; Mostafa *et al.* 2017; Hemmat-Jou *et al.* 2023
Rubiaceae	*Morinda tinctoria*, *Gardenia jasminoides*	Tetranychidae	*T. urticae*, *O. coffeae*	Adulticidal, ovicidal, repellent and ovicidal deterrent activity	Vasanthakumar *et al.* 2012; Wagan *et al.* 2018
Cannabaceae	*Humulus lupulu*, *Cannabis sativa*	Tetranychidae	*T. urticae*	-	Yanar *et al.* 2011; Górski *et al.* 2016

Advance management strategies

The overreliance on conventional acaricides has led to increased resistance in mite populations and raised environmental and safety concerns, underscoring the urgent need for advanced, species-specific management strategies (Damalas and Eleftherohorinos 2011; Nicolopoulou-Stamati *et al.* 2016). Given these challenges, there is a pressing need to explore safer, more targeted solutions for pest management. Among the most promising next-generation strategies are oligonucleotide acaricides and reverse genetic tools, including CRISPR/Cas 9 and RNAi which are now considered as advanced species-specific resistance management techniques.

Oligonucleotide acaricides (Olacaricides)

Oligonucleotide acaricides are short, single-stranded antisense DNA molecules (13–25 nucleotides), which may be unmodified or chemically stabilized. Their application is limited by rapid degradation through intracellular endo- and exonucleases, typically via 3' to 5' activity (Wickstrom 1986; Akhtar 1991; Eder *et al.* 1991). Based on their mechanism of action, they are classified into two types: (a) RNase H-dependent oligonucleotides, which degrade mRNA, and (b) steric-blocker oligonucleotides, which inhibit splicing or translation by physically blocking the machinery. In insects and mites, internalization of antisense oligonucleotides likely primarily occurs through adsorptive endocytosis and fluid-phase pinocytosis, with uptake efficiency varying based on oligonucleotide concentration (Dias and Stain 2002) (Fig. 3a).

The first bioformulation combining the 11-mer antisense oligonucleotide acaricide Tur-3 and the fungus *Metarhizium robertsii* was highly effective against *T. urticae*, significantly reducing mite reproduction and survival. The synergistic application increased mortality rates by 7-fold and reduced fecundity by 5-fold, while Tur-3 alone suppressed target pre-rRNA expression by 2.5-fold and inhibited detoxifying enzymes (phenoloxidase, esterase, and glutathione-S-transferase) by 2–3 times (Gavrilova *et al.* 2024).

CRISPR/Cas9 technology

CRISPR (Cluster Regularly Interspace Short Palindromic Repeats – protein) and Cas 9 (DNA endonucleases associated with CRISPR protein) are bacterial adaptive immune system components. The DNA sequence specificity of Cas9 was determined by crRNA (CRISPR RNA), tracrRNA (Trans

activating crRNA) or sgRNA (Single guide RNA – a combination of crRNA and tracrRNA) (Jinek *et al.* 2012). Cas9 induces double-stranded breaks in the genome of eukaryotes that could be repaired by HDR (Homology Directed Repair) and NHEJ (Non-Homologous End Joining) (Fig. 3b). Genome editing using CRISPR/Cas9 is typically delivered to oocytes via microinjection of sgRNA and Cas9 protein. (Bajda *et al.* 2017; Douris *et al.* 2017; Gantz and Akbari 2018).

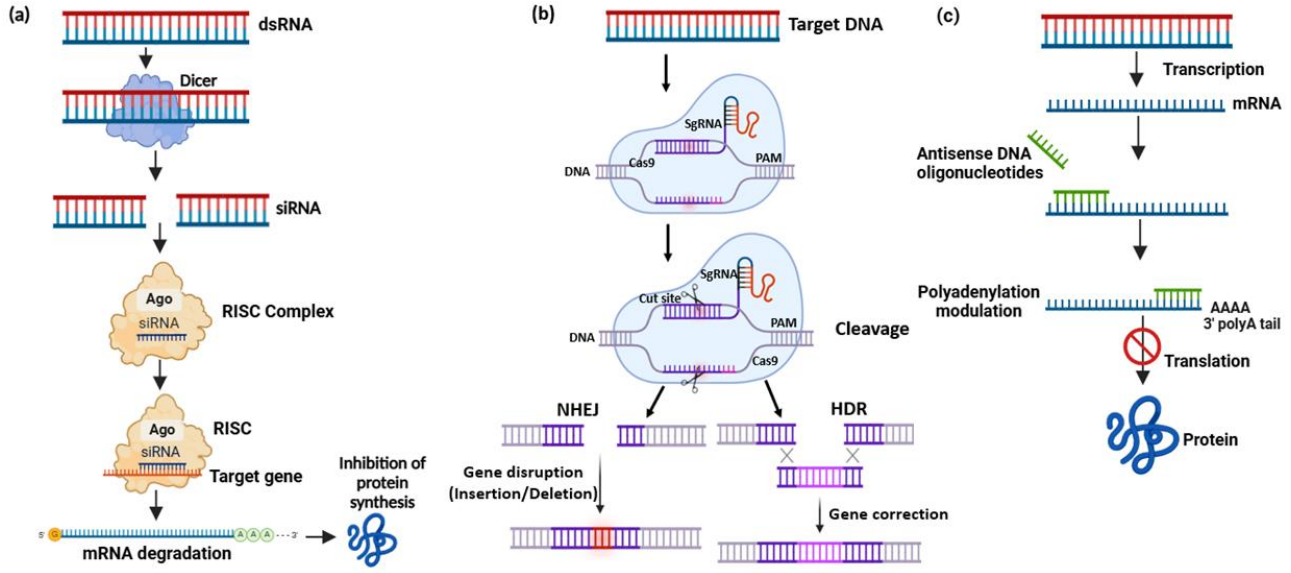

Figure 3. a. dsRNA Mechanism. dsRNA is taken up by the insect cells and cleaved by the enzyme Dicer into small interfering RNAs (siRNAs). These siRNAs are incorporated into the RNA-induced silencing complex (RISC), which guides the complex to degrade complementary mRNA. This process silences mRNA expression that inhibits protein synthesis **b.** CRISPR/Cas 9-based genome editing. The CRISPR/Cas9 system targets DNA by recognizing a protospacer adjacent motif (PAM) site, where it creates double-stranded breaks (DSBs). At the proximal end, blunt-ended DSBs are generated, while cohesive-ended DSBs form at the distal end. These breaks are repaired by the mite's endogenous mechanisms: non-homologous end joining (NHEJ) or homologous recombination (HR). NHEJ often introduces insertions or deletions (InDels), leading to gene inactivation through premature stop codons or frameshift mutations. Conversely, HR enables precise gene replacement or insertion in the presence of a donor DNA template. **c.** Oligonucleotide acaricide. Antisense DNA binds to target mRNA, blocking ribosome attachment and preventing protein translation, effectively silencing gene expression.

While embryonic microinjection is effective for sgRNA in *Drosophila melanogaster* (Diptera: Drosophilidae), it leads to lethality in Chelicerata embryos (Korona *et al.* 2017; Garb *et al.* 2018). An alternative approach to avoid injecting into eggs or embryos involves delivering sgRNA directly to the germline by injecting it into the mother animals. This approach has been demonstrated to be effective in insects (Kotwica-Rolinska *et al.* 2019), and nematodes (Cho *et al.* 2013; Witte *et al.* 2015). In 2020, Dermauw *et al.* (2020) injected *T. urticae* with a CRISPR/Cas9 mix, including Cas9 protein and chloroquine reagent (endosomal escape reagent). Nevertheless, the genome editing efficiencies were very low, with less than 0.2% edited offspring (Dermauw *et al.* 2020). This limited success is likely due to several factors, including challenges in delivering CRISPR/Cas9 components effectively into the mite's cells, the species' unique reproductive biology, and the potential for rapid degradation of introduced nucleic acids, all of which can impede the gene-editing process (Sun *et al.* 2017; Dermauw *et al.* 2020; De Rouck *et al.* 2024). De Rouck *et al.* (2024) observed the synergistic effect between peptide capsules and saponins led to a notable enhancement in CRISPR/Cas9 knock-out effectiveness, surpassing 20%. This specific formulation of CRISPR/Cas9, is labeled as SYNCAS. Furthermore, Receptor-Mediated Ovary Transduction of Cargo (ReMOT Control) technology was developed to deliver the Cas 9 RNP complex into microarthropods (Chaverra-Rodriguez *et al.* 2018). Utilizing this genome editing tool to target resistance-associated genes may help reduce acaricide resistance in phytophagous mites.

RNA interference strategy

RNA interference (RNAi) is a natural gene-silencing mechanism with promising potential for pest

management, mediated by double-stranded RNA (dsRNA). A groundbreaking milestone in molecular biology occurred in 1998 with Fire and Mello's discovery of RNAi, leading to a Nobel Prize in Physiology and Medicine in 2006. This revelation deepened our understanding of gene control and paved the way for RNAi-based treatments.

RNAi offers a sequence-specific approach to reduce the expression of targeted genes, tailor-made for each species due to the uniqueness of their gene sequences. RNAi can selectively suppress them without harming non-target species by focusing on specific genes crucial for the growth, development, or reproduction of insect pests (Whyard *et al.* 2009) (Fig. 3c). Within the *T. urticae* genome, key RNAi machinery genes, including Pasha, Ago, Drosha, RdRp, Loquacious, Dicer, and Piwi/Aub/Ago3, were identified (de la Fuente *et al.* 2007; Grbić *et al.* 2011; Marr *et al.* 2015; Mondal *et al.* 2018; Niu *et al.* 2018). Interestingly, *T. urticae* possesses five distinct forms of RdRp, which are absent in insects, instead of SID-1 suggesting enhanced RNAi processing potential. Additional RNAi factors have been documented in various tick and mite species (Niu *et al.* 2018; De Rouck *et al.* 2024; Yu *et al.* 2025).

RNA interference operates as a post-transcriptional gene silencing mechanism, involving small RNAs of 18–30 nucleotides associated with the protein Argonaute (Ago) (Höck and Meister 2008). Three main groups of small RNAs – P-element induced wimpy tesis (Piwi-interacting RNAs) (piRNAs), small interfering RNAs (siRNAs), and microRNAs (miRNAs) – have been discovered in animals (Okamura and Lai 2008). However, among these, only siRNAs are currently employed in pest control strategies due to their ability to trigger sequence-specific mRNA degradation, making them suitable candidates for RNAi-based pest management (Christiaens *et al.* 2020; Nitnavare *et al.* 2021). The siRNA pathway can be triggered endogenously and exogenously, miRNAs and piRNAs are typically activated endogenously (Ghildiyal and Zamore 2009). Despite their conserved function in gene regulation networks, miRNAs differ by clade. In invertebrates, a common strategy for inhibiting gene expression through RNAi involves introducing long dsRNA, processed by the RNase III enzyme Dicer, into short RNAs of the siRNA class (Christiaens *et al.* 2020). Unlike vertebrates with a single Dicer, arthropods like *D. melanogaster* possess Dicer-1 (miRNA) and Dicer-2 (siRNA) for pathway specialization (Lee *et al.* 2004). The introduction of exogenous dsRNA into eukaryotic cells prompts rapid degradation of mRNAs with complementary sequences, serving as an evolutionarily conserved mechanism for post-transcriptional gene silencing, essential for defense against viral infection and transposable elements, as well as developmentally regulated translational suppression (Mello and Conte 2004; Ding 2010). In mites, this allows researchers to silence genes involved in acaricide resistance or reproduction. Detailed documentation of the successful implementation of RNA interference (RNAi) for the targeted silencing of resistance genes in phytophagous mites is presented in Table 3.

Table 3. RNA-based inhibition of resistance genes in phytophagous mites

Species	Genes	Acaricides	Reference
T. urticae	NADPH- cytochrome P450 reductase	Bifenthrin, fenpyroximate and abamectin	Adesanya *et al.* (2020)
T. urticae red form	NADPH- cytochrome P450 reductase	Fenpropathrin	Shi *et al.* (2015)
	Esterase gene	Fenpropathrin, cyflumetofen	Shi *et al.* (2016)
	3 – aminobutyric acid chloride channel	Abamectin	Xu *et al.* (2017)
	GABA transaminase	Abamectin	Xu *et al.* (2017)
	Intradiol Ring-Cleavage Dioxygenase	Abamectin	Xu *et al.* (2019)
P. ulmi	Glutathione-S-transferase mu-class 5	abamectin	Liao *et al.* (2016)
	Carboxylesterases (CarEs-1, CarEs-7 and CarEs-9)	Fenpropathrin	Shen *et al.* (2016)

CONCLUSION

The escalation of acaricide resistance among phytophagous mites underscores the need for alternative

and sustainable control methods. Integrating secondary metabolites from microorganisms, plants, and fungi offers a promising solution by providing a multi-targeted mode of action and mitigating the development of resistance. Additionally, the advancements in genetic technologies, such as CRISPR/Cas9 and RNA interference, hold significant potential for targeted and precise mite management, although their application in field settings remains limited and requires further validation. These innovative strategies, combined with improved resistance management approaches such as acaricide rotation and resistance monitoring, create a holistic, eco-friendly framework for mite suppression. Future perspectives should prioritize overcoming current limitations, optimizing delivery systems, ensuring regulatory approval, and promoting farmer adoption to achieve effective, long-term, sustainable acaricide resistance management. Additionally, validating these innovative tools under real-world conditions and developing supportive policies will promote their practical implementation, reduce reliance on chemical pesticides, and ensure sustainable success in agricultural systems.

ACKNOWLEDGEMENTS

We would like to express our gratitude to all researchers whose work has contributed to this field. We also extend our apologies to authors whose papers were not referenced in our work. Finally, we thank the reviewers for their insightful comments and constructive feedback, which significantly improved the quality of this review.

Author contributions: S.S.P.: Conceptualization, Methodology, Writing – Original Draft, Visualization; E.S.: Writing – Review & Editing, Supervision; P.R.: Writing – Review & Editing; M.M: Writing – Review & Editing; K.K.K.: Writing – Review & Editing; S.P.T.S.: Writing – Review & Editing.

Funding: The research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Data availability: No new data was produced or examined to support this study. Instead, this review relies on previously published data derived from various studies.

Ethics approval: This study only included arthropod material, and all required ethical guidelines for the treatment and use of animals were strictly adhered to in accordance with international, national, and institutional regulations. No human participants were involved in any studies conducted by the authors for this article.

Conflict of interest: The authors declare that they have no conflict of interest.

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شکستن مقاومت کنه‌کش‌ها: راهبردهای پایدار برای مهار کنه‌های گیاهخوار با راه‌حل‌های طبیعی و پیشرفته

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چکیده

کنه گیاهخوار *Tetranychus urticae* Koch به طور فزاینده‌ای در برابر ۵۵۸ کنه‌کش در سراسر جهان مقاومت پیدا کرده و عملکرد محصول را در مناطق کلیدی کشاورزی تهدید می‌کند و بر محصولات مهم اقتصادی مانند گوجه‌فرنگی، توت‌فرنگی و مرکبات تأثیر می‌گذارد که منجر به اتکای بیشتر به مهار شیمیایی می‌شود. از این رو، استفاده جهانی از کنه‌کش‌ها در مدیریت کنه‌ها سطح بالایی را ثبت می‌کند. این مقاومت از سازوکارهای مختلفی از جمله جهش‌های ژنتیکی، کاهش جذب کنه‌کش‌ها و افزایش سم‌زدایی ناشی می‌شود. چنین مقاومتی اثربخشی مهار شیمیایی را کاهش می‌دهد و نیاز به راهبردهای‌های جایگزین را ضروری می‌کند. این بررسی، استراتژی‌های مدیریت مقاومت فعلی برای کنه‌های گیاهخوار را با تمرکز بر رویکردهای مرسوم و نوآورانه خلاصه می‌کند. راهبردهای مدیریت تلفیقی آفات (IPM) بر اهمیت ادغام روش‌های مهار شیمیایی، زیستی و زراعی برای کاهش سرعت توسعه مقاومت تأکید دارند. متابولیت‌های ثانویه تولید شده توسط میکروارگانیسم‌ها، گیاهان و قارچ‌ها، راه‌حل‌های طبیعی امیدوارکننده‌ای را برای مهار جمعیت کنه‌ها با طیف وسیعی از عملکرد ارایه می‌دهند. این ترکیبات با کاهش اتکا به درمان‌های شیمیایی و در عین حال حفظ کنترل مؤثر کنه‌ها، به تأخیر در مقاومت کمک می‌کنند. همچنین، عوامل مهار زیستی طبیعی، مانند شکارگران حشرات، کنه‌های شکارگر، باکتری‌ها، قارچ‌ها و ویروس‌ها، پتانسیل خوبی برای کنترل آفات نشان داده‌اند. افزون بر این، ترکیبات مشتق شده از گیاهان، جایگزینی سازگار با محیط زیست با اثرات چند هدفی بر فیزیولوژی کنه‌ها ارایه می‌دهند. راهبردهای پیشرفته، مانند کنه‌کش‌های الیگونوکلئوتیدی، فناوری CRISPR/Cas9 و تداخل RNA، نتایج امیدوارکننده‌ای را در مطالعات آزمایشگاهی برای مبارزه با مقاومت کنه‌کش‌ها نشان داده‌اند، اگرچه موفقیت عملی و کاربرد گسترده آنها در شرایط مزرعه هنوز در دست بررسی است. این راهبردها فرصت‌های مشخصی را برای کاهش بسیار اتکا به آفت‌کش‌های شیمیایی، کاهش مؤثر مقاومت به کنه‌کش‌ها و افزایش پایداری و تاب‌آوری سامانه‌های تولید محصولات جهانی ارایه می‌دهند و در نتیجه به شیوه‌های کشاورزی ایمن‌تر و سازگارتر با محیط زیست کمک می‌کنند.

واژگان کلیدی: مدیریت مقاومت به کنه‌کش‌ها، CRISPR/Cas9، کنه‌کش الیگونوکلئوتیدی، کنه‌های گیاهخوار، تداخل RNA، متابولیت‌های ثانویه.

CITE: Sathiya Priya, S., Sumathi, E., Renukadevi, P., Murugan, M., Kumar, K.K. & Thamarai Selvi, S.P. (2025) Breaking acaricide resistance: Sustainable strategies for phytophagous mite control with natural and advanced solutions. *Persian Journal of Acarology*, 14(4): 140403.
https://doi.org/10.22073/pja.v14i4.87081