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REVIEW ARTICLE

Role of endosymbionts in sap feeding insects and their potential in pest management strategies

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Abstract

Endosymbionts are microorganisms living within another organism and are closely associated with their biological functions. Sucking insects *viz.,* aphids, whiteflies, leafhoppers, planthoppers and mealybugs, are major sap-feeding insects that cause considerable damage to crop plants. These homopteran insects have a strong relationship with facultative and obligate bacterial endosymbionts. Through symbiotic adaptations, insects can exploit plant resources and escape from the plant defenses. Endosymbionts play a critical role in physiological adaptation and ecological interactions, greatly affecting host fitness, detoxification processes and interactions with their natural enemies. For example, the endosymbiont *Buchnera aphidicola* helps the pea aphid, *Acyrthosiphon pisum,* neutralize hydroxamic acids like DIMBOA derived from plants. It also aids in detoxification processes and improves amino acids metabolism. Beyond detoxification, they also reduce plant defense mechanisms by interfering with communication pathways, triggering susceptibility genes in plants and altering the distribution of nutrients inside host plants. Endosymbionts influence the coevolutionary dynamics between plants and insects as well as the developmental paths of insect host plant ranges, allowing insects to quickly adapt to new plant defenses through the acquisition or change of their symbiont communities. This complex tri-trophic interaction between homopterans, plants and endosymbionts drives the evolution of plant defense and host-plant interaction. The manipulation of these endosymbionts contributes to the development of biological control methods. These modern approaches provide alternatives to established chemical interventions, thus achieving more sustainable and environmentally consistent pest management strategies.

Keywords: detoxification; endosymbionts; homopteran; pest management

Introduction

Symbiosis is a close, usually long-lasting relationship between two or more organisms. Endosymbiosis describes an organism living within another organisms. The association between insects and microbes is often mutualistic and has a significant impact on the biological functions of the host insects. An endosymbiont is any type of organism which lives within an organism's body and forms an endosymbiotic relationship. It may take various forms like parasitism (one organism benefits at the expense of the other), mutualism (both organisms' benefit), commensalism (one organism benefits without affecting the other), amensalism (one is harmed while the other is unaffected), commensalism (one benefits without affecting the other), synnecrosis (both are harmed), or neutralism (neither is significantly affected) (1). Approximately fifty percent of insects are estimated to harbour endosymbiotic bacteria, especially those that rely exclusively on nutritionally restricted diets (2, 3). There are two types of endosymbionts in insects. They are primary (obligate) and secondary (facultative) symbionts. Obligate symbionts are important for growth and development and also provide nutritional supplements to the host. For example, *Buchnera aphidicola*, *Portiera aleyrodidarum*, etc. are known as primary endosymbionts. *B. aphidicola* synthesizes essential amino acids such as tryptophan and lysine, which are lacking in the aphid's diet of phloem sap, thus facilitating the host's development and reproduction. Likewise, *P. aleyrodidarum* supplies whiteflies with essential amino acids and carotenoids, making up for the dietary deficiencies of plant sap. Such endosymbionts are normally accommodated in specialized cells known as bacteriocytes and are transmitted maternally, establishing an obligate mutualistic association that is vital to the host's fitness. Facultative endosymbionts are not significant for host survival or fecundity and can be found within various host tissues, like *Fritschea bemisia*, *Serratia symbiotica*, etc (4). These symbionts are housed in specialized structures called bacteriocytes or mycetocytes and are transmitted from one generation to the next through vertical transmission (3, 5).

Endosymbionts become heritable by acquiring mechanisms that ensure vertical (maternal) transmission to offspring. The association becomes obligate or beneficial for host growth because the host depends on this association and horizontal transmission does not occur; the phylogeny of the endosymbionts aligns with the phylogeny of the hosts (6). Insects feeding predominantly or exclusively on plant xylem and phloem sap must penetrate plant tissue with flexible tubular mouthparts (stylets) to ingest plant phloem sap. This diet is unbalanced, rich in carbohydrates but deficient in amino acids and other nitrogenous compounds (7). Due to the low concentrations of nitrogenous compounds, phloem-feeding insects ingest large amounts of plant sap and excrete the excess sugar as honeydew. This feeding mode facilitates the transmission of plant viruses, making members of the Homoptera significant vectors of viral plant pathogens and it became resistant to different insecticides and resistant varieties (8). Furthermore, these insect populations can become enormous on plants, causing malnutrition, leaf bending and gall formation. Such damage not only reduces the photosynthetic efficiency and overall vigour of the host plant but also leads to significant yield losses in agricultural systems. In severe infestations, the structural deformities and resource depletion can compromise plant growth, making them more susceptible to secondary infections and reducing their commercial value. The review emphasizes the role of endosymbionts among different sap-feeding insects and how these endosymbionts determine insect nutrition and physiology. Various endosymbiont groups among the major homopteran pests like mealybugs, planthoppers, leafhoppers, aphids and whiteflies were narrated. Insect adaptation to different plant defenses, utilizing endosymbiont activity and interaction of insect symbionts with plant secondary metabolites, was critically explained. Symbiont-mediated detoxification processes, physiological function and genetic classification of symbionts among the insect hosts are further explored in the succeeding sections. Novel approaches of using symbionts as a tool in pest management strategies like chitinase and protease degrading bacterial isolates, RNA technology, Sterile insect technique, etc. and its scope were elucidated.

Role of endosymbionts in insects

Endosymbionts, such as bacteria, fungi, yeast and protozoa, form symbiotic relationships by residing inside insects. This relationship is particularly beneficial for herbivorous insects, including both chewing and sap sucking types. These microscopic partners assist with digestion, nutrient synthesis and the detoxification of plant compounds. They act as internal biochemical factories that produce essential vitamins and amino acids that insects cannot obtain from their plant-based diets alone.

Chewing insects, such as caterpillars, beetles and grasshoppers, have shown significant benefits from these partnerships. These insects use symbiotic bacteria to break down plant cell walls and neutralize toxic compounds, enabling them to extract more energy from their food. For instance, *Spodoptera* (armyworms) benefits from bacteria that help digestion of indigestible plant material. In contrast, sap-feeding insects like aphids, whiteflies and leafhoppers rely even more heavily on their endosymbionts due to their nutrient-poor diet of plant sap, which is rich in sugars but lacks essential nutrients (9). Aphids depend on *B. aphidicola* to produce vital amino acids such as proline and serine, which their diet does not provide (10). To enhance the nutrient synthesis and reproduction rates in psyllids, it mainly depends on *Wolbachia* and *Carsonella ruddii* (11).

Losing their microbial relationship would severely impact survival, as these microbes are essential for nutrient production. Both chewing and sap-sucking insects build beneficial microorganisms. Chewing insects consume a very wide range of plant material, such as leaves, stems and roots, that tend to encompass more diverse and balanced nutrients compared to sap feeders. Sap feeders consume only plant sap, especially phloem and xylem sap, which is high in carbohydrates but extremely low in essential amino acids, vitamins and other minerals. They need more symbionts to obtain essential nutrients for their survival and development. To compensate for this low nutrient supply, sap-feeders depend heavily on their symbiotic microorganisms compared to chewing insects. (12). This underscores the vital importance of these symbiotic relationships, especially for insects that have evolved to survive on a highly specialized diet.

Phloem-feeding insects like leafhoppers, planthoppers, whiteflies, depend on endosymbionts for essential elements that are lacking in their diet. In this relationship, the bacterial endosymbiont *Sulcia mulleri,* found in many pests like tree hoppers, green leaf hoppers, plays a crucial role. It plays a crucial role by providing essential cofactors, vitamins, amino acids for their growth and development (13) and facilitates nutrient exchange through membrane transporters (5). Nevertheless, whiteflies exhibit a complex symbiotic system such as *Rickettsia* sp., *P. aleyrodidarum, Hamiltonella defensa*. *H. defensa*, a secondary endosymbiont, helps supplement the host's nutritional needs (14). Aphids contain endosymbiont *B. aphidicola* which release nutrition and vital amino acids (15).

Whiteflies have a complex symbiotic system that contains *Rickettsia* sp., *Portiera aleyrodidarum and Hamiltonella defensa*. Another symbiont that helps to supply the nutrients to the host is *H. defensa* (14). Similarly *Moranella endobia* and *Tremblaya princeps* exhibit a nested symbiosis in mealybugs (16).

Endosymbionts also contribute to enhanced host adaptation (17), reproductive success (18), stress resilience and genetic diversity (19). For instance, *Wolbachia* improves whitefly fitness by supplying B vitamins (20, 21). At the same time, elevated levels of *Arsenophonus* in viruliferous *Bemisia* tabaci Asia-I suggest a role in facilitating viral transmission by evading host immunity (22).

Some of these endosymbionts, *Wolbachia, Arsenophonus, Cardinium* and *Rickettsia*, exert parasitic effects through the manipulation of insect reproduction by mechanisms like cytoplasmic incompatibility, male-killing, feminization and parthenogenesis induction, ensuring their transmission (18, 23, 24). T. princeps in mealybugs is a primary symbiont that controls the rapamycin pathway and has been implicated in fecundity and survival on resistant host plants, which aids in plant defense evasion (25) (Table 1).

Diversity of endosymbionts in homopteran insects

Endosymbiotic relationships in homopteran insects exhibit remarkable diversity, both in the roles of the endosymbionts within their hosts and in the taxonomic classification of these microbes. Certain homopteran insects, such as leafhoppers and treehoppers, have evolved even more complex

Table 1. Different types of endosymbionts and their role in major sucking insects

Insects	Endosymbionts	Symbiont type	Symbiont locality	Symbiont role
Leafhopper and planthopper	Yeast-like symbionts - *Pichia guilliermondii, Saccharomycetales* sp., *Debaryomyces hansenii*	Primary/ obligate	Abdominal fat body; ovary, eggs	Nitrogen waste recycling, supply proteins for embryonic development, Sterol and amino acid metabolism
Brown planthopper	*Wolbachia*	Secondary/ facultative	Reproductive organs	Fertility and sex ratio distortion, Sex determination
Aphid - *Acyrthosiphon pisum*	*Buchnera aphidicola*	Primary /obligate	Bacteriocytes	Essential amino acids
Aphid	*Regiella insecticola*	Secondary/ facultative	Gut and ovaries	Host plant adaptation and reproduction
Aphid	*Rickettsiella*	Secondary/ facultative	Secondary bacteriocytes, sheath cells, various tissues and the hemolymph (Tsuchida)	Increasing blue-green polycyclic quinones in the body, whichconfer protection from predators
Whitefly	*Portiera aleyrodidarum*	Primary/ obligate	Bacteriocytes	Lipid and amino acid synthesis
Whietfly	*Arsenophonus* sp.	Secondary/facultative	Salivary gland and gut	Potentially host interactions and adaptation, detoxification
Mealybug	*Tremblaya princeps & Moranella endobia*	Primray/obligate	Bacteriocytes and gut	Nutrient metabolism and host adaptation
Mealybug	*Mikella endobia & Sodalis* sp.	Secondary/facultative	Fat bodies	Potential nutritional supplementation
Mealybug	*Cardinium & Wolbachia*	Secondary/ facultative	Ovaries	Cytoplasmic Incompatibility & Feminization

endosymbiotic systems including many bacterial companions. For example, the green leafhopper *Nephotettix cincticeps* harbours two distinct endosymbionts, *Nasuia and Sodalis*, belonging to the Proteobacteria and Bacteroidetes phyla, respectively (26). In brown planthopper, Yeast-Like Symbionts (YLS) such as *Ascomycetes* symbionts, *Pichia*-like symbionts and *Candida*-like symbionts play a major role in amino acid metabolism through the recycling of uric acid, but it is difficult to culture in vitro condition because of their unique environmental requirements, which are specifically provided by the insect host. It may be related to virulence and to improve the adaptation of resistant rice varieties. YLS are the primary endosymbionts that are exclusively housed in bacteriomes (specialized organs), these bacteriomes are present in midgut and fat bodies. The secondary endosymbionts are present in various tissues like haemolymph, midgut lumen, midgut epithelium and reproductive organs (Fig. 1). Secondary endosymbionts include *Asaia* sp., *Aeromonas* sp. *and Enterobacter* in midgut region (27), *Hirsutella proturicola,* (28), *Cryptococcus*-like symbionts and *Pichia*-like symbionts (29) in the fat bodies, *Wolbachia and Arsenophonus* (26) in the reproductive organs and *Yarrowia lipolytica* and *Sterigmatomyces halophilus* in the eggs of planthoppers (30).

Mealybugs serve as hosts to several endosymbionts belonging to the phylum Bacteroidetes, including *Tremblaya* and *Moranella*. These symbionts play a crucial role in supplementing the insect's nutrient-deficient phloem sap diet. One of their primary functions is the synthesis of essential amino acids and vitamins. They are involved in a unique nested symbiosis, where both contribute to complementary steps in metabolic pathways, enabling efficient nutrient production. This cooperative system also helps in recycling nitrogenous waste products into usable compounds. These nutritional contributions are vital for the mealybug's growth, development and reproductive success (31). Among these, *T. princeps* and *M. endobia* are the primary endosymbionts that reside inside the midgut bacteriocytes (32) (Fig. 2). The secondary endosymbionts like *Mikella endobia* & *Sodalis glossinidius*. Both are gamma proteobacteria closely related to fat bodies (33) *Arsenophonus* sp.*, S. symbiotica* - hemolymph (34), *Spiroplasma* sp. tracheae*, Wolbachia & Rickettsia* sp. reproductive organs (35).

The link between aphids and their endosymbiont *B. aphidicola,* an obligatory endosymbiont belonging to the Proteobacteria phylum and found in all aphid species, is a well-researched example of such a relationship. Nearly all aphid species have the obligatory endosymbiont *B. aphidicola*, which has co-evolved with its host for more than 100 million years. It plays a vital function in the nutrition of the host by supplying vitamins and amino acids that are absent in the diet of aphid's phloem sap. The intracellular long-term lifestyle of the bacterium is indicated by its vastly diminished genome. Since this mechanism is transmitted maternally, symbiont persistence is guaranteed from generation to generation. It is a critical model for symbiosis and evolutionary biology studies due to its function in nutrition, evolutionary stability and genomic discovery (5). Bacteriomes are the specialized organs in the midgut having a primary endosymbiont, B. *aphidicola*. Secondary endosymbionts occur around many tissues, including *Rickettsia* sp.*, Erwinia sp., H. defensa* - haemolymph, *Spiroplasma* sp. - tracheae, *Fukatsuia symbiotica, Rickettsiella viridis* - fat bodies, *H. defensa, Regiella insecticola and Spiroplasma* sp. - reproductive organs (36) (Fig. 3).

On the other hand, whiteflies have a dual endosymbiont system consisting of *Hamiltonella and Portiera,* both belonging to the Proteobacteria phylum (22). Primary endosymbionts found in midgut and fat bodies of whiteflies -*P. aleyrodidarum* while the secondary endosymbionts include *Rickettasia, Arsenophonus* sp.*, Orientia* sp. *and Erwinia* sp. of the midgut (19, 37), *Arsenophonus* sp., - salivary gland (38). *Wolbachia, H. defensa*, (39). *Arsenophonus* sp.*, caridnium* sp. (40) - reproductive organs, *F. bemisia, Cardinium hertigii* of fat bodies (41) (Fig. 4).

This endosymbiotic system with numerous associates demonstrates the complex evolutionary adaptations to meet the diverse nutritional needs of various insect hosts. Homopteran insects have a diverse range of endosymbionts due to differences in their evolutionary paths, genetic traits and taxonomic connections. Due to their long-term relationships

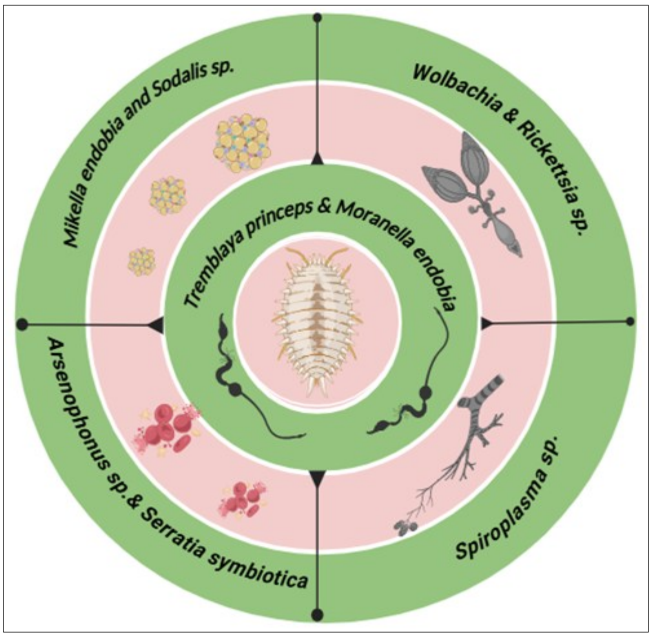


Fig.1. Endosymbionts present in mealybug.

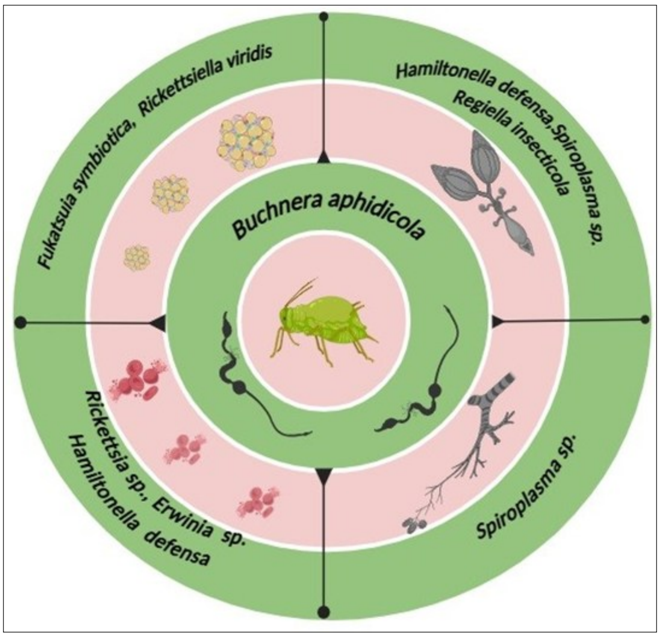


Fig. 2. Endosymbionts present in aphid.

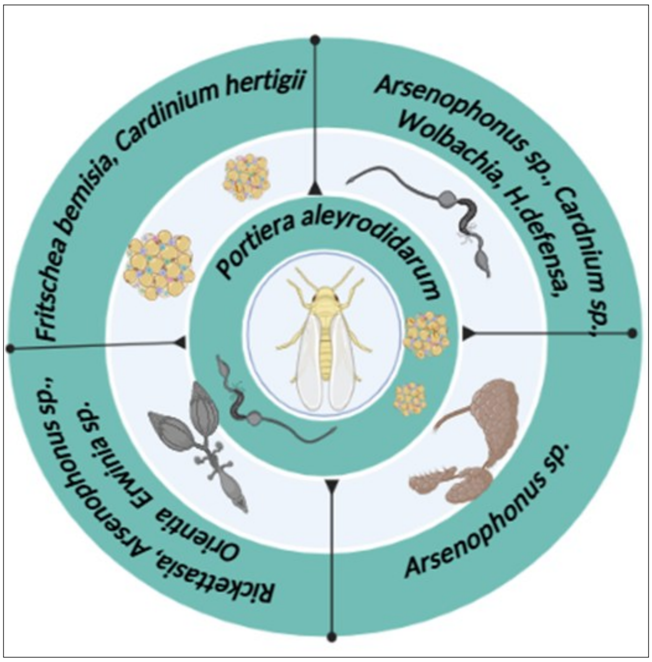


Fig. 3. Endosymbionts present in whitefly.

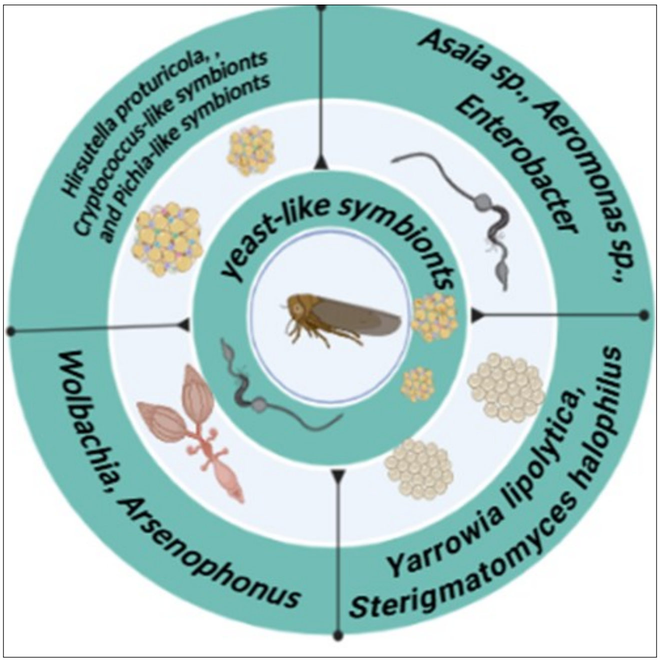
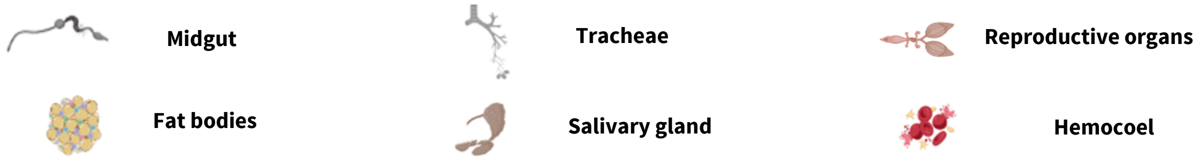


Fig. 4. Endosymbionts present in hoppers.



In the above figures, the second inner layer depicts the primary (obligate) endosymbionts, the third layer depicts the location of the secondary (facultative) endosymbionts and the fourth layer depicts the diversity of secondary endosymbionts.

with their hosts and adaptation to certain ecological niches as well as many endosymbionts have close association with sucking insects. Certain symbionts aid in the spread of viruses, while others are involved in detoxification of the pesticides or help pests adapt to resistant plants. Pest populations can be decreased by focusing on these microorganisms, particularly those that are specific to the insect. Biocontrol techniques can also make use of symbionts like *Wolbachia* to reduce pest populations. Understanding their functions facilitates the creation of eco-friendly, selective and efficient pest control techniques based on their diversity.

Interaction between symbionts of sucking insects and plant secondary metabolites

Plant Secondary Metabolites (PSMs) make up a complex group of compounds that do not directly influence the growth or reproduction of the plant but have crucial roles in insect-plant interactions. Since some secondary metabolites may have indirect effects on plant fitness. However, insects have co-evolved and have highly specialized adaptations to chemical defences. Some specialists evolve detoxifying mechanisms through the upregulation of cytochrome P450 enzymes (42), while others incorporate these compounds for their defence against predators. However, the plasticity of such interactions is interesting; as insects adapt to specific PSMs, the plants respond by generating new compounds or altering old ones (43).

The three major classes of plant secondary metabolites include terpenes, phenolics and nitrogen-containing compounds. These metabolites act as feeding deterrents, toxins, or digestibility reducers against insect herbivores. For example, glucosinolates in Brassicaceae plants have considerably reduced the rate of feeding behaviour and development of lepidopteran larvae (44).

PSMs can also eliminate insect endosymbionts, by creating contact and stomach poisoning. These substances may affect insect symbiotic organisms (45). In leaf sheaths and phloem exudates, the brown planthopper (BPH) attack greatly raised 'Sakuranetin'. Sakuranetin is a compound produced by plants to defend against fungal infections. It is made from another substance called naringenin, with the help of a special plant enzyme. The number of fungal endosymbionts decreases at the time of release of sakuranetin. Microbes inside insects supply essential nutrients, help in hormonal regulation and assist in recycling nitrogen to keep the insect healthy. Additionally, sakuranetin suppressed *Candida carpophila,* a symbiont that is eaten by a different insect. The related endosymbiont species *C. carpophila* and *H. chrysospermus* were directly inhibited in their growth by sakuranetin (46). Salicylic acid and benzyl benzoate have significantly increased the mortality rate and have profound effects on survival rate, weight gain, fertility and symbiotic populations. Methyl jasmonate, a plant chemical involved in defense, can reduce the number of certain yeast-like symbionts inside the insects. These microbes are important for the insect's growth, reproduction and feeding (47). A species of whitefly found on tomatoes carries helpful bacteria that help it detoxify harmful compounds like tomatine. When tomatine levels increase, these bacteria multiply and help the insect continue feeding safely.

Aphid fitness and plant defensive responses are influenced by endosymbionts such as *Arsenophonus*. There is an important relationship between the number of secondary metabolites, like gossypol and the number of endosymbionts, such as *Arsenophonus*, in aphid populations (48). The possible impact of gossypol on endosymbionts' is to increase the insect host's fitness, highlights the interaction between plant defensive mechanisms and symbiont-mediated benefits.

The greenhouse whitefly harbours both *P. aleyrodidarum* and *Arsenophonus* sp. endosymbionts. These endosymbionts facilitate the metabolism of the phenolic compounds of cucurbit plants, primarily altering the process of conversion of cucurbitacins (49). *P. aleyrodidarum* as the primary endosymbiont found in *B. tabaci* MEAM1 on tomatoes carries helpful bacteria that help it detoxify harmful compounds like tomatine. When tomatine levels increase, these bacteria multiply and help the detoxification activities of insect (Fig. 5) (30).

The Asian citrus psyllids host *C. ruddii*, which is reported to assist in the metabolism of citrus flavonoids. Studies indicate that the populations of endosymbionts correlate with citrus varieties and secondary metabolite profiles (50).

Endosymbionts mediated detoxification mechanism

Detoxifying symbiosis describes the mechanism by which microorganisms connected to insect's aid in the detoxification of pesticides and plant toxins (51). Bacterial gut symbionts that metabolize these substances often contribute to insecticide resistance. In addition to helping the host break down toxic compounds, the microbiota presents in hosts exposed to pesticides can serve as a source of selection pressure. In addition to offering genetic diversity, this microbial community helps to reduce the pesticide susceptibility, which causes the

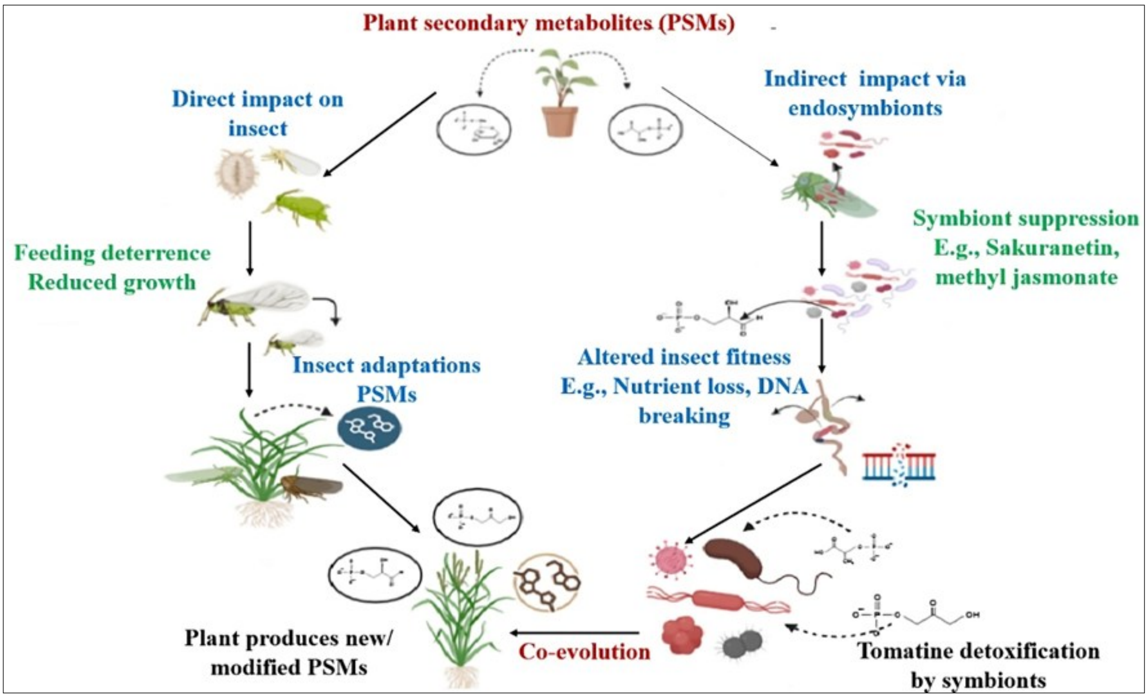


Fig. 5. This diagram illustrates the dynamic interaction between plant secondary metabolites (PSMs), microbes and insect herbivores.

insects to become resistant (52). Numerous studies have discovered a variety of bacteria that break down pesticides in several insect orders, such as the Diptera, Coleoptera, Hemiptera and Lepidoptera.

Brown planthopper: The brown planthopper is one of the most destructive pests of rice in Asia. Advanced biochemical adaptation mechanisms and endosymbiont diversity allow the species to avoid both plant defensive responses and insecticide interventions. The monophagous nature of this pest is further supported by its advanced interactions with endosymbionts, particularly Yeast-Like Symbionts (YLS) and bacterial symbionts. These symbionts are crucial for their metabolic processes as well as detoxification pathways.

In certain instances, the brown planthopper has ingested symbiotic bacteria from water and soil sources, such as *Serratia marcescens*, which gives it resistance to the popular insecticide buprofezin. Still, antibiotic treatment causes the susceptible brown planthopper to become vulnerable again. The capacity of *S. marcescens* to digest the insecticide and increase host resistance has been further highlighted by the discovery of putative genes linked to buprofezin degradation through genomic research (53).

Similarly, it has been observed that imidacloprid exposure increases the number of *Wolbachia* in brown planthopper. This increase does not directly contribute to insecticide resistance, but rather indicates a physiological stress response, likely aiding in host resilience or maintenance of host fitness under chemical exposure. Eliminating this bacterium lowers the transcript levels and enzyme activity linked to insecticide metabolism, suggesting that *Wolbachia* plays a role in enhancing the host resistance to imidacloprid, acephate, imidacloprid, thiamethoxam and buprofezin resistance is present in the Insecticide Susceptible (IS) and Insecticide Resistance (IR) populations. The IR population has greater bacterial diversity and richness than the IS population. In the IS population, the majority phylum was Proteobacteria (99.86%), whereas in the IR population, Firmicutes (46.06%), Bacteroidetes (30.8%) and Proteobacteria (15.49%) were dominant. Shared genera of the two populations are *Enterococcus, Weissella and Morganella* and probably form the core microbiota related to brown planthopper. IR population contains an abundance of detoxifying bacteria (54).

Aphids: Aphids have some strong adaptations, among which their obligate association with bacterial endosymbionts, that empower them to exploit a broad range of host plants and achieve complex detoxification mechanisms (55). The very high impact on their host range, including their adaptive ability, varies from one species of aphid to another with different endosymbiont communities. For example, a complex community of *A. pisum* endosymbionts aids in exploiting several legume hosts (56). Likewise, *Myzus persicae* possesses unique mechanisms of adaptation through endosymbiont mediation to considerable plant defensive compounds at its high host range (57).

The detoxification of imidacloprid in aphids is achieved through mutations in the nAChR β1 subunit, uridine 5-diphosphate glucuronosyltransferases (UGTs) and overexpression of cytochrome P450s (CYP6CY22 and CYP6CY13). Several endosymbionts have been known to influence imidacloprid metabolism, which may improve resistance in insect hosts, these bacteria include *Pseudomonas sp*, *Stenotrophomonas maltophilia, Klebsiella pneumoniae, Bacillus alkalinitrilicus and Mycobacterium* sp. (58).

Also compared to the spirotetramat-susceptible strain (SS), the spirotetramat-resistant strain (SR) showed a significant reduction in Alphaproteobacteria and an increase in Gammaproteobacteria. During spirotetramat selection between SS and SR populations, there were no differences among them and the remaining 11 bacterial classes are *Bacilli, Betaproteobacteria, Clostridia, Deinococci, Bacteroidia, Anaerolineae, Negativicutes, Sphingobacteria, Actinobacteria, Epsilonproteobacteria and Deltaproteobacteria*. The SR aphids showed a notable increase in the abundance of *Enterobacteriaceae, Lactobacillaceae and Caulobacteraceae* compared to the SS sample. In contrast, families such as *Rhodobiaceae, Streptococcaceae, Thermaceae, Moraxellaceae and Staphylococcaceae* exhibited a significant decrease in the SR sample (59).

Whitefly: Recent molecular studies indicated that *B. tabaci* is a cryptic species complex, comprising at least 44 different species with different biological and ecological traits (60). Out of these species, the most limiting and economically essential members of the complex are MEAM1 formerly known as biotype B, Middle East-Asia Minor 1 and MED formerly referred to as biotype Q, Mediterranean (61). In fact, these have tremendous adaptability to various host plants and environmental conditions that make them difficult to manage with considerable effects even though the application of pesticides is not effective (62). This is because of the gut microbiota and enzyme resides inside the host.

The three major enzyme systems are cytochrome P450 monooxygenases (P450s), carboxylesterases (COEs) and glutathione S-transferases (GSTs), are responsible for the advanced detoxification mechanism based on whiteflies' adaptation against different insecticides. Furthermore, endogenous and xenobiotic chemicals like DDT, abamectin and organophosphate pesticides must be detoxified by glutathione-S-transferase enzymes. These enzymes are primarily host-encoded, not symbiont derived. However, the GST enzymes themselves are encoded by the host genome and are part of the insect’s intrinsic metabolic detoxification efficiency by modulating host gene expression or providing co-factors. It has been proved in different strains of *B. tabaci* that higher GST activity is related to a decrease in susceptibility to pesticides (63). Higher relative densities of *Wolbachia or Rickettsia* have been associated with enhanced susceptibility to pesticides in whiteflies*,* *B. tabaci* (64). On the other hand, compared to the susceptible population, thiamethoxam-resistant whiteflies were shown to have a greater abundance of Rickettsia and a lower abundance of *Portiera* sp. *and Hamiltonella* symbionts. The *Arsenophonus* and *Wolbachia* found in the *B. tabaci* (Asia II 7 and Asia II 5) from West Bengal populations became resistant to imidacloprid and thiamethoxam while only *Wolbachia* was correlated with the acetamiprid resistance (65). *Aleurodicus dispersus* (rugose spiralling whitefly), which has invaded new geographical regions and became resistance to systemic neonicotinoid and indirectly affects the natural enemy of coconut (66), this is because of the detoxification mechanism developed by endosymbionts of whitefly.

Mealybugs: Mealybugs are a serious polyphagous pest due to its short developmental period and asexual reproductive behaviour. The pesticide tolerance patterns in mealy bugs are shaped by their sophisticated associations with internal bacterial partners. The essential bacterial symbiont *T. princeps* and *M. endobia* exists across *Planococcus citri* supports basic biochemical functions that could indirectly support chemical breakdown processes and potentially contributing to insecticide resistance (67). These bacterial partners carry genetic material involved in protein building blocks and chemical processing pathways, suggesting possible involvement in breaking down foreign compounds (33).

Within the agricultural pest, investigators identified a newly discovered optional bacterial partner, *Wolbachia* strain PS -23, that generates specific detoxifying enzymes (glutathione S-transferases) that successfully deactivate modern insecticides from the neonicotinoid family, with effectiveness against imidacloprid (68). The *Bacillus* sp. in papaya mealy bug might have a role in the detoxification of profenophos and chlorpyrifos OP compounds that were used for the management of the mealy bug complex (69).

New approaches to pest management are made possible by our expanding knowledge of endosymbiont-mediated detoxification. Restoration of sensitivity is possible by perturbing microbial partners involved in pesticide resistance. For example, the removal of *S. marcescens* from brown planthoppers makes them sensitive to buprofezin (53). Additionally, detoxifying genes of major symbionts can be knocked down through RNA interference (RNAi). Manipulation of symbionts can enhance the efficacy of biological control agents, but microbiome-derived monitoring technologies can aid in detecting the emergence of insecticide resistance. Through population dilution, releasing pests that are designed or devoid of symbionts may further decrease resistance.

Despite its potential, pest control based on endosymbionts possesses several demerits. Because insect-symbiont relationships are so unique, cross-species (that works well in one insect species may not work in another species) applications are challenging. Beneficial ecological associations would be disrupted by redefining symbiont associations. Obligatory symbiont culture on an in vitro level is still technically difficult, restricting experimentation and application in the field. Insect populations would even become accommodated to such through novel detoxifying mechanisms or symbionts. Additionally, there is the lack of information regarding functional participation of detoxification genes by hosts. Regulatory and biosafety issues, particularly those compared to genetically manipulated organisms, would have to be resolved prior to extensive application (51).

Physiological role of endosymbionts in insects

Essential amino acids, which are deficient in the insect’s diet or plant phloem sap, are supplemented by symbionts. For their survival, insects such as planthoppers and leafhoppers depend on symbiont-provided nutrients because they feed on resistant rice cultivars that are deficient in sugars, amino acids and vitamins. Symbionts can mitigate the negative effects of lacking essential amino acids by supplying the necessary nutrients. Also, they contribute to maintaining nutritional homeostasis during low nitrogen content then it is transforming stored uric acid into beneficial chemicals (3, 70).

Insects that feed on plant sap often develop endosymbiotic relationships with bacteria that supply essential nutrients deficient in their diet. Most of the aphid species have a bacterial symbiont *B. aphidicola* which belongs to a group Gammaproteobacteria. This helps them to survive on their low nutrient diet (71). But in case of *Geopemphigus* sp., the typical *Buchnera* is no longer present. Instead, they have a different symbiotic bacterium, passed from mother to offspring, which belongs to the Bacteroidetes group. Even though it's not *Buchnera*, this new symbiont can still perform similar functions like producing amino acids and vitamins which are crucial for the insect's survival (26). The *Bacillus* sp. isolated from *Rhizoecus amorphopalli*, a retained-tuber mealybug, showed positive findings for tests of carbohydrate fermentation and citrate consumption but negative results for tests of indole synthesis (72).

The ability of the host to use resistant rice types and overcome plant defenses in leafhoppers has been associated with the gut endosymbiont *S. muelleri* (73). To improve the host's ability to flourish on nutrient-poor or defensive plant hosts, *S. muelleri* synthesizes amino acids and other vital nutrients (26).

Genetic characterization of endosymbionts in homopteran insects

Endosymbionts, especially those from the genera *B. aphidicola, S. mulleri, Tremblaya, Wolbachia*, have been established to provide major benefits to aphids, whiteflies, mealy bugs, hoppers and other nutrient-deficient hosts. Each insect has varied bacterial diversity. Bacteria have certain genes that benefit the insect in many ways. They provide the insect with nutrients, help in digestion, improved resistance to pathogens, regulation of physiological responses and gene expression and aid in digestion, enhance resistance to pathogens, regulate physiological responses and control gene expression, as well as synthesize vital compounds like vitamins.

Both insect and bacteria have evolved independently. These associations are so unique and diverse (74). Some of the genes are involved in the production of pantothenic acid (*panB, panC*) (75), biotin (*bioA, bioD*) (76) and riboflavin (*ribA, ribB, ribC*) (77).

Insecticide-treated whitefly alterations in the relative quantity of symbionts and the expression pattern of two cytochrome P450 (cyp) genes were also evaluated. The CYP6CM1 and CYP6CX1 genes were consistently expressed more in imidacloprid-treated whiteflies, according to quantitative PCR (qPCR) research, indicating a relationship between gene expression and the insect's capacity to detoxify harmful substances such as pesticides (65). The important gene leuABCD encodes the enzymes required to produce the branched-chain amino acid leucine. Since leucine is lacking in their phloem-sap diet. (Ganter, 2006) Recent transcriptomic analysis showed that it is mainly the gene CYP6CM1 that causes a degree of neonicotinoid resistance while many GST genes are connected with organophosphate resistance (78).

A positive correlation was obtained from the endosymbionts and level of resistance, especially between *Arsenophonus* and *Wolbachia* for imidacloprid and thiamethoxam resistance while only *Wolbachia* was in correlation with the acetamiprid resistance in whitefly population (Asia II 7 and Asia II 5) from West Bengal. Expression analysis showed the upregulation of such P450 genes as CYP6CM1, CYP6DZ7, CYP4C64, CYP6CX1 and CYP6DW2 in resistant populations. This suggests that both P450 mono-oxygenases and symbiotic bacteria may confer whitefly resistance to neonicotinoids (65).

Aphids must depend on *Buchnera* for this amino acid. The genes for anthranilate synthase (*trpEG*) are located on plasmids in the bacterial endosymbionts (*Buchnera*) of the aphids *Rhopalosiphum padi, R. maidis, Schizaphis graminum and A. pisum.* The trpEG amplification on plasmids may lead to an excess of this vital amino acid, which is needed for the aphid host and an increase in enzyme protein (79) . The *glnA* gene which encodes the glutamine synthetase, helps to assimilate the ammonia content byproduct of amino acid metabolism (5) and also the synthesis of riboflavin is carried out by the gene *ribA*. *B. aphidicola* produces the bacterial chaperonin GroEL, which is a major compound of plant defensive mechanism. It causes plants to create reactive oxygen species and deposit callose (80).

In case of mealybug, the endosymbiont Tremblaya having a gene called *pabABC* which encodes the enzymes involved in the biosynthesis of folate. It is an important vitamin for the growth and development (32)

Interaction of endosymbionts with natural enemies of crop pests

Several studies have emphasized certain defense substances produced by endosymbionts that protect their homopteran hosts from diseases, parasitoids and predators. For example, in *B. tabaci,* the endosymbiont *H. defensa* produces cytoplasmic toxins associated with bacteriocytes, such as the type II toxin-antitoxin system (ToxIN) and YD-repeat toxins, which provide defense against fungi and parasitoid wasps (81). In the same way, the endosymbiont *R. insecticola* in the aphid *A. pisum* produces a toxin called "Diplorickettsia," which confers resistance to the parasitoid wasp *Aphidius ervi* (82).

S. symbiotica plays a crucial role in the defense mechanisms of aphids; indeed, it causes mortality of parasitoid larvae that emerge around four- or five days following oviposition (83). In addition, *S. symbiotica* along with *H. defensa*, confers protective effects against predators like lady bird beetles (*Hippodamia convergens*) leading to a reduction in the reproduction fitness (84).

Pest management strategies - Symbionts as a novel tool for IPM

Modern agricultural systems integrate with Integrated Pest Management, which includes different approaches to control or reduce the pest populations. It makes use of diverse techniques such as planting resistant crop varieties, biological control techniques and biotechnological applications (85). Endosymbionts are utilized in several innovative pest control tactics like sterile insect techniques (SIT), chitinase and protease degrading bacterial isolates, paratransgenesis, RNA interference and other sophisticated manipulation of bacterial symbionts have shown outstanding potential (86).

Chitinase and protease degrading bacterial isolates: Chitin microfibrils embedded in a protein-carbohydrate matrix make up the Peritrophic Membrane (PM) lining the midgut of insects (87). This chitin serves as a source of carbon and nitrogen for the growth of gut bacteria and is beneficial to the host insect (88). As microbial enzymes are difficult for insects to acquire resistance to, exploiting the chitinous morphological framework to disrupt the structural portion of the insect using enzymes produced by gut bacteria is an environmentally benign strategy. In insects, the old cuticle is partially broken down by gut bacterial chitinases. In pest management strategies, gut bacteria that produce protease and chitinase have been shown to penetrate the host's gut through feeding and interfere with the peritrophic membrane's thickness. This results in a nutritional imbalance in the host insect and ultimately causes insect mortality (69, 89).

The enzymatic activities of the bacterial isolates from the Rugose Spiralling Whitefly (RSW) were different in different host plants. The chitinolytic activity was highest for *Bacillus siamensis* SBRSW9 and *Bacillus altitudinis* SBRSW2 at 3.96 μmol^{-1} min^{-1} mL^{-1} and 3.01 μmol^{-1} min^{-1} mL^{-1} respectively, obtained from banana plants. The lowest chitinolytic activity was reported for *Bacillus altitudinis* SSRSW18 from sapota plants at 0.07 μmol^{-1} min^{-1} mL^{-1}. Proteolytic activity ranged from one isolate to other isolate with greater variations. *Bacillus subtilis subsp. stercoris* SBRSW19 had the highest proteolytic activity at 71.43 % and the lowest at 76.93 % was by *Bacillus albus* SCRSW11. Proteolytic activity recorded the lowest at 10.01 % by *Bacillus altitudinis* SSRSW13, which was obtained from RSW on coconut, banana and sapota plants (90).

Siderophore production also differed among bacterial isolates. This variation in siderophore production is important in pest management. Siderophores are iron-chelating compounds produced by microbes. Some bacteria could be developed into biocontrol agents. For example, introducing bacteria that produce too much siderophore that disrupt the gut balance and it could harm the pest or stop its growth and development. For instance, replacing the beneficial gut microbes with less supportive or even antagonistic strains may weaken the pest or make it as a microbial biopesticide. This aligns with the broader goal of eco-friendly pest management by targeting pest-associated microbiota instead of relying solely on chemical control methods. *Bacillus subtilis subsp. stercoris* SBRSW19 from bananas produced the highest amount of siderophores at 83.40 %, while *Bacillus zanthoxyli* SCRSW13 from coconuts produced the lowest amount at 2.10 %. The glutathione-S-transferase activity of RSW gut bacterial isolates ranged from 5.21 to 24.48 $nmol^{-1}$ min^{-1} mL^{-1} μg $protein^{-1}$. These gut bacteria can destroy the host insect physiology through chitinase, siderophores and proteases production. Due to its high fecundity, it is rapidly spreading through the host plants (91).

The longevity, reproductive potential and offspring weight of the pink hibiscus mealybug, *Maconellicoccus hirsutus* was influenced by the ability of bacteria such as *S. marcescens, Pseudomonas aeruginosa* and *B. subtilis* to degrade wax (92). Over 50 % of the bacterial strains linked to mealybugs could use the bug's wax as a carbon source. One essential class of detoxifying enzymes involved in the metabolism of foreign substances is Glutathione S-Transferases (GST). These enzymes have an important role in mechanisms of resistance against natural and synthetic toxins. GSTs make it possible for pests to become resistant to environmental stress by detoxifying insecticides and plant secondary metabolites through glutathione conjugation, which lowers their toxicity and allows for easier elimination from the body. GSTs also have a protective function by avoiding oxidative stress, which is otherwise caused by chemical or environmental exposure (93). The two species with the highest mortality rates among papaya mealybugs were *Bacillus cereus* PYP3 (78.7 %) and *Bacillus sp.* PLB1 (74.0 %). Chitinase, protease activity and the capacity to break down wax were demonstrated by both strains (69). Citrus mealybug populations were successfully managed by using *Bacillus amyloliquefaciens* A1, *Paenibacillus polymyxa* AB3 and *Providencia rettgeri* K10 (94). A toxin generated by the bacterial strain *Xenorhabdus nematophilus* MDUStBa15 was shown to be effective in controlling two-tailed mealybugs in field trials (95). The use of leaf dip approach to evaluate the effectiveness of bacterial-mediated mealybug management. *Enterobacter* sp. L3 and *Bacillus subtilis* strain CAF3, which led to 95 % and 81 % of mealybug (*Phenacoccus parvus*) mortality rates, respectively (96).

RNA interference technology: RNA interference, or RNAi for short, is a conserved biological phenomenon where double-stranded RNA (dsRNA) is implicated in the breakdown of homologous messenger RNA (mRNA), causing post-transcriptional gene silencing (97). When the insects take in dsRNA targeting essential genes, the cellular machinery including Dicer-2 converts it into small interfering RNAs (siRNAs) and these siRNAs direct the (RNA-inducing silencing complex) RISC to degrade complementary mRNA sequences that effectively silencing the target gene (98).

This mechanism can have direct effects on pest populations. By silencing genes which is essential for survival, reproduction, or development, the pests may experience reduced growth, impaired fertility, or death. Aphids are controlled through symbiont-mediated RNAi represents an important new step forward in pesticide or formulated product management. In previous work, traditional RNA interference methods were effective against aphids but were not implemented due to high costs of synthesis and limited dsRNA availability. It has recently been demonstrated that *S. symbiotica* in aphids can be cultured on axenic media. This symbiont can be engineered to produce specific dsRNAs inside the aphid's body, a process called symbiont-mediated RNA interference (SMR). This allows for a continuous and targeted gene-silencing effect without needing repeated dsRNA applications. This has made it possible to engineer this symbiont along with the *B. aphidicola* to produce dsRNA for specific genes in the host, thus making SMR a viable approach. Success in these different insect pests indicates that it may be its potential usefulness as a sustainable cost of pest control, but it still needs further research to optimize its field application (99).

Other advanced technologies, like CRISPR-Cas9 gene editing, have also been demonstrated for targeted suppression via the mechanism of Incompatible insect technique (IIT), which disrupts reproductive compatibility by modifying the male insect microbiota that becomes reproductive incompetents. In the case of Sterile Insect Technique (SIT), sterile males mated to fertile females lay eggs that are not viable and thus cannot continue through embryogenesis. It is a form of intervention that gradually lowers the population density of the target species to extinction (86). Microbial bioinsecticides make use of naturally occurring entomopathogenic bacteria to kill pests. For example, the *Bacillus thuringiensis* strain VKK-BB2 has been effective in controlling *Leucinodes orbonalis*, a major pest of brinjal. The manipulation of gut symbionts, which means altering or disrupting the microbial communities within insect guts to negatively affect their growth, reproduction, or survival. For instance, feeding genetically modified *E. coli* to *Bactrocera dorsalis* (oriental fruit fly) significantly increased mortality. Another approach is the use of antibiotics to suppress or eliminate beneficial symbionts, thereby making pests more susceptible to insecticides and reducing their overall fitness. In the case of *Nilaparvata lugens* (brown plant hopper), treatment with tetracycline and ciprofloxacin downregulated genes responsible for detoxification, enhancing insecticide susceptibility. In the paratransgenesis technique, the natural bacterial flora of disease-transmitting vectors has also been isolated and genetically modified to create molecular interventions interfering with the mechanisms of pathogen transmission. This has been effectively used in tsetse flies by disrupting their symbionts like *Wigglesworthia*, leading to sterility (100). These are the new strategies in pest management that simultaneously maintain ecological balance. Using chitinase and protease degrading bacterial isolates and RNA interference technology only reduces the microbiota population of the homopteran insect. Other techniques are not described or utilized in homopteran. Endosymbiont manipulation in homopteran pest control may perturb ecosystem equilibrium through impact on non-target species and microbial diversity. While these methods are efficient, they may be injurious to beneficial insects or disrupt predator-prey balance. To prevent hazards, targeted methods, accurate environmental evaluation and complementation with other pest control methods, e.g., crop rotation and natural enemies, are critical to ensure ecological stability. Further studies are needed to optimize these methods in an environmentally friendly context (89).

Conclusion

Endosymbionts play a crucial role in altering the biology and ecology of sucking pests by influencing their nutritional supply, interactions with natural enemies and secondary metabolites and detoxification mechanism causes resistance to plant defenses from the environment and it has several kinds of advantages associated with it. As the sucking pests are mostly reproduced by asexual reproduction, the impact on the symbionts and carry over to next generation is quite fast in these sap feeders. They provide adaptive advantage to insects for their survival and multiplication in the adverse condition. Their impact on nullifying the toxins from plant metabolites as well as insecticides makes pest management strategies tough. Using symbiont-target antibiotics by modifying plant defensive mechanisms to target the development of endosymbionts offers a promising solution. But, considering their significant impact on ecosystem dynamics and possible knock-on effects on non-target animals, it is still crucial to thoroughly consider the ecological consequences of disturbing endosymbiont communities. More effective and long-lasting approaches to pest management may be developed by understanding the complex processes by which endosymbionts influence host-plant interactions. Another strategy recently developed in utilizing endosymbionts as one of the components in the pest management. However, few studies have explored the potential of symbionts as tools in pest management. Follow-up studies need to be aimed at the development of pest-specific microbiome profiles for targeting specifically, assessing the long-term ecological impact of symbiont-mediated therapy and improving their delivery technology under field settings. Additional justification for the development of ecologically balanced and targeted pest control programs will be based on the discovery of plant cultivars that naturally disrupt symbiont function and the use of paratransgenesis in homopterans. Promoting microbial and gene-targeted pest control strategies and reducing the reliance on chemical pesticides, these discoveries facilitate further development toward sustainable agriculture. The present study comprehends the complex interactions between sucking pests, endosymbionts and host plants, as well as to pest management methods. It is useful to capitalize on these endosymbionts; a significant amount of research is required. More research on understanding function of endosymbionts in sucking pests and their interactions with host plants is crucial to capitalize for development of pest control strategies.

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Authors' contributions

RM drafted the initial manuscript, revised, designed the manuscript, RPS conceptualized the idea, critically reviewed and revised the manuscript, MM, RA provided relevant inputs for the endosymbionts and their practical utility based on his earlier research works in the lab, SJ, NS critically revised the manuscript. All authors read, reviewed and approved the final manuscript.

Compliance with ethical standards

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