

Plants- Insect Interactions and Involvement of Insect's Microbiota

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Abstract

We're just at the beginning to learn about the vast array of microorganisms that are connected to insects and how they influence the relationships between insects and plants. Insects are excellent transporters and possible recipients of plant diseases and bacteria that modify plant defenses, in addition to directly profiting from symbiotic microbial metabolism, insects also acquire and spread pathogens within their surroundings. Plants induce stress-specific defenses to fight off insects and their bacteria in order to avert damage. Nonetheless, a multitude of modifications found in both bacteria and insects enable them to evade the activation of plant defense mechanisms. It has become clear in recent years that the vast diversity and metabolic capability of microorganisms associated with insects may influence insect-plant interactions significantly more than previously thought. The latter could have an impact on how sustainable pest management techniques can be designed and developed. Thus, in a fast-developing field of study, this review clarifies the state of our understanding regarding multitrophic insect-microbe-plant interactions.

Keywords: Defenses, Plant interaction, transporter, symbiotic, metabolic capability, pathogens, multitrophic etc.

Introduction

The relationship between plants and microbes is a dynamic, intricate process that has existed for as long as plant colonization on Earth. An assembly of host and non-host species has developed over millions of years as a result of plants' connection with microbes; this distinct ecological unit is known as a "holobiont." Plants are frequently invaded by both useful and pathogenic microorganisms, primarily bacteria and fungi, in both natural and farmed ecosystem. Beneficial interactions include a variety of direct and indirect mechanisms, including the transfer of nutrients by mycorrhizal fungi and rhizobia, which bind to roots and supply plants with fixed nitrogen and mineral nutrients, respectively; direct growth stimulation through phytohormones; antagonistic relationships with pathogenic microorganisms; and stress mitigation. However, because the invasive microorganisms may be saprophytic and induce necrotrophy in the colonizing plants, the negative interactions are harmful for the plants. Understanding the relationship between plants and microorganisms is therefore essential to understanding both the advantages and disadvantages of microbes on plants.

Microorganisms have been gaining a lot of interest lately because of their function in both plants and animals. In addition to being known to cause major health problems in their hosts, microorganisms are recognized as well for the advantages they bestow upon them. We cannot ignore the advantages that microorganisms offer to their host cells. Microbes aid in the production of vital nutrients like vitamins and

amino acids during the digestive process of the host animal. Microbes play comparable roles to plants. By enabling effective nutrient uptake and enhancing plant responsiveness to possible threats, soil microbes can enhance plant growth and support the plant's defence mechanism ^[1]. Microbes also break down organic material and release nutrients. There are nearly more than 5.5 million species of *Arthropoda* phylum- insect among which one million is estimated to be identified. More than 6000 species of mites associated with arachnids belongs to an important class of insects which feeds on plants. Plants eating insects such as *Hymenoptera* (sawflies), *Orthoptera* (grasshoppers), *Coleoptera* (beetles) and *Lepidoptera* (butterflies) are mostly seen in area of horticulture, forestry pests and agriculture. Insects feeding on other insects belongs to orders such as, *Thysanoptera*, *Hemiptera* and invertebrates such as joint legged class *Arachnida* along with other orders of *Tetranychidae* and *Eriophyoidae* (gall mites and spider mites) ^[2].

Indirect effects of insect-induced microbial transmission are thought to account for 30%–40% of crop yield reduction, while direct insect damage is thought to account for 18%–20% of crop losses ^[3]. The host range of insects is mostly determined by adaptations that evolved during coevolution with plants. As a result, some insects (specialists such as monophages or oligophages) are limited to specific plant families or species, while others (generalists, such as polyphages,) have a very wide host plant range ^[4]. The top 10 crops with the largest agricultural gross production value (FAO, 2016) are rice, maize, wheat, soybean, tomato, potato, sugar cane, vegetables (such as celery, bamboo shoots, celery, parsley, beets etc.), apples and grapes. These are the major food crops that are impacted by insects. Both forestry and floriculture, which deal with a variety of insects, are quite important economically. While forestry deals with large eating insects like grasshoppers and beetles, floriculture frequently involves greenhouse cultivation, which provides perfect conditions for thrips and aphids (CABI 2020).

Microbes are vital to a lot of insects that feed on plants. Insect survival and health are drastically compromised, or life itself is rendered impossible, in the absence of their symbiotic microbiome ^[5]. Furthermore, it has been demonstrated that microorganisms associated with insects influence how insects interact with their host plants ^[6]. This review will shortly discuss the surface of viral transmission and its impact on insect–plant interactions, since insect vectors transmit 80% of the approximately 900 known plant viruses ^[7]. This review focuses on the influence of insect-associated microorganisms on insect–plant interactions in order to gain a better understanding of the multitrophic interactions between insects and their host plants.

Microbiota associated with Insects

Numerous microorganisms are associated with insects. These include symbionts, which can have a relationship with their host in which both participants benefit (mutualism), non-benefit (commensalism), or one benefit while the other suffers (parasitism) ^[8]. Transient microorganisms can also be pathogenic to either the insect or the host plant. These microorganisms, which are derived from insects or are spread by insects amongst visited host plants, comprise bacteria, archaea, fungus, protists, and viruses ^[9].

Plant-beneficial bacteria, pathogens, and transient microbiota

The environment, which includes soil and plant-associated bacteria, plant symbionts (such as endophytes), plant-beneficial and growth-promoting microbes, and pathogens, is the source of transient insect microbiota, which is momentarily linked to its host ^[10]. According to recent reports, plant-piercing and sucking insects like mirids and leafhoppers (*Hemiptera*) can transfer beneficial endophytes that encourage plant growth and, in turn, provide their host insect with enough food ^[11]. Plant pathogen transfer is also a

possibility. One such instance is the spread of the infamous hemibiotrophic plant pathogen *Pseudomonas syringae*, whose pathovars are capable of infecting the majority of significant crop species globally ^[12]. Kiwifruit trees develop bacterial canker as a result of this, bacterium being spread by the citrus flatid planthopper (*Metcalfa pruinosa*) ^[13]. But *P. syringae* has also been demonstrated to suppress plant defences that pose a threat to insects, therefore making them perfect insect partners ^[14]. However, some *P. syringae* strains associated with leaves are harmful to insects, such as *aphids*, which alters the outcome of the plant-insect interaction ^[15].

Transfer of insect symbionts

Many insects depend on symbiotic bacteria for survival; without them, life is either impossible or significantly impacted. Microbial symbionts in insects are crucial for their host's nutrition, defence against infections, and digestion ^[16]. Insects that feed on plant xylem and phloem sap, which are low in key nutrients, are particularly dependent on microorganisms to augment their diet with vital amino acids ^[17]. Nevertheless, some insects, such as caterpillars (*Lepidoptera*), grasshoppers (*Orthoptera*), thrips (*Thysanoptera*), and spider mites (*Tetranychidae*), appear to be less affected by the removal of their microbiota ^[18]. Microbes can be acquired by insects through either horizontal or vertical transmission, depending on whether they depend on symbionts for necessary or advantageous functions (i.e., obligate vs facultative symbionts). Required symbionts are vertically passed from the mother to the young before or during birth, through the surfaces of the eggs, or by particular behaviour that facilitate the transfer of necessary microorganisms. Usually obtained from the environment by feeding or interaction that results in horizontal transmission, facultative symbionts facilitate advantageous non-essential tasks for their host ^[19]. Pseudo-vertical transmission is one of the mixed forms of transmission that allows symbionts to be obtained both horizontally and vertically ^[20]. For their host, facultative symbionts perform a wide range of functions, such as body pigmentation, sex determination, and tolerance to high temperatures. For example, the formation of blue-green polycyclic quinones caused red-colored pea aphids infected with a Rickettsial facultative endosymbiont to change green ^[21].

Variability among insect symbionts

Even though the field of study on insect microbiota is developing quickly, our understanding of the complexity and diversity of the microbial communities linked to insects is still in its infancy. Microbes like *Asaia*, *Arsenophonus*, *Buchnera*, *Burkholderia*, *Blattabacterium*, *Blochmannia*, *Carsonella*, *Coxiella*, *Hamiltonella*, *Pantoea*, *Portiera*, *Phytoplasma*, *Pseudomonas*, *Rickettsia*, *Spiroplasma*, *Sodalis*, *Uzinura*, *Wolbachia*, *Zinderia* and numerous other (uncultured) bacteria are examples of insect symbionts ^[8]. A portion of these insect symbionts also pose a threat to plants. For example, insects include intracellular Gram-negative bacteria known as *Rickettsia*-like organisms (RLOs), which play important roles in primary feeding. They spread to plants where they are harmful and have the ability to control insect reproduction. Leafhoppers, White flies, cicadas and psyllids are the insects that spread RLOs ^[22]. RLOs cause several diseases in plants, including papaya bunchy top disease, grapevine yellows, strawberry green petals, and strawberry deadly yellows ^[23].

In another example, according to Sugio *et al.* (2011) ^[24], phytoplasma are a highly varied collection of pleomorphic-shaped, Gram-positive phytopathogenic bacteria that intracellularly colonize both insects and plants. They do not need sophisticated genomes because, as they colonize host cells, they can benefit from the host's biological activities. Of all the phytopathogenic bacteria that have been identified,

phytoplasma have the smallest genomes, averaging 0.7 Mb and having a low G+C content ^[25]. They infect around 800 distinct plant species and cause over 1000 plant diseases, indicating their broad host range ^[26]. The most effective vectors for the spread of phytoplasmas are hemipteran insects. Only some of the Gram-positive, helical-shaped, internal bacteria known as *Spiroplasma* are phytopathogens; they are not closely related to Phytoplasma ^[27]. According to Özbek *et al.* (2003) ^[28] *Spiroplasma kunkelii* causes maize stunting disease, which is spread by leafhoppers and, in extreme situations, results in the total loss of corn seed production. Citrus obstinate disease, or *Spiroplasma citri*, is caused by leafhoppers and spreads to other plant species, such as carrot and periwinkle, discolouring the leaves ^[29].

Parts of insects that are symbiont-hosting

Both the inside and the outside of insects can contain insect symbionts. According to Heine *et al.* (2018) ^[30], leafcutter ants have symbiotic *Pseudonocardia* bacteria on their exterior, which shields *Leucoagaricus* from the destructive parasitic fungus *Escovopsis*. Leafcutter ants harvest tree leaves in order to establish a *Leucoagaricus* fungus as their food source. Perlmutter and Bordenstein (2020) ^[8] reported that most insect symbionts, on the other hand, are more closely related to their host insect and reside in the stomach, malpighian tubules, haemolymph, fat body, and specialized symbiont organs (such as bacteriocytes and bacteriomes in aphids). Owing to their smaller genomes, obligate insect symbionts have developed close bonds with their hosts as a result of their dependence on host metabolism. They are frequently found inside insects as endosymbionts or even inside cells that shield the insects' immune systems ^[31].

Adaptation of cosymbionts and symbionts

Due to their rapid mutation rate and need on their host's and other symbionts' metabolism for survival and reproduction, many endosymbionts have short genomes as a result of gene loss ^[32]. These symbionts may eventually unintentionally lose genes necessary for their host, which would cause other symbionts to take its place. The *Sulcia* obligatory symbionts of xylem-feeding insects including spittlebugs, sharpshooters, and cicadas (*Hemiptera*) are one example of such integrated metabolic processes. According to Ankrah *et al.* (2020) ^[16], arginine, leucine, isoleucine, lysine, phenylalanine, tryptophane, valine and threonine are the eight necessary amino acids that *Sulcia* supplies to its host. *Zinderia*, *Sodalis*, *Baumannia*, and *Hodgkinia* are co-obligatory symbionts that provide the other required amino acids, such as histidine and methionine, that the primary obligate symbiont is unable to manufacture. According to McCutcheon and Moran's 2010 study ^[32], *Zinderia*, a co-obligate symbiont, effectively compensated for the loss of the tryptophane biosynthesis pathway in *Sulcia*-CARI of sharpshooters. However, *Zinderia*'s genome is merely 208 kb in size. Another illustration is *Buchnera*, an aphid endosymbiont that continuously loses genes ^[33]. While the coexisting endosymbiont *Serratia* was discovered to be able to manufacture tryptophane, covering critical metabolism for both endosymbionts, the *Buchnera aphidicola* symbiont of the aphid *Cinara cedri* has lost its ability to produce riboflavin and tryptophane ^[33]. Furthermore, obligate symbionts with severe genome reductions may develop their own endosymbionts, as the mealybug *Tremblaya* symbiont's *Moranella* ^[34]. In other situations, eukaryotes may take the place of bacterial obligate symbionts. For example, in cicadas, the absence of bacterial *Hodgkinia* symbionts led to the replacement of a fungal associate that resembled yeast, highlighting the significance of the microbial community that extends beyond bacteria ^[35]. As a result, rather than being a static relationship, microbial insect symbiosis appears to be a more dynamic state of cooperation.

Microbiological transfer from insects to vegetation

Given the ubiquitous nature of bacteria, transmission is unavoidable. Microbes are taken from colonized tissues when an insect feeds, and they are then spread by saliva and oral secretions in the form of regurgitant, which comes from the front of the insect's digestive tract, or by frass^[36]. The non-destructive feeding technique of plant sap eating insects helps microorganisms to safely pass through physical and chemical barriers in plants, making them the most effective vectors for spreading bacteria to plants. But insects that eat leaves can also spread bacteria into open wounds, where they are exposed to the poisonous chemicals that protect injured plants. While generalist insects have the ability to inoculate a wider range of plant species and thereby potentially indirectly transmit microbes to specialist insects, specialist insects are likely to only transmit microbes to a very limited group of plant species, depending on their range of plant hosts^[29]. According to Hosokawa *et al.* (2007)^[37], the latter may result in non-pest insects developing microbial modifications that enable them to feed on different plant species.

Pest status and the microbiome of insects

It has been demonstrated that the transfer of pest insects' gut microbiota to non-pest insects can result in the acquisition of the pest status. Insect performance on soybean was reversed when non-pest *M. cribraria* egg-transmitted symbionts and soybean pest shield bug *Megacopta punctatissima* were switched^[37]. It has also been demonstrated that the microbiota of pea aphids (*Acyrtosiphon pisum*) is crucial for facilitating effective reproduction on particular plants^[38]. Antibiotics were used to eradicate the microbiota of genetically identical animals, selectively removing the microbiota of their progeny, while leaving their obligatory symbiont *Buchnera* intact. Antibiotics were used to eradicate the microbiota of genetically identical animals, selectively removing the microbiota of their progeny, while leaving their obligatory symbiont *Buchnera* intact. In contrast to control offspring, the progeny of antibiotic-treated insects reproduced equally well on vetch plants (*Vicia sativa*), but they lost nearly 50% of their fecundity on white clover (*Trifolium repens*), highlighting the significance of the insect microbiota for host–plant interactions^[38]. It is also known that phytoplasmas spread by insect vectors can change the host range of insects through as-yet-unidentified processes. On the one hand, Aster yellows phytoplasmas (AYPs) boost the fertility or growth of their vector, such as the general leafhopper *Macrostelus quadrilineatus*, which spreads the AYPs to a variety of plants. However, *Dalbulus maidis*, a monophage leafhopper, lives longer on nonhost plants infected with AYPs, suggesting that the host range of specialised leafhoppers is affected by the generalist leafhoppers' dissemination of AYPs^[39]. The "vector manipulation" theory suggests a mechanism by which insect behaviour and pest status are altered^[40]. According to this theory, microorganisms influence the insect's choice of host plant in order to facilitate their spread. It has been demonstrated that the corn-specialist leafhopper *D. maidis* is drawn to phytoplasma-infected plants and subsequently favours healthy plants, which promotes the spread of infection. On the other hand, oviposition on infected plants was significantly decreased^[41]. The underlying processes of these kinds of interactions are still unknown. Given that polyphagous insects have the capacity to visit a broad variety of plant species, the exchange of symbionts across various insect species may be facilitated by the transfer of microorganisms, including symbionts, through plant surfaces, with unidentified effects. Furthermore, spread microorganisms have the ability to change the physiology and defence state of plants, which may allow insects to feed on defense-compromised plants that would not have been accessible to them otherwise.

Plant-microbe-insect interactions

Because various organisms are a component of food webs, direct and indirect interactions between members of an ecosystem are not uncommon. Organisms influence or assist one another in the battle for survival. An example of a factor influencing a plant-insect connection is other species, such as phytopathogens, by altering how much plant resource is consumed [42]. Time, which attacks both nature and the genetic makeup of plants, determines the defence responses to insects or viruses [43]. Plant defence mechanisms are precise in their responses to diseases or insect attacks [44].

Plants are not defenceless against insects and bacteria that try to take advantage of their resources. Advanced defence mechanisms have developed in plants to fend off intruding threats and draw in insect parasitoids [45]. These mechanisms include constitutive physical and chemical barriers, stress-specific detection systems, downstream cross-communicating phytohormonal defence signalling pathways, enhanced defence mechanisms that enable fast response, and the production of secondary metabolites (Fig. 1).

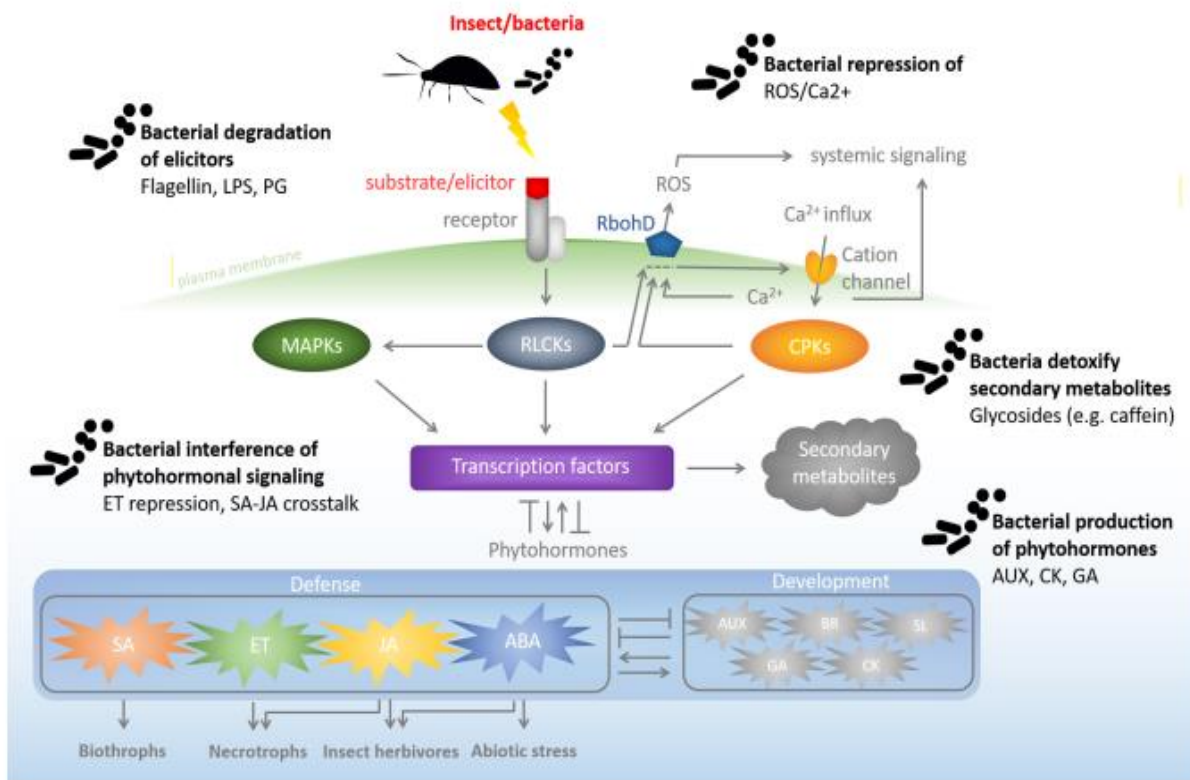


Figure 1: A summary of the disruption of plant defence signalling by microbes linked with insects. Plants sense stress via activating mitogen activated kinases (MAPKs), receptor-like cytoplasmic kinases (RLCKs), and Ca²⁺ influx, which in turn activates calcium-dependent protein kinases (CPKs). RbohD is activated by Ca²⁺, RLCKs, and CPKs. This results in the production of extracellular reactive oxygen species (ROS), which function as a second messenger in systemic signalling throughout the plant in conjunction with Ca²⁺. The downstream stress signalling pathway, which involves the activation of transcription factors that control the synthesis of phytohormones and secondary metabolites, is initiated by the activation of CPKs, RLCKs, and MAPKs. In the main text, crosstalk between (phytohormonal) signalling channels are further explained. Abscisic acid (ABA); Auxin (AUX); Brassinosteroids (BR); Cytokinins (CK); Ethylene (ET); Gibberellin (GA); Jasmonic acid (JA); Lipopolysaccharides (LPS);

Peptidoglycan (PG); Salicylic acid (SA); and Strofalactones (SL). (Silvia Coolen *et al.*, 2022- The secret life of insect- associated microbes and how they shape insect- plant interactions).

overcoming and profiting from physical limitations found in plants

Plants have inherent physical and chemical barriers, such as waxy cuticles, strengthened cell walls, trichomes and preformed metabolites, and antifeeding chemicals, as a first line of defence against invasive bacteria and insects [46]. These initial plant defences provide a rich carbon supply for organic polymers and complex polysaccharides, such as cellulose, pectin, and lignin, which microbes can exploit to their advantage. Chewing insects secrete saliva and regurgitant-containing enzymes during eating, which aid in the digestion of plant material and promote the absorption of nutrients [47]. For example, the tortoise beetle *Cassida rubiginosa* can use symbionts *Ca. Stammera capleta*, which enables pectin degradation with the help of two secreted pectinolytic enzymes, in order to supplement their absence of critical digestive enzymes. These microbial enzymes are necessary for the survival of the tortoise beetle [48]. It was discovered that the cellulose-degrading *Citrobacter* (*Enterobacteriaceae*) bacteria in the larvae of root-feeding white grub beetles, *Lepidiota mangoeta*, were probably providing their host with cellulose breakdown [47]. Additionally, it was discovered that *Enterobacteriaceae* were the most active in the phytophagous Forest Cockchafer (*Melolontha hippocastani*, *Coleoptera*) in terms of cellulose degradation, as evidenced by a high level of ¹³C isotope-labeled carbon incorporation into bacterial DNA following insect feeding from ¹³C-cellulose [49]. Because of the obligate symbiotic nature of their relationship, it is still unclear to what extent the symbionts are responsible for lignin digestion. However, it was discovered that *Reticulitermes flavipes* termites rely on both symbiotic protists and their host for the degradation of cellulose and lignin [50]. According to Kos *et al.* (2012) [51] and Yang *et al.* (2018) [52], plant preformed chemical barriers are made up of constitutively produced metabolites, or toxins, such as breakdown products of glycosides that contain sulphur and nitrogen, such as isothiocyanates, which can also be utilized as sources of carbon and nitrogen.

Blocking the plant's ability to recognize

Plants developed an innate immune system as a post invasive line of defence. Through this system, they are able to identify signals from stressed or wounded cells and nonself-molecules, activating a stress-specific counterreaction in response (Fig. 1). Insect-associated compounds like lipids, fatty acids, and fatty acid conjugates are released into the plant along with digestive enzymes like pectinase, β -glucosidase, and glucose oxidase when they begin feeding on host plants [53]. The plant's pattern recognition receptors (PRRs) can identify these compounds, which are sometimes referred to as herbivore associated elicitors (HAEs) or herbivorous-insect associated molecular patterns (HAMPs). These molecules then trigger a plant defence response. Plants can identify microorganisms using comparable chemicals known as microbe or pathogen associated molecular patterns (MAMPs or PAMPs), just like they can identify insects. Among these compounds include peptidoglycan (PGN), lipopolysaccharide (LPS), bacterial elongation factor thermo-unstable (EF-TU), fungal chitin, and flagellin (FLG) [54]. Furthermore, plant-derived elicitors known as damage-associated molecular patterns (DAMPs, such as peptides and oligogalacturonides) that are a component of the plant's wound response may be released in response to insect feeding or microbial invasion [55]. PRRs' recognition of elicitors triggers downstream signalling that is particular to stress and a defence response. Stress-specific PRRs that evoke particular responses let plants differentiate between different types of stress and lead to pattern-triggered immunity. Plant defence

signals can be targeted by effector molecules of invasive insects and microorganisms, which can compromise this response. When plants respond to these manipulative molecules with intracellular resistance proteins, effector triggered immunity results ^[56].

Effective pattern-triggered immune defences are activated when host plants recognize insects and the microorganisms they are connected with. To allow an unhindered invasion into the host plant, microbes have, nevertheless, evolved defence mechanisms against recognition by the plant. For example, the plant disease *P. syringae*, which is spread by insects, can inhibit the plant's ability to recognize its own flagellin molecules by secreting alkaline protease A (AprA), an enzyme that breaks down flagellin ^[57]. This mechanism has been demonstrated to be successful in keeping bacteria from recognizing their attackers, making them invisible to plants, in both human and plant cell cultures. It has been demonstrated that the *X. fastidiosa* plant pathogen, which is likewise spread by insects, responds to an effective pattern that triggers immunity by delaying LPS recognition in plants ^[58]. Insect-associated microorganisms may be able to stop their host insect from being identified by the host plant in addition to preventing recognition of themselves. It has been demonstrated that *Wolbachia* symbionts' short noncoding RNAs may impact the genes of their insect hosts, which may then indirectly change HAMPs that plants can identify ^[59].

Early plant defence signal interference

Plant receptor binding causes immediate release of calcium (Ca²⁺) influx, glutamate, phosphorylation of downstream receptor-like cytoplasmic kinases (RLCKs), calcium-dependent protein kinases (CPKs) and local phosphorylation of receptor kinases, that recruit and phosphorylate respiratory burst oxidase homologue D. (Fig. 1) (RbohD) ^[60]. Within minutes of an elicitor's recognition, plant cells depolarize as a result of extracellular reactive oxygen species (ROS) produced by RbohD activation. At an astounding rate of up to 2.4 cm min⁻¹ for Ca²⁺ and 8.4 cm min⁻¹ for ROS, both serve as second messengers that activate plant stress signalling throughout the entire plant ^[54]. It has been demonstrated that glutamate release plays a major role in facilitating Ca²⁺ long-distance signalling by activating cation-permeable ion channels that resemble glutamate receptors ^[61]. Moreover, the magnitude and character of Ca²⁺ signalling vary depending on the elicitor, suggesting that this general defence signal may contain information particular to stress ^[62].

Blocking Ca²⁺ signalling is crucial for piercing and sucking insects to avoid clogging plant sieve components, which are necessary for supplying phloem sap ^[63]. It is also known that bacteria spread by insects can affect plant defence signalling by interfering with the calcium signal. The plant's Ca²⁺ sensor, calmodulin, is the target of phytopathogenic *P. syringae* bacteria, which are spread by a variety of insects, including leaf mining fly larvae. This alters the production of ROS and increases the susceptibility of the plant to the pathogen ^[64]. Due to the well-known antimicrobial properties of ROS, microorganisms attempt to suppress their synthesis, which in turn helps insects who consume the same plant. By inhibiting the ROS-burst upon recognition, *Pseudomonas syringae* has been demonstrated to improve insect herbivory in *Arabidopsis* leaf mining fly larvae (*Scaptomyza flava*) ^[65]. As evidence of their advantageous impact on insects, *S. flava* larvae prefer to eat on *P. syringae*-infected leaves and grow there more quickly. In addition to the rapid second messenger-induced signalling caused by Ca²⁺ and ROS, activation of plant receptors also activates transcription factors (TFs) involved in stress signalling regulation, causes cross-communication between various stress signalling pathways, and amplifies phytohormone-driven and plant stress responsive pathways ^[66]. These signalling pathways downstream are targets for microorganisms as well.

Plant hormones

The modulation and amplification of plant defences are significantly influenced by plant hormones. Plants use a variety of phytohormone-driven signalling pathways, such as the production and accumulation of ethylene, salicylic acid, jasmonic acid, and abscisic acid, depending on the type of stress they are experiencing^[67]. One or more phytohormones must function laterally or concurrently in order for plants to respond to various biotic and abiotic stressors^[68]. In response to infections that feed on live cells, plants typically develop defences against them using salicylic acid. Defences against necrotrophic pathogens—pathogens that feed on dead plant tissues—are triggered by jasmonic acid and ethylene. In their necrotrophic stage, hemi-biotrophic infections (like *P. syringae*) cause plant defences against salicylic acid and then jasmonic acid. Chewing herbivores causes the induction of both jasmonic acid and abscisic acid; in contrast, abscisic acid is the hormone that reacts to abiotic stress. Two separate antagonistic signalling branches that are influenced by ethylene and abscisic acid are the outcome of jasmonic acid signalling^[69]. Plants employ development and growth related phytohormones such as auxin, gibberellin, cytokinins, brassinosteroids, and strigolactones in addition to phytohormone stress-driven plant signalling pathways. These phytohormones interact and cross-communicate with defence hormones^[70].

Bacteria have a wide range of adaptations that enable them to influence certain plant signalling pathways to guide their interactions. They are also known to produce phytohormones and their copies. Plant beneficial endophytes are known to boost nutrient acquisition (e.g., nitrogen fixation) or modulate plant hormones (e.g., auxin, gibberellin and cytokinin,) and are spread by piercing and sucking insects^[69]. Many bacteria, including *Acetobacter*, *Azotobacter*, *Azospirillum*, *Alcaligenes*, *Burkholderia*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Herbaspirillum*, *Pseudomonas*, *Pantoea*, *Rhizobium*, *Rhodococcus*, and *Streptomyces* are well known for their capacity to produce the primary auxin found in plants, namely indole-3-acetic acid^[71]. The latter is not surprising, given it was recently found that the production of indole-3-acetic acid in plants originates from horizontal gene transfer in bacteria. This explains the significance of the organisms in their interactions with one another as well as for both of them^[72]. Auxin signalling in plants is utilized by both insects and bacteria to encourage plant growth and guarantee enough food resources for their growth^[73]. Plant endophytes are known to stimulate plant development not only by increasing indole-3-acetic acid but also by reducing the plant stress hormone ethylene through the synthesis of the enzyme 1-aminocyclopropane-1-carboxylase deaminase^[74]. Additionally, the ethylene-repressive plant-beneficial bacterium *Klebsiella oxytoca* stimulates plant development^[75]. These likely influences plant defences against infections and insects through ethylene signalling. The phytopathogen *P. syringae*, which is carried by insects, also inhibits ethylene signalling, which stops ethylene-induced stomatal closure by using its HopM1 effector to facilitate entry into the plant's apoplast^[76]. Furthermore, *P. syringae* uses its AvrPto effector protein to suppress the production of DAMP-induced plant stress signalling as well as PAMP (flagellin and EF-Tu)^[77]. *P. syringae* AvrPto may help insects because DAMP responses are also seen in plant defences against eating insects.

It is also known that certain bacteria synthesise cytokinins, which have a direct impact on plant physiology. For instance, the leaf miner caterpillar insect symbiont *Wolbachia* (*Phyllonorycter blancardella*, *Lepidoptera*) releases cytokinins that induce a photosynthetically active green patch phenotype known as a "green island," increasing the insect host's survival as a result of an increase in Chlorophyll concentration in plants^[78]. Plant hormonal imbalance that spreads to uninfected tissues has also been linked to phytoplasma infection, providing a favourable nutritional state for insects on the plant^[79]. However, the synthesis of cytokinins has the potential to transform commensal plant bacteria into phytopathogens. It

appears that *P. agglomerans*, an insect symbiont and plant commensal, has acquired a plasmid harbouring genes for cytokinin production, which transforms the bacteria into a plant pathogen that forms galls^[80]. Moreover, it has been demonstrated that the galling mite *Fragariocoptes setiger* (*Eriophyoidea*) harbours other microbiota, such as *Agrobacterium*, *Pseudomonas*, *Rhodococcus* and *Erwinia*, that have the capacity to develop plant galls^[81]. Additionally, bioactive gibberellin produced by the plant pathogen *Xanthomonas oryzae* pv. *oryzicola* lowers the defences against jasmonic acid in plants, which indirectly benefits insects that feed on the affected plant. It was demonstrated that the gibberellin production route in bacteria and plants is identical, suggesting the possibility of cross-kingdom contact and perhaps horizontal gene transfer^[82].

Stress phytohormone interference and cross-communication

Plants depend on a cross-communicating, well-balanced signalling system to withstand a wide range of stressors (Fig. 2). Plant growth and development are frequently reported to be negatively regulated by stress signalling, indicating that stress signalling takes precedence over these processes in plants. On the other hand, stress signalling is adversely regulated by plant growth-related signalling, and both insects and microorganisms take advantage of this antagonistic relationship^[83]. Antagonism and synergism in the interaction between plant phytohormonal pathways have been well-documented and are quite intricate. Salicylic acid and jasmonic acid are the phytohormones that have been investigated the most among those recognized for their capacity to facilitate cross-communication^[84].

According to Verhage *et al.* (2011)^[85], insects' saliva and oral secretions are enough to suppress plants' unwanted jasmonic acid defences when they are fed on them. Additionally, bacteria found in oral secretions may be absorbed by the plant during feeding and trigger defensive mechanisms that prevent the plant from responding normally to insects that invade it. It has been shown that *Stenotrophomonas*, *Pseudomonas*, *Enterobacter*, and *Pantoea* bacteria within oral compartments induce plant salicylic acid defences, thereby repressing jasmonic acid-defenses and promoting optimal growth of the beetles (*Leptinotarsa decemlineata*) and its closely related false potato beetle (*L. juncta*)^[86]. Additionally, *Bemisia tabaci*, a whitefly that feeds on phloem, uses its *Hamiltonella defensa* symbionts to repress plant jasmonic acid defences against insects through salicylic acid-jasmonic acid antagonistic interactions. It has also been demonstrated that oral secretions of *Spodoptera litura*, which contains *Staphylococcus epidermidis*, can suppress jasmonic acid and produce salicylic acid^[87]. Similarly, *P. syringae* -induced salicylic acid-jasmonic acid antagonistic effects are advantageous for the cabbage looper moth *Trichoplusiani*. However, by suppressing salicylic acid defences, *P. syringae* bacteria may be harmful to generalist insects.

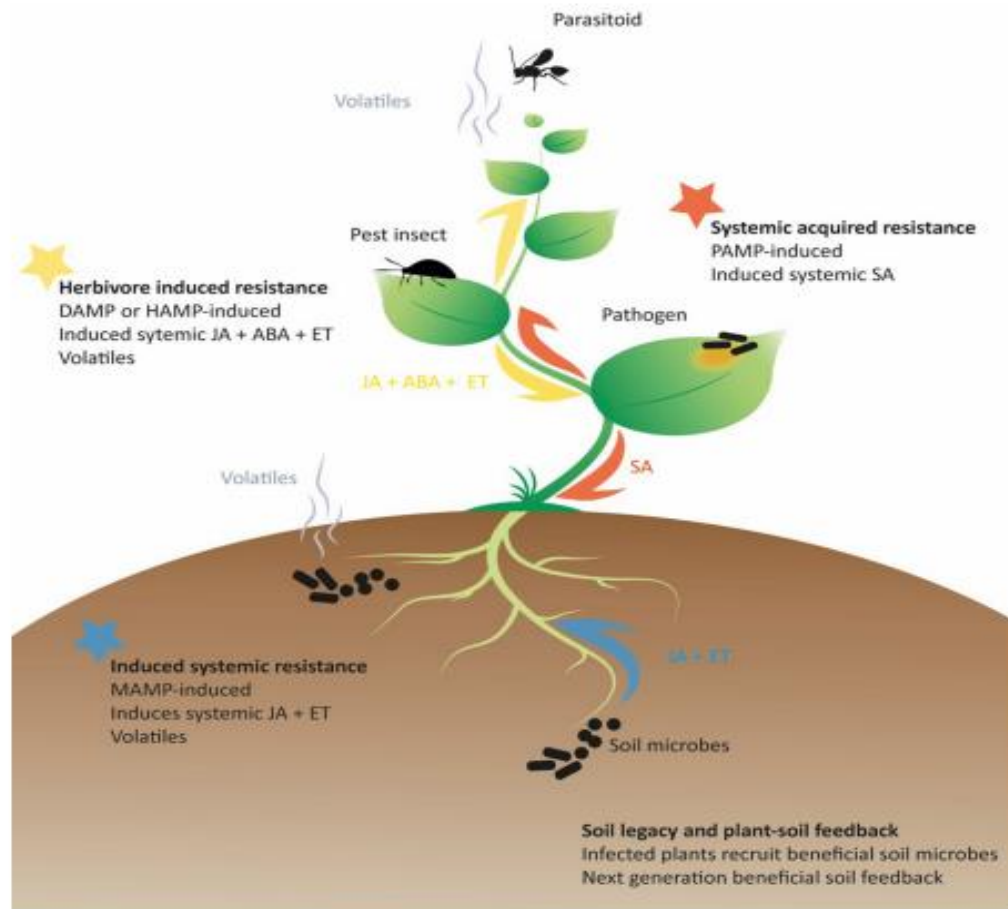


Figure 2: An outline of the main mechanisms involved in induced systemic plant defence.

In plants, herbivorous insects cause damage or herbivore-induced resistance (shown in yellow), which results in defence priming for ethylene (ET), abscisic acid (ABA), and jasmonic acid (JA). The generation of herbivore-induced plant volatile emissions, which draws in insect parasitoids that parasitize insects, is another aspect of herbivore-triggered resistance. Plant PAMP-induced systemic acquired resistance (SAR, in red) is a response to pathogenic microorganisms, which are frequently spread by insects. This response primes plants' defences against salicylic acid (SA). Beneficial soil bacteria for plants have the ability to cause induced systemic resistance (ISR), which prepares plants for ethylene and JA defences and the subsequent release of volatiles. This process may be carried out by insects. Additionally, beneficial bacteria that are attracted to infected or diseased plants shield subsequent plant generations from infection by means of a microbial soil legacy and plant–soil feedback.

Coronatins are jasmonic acid-mimics that stimulate stomatal opening and facilitate the entry of germs into the plant's apoplast. The tomato yellow leaf curl virus C2 protein, which is carried by the white fly *B. tabaci*, has been shown to suppress plant jasmonic acid responses to insect feeding while promoting insect survival and reproduction [88]. Plant JASMONATE ZIM DOMAIN (JAZ) transcriptional repressor proteins necessary for plant jasmonic acid responses were shown to be protected from degradation by the viral C2 protein [55]. Additionally, aphids are known to transmit a variety of viruses, such as the cucumber mosaic virus [89], which weaken plant defences. It has been demonstrated that the CMV 2b protein suppresses plant responses to jasmonic acid, and that plants become highly resistant to aphids when the

protein is absent during infection, highlighting the significance of insect-associated microbes in insect-plant interactions ^[90].

Enhanced defensive capacity

Different enhanced defence response states that plants have an impact on insects and their microbiota (Fig. 2). Plant resistance to insects and pathogens is largely dependent on the microbiota of the rhizosphere (underground) and phyllosphere (above ground), which are linked to soil bacteria that promote defence and beneficial growth ^[91]. Plant-beneficial rhizobacterium *K. oxytoca*, for example, can cause systemic resistance (ISR) by preparing plants for defences against necrotrophic diseases and insects through the production of ethylene and jasmonic acid ^[67]. The plant can react to a threat more swiftly and forcefully while it is in this prepared state. One pathogen that would be impacted by ISR is *Pectobacterium*, a necrotrophic plant pathogen that lives in the gut of *Delia radicum* larvae, the cabbage root fly ^[92]. Systemic acquired resistance is another kind of improved state of plant defences (SAR). Systemically elevated salicylic acid levels are a hallmark of SAR. This phenomenon occurs when an earlier infection with a pathogen, which can be spread by insects, sets off pattern- or effector-triggered immunity, making uninfected systemic tissue more susceptible to salicylic acid-signaling against biotrophic and hemibiotrophic pathogens. Furthermore, herbivore-induced resistance describes the systemic accumulation of proteinase inhibitors caused by herbivores (DAMP or HAMP), which prevents insect digesting enzymes.

Rooted in the soil

The impact of bacteria and insects on plant defences is mediated by a soil-born legacy, according to a highly intriguing new discovery (Fig. 2). The establishment of a beneficial soil microbiota following plant pest infestation or infection by (vector-transmitted) diseases offer plants grown on the same soil in subsequent generations with protective plant-soil feedback ^[19]. Friman *et al.* (2021) ^[93] conducted a sophisticated experiment in which cabbage plants were subjected to several herbivorous insects, such as *D. radicum* larvae, Aphids, or *Plutella xylostella* caterpillars. Following this, the soil from these plants was used to challenge a second generation of plants with *D. radicum* larvae, and the performance of the insects was evaluated.

Plant's volatile compounds

Insect deterrent and parasitoid or vector-attracting herbivore-induced plant volatiles are eventually produced and released as a result of plant defence signalling (Fig. 2) ^[94]. According to Casteel *et al.* (2012) ^[95] *Ca. L. asiaticus* and *Ca. Liberibacter psyllaourous* repress the salicylic acid and jasmonic acid defences caused by their psyllid vector. They also release volatile methyl-salicylic acid, which draws in psyllid insects that carry the bacteria. A similar situation for apple plants infected with phytoplasma has been reported. Apple tree pests *Cacopsylla picta* psyllids are drawn to infected trees by their emitting a sesquiterpene called E- β -caryophyllene, which serves as a vector ^[24]. Conversely, insect symbionts may also lessen the volatile emissions from plants, so preventing the attraction of parasitoids. *H. defensa*, an endosymbiont of the pea aphid (*A. pisum*), decreased the systemic release of plant volatiles, which in turn decreased the recruitment of parasitoids (*Aphidius ervi*) ^[6]. Bacteria can also produce volatiles. Fruit containing volatile terpenes, such as 2-methylisoborneol generated by *Streptomyces* bacteria, attracts fruit flies (*Drosophila melanogaster*) to oviposit on it ^[96]. Nonetheless, the bacterium's chemical defences cut

off larvae growing on fruit colonized by *Streptomyces*, indicating that this process may be used for biocontrol techniques.

Microbial detoxification of defence chemicals in plants

Eventually, phytoalexins, glycosides, and their breakdown products, as well as antifeeding compounds like lectins, are produced as a result of plant defence signalling. These compounds primarily target the digestive system of insects and have an impact on their gut barrier ^[97]. There are hundreds of identified secondary plant metabolites, including glucosinolates, alkaloids, flavonoids, terpenes, and compounds generated from fatty acids, that have an impact on insect herbivores ^[98]. Several well-known plant secondary metabolites, such as solanine, tomatine, caffeine, and nicotine, have insecticidal effects. Insect poisoning can pose a serious risk even though their meal retention period is brief. Insects possess a multitude of adaptations that enable them to consume plants with specific defence mechanisms since they have coevolved with their host plants ^[99]. Target-site modifications, inactivation by gut alkalization, fast excretion, sequestration, degradation, and detoxification by glutathione transferases, carboxylesterases, and cytochrome P450 monooxygenases are some of these resistance mechanisms ^[100]. There are known to be over 660 P450 monooxygenases in insects, and these enzymes, along with the reductases they are linked with, give insects resistance to every known kind of pesticide ^[101]. Furthermore, the act of consuming harmful plants creates significant selective pressure on the gut microbiota of the insect and increases the likelihood of microbial modifications that may be advantageous to their host insect ^[102]. Numerous writers have discussed the significance of symbiotic bacteria in detoxification and their effect on the functionality of insects ^[103]. For example, Ceja-Navarro *et al.* (2015) ^[104] showed that the ability to degrade oleuropein and caffeine was lost in insects without microbiota. One of the most important issues facing agriculture today is detoxifying microbial symbiosis, a special coping mechanism that insects use to deal with poisonous secondary plant compounds and pesticides ^[105].

Conclusion

Insect-associated microorganisms are crucial in influencing plant responses during insect-plant interactions ^[59]. It is still mostly unclear how bacteria accomplish this, which has led to an intriguing and quickly developing field of study. Numerous insects have microbial associations, with a subset recognized to be phytopathogenic or capable of modulating plant defence mechanisms for the advantage of their host insect. The diversity of microbes found in insects is immense, and our knowledge of how they can influence interactions between insects and plants is still developing. Microbes can undermine plant defences in a variety of ways, including by blocking the activation of defences, altering phytohormonal signalling in plants, and detoxifying secondary metabolites in plants. Because microbial changes dictate an insect's range of plant hosts, it has even been demonstrated that the microbiota of the insect influences whether the insect is classified as a pest. Different from single interactions, multitrophic interactions are unpredictable and might result in unforeseen consequences ^[106]. The relationships between the microbiota of the insect and its host plants are also true. Beyond microbes, one should also carefully explore the complexity of insect-plant interactions. Via volatile alarm signals, plants can communicate with one another and prepare defences against insects and viruses that they see as threats. Even plants can pass on epigenetic markers to their progeny in the form of inherited changes that shield off dangers in subsequent generations ^[107].

Additionally, plants may come across several insects that change how they interact with other insects and the bacteria they are linked with and depending on the pathogen's lifecycle, the presence of several microorganisms or pathogens can result in different consequences. plant reaction ^[44]. Looking ahead, plants and crops will probably face complex multitrophic interactions more often because of our changing climate, which will allow insects and pathogens to spread more easily and even outside of their typical growing seasons ^[108].

Food security is expected to face significant challenges due to the fast-growing human population, which is expected to reach 9.3 billion people by 2050 ^[109]. To fulfil future food demands, a significant increase in efficient food production is necessary (UN 2011, FAO 2012). Effective pest management is essential to meeting these needs. Pesticides were formerly essential instruments for controlling pests, but due to health concerns and resistance development, their use is now drastically decreased ^[110].

Consequently, without negatively influencing the ecological footprint, employing and enhancing the naturally occurring adaptive mechanisms of plants, insects, and the microbes that they are associated with may offer sustainable options. Further understanding of the multitrophic interactions between insects, plants, and the microbes that coexist with them is necessary to efficiently design strategies for managing pests and plant diseases. Given that insects depend on the microbial services provided by these microorganisms, they could make excellent targets for pest control efforts.

Conflict of interest

The author states no conflict of interest.

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