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REVIEW



Unlocking agro-ecosystem sustainability: exploring the bottom-up effects of microbes, plants, and insect herbivores

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Abstract

Agricultural ecosystem formation and evolution depend on interactions and communication between multiple organisms. Within this context, communication occurs between microbes, plants, and insects, often involving the release and perception of a wide range of chemical cues. Unraveling how this information is coded and interpreted

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is critical to expanding our understanding of how agricultural ecosystems function in terms of competition and cooperation. Investigations examining dual interactions (e.g. plant–microbe, insect–microbe, and insect–plant) have resolved some basic components of this communication. However, there is a need for systematically examining multitrophic interactions that occur simultaneously between microorganisms, insects, and plants. A more thorough understanding of these multitrophic interactions has been made possible by recent advancements in the study of such ecological interactions, which are based on a variety of contemporary technologies such as artificial intelligence sensors, multi-omics, metabarcoding, and others. Frequently, these developments have led to the discovery of startling examples of each member manipulating the other. Here, we review recent advances in the understanding of bottom-up chemical communication between microorganisms, plants, and insects, and their consequences. We discuss the components of these “chemo-languages” and how they modify outcomes of multi-species interactions across trophic levels. Further, we suggest prospects for translating the current basic understanding of multitrophic interactions into strategies that could be applied in agricultural ecosystems to increase food safety and security.

Key words: chemical languages, communication, herbivorous insects, multitrophic interactions, plant cues, plant-associated microbes

INTRODUCTION

Ecosystems comprise ecological units, such as populations, species, and communities (Krebs *et al.* 2024), that are intertwined within complex networks that affect agricultural productivity, fertility, and sustainability (Guimarães 2020). In recent decades, expanding human activities have progressively increased the frequency and severity of disturbance events that alter the complexity, dynamics, and function of ecosystems, including those used for cultivation (Hoque 2023). In some instances, the intensity and extent of ecosystem alteration can be so severe that it may cause ecosystem collapse or reach a “point of no return,” as, for instance, reported for environmental pollution with microplastics (Priya *et al.* 2022). There is a consensus that the overgrowth of livestock and crops and intensive agriculture in general, combined with the degradation and destruction of natural habitats caused by urbanization, industrialization, and overexploitation of natural resources, are threatening the stability and resilience of ecosystem units and their networks.

The increase in the global human population is accompanied by rising food demand, making sustainable agricultural productivity essential for meeting food security demands. In parallel, awareness of the importance of environmental quality, whether in terms of maintenance or restoration has led to greater demands for the development of “greener,” that is, sustainable and renewable, agricultural practices, so that environmental degradation and/or pollution can be contained or even reversed (Sridhar *et al.* 2023). Crop production is one activity where production demands and environmental concerns intersect, as this sector has long re-

lied on the (over-) use of chemical fertilizers, insecticides, antimicrobials, and other potentially environmentally harmful activities (Çakmakçı *et al.* 2023). Some of the negative consequences of these practices include the emergence of pesticide-resistant insects and antibiotic-resistant microbes, as well as environmental pollution that can affect water quality, species diversity, soil and plant health, interactions between trophic levels, and even the quality of the cultivated crop (Zhang *et al.* 2018).

Microorganisms, plants, and insects are three important actors in both man-made and natural ecosystems. Plants provide food sources and habitats for large numbers of microorganisms and insects, and, in turn, can significantly benefit from the presence of beneficial microorganisms and insects. There has been considerable research focused on di-trophic interactions occupying different trophic levels, that is, on microorganism–plant, plant–insect, or microorganism–insect interactions (Biedermann & Rohlf 2017; Jones & Agrawal 2017; Vurukonda *et al.* 2018; Alhoraibi *et al.* 2019; Chen & Mao 2020; Ye *et al.* 2021; Wang *et al.* 2023). These investigations have often yielded insights into practical applications such as the development of novel pest and/or disease-specific remediation strategies (Beck & Vannette 2017; Cellini *et al.* 2021). Yet, our understanding of the interactions remains highly limited without considering three or more interactions across trophic levels simultaneously.

Examining such tri-trophic interactions, that is, between microorganisms, plants, and insects should yield insights for practical interventions to maintain or increase agricultural productivity and resilience. For instance,

inoculation of soil with beneficial microbes may induce tolerance or defenses among plants against insects, reducing damage and crop loss associated with herbivores (Pangesti *et al.* 2020). On the other hand, certain fungal microbes, for example, symbionts, can assist insects in detoxifying plant-produced defensive compounds, thus increasing their performance and/or host range (Li *et al.* 2021). These multitrophic interactions can also act as a driving force mediating biodiversity and adaptation, with imbalance disruptions between partners potentially resulting in significant negative consequences for ecosystem function and biodiversity (Jeavons *et al.* 2022; Ali 2023). Increased invasions of non-native (plant, microbial, and/or insect) species because of human activity (e.g. increasing global trade and travel) and/or climate change are a prime example. A variety of invasive plants have been shown to significantly change soil microbial communities, affecting the abundance and diversity of native insects, animals, and other plants (Tobin 2018; McLeod *et al.* 2021). Invasions by non-native microbial plant pathogens and insect pests can even lead to the functional extinction of indigenous plant species (Tobin 2018). Therefore, an increased understanding of multitrophic interactions may facilitate the restoration of ecological balances, and, in terms of pathogen and pest control, can help improve applications of integrated pest management practices in cultivated ecosystems (Stelinski *et al.* 2019).

Unraveling the functional characteristics of multitrophic interactions is crucial for establishing sustainable foundations for modern crop production that seek to maintain both food and environmental security. Recent progress in the application of emerging technologies such as metabarcoding, multi-omics, artificial intelligence, and various sensors has shed new insights into the mechanisms governing microbe–plant–insect interactions (Grunseich *et al.* 2019; Liu *et al.* 2019; Mason *et al.* 2019; Wan *et al.* 2020; McCary *et al.* 2021). One striking discovery is that plant-associated microbes can affect herbivore behavior and performance by altering plant-produced visual, olfactory, and gustatory cues (recognized by plant pests). These effects likely place selective pressure on the formation of ecological traits and evolutionary (co-) adaptations for each player, leading to competing changes to pest tolerance among plants and herbivore performance on those hosts (Kamali *et al.* 2022).

It should be kept in mind that both outcomes can occur, as the same physiological effects caused by microbes on plants can result in the repellence of some insects but attraction for others. Here, we explore potential mechanisms that regulate these tritrophic interactions and summarize the current understanding of how microbes affect

plants, which in turn affect the behavioral responses of insects (Fig. 1). Furthermore, we discuss how investigations of these multi-trophic interactions integrate tools and techniques from related disciplines and may increase translation of results into practical outputs that could be integrated into pest and/or plant disease control. This information will facilitate further development of models in molecular ecology, increasing our understanding of ecosystem homeostasis for the purpose of managing and/or improving agroecosystems from the perspective of functional ecology.

Microorganisms are key players affecting the biochemical and physical traits of plants, such as size, biomass, shape, structure, growth (root, stem, and leaf rates), spectral reflectance, color, and metabolite content. Some microbes, for example, rhizobia, may additionally increase the nutritional quality of plants by providing scarce or needed nutrients (e.g. nitrogen in exchange for carbon), which not only affects the plant but also modulates the quality and quantity of available plant metabolites attractive to insect herbivores (Shikano *et al.* 2017). Conversely, some plant microorganisms can stimulate plant defenses by promoting induced systemic resistance, in turn reducing attacks by insect herbivores (Pieterse *et al.* 2014). Thus, microorganisms can play important roles in determining the nature, persistence, and consequences of insect–plant interactions by shaping the gustatory, olfactory, and visual cues perceived by insect herbivores and by providing real-time information on the location and status (healthy or diseased) of a potential host plant and/or its nutritional and defense status. The feeding and oviposition behaviors of insect herbivores are also adjusted as a function of the information perceived by plants (Fig. 2).

MICROBIAL CHANGES TO VISUAL CUES PRODUCED BY PLANTS INDIRECTLY AFFECT INSECT BEHAVIOR

Beneficial plant microbes are usually thought to enhance plant growth and biomass; therefore, such microorganisms may induce visual cues associated with higher plant vigor and/or nutritional/defense status to potentially facilitate foraging and oviposition by insect herbivores (Grunseich *et al.* 2019). Increased plant biomass and resistance against abiotic stress are known to result from plant associations with arbuscular mycorrhizal fungi (AMF), for example, the association of *Glomus intraradices* with various herbaceous plants (Kempel *et al.*

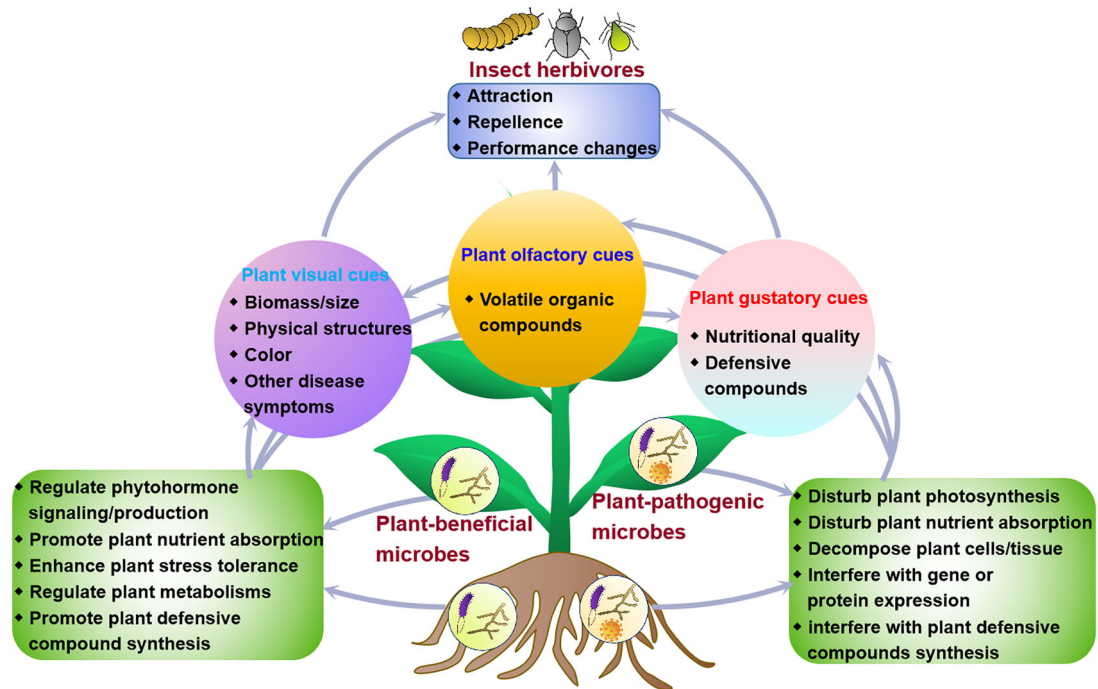


Figure 1 Model diagram of microbes regulating behaviors of insect herbivores via modification of plant-produced cues.

2010). In turn, such plant growth stimulation has been shown to enhance insect biomass, for example, increased growth of Egyptian cotton leafworm (*Spodoptera littoralis*) developing on AMF-inoculated plants. Moreover, by altering plant physical defense structures, AMF may also increase the foraging behavior of herbivorous insects. For example, plant trichomes act as the first line of plant defense against herbivory, and their density can be reduced in AMF-associated plants, for example, tomatoes (Malik *et al.* 2018). In turn, this may increase herbivore performance/damage, as has been reported for early-stage potato beetle larvae (*Leptinotarsa decemlineata*). These data suggest the importance of considering microbial-mediated trade-offs when considering their applications; that is, the increase in plant growth seen in applying AMF may be offset by increased pest density, activity, and crop damage.

Plant growth and development can be promoted by microorganisms via regulation of different plant hormone-growth and defense-related pathways, including those involved in the production of auxin, cytokinin, ethylene, gibberellin, abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA) (Puga-Freitas & Blouin 2015). For example, ethylene acts as an inhibitor of root elongation, lateral growth, and root hair formation. Therefore, beneficial microorganisms may promote plant growth by re-

ducing plant ethylene levels through the production of microbial 1-aminocyclopropane-1-carboxylate (Nascimento *et al.* 2018). Microorganisms may also tap into host signal transduction pathways to induce the production of plant growth-promoting hormones, such as auxin, and, in many cases, may themselves produce plant growth-stimulating hormone analogs that target the growth of their hosts (Mastretta *et al.* 2006).

A number of microorganisms increase plant biomass by enhancing nutrient absorption. Nitrogen-fixing bacteria convert atmospheric N_2 into ammonia via nitrogenase activity, which is then directly absorbed and used by plants (Pineda *et al.* 2010). Other soil- or root-associated microorganisms secrete organic acids (e.g. gluconic acid, 2-ketogluconic acid) that dissolve inorganic phosphate, solubilizing this essential nutrient for plant use (Hameeda *et al.* 2008). Various plant-associated microbes release extracellular phosphatases that mineralize organophosphate esters for plant utilization (Kim *et al.* 1998). Furthermore, some microorganisms bind Fe^{3+} for plant use by secreting siderophores that can then be taken up by plant cells via specific transporters (Compant *et al.* 2005).

Microorganisms also promote plant tolerance to a range of abiotic stresses, including drought, salt, and heavy metal stress in soils, thus increasing plant health and growth (Weyens *et al.* 2009; Yang *et al.* 2009; Pineda

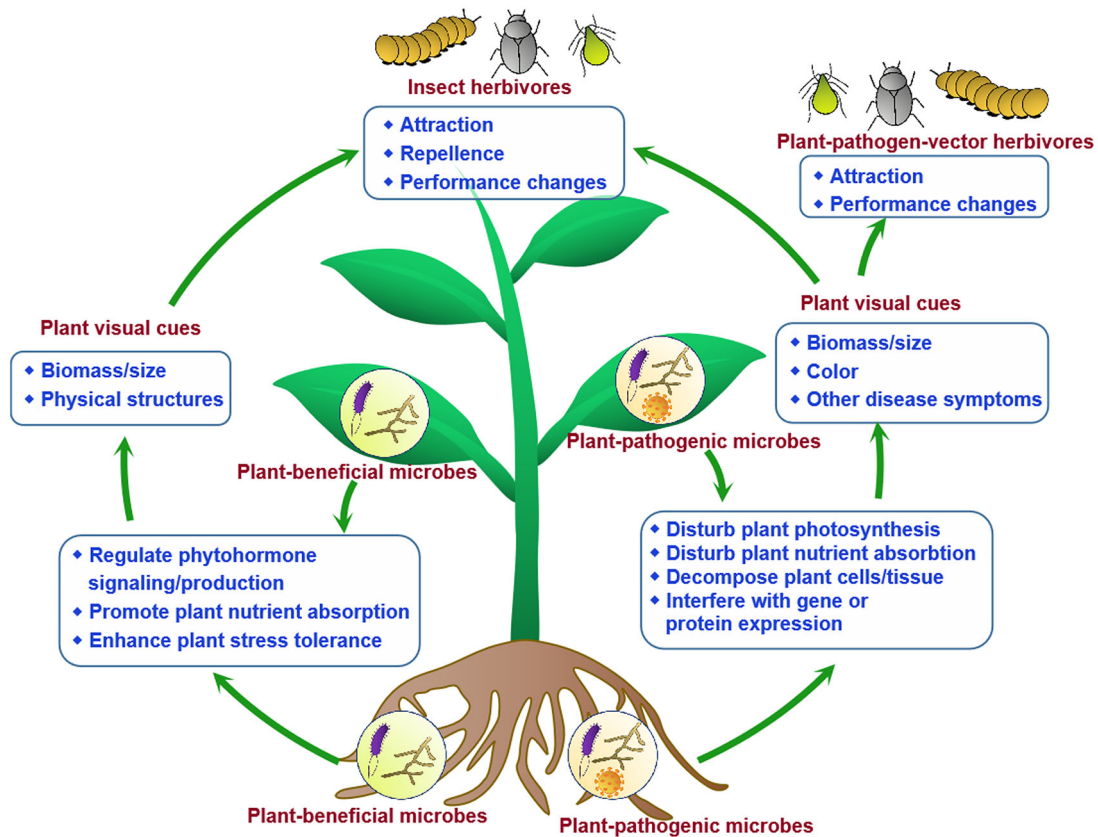


Figure 2 Model diagram of microbes regulating behaviors of insect herbivores via modification of plant-produced visual cues.

et al. 2010). In terms of drought stress, various plant growth-promoting rhizobacteria (PGPR) increase plant resistance by altering the expression of genes associated with stress response and modulating activity levels of antioxidant enzymes (Vurukonda *et al.* 2016). PGPR may even alter root morphology by producing extracellular polysaccharides, phytohormones, and phytohormone analogs (e.g. indole-3-acetic acid, gibberellin, and ABA), specific enzymes (e.g. 1-amino cyclopropane-1 carboxylate deaminase), volatiles (e.g. 2R,3R-butenediol), and osmolytes (e.g. proline, trehalose, and choline) (Vurukonda *et al.* 2016) that promote root health and growth. AMF (e.g. *Glomus etunicatum* and *Glomus mosseae*) have been shown to improve the salt tolerance of plants [e.g. soybean (*Glycine max*) and maize (*Zea mays*)] by (1) promoting the acquisition of plant nutrients (phosphorus, nitrogen, magnesium, and calcium), (2) facilitating the accumulation of osmoprotectants and/or antioxidants, (3) helping to maintain optimal $K^+ : Na^+$ ratios, (4) regulating physiological processes (e.g. improving photosynthetic efficiency, maintaining water content, stimulating

ABA accumulation, enhancing nodulation, and improving nitrogen fixation), and (5) affecting expression levels of drought resistance genes such as *PIP*, *Lsnced*, *Lslea*, *LsP5CS*, and various Na^+ / H^+ antiporters (Evelin *et al.* 2009).

Unlike beneficial plant microbes, plant-pathogenic microbes often cause obvious disease symptoms, such as necrosis of leaves, stems, roots, flowers, and/or fruit, as well as changes to color, which can affect insect foraging and oviposition behavior (Hodge & Powell 2010; Jagiello *et al.* 2019). In fact, vector-borne phytopathogens can enhance the attractiveness of plants to insect vectors by inducing plant disease symptoms, ultimately promoting the spread of the pathogenic microorganisms. For example, barley, wheat, and oats infected with the *Barley yellow dwarf virus* exhibit reduced leaf size and yellowing, which increases the attractiveness of infected host plants to the associated vectors (e.g. the aphids *Metopolophium dirhodum* and *Sitobion avenae*) (Ajayi & Dewar 1983). Similarly, pea plants (*Pisum sativum*) infected with the *Pea enation mosaic virus* exhibit symptoms of yellow spots

and leaf curling. Compared to healthy plants, these visual attributes enhance the attractiveness of infected plants to pea aphids (*Acyrtosiphon pisum*). Furthermore, aphid growth and reproduction are increased on plants with well-developed *Pea enation mosaic virus* symptoms than on non-infected, healthy counterparts (Hodge & Powell 2010). Other examples include the leaves of broad bean (*Vicia faba*) and grapevines (*Vitis vinifera*), which become yellowish after infection by the bacterial agent, *Flavescence dorée* phytoplasma. This color change increases the attraction/prevalence of *Scaphoideus titanus* leafhopper nymphs and/or adults feeding on diseased bean plants and grapevines (Chuche *et al.* 2016).

Intriguingly, plant visual cues modified by non-vector-borne phytopathogens are often also recognized by non-vector herbivores but result in avoidance of egg laying on infected plants. For example, the non-vectoring leaf-miner species *Cameraria ohridella* selectively avoids ovipositing in the red-brown necrotic areas of leaves of horse chestnut (*Aesculus hippocastanum*) infected by the pathogenic fungus, *Phyllosticta paviae* (Desmazières) (Jagiello *et al.* 2019). A similar phenomenon has also been documented for the light brown apple moth, *Epiphyas postvittana*, a polyphagous pest on pome and stone fruits that avoids laying eggs in the necrotic areas of moderately and heavily gray mold (*Botrytis cinerea*)-infected grapevines exhibiting soft rot symptoms (Rizvi *et al.* 2015). From an adaptive perspective, such behavior of non-vector insects to selectively avoid laying eggs on microbially infected plants or tissue sites should reduce the likelihood of them or their progeny becoming also infected by the same microbe(s) and/or suffering from potential performance loss on diseased and sub-optimal host plants.

Infection of host plants by pathogenic microorganisms may obstruct and/or decrease the efficiency of photosynthesis *via* tissue damage and loss of chloroplasts/chlorophyll content or other pigment molecules, resulting in nutrient deficiency, disruption of carbon fixation, and reduced carbohydrate synthesis. Depending on the severity or progression of the disease, such damage becomes noticeable as changes to plant color (e.g. chlorosis and yellowing) (Pontes *et al.* 2020). Many pathogenic fungi and bacteria decompose and destroy plant cells and tissue structures by secreting a variety of enzymes. These enzymes include endo- β -1,4-xylanases and polygalacturonases that target plant xylan and homogalacturonan, respectively (Misas-Villamil & van der Hoorn 2008). The enzymes may also interfere with gene or protein expression levels in host plants by producing a variety of virulence factors, including effector proteins, secondary

metabolites, and even small RNA molecules (Doehle-*mann et al.* 2017). Ultimately, this infection may result in plant cell necrosis or decay (Pontes *et al.* 2020).

Pathogenic microorganisms may also disrupt the normal balance of plant metabolism and the production of hormones, which may either result in inhibition of plant cell growth or, conversely, in excessive proliferation leading to “tumors” or abnormal plant forms. For example, *Agrobacterium tumefaciens* and *Agrobacterium rhizogenes* regulate plant auxin, ethylene, and SA pathways to form tumors or galls on plant tissues, within which the bacteria proliferate and reside, accessing nutrients from the host (Lee *et al.* 2009).

MICROBIAL CHANGES TO OLFACTORY CUES PRODUCED BY PLANTS INDIRECTLY AFFECT INSECT BEHAVIOR

Plant-associated microorganisms affect the quantity and/or quality of plant volatile organic compounds (VOCs), many of which affect the behavioral response patterns of herbivorous insects. These VOCs reveal information regarding plant identity (Bruce *et al.* 2005), nutritional composition (Goff & Klee 2006), health/defense status, and/or the degree of predation risk by potential natural predators to foraging herbivores (Helms *et al.* 2019). Some VOCs, known as allomones, repel or deter insect herbivores as part of direct plant defense, whereas others, referred to as kairomones, may serve as host-finding or oviposition cues to herbivorous insects (Dicke 2016). Insects perceive changes in microbially altered, plant-emitted chemical cues and respond accordingly (Kessler & Baldwin 2001; Touhara & Vosshall 2009). This process is dynamic, with plants under selection pressure to develop “deceptive” cues to ward off potential insect herbivores and insects under selection pressure to properly decode these cues to find suitable feeding and ovipositing sites.

Both direct and/or indirect plant defenses may be enhanced following inoculation of plants with beneficial microorganisms via changes in VOC composition and subsequent modulation of herbivore feeding and oviposition behavior (Table 1). For example, treating Lima bean plants (*Phaseolus lunatus*) with a combination of rhizobium (genus *Bradyrhizobium*) and JA resulted in a significant decrease in total volatile release (Ballhorn *et al.* 2013). However, this co-treatment also results in a significant increase in indole levels, a derivative product of the

Table 1 Alterations of plant volatile organic compounds released after microbial inoculation and the corresponding behavioral changes occurring in insect herbivores

Microorganism species	Plant species	Plant-produced olfactory cues	Herbivorous insect species	Insect behaviors	References
Beneficial bacteria					
Genus <i>Bradyrhizobium</i>	Lima bean (<i>Phaseolus lunatus</i>)	Total volatiles↓, indole↑	Mexican bean beetle (<i>Epilachna varivestis</i>)	Repellent	Ballhorn <i>et al.</i> (2013)
<i>Pseudomonas fluorescens</i> WCS417r	<i>Arabidopsis thaliana</i>	Terpene (E)- α -bergamotene↓, methyl salicylate↓, linalil↓	Cabbage moth (<i>Mamestra brassicae</i>)	\	Pangesti <i>et al.</i> (2015a)
<i>Bacillus velezensis</i> strain INR-7	Maize (<i>Zea mays</i>)	(E)-5-Methyl-2-methylene-2-hexen-1-ol↓, 3-Hexen-1-ol↓, linalool↑	European corn borer (<i>Ostrinia nubilalis</i>)	Repellent	Disi <i>et al.</i> (2017)
<i>Bacillus velezensis</i> strain AP-188, <i>Bacillus mojavensis</i> strain AP-209, <i>Ficibacillus solisalsi</i> strain AP-217, and <i>Bacillus velezensis</i> strain AP-218	Maize (<i>Zea mays</i>)	(E)-5-Methyl-2-methylene-2-hexen-1-ol↓, 3-hexen-1-ol↓	European corn borer (<i>Ostrinia nubilalis</i>)	Repellent	Disi <i>et al.</i> (2017)
<i>Bacillus velezensis</i> strain AP-136, <i>Bacillus velezensis</i> strain AP-219, and <i>Bacillus velezensis</i> strain AP-295	Maize (<i>Zea mays</i>)	(E)-5-Methyl-2-methylene-2-hexen-1-ol↓, 3-hexen-1-ol↓	European corn borer (<i>Ostrinia nubilalis</i>)	Repellent	Disi <i>et al.</i> (2017)
Beneficial fungi					
<i>Neophodidium lolii</i> “wild-type” strain (E ^{WT})	Perennial ryegrass (<i>Lolium perenne</i>)	2-Ethyl-1-hexanol acetate↑, (Z)-2-octen-ol↑, butylated hydroxytoluene↑	African black beetle (<i>Heteronychus arator</i>)	Repellent	Qawasmeh <i>et al.</i> (2015)
<i>Neophodidium lolii</i> AR1 strain (E ^{AR1})	Perennial ryegrass (<i>Lolium perenne</i>)	2-Ethyl-1-hexanol acetate↑, (Z)-2-octen-ol↑, butylated hydroxytoluene↑, octanal↑, 5-methyl-1-heptene↑, (E)-2-hexen-1-ol↑	African black beetle (<i>Heteronychus arator</i>)	Repellent	Qawasmeh <i>et al.</i> (2015)
<i>Neophodidium uncinatum</i>	Grass hybrid (<i>Festuca pratensis</i> × <i>Lolium perenne</i>)	Acetic acid↓, ethanol–water cluster↓, hexanal/hexanols↓, monoterpenes↓, acetaldehyde↓, dimethylsulphide↓, CO ₂ ↑	Grass grub (<i>Costelytra zealandica</i>)	Repellent	Rostás <i>et al.</i> (2015)

(Continued)

Table 1 (Continued)

Microorganism species	Plant species	Plant-produced olfactory cues	Herbivorous insect species	Insect behaviors	References
Pathogenic bacteria					
<i>Erwinia tracheiphila</i>	Wild gourd (<i>Cucurbita pepo</i> ssp. <i>texana</i>)	Foliar volatiles: 1-pentanol↑, Toluene↑, Hexenal↑, <i>c</i> -2-hexenal↑, <i>z</i> -3-hexen-1-ol↑, Xylenes↑, Ocimene↑; Floral volatiles: Linalool↓, Nonatriene↓, 1,4-methoxybenzene↓	Striped cucumber beetle (<i>Acalymma vittatum</i>)	Attracted to leaves; repellent to flowers	Shapiro <i>et al.</i> (2012)
<i>Candidatus Liberibacter asiaticus</i>	Citrus (<i>Citrus sinensis</i>)	Methyl salicylate↑, methyl anthranilate↓, D-limonene↓	Asian citrus psyllid (<i>Diaphorina citri</i>)	Attractive then repellent	Mann <i>et al.</i> (2012)
Pathogenic fungi					
<i>Botrytis cinerea</i>	Grapevines (<i>Vitis vinifera</i>)	3-Methyl-1-butanol↑	European grapevine moth (<i>Lobesia botrana</i>)	Repellent	Tasin <i>et al.</i> (2012)
Rose powdery mildew (<i>Podosphaera pannosa</i>)	China rose (<i>Rosa chinensis</i>)	\	Beet armyworm (<i>Spodoptera exigua</i>)	Repellent	Yang <i>et al.</i> (2013)
Anther smut fungus (<i>Microbotryum violaceum</i>)	White campion (<i>Silene latifolia</i>)	Lilac aldehyde↓, (<i>Z/E</i>)-arbusculone↓, phenylacetaldehyde↓, lilac degradation↓, (<i>E</i>)- β -ocimene↓	Noctuid moth (<i>Hadena bicruris</i>)	Repellent	Dötterl <i>et al.</i> (2009)
Virus					
<i>Cucumber mosaic virus</i> (family <i>Bromoviridae</i>)	Cultivated squash plants (<i>Cucurbita pepo</i> cv. Dixie)	Total volatiles↑	<i>Myzus persicae</i> ; <i>Aphis gossypii</i>	Attractive then repellent	Mauck <i>et al.</i> (2010)
<i>Potato leaf roll virus</i>	Potato (<i>Solanum tuberosum</i>)	2-Hexen-1-ol↑, nonane↑, myrcene↑, limonene↑, pinene↑, nonanal↑, undecane↑, decanal↑, cadinene↑, caryophyllene↑, α -humulene↑, 7-11-dimethyl-3-methyl-dodecatriene↑, β -sesquiphellandrene↑, longifolene↑	<i>Myzus persicae</i>	Attractive	Eigenbrode <i>et al.</i> (2002)
<i>Barley yellow dwarf virus</i>	Barley (<i>Hordeum vulgare</i>)	Methoxybenzene↑, (<i>Z</i>)-3-hexenyl acetate↑, undecane↑, nonanal↑, naphthalene↑, dodecane↑, decanal↑, 2-methyl dodecane↑, tridecane↑, 2-methyl tridecane↑, copaene↑, tetradecane↑, caryophyllene↑, unidentified sesquiterpene↑, 9-methyl nonadecane↑, pentadecane↑, 2-methyl pentadecane↑, hexadecane↑	Bird cherry-oat aphid (<i>Rhopalosiphum padi</i>)	Attractive	Jiménez-Martínez <i>et al.</i> (2004)

plant shikimic acid pathway. These changes, in turn, affect insects, in particular reducing feeding by the Mexican bean beetle (*Epilachna varivestis*) (Ballhorn *et al.* 2013). Indole has also been shown to promote the synthesis of volatiles such as terpene, JA-isoleucine conjugate, and ABA. These compounds act to enhance plant systemic resistance to insect herbivores (Erb *et al.* 2015). Similarly, the generalist herbivore, Egyptian cotton leafworm (*S. littoralis*), prefers feeding and ovipositing on indole-deficient maize mutants over wild-type plants (Veyrat *et al.* 2016).

Microbial infection of plants causing reduced VOC production may also indirectly affect plant defense processes (Table 1). Plants inoculated with *Pseudomonas fluorescens* WCS417r respond to the cabbage moth, *Mamestra brassicae*, by releasing lower amounts of (*E*)- α -bergamotene and methyl salicylate, which is associated with reduced expression of the terpene synthase genes *TPS03* and *TPS04*. This results in increased attraction of the parasitoid wasp, *Microplitis mediator*, which acts as an indirect defense against the cabbage moth (Pangesti *et al.* 2015a, 2016). Various strains of the endophytic fungus, *Neotyphodium lolii*, colonizing ryegrass (*Lolium perenne*) differentially affect the VOC composition of the plants they infect (Qawasmeh *et al.* 2015). Specifically, colonization by E^{WT} and E^{ARI} strains causes infected hosts to produce higher levels of 2-ethyl-1-hexanol acetate, (*Z*)-2-octen-ol, and butylated hydroxytoluene relative to control plants without fungi. The African black beetle (*Heteronychus arator*) was less attracted by E^{WT} and E^{ARI}-infected ryegrass compared to control plants (Qawasmeh *et al.* 2015). In addition, colonization of maize with different PGPR strains reduced VOC production. For example, three strains of PGPR inoculation suppressed the release of 3-hexen-1-ol and significantly decreased the levels of (*E*)-5-methyl-2-methylene-2-hexen-1-ol in maize. These changes were associated with decreased oviposition by the European corn borer (*Ostrinia nubilalis*) on PGPR-colonized maize as compared to control plants (Disi *et al.* 2017). Colonization of the vegetative portion of the grass hybrid *Festuca pratensis* \times *L. perenne* by the endophytic fungus *Neotyphodium uncinatum* decreased total VOC production but increased CO₂ content in roots. These changes decreased the attractiveness of the endophytic fungus-treated grass to the root herbivore, grass grub (*Costelytra zealandica*), as compared to uncolonized plants, thus benefiting the plant (Rostás *et al.* 2015).

The transmission and spread of many phytopathogens are mediated by insect vectors. Certain pathogens indirectly manipulate insect vector behavior by changing the

composition or concentration of VOCs released by their host plants to recruit potential insect vectors to infected plants (Table 1), which may result in increased pathogen transmission (Sharifi *et al.* 2017). For instance, the total amount of VOCs released by cultivated squash plants (*Curcubita pepo* cv. Dixie) increases after infection by the non-persistently transmitted *Cucumber mosaic virus* (family *Bromoviridae*). The increased emission of these VOCs, in turn, renders infected plants more attractive to the aphids, *Myzus persicae* and *Aphis gossypii*. Although aphids are initially attracted to infected plants as a result of the pathogen-altered VOCs, over time, the aphids disperse to uninfected plants because diseased plants are of lower nutritional quality, which ultimately promotes the spread of the virus (Mauck *et al.* 2010). Also, persistently transmitted viruses, such as the *Potato leaf roll virus*, cause an increase in the total amount of VOCs released by potato plants (*Solanum tuberosum*). These include greater production of β -sesquiphellandrene, 2-hexen-1-ol, and cadinene, which causes the aphid vector, *M. persicae*, to preferentially feed on infected over uninfected potato plants (Eigenbrode *et al.* 2002). Barley yellow dwarf virus is also a persistently transmitted virus and induces an increase in the total amount of volatiles in infected plants. This causes the vector insect, that is, the bird cherry-oat aphid (*Rhopalosiphum padi*), to preferentially feed on infected than uninfected barley (*Hordeum vulgare*) (Jiménez-Martínez *et al.* 2004).

In addition to plant viruses, bacterial pathogens transmitted by phytophagous insects also promote the spread of pathogens by modifying plant VOC release (Martini *et al.* 2016) (Table 1). For example, wild gourd (*Cucurbita pepo* ssp. *texana*) infected with the bacterial pathogen, *Erwinia tracheiphila*, exhibits increased leaf VOC content (e.g. 1-pentanol, toluene, and hexenal) and decreased floral VOC content (e.g. linalool, nonatriene, and 1,4-methoxybenzene), which increases the attractiveness of leaves to the insect vector, the striped cucumber beetle (*Acalymma vittatum*). In this pathosystem, the pathogen is thought to indirectly modulate vector behavior by initially attracting vectors to the leaves of infected plants for pathogen acquisition and subsequently attracting vectors to the flowers of healthy plants for pathogen inoculation (Shapiro *et al.* 2012). In citrus (*Citrus sinensis*), infection with a bacterial pathogen (*Candidatus Liberibacter asiaticus*) increases the release of methyl salicylate, which attracts the Asian citrus psyllid (*Diuraphis citri*) vector to infected over uninfected plants (Mann *et al.* 2012). Congruent with the “deceptive host phenotype hypothesis” (Mauck *et al.* 2010), the Asian citrus psyllid subsequently disperses to healthy plants,

possibly because they are nutritional superior to infected counterparts (Mann *et al.* 2012). With the broad use of various odor collection/adsorption devices coupled with gas or liquid chromatography–tandem mass spectrometry, it is becoming easier to describe the quantitative and qualitative changes in VOCs released by plants as mediated by disease progression. These techniques may be further combined with assays of insect behavior or GC-electroantennography to screen and identify critical VOCs released by plants after microbial colonization that affect insect behavior.

In contrast to the indirect effects of pathogens on insect vectors, pathogen-induced changes to plant cues (i.e. VOCs) typically reduce behavioral responses of non-vectors to infected plants (Table 1). For example, infection of grapevines by the fungal gray mold (*B. cinerea*) pathogen increases the production of 3-methyl-1-butanol, which in turn decreases the attractiveness of infected plants to the non-vector insect herbivore, the European grapevine moth (*Lobesia botrana*). This presumably benefits the insect by decreasing egg laying on fungus-infected plants suffering from rot symptoms, which would be sub-optimal for offspring development (Tasin *et al.* 2012). Yang *et al.* (2013) found a similar phenomenon in China rose (*Rosa chinensis*) after infection by rose powdery mildew (*Podospheera pannosa*); VOC release reduced feeding and oviposition behavior of the non-vector insect, beet armyworm (*Spodoptera exigua*), on infected plants. In addition, the total amount of volatiles released by the white campion, *Silene latifolia*, decreased after infection by the anther smut fungus, *Microbotryum violaceum*, including decreased release of lilac aldehyde, an attractant cue for the non-vector noctuid moth, *Hadena bicruris*. Consequently, *H. bicruris* avoids feeding and ovipositing on infected plants that are presumably rendered sub-optimal for offspring development (Dötterl *et al.* 2009). A summary of VOC production results following inoculation of plants with various microorganisms and the corresponding changes in herbivore behavior is provided in Table 1.

Microorganisms affect insect behavior via changes to VOC release by modulating plant signaling cascades (Sharifi *et al.* 2017). For example, the plant hormone JA induces the expression of genes related to the synthesis of a spectrum of volatile compounds, with JA levels regulated by a series of signal transduction pathways. However, the jasmonate ZIM domain (JAZ) protein has a negative regulatory effect on volatile biosynthetic gene expression induced by JA (Thines *et al.* 2007). In the resting state, JAZ binds to the transcription factor MCY2, which in turn binds to the G-box region of the JA re-

sponse gene promoter, thereby inhibiting the expression of JA-responsive genes (Wasternack & Hause 2013). In the presence of an external stimulus that can include the addition of JA itself, CO11 recruits the JAZ protein to the Skp1/Cullin/F-box protein complex via E3 ubiquitin ligase activity. This leads to JAZ protein ubiquitination and subsequent degradation by the 26S proteasome. With the degradation of the JAZ protein, MCY2 is free to activate the expression of JA-responsive genes (Wasternack & Hause 2013). Recent studies have shown that some pathogenic microorganisms alter plant volatile profiles (in some cases increasing and in others decreasing VOC production) by targeting the JAZ protein. For example, the effector protein 2b released by the *Cucumber mosaic virus* interacts with and prevents JA-induced degradation of the host JAZ protein. This inhibits the expression of volatile synthesis genes in plants, resulting in changes to the VOC content emitted by infected plants. The altered profile, in turn, increases the attractiveness of infected plants to the phytopathogen vector, *M. persicae* (Wu *et al.* 2017). Conversely, coronatine, a toxin secreted by *Pseudomonas syringae*, promotes the interaction between JAZ and CO11 (Melotto *et al.* 2008). This might lead to the degradation of JAZ and the subsequent promotion of the expression of JA-dependent volatile biosynthetic genes, which requires further investigation. Pathogen-associated molecular patterns (PAMPs) produced by pathogenic microorganisms have also been shown to affect levels of plant volatiles that regulate the behavior of insect herbivores. For example, the treatment of plants with the bacterial flagellin peptide Flg22, a typical bacterial PAMP, significantly increases JA levels. Moreover, longer durations (2 and 3 h) of plant exposure to Flg22 significantly increase volatile content, which can include heptanal, nonanal, hendecanal, and other compounds (Tu *et al.* 2017). Considering that plant hormone signals play pivotal roles in both VOC production and growth regulation, the indirect effects of microorganisms (PAMPs and effectors) on insect behavior via plant hormone signaling pathways deserve further investigation.

MICROBIAL CHANGES TO GUSTATORY CUES PRODUCED BY PLANTS INDIRECTLY AFFECT INSECT BEHAVIOR

The interaction between microorganisms and plants often causes changes in plant quality with respect to nutrients made available to insect herbivores. These may

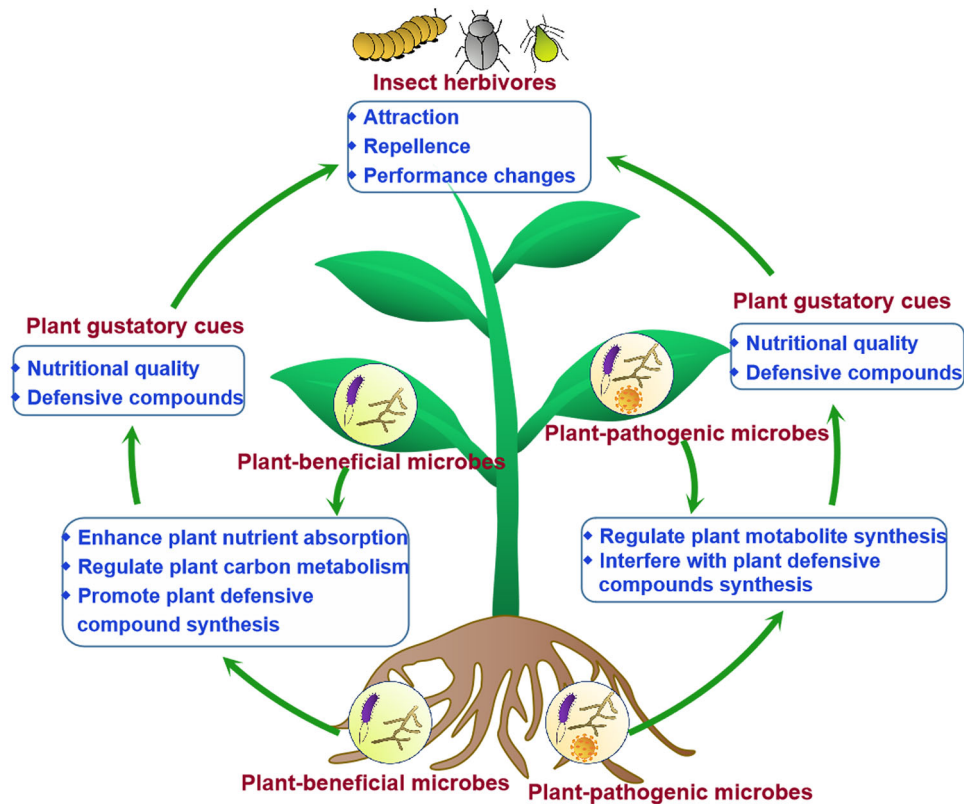


Figure 3 Model diagram of microbes regulating the behaviors of insect herbivores via modification of plant-produced gustatory cues.

include altered levels of carbohydrates, amino acids, and/or plant-defensive secondary metabolites, which may directly affect host-plant selection and/or reproductive strategies employed by herbivorous insects (Aqueel *et al.* 2014). These non-volatile compounds are important gustatory cues specifically perceived by various receptors on insect herbivore antennae, mouthparts, tarsi, and/or ovipositor structures, which may affect various behaviors, including feeding and/or oviposition (Grunseich *et al.* 2019) (Fig. 3).

Beneficial microbes improve plant nutritional status by promoting nutrient absorption, thus affecting host selection by insect herbivores. For example, the rice water weevil, *Lissorhoptrus oryzophilus*, usually lays its eggs in the sheath of rice leaves, and emerging larvae feed on rice roots. Association of the AMF, *Glomus intraradices* with rice, increases concentrations of phosphorus and nitrogen in rice shoots and increases nitrogen content in roots, which enhances insect oviposition on AMF-colonized plants (Cosme *et al.* 2011). Given the microbe-mediated sequestration of nutrients in AMF-colonized plants, preferential oviposition on such plants

results in higher survival rates of subsequent offspring, thus favoring insects that are able to recognize AMF-colonized plants.

Beneficial microorganisms may also affect insect behavior by modulating levels of plant defensive compounds. For example, colonization of cotton (*Gossypium hirsutum*) by PGPR (*Bacillus* sp.) increases levels of gossypol, a phenolic yellow pigment that inhibits dehydrogenase activity in cotton seeds, roots, and stems (Zebelo *et al.* 2016). Gossypol acts as a plant defense against insect herbivores by decreasing insect fertility, and *Bacillus* sp. increases the expression of several gossypol synthesis-related genes in plants (e.g. (+)- δ -cadinene synthase gene family members). Ultimately, this effect decreases the survival/reproductive rates of beet armyworm larvae on PGPR-colonized plants (Zebelo *et al.* 2016). With respect to beneficial fungi, AMF colonization has been shown to change the nitrogen and phosphorus contents of milkweed (*Asclepias* spp.), as well as alter levels of several defensive compounds, including cardenolide and latex; cardenolide is a toxic steroid while latex inhibits feeding (Tao *et al.* 2016). The monarch butterfly

(*Danaus plexippus*) preferentially lays eggs on milkweed plants with low levels of cardenolides, likely to facilitate offspring survival (Jones & Agrawal 2019).

Pathogenic microorganisms may also affect insect behavior by modulating nutritional content and/or defensive metabolites in plants, which can be perceived by herbivores as changes in gustatory cues. For example, infection of peanut (*Arachis hypogaea*) with the pathogenic fungus, *Sclerotium rolfsii* Sacc., increases concentrations of soluble sugars, with a concomitant decrease in levels of defensive compounds (e.g. soluble phenolics) (Cardoza *et al.* 2003a,b). Infected plants often receive greater oviposition from the beet armyworm. Overall, insect larvae exhibit higher survival, develop faster, and achieve greater pupal weight when developing on infected plants (Cardoza *et al.* 2003b). When compared with uninfected coffee beans, female coffee berry borers (*Hypothenemus hampei*) produce more offspring on beans infected with *Fusarium solani*, where the fungal infection causes increased production of ergosterol (Morales-Ramos *et al.* 2000). Ergosterol plays an important role in regulating the growth and development of insects (Wen *et al.* 2023), and because insects are unable to synthesize ergosterol *de novo*, they must obtain it from food. Thus, *F. solani* indirectly promotes the growth and development of beetles by providing enriched sources of ergosterol in infected plants (Morales-Ramos *et al.* 2000).

In some instances, plants may transfer anywhere between 4% and 20% of the carbon fixed by photosynthesis to the AMF mutualists in the form of sugars and lipids (Kaur & Suseela 2020). The consumption of plant carbon by these fungi increases the photosynthetic activity of the plants by forming a carbon “sink” in the roots. Consequently, levels of carbon metabolism in AMF-associated plants are usually higher than in their AMF-lacking counterparts, resulting in very different levels of carbon-containing compounds (e.g. sugars and amino acids) between the two (Kaur & Suseela 2020). The influence of microorganisms on non-volatile defensive compounds (e.g. isoflavonoids, alkaloids, tannins, and phenolics) often depends on the particular plant and microbial species associated with the plant (Korenblum & Aharoni 2019). However, in most instances, the underlying regulatory mechanisms that cause these differences remain unclear, with further research needed to better understand the mechanisms affecting plant nutritional status as well as how insect herbivores perceive the associated changes via gustatory cues.

MICROBES INDUCE PLANT-MEDIATED CROSSTALK VIA MULTIPLE CUES TO AFFECT INSECT BEHAVIOR

Tritrophic interactions between microbes, plants, and insect herbivores are mediated by visual, olfactory, and gustatory perception. Insects usually do not rely on a single sensory system to locate host plants (George *et al.* 2020). Microbial colonization of plants may simultaneously affect multiple plant cues, and the resulting changes are likely to act in concert to affect the behavior of insect herbivores. For instance, colonization of cucumber with the PGPR, *B. pumilus* (strain INR-7), promotes an increase in biomass but also reduces the concentration of cucurbitacin (Zehnder *et al.* 1997a,b). Cucurbitacin is a bitter secondary metabolite produced by cucurbitaceous plants that is toxic to most insect herbivores. However, the cucumber beetle (*Diabrotica undecimpunctata*) is not only able to tolerate this metabolite but actually sequesters it as a defensive compound against its own natural enemies (Brzozowski *et al.* 2020). Moreover, the number of beetles feeding on cucumbers is positively correlated with total cucurbitacin content. In this instance, the bacterial association with host plants affects both plant visual and gustatory cues and results in a decreased prevalence of cucumber beetles on infected plants with lower cucurbitacin levels (Zehnder *et al.* 1997a,b).

Another example of behavioral manipulation of herbivores caused by plant viruses occurs in rice infected with a combination of two viruses (*Rice tungro bacilliform virus* and *Rice tungro spherical virus*) causing tungro disease. Infection of rice by these viruses modifies plant cues to attract the vector insect, green leafhopper (*Nephotettix virescens*). Whereas the vector initially prefers to feed on infected plants, 24 h after the initial feeding, the insects disperse and aggregate on healthy plants as their preferred food source (Khan & Saxena 1985). Free sugars and soluble protein content in tungro disease-infected rice are increased, yet the palatability of the infected plants to the leafhoppers is reduced. Although the mechanism causing the initial attractiveness of infected plants to the planthopper remains unclear, it is likely the result of altered visual and/or olfactory cues released by virus-infected plants. The coordinated direct versus indirect effects that microbes have on vector behavior following plant infection (which may result in either attraction or deterrence of specific insects) are worth exploring further,

particularly with respect to how these coordinated effects operate through integrated visual, olfactory, and gustatory cues. One hypothesis is that insects rely on olfactory cues for long-distance orientation and subsequently switch to visual cues to distinguish between potential plant hosts and identify specific targets for oviposition to maximize the growth and development of their progeny.

Plants simultaneously confront a variety of pathogenic microorganisms in both natural and agricultural ecosystems. Due to the highly diverse range of species of plant-associated microorganisms, the modulation of herbivore behavior by microorganisms should be considered a dynamic process that may change over time (even within a single day), and these changes are likely affected by factors including circadian rhythms, fluctuations in abiotic conditions, changes in soil constituent contents (e.g. phosphorus and nitrogen levels), and interactions among the microbes themselves as they co-occur in various combinations on different species of host plants. For example, infection of the broad bean by the rust fungus (*Uromyces viciae-fabae*) increases nitrogen concentration in plants (Al-Naemi & Hatcher 2013). The black bean aphid (*Aphis fabae*) prefers feeding on *U. viciae-fabae*-infected leaves to uninfected counterparts, as these plants improve aphid growth rates and fertility (Al-Naemi & Hatcher 2013). Conversely, infection by the necrotrophic fungus gray mold (*B. cinerea*) results in decreased nitrogen content in the broad bean. In this case, the growth rate and fecundity of the aphids are reduced on gray mold-infected plants compared with healthy plants. Under conditions where the two fungi simultaneously infect the broad bean, there is a decrease in plant nitrogen content, but this does not seem to affect the growth rate and/or fecundity of the insects. However, when the two fungi successively infect the broad bean, the nitrogen content is decreased, and aphid fecundity is decreased (Al-Naemi & Hatcher 2013). These results highlight the complexity of interactions that can occur even when there are relatively few species interacting and the potential importance of succession, that is, the order of microbial association.

A similar phenomenon was also observed in a plant–virus–herbivore interaction (Peñaflor *et al.* 2016). Soybean plants infected with the *Bean pod mottle virus* exhibit increased levels of glucose and several amino acids in their leaves. These infected plants were more attractive to Mexican bean beetles (*E. varivestis*) than uninfected counterparts (Peñaflor *et al.* 2016). In the case of the *Soybean mosaic virus*-infection, soybean plants are characterized by decreased JA levels, increased SA levels, and increased leaf glucose, leaf and phloem sucrose, and total and specific amino acid concentrations. The attractiveness

of infected plants to both Mexican bean beetles and soybean aphids, *Aphis glycines*, is greater than that of their uninfected counterparts (Peñaflor *et al.* 2016). *Bean pod mottle virus* and the *Soybean mosaic virus* co-infected soybean plants exhibit decreased JA levels, increased SA levels, and increased phloem sucrose, and total and partial amino acid content. However, the co-infected plants only showed increased attractiveness to the soybean aphids (Peñaflor *et al.* 2016). Collectively, these studies suggest that co-infection of pathogenic microorganisms in plants may have differential effects on the interaction between plants and insect herbivores, and this can change the dynamics of pathogen spread.

CONCLUSIONS AND OUTLOOK

In natural ecosystems, tritrophic interactions among plants, insects, and microorganisms facilitate stability. Plant-associated microorganisms regulate the preference and performance of insect herbivores by modulating variable plant-produced cues. Plant associations with both beneficial and pathogenic microbes affect various physiological and molecular processes in plants, such as phytohormone signaling, biosynthesis, and nutrient absorption, and this includes regulation at the gene and protein expression levels. The consequences of these activities are changes in plant-produced visual, olfactory, and gustatory cues that can subsequently affect the growth, survival, feeding, and ovipositing preferences of insect herbivores. The fluid nature of horizontal gene transfer between microbes, insects, and plants confers selective advantages to the recipient organism and may provide important evolutionary mechanisms for enhanced adaptations for all three associates (Matveeva *et al.* 2012; Stritzler *et al.* 2018). Discovering not only additional examples of horizontal gene transfer events, but also considering gene loss, diversification, and convergent evolution (e.g. genes affecting plant hormone levels) is necessary for a more detailed understanding of how these systems function.

Insect herbivore-associated microbes also play important roles in the ecology and evolution of insect–plant interactions (Ma *et al.* 2023; Zhang *et al.* 2023). The effects of both plant- and insect-associated microbes should be considered simultaneously in future studies. Furthermore, most recent investigations of plant–insect–microbe interactions continue to be conducted in a largely controlled lab or semi-field environments. However, in real-world scenarios, biotic factors like co-infection or co-infestation by multiple species of microbes or insect herbivores and abiotic factors like salt stress, drought stress, and

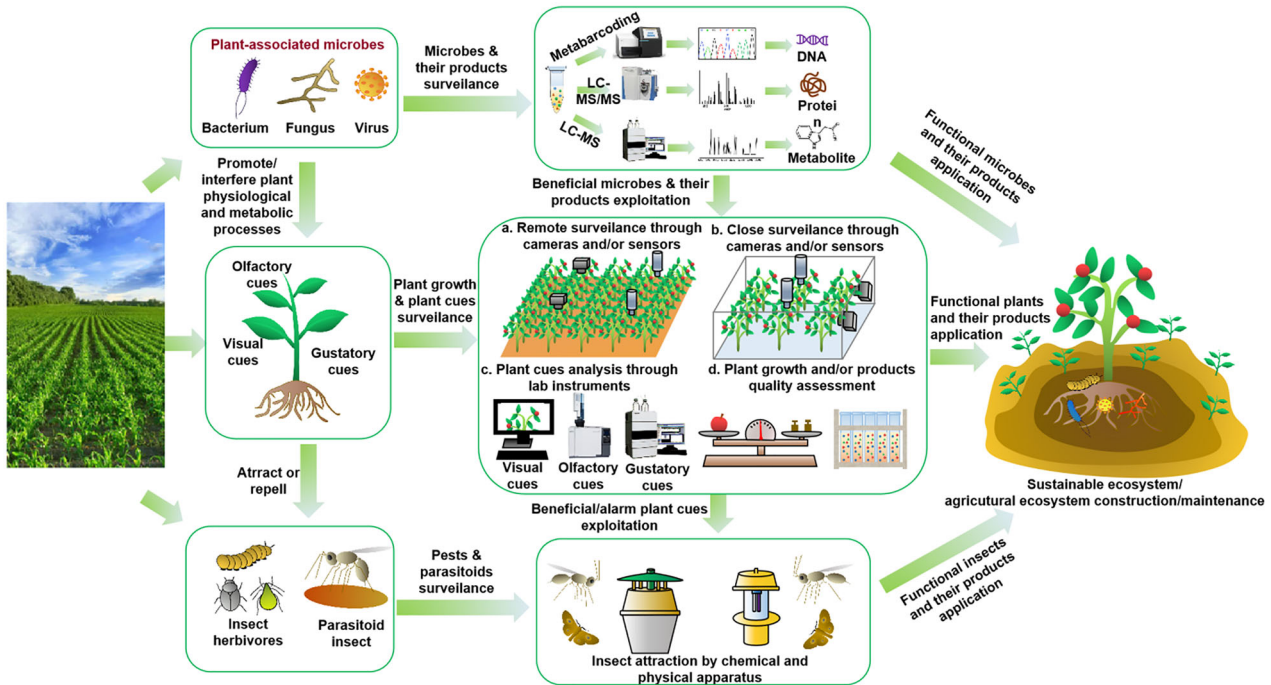


Figure 4 Future directions to monitor the dynamic changes occurring during interactions among various organisms in agricultural ecosystems. Construction of such surveillance networks with capabilities in metabarcoding, image capture, and gustatory and olfactory cue surveillance combined with insect-attractant traps could identify critical organisms or their components modulating ecosystem changes and facilitate understanding of the “languages” that mediate interactions among organisms.

nutrient deficiency also affect tritrophic interactions. Future research integrating the effects of various abiotic factors is needed to better understand the mechanisms governing tritrophic interactions.

In particular, this research may have important applications for the improvement of pest control strategies for agricultural applications. For example, understanding how microbial associations with plants affect pest behavior could determine the timing and nature of integrated pest management practices (Stelinski *et al.* 2019; Bai *et al.* 2023). For instance, some entomopathogenic fungi not only promote plant growth but also increase plant defense responses against insect herbivores (Jaber & Enkerli 2017). Therefore, reshaping the soil microbiome is one possible strategy for pest management in agroecosystems or for restoration in degraded natural ecosystems (Pineda *et al.* 2017). This can be accomplished by developing and commercializing beneficial microbial inoculants (Bai *et al.* 2015; Yu *et al.* 2022). Similarly, microbial inoculates can stimulate host plants to produce insect-repellent volatiles and/or defensive compounds. Furthermore, soils with beneficial bacterial and/or fungal communities could be purposefully transplanted to promote

soil disease-suppressive properties (Mendes *et al.* 2011; Raaijmakers & Mazzola 2016; Wubs *et al.* 2016) and/or to regulate environmental factors (e.g. soil temperature or moisture levels) to alter the residing soil microbiome composition to a desired beneficial state (Dessaux *et al.* 2016; Raaijmakers & Mazzola 2016; Kolton *et al.* 2017; Chen *et al.* 2020; DuPont *et al.* 2021; Liu *et al.* 2021). Plant factors, including plant species, ontogeny, and root exudates, may modify the soil microbiome directly or indirectly. Thus, crop rotation, intercropping, or cover crops are also useful tactics for shaping the desired soil microbiome in agroecosystems.

Future investigations should also aim to classify and resolve the cues involved in tritrophic interactions that shape natural and agricultural ecosystems (Fig. 4). For instance, specific microbial species or their components may be identified and then employed to either attract natural predators or parasitoids or to repel herbivorous pests by modifying plant visual cues. For example, the use of light and/or infrared light detection in agricultural crops via cameras has been applied to monitor coloration as a marker for plant health and/or pest infestations. Combining such data outputs with insect trapping and

metabarcoding technologies may enable automated quantification of human influence within small ecosystems and allow manipulation for pest management within agroecosystems.

Unraveling the chemistry of multitrophic interactions in phytoplasma disease systems may advance the applications for pest control. For example, synthetic mixtures of phytopathogen-induced volatile odorants may be used to manipulate vector behavior. In addition, certain microbial or herbivore-induced odorants may be used to attract parasitoids. Dynamic monitoring of plant volatiles by GC-MS combined with microbial metabarcoding and insect behavioral assays can be employed to understand these interactions for the development of practical tools.

Similarly, many microbial or herbivore-induced metabolites exhibit antiviral, insecticidal, and fungicidal activities. Determining the factors that induce the production of these metabolites might yield applications with limited negative effects on ecosystems (Elshafie *et al.* 2023). For instance, dynamic surveillance of plant/soil/water microbes or their products during ecosystem change or growth could facilitate the re-construction of functional networks that resolve interactions between the species involved. This could be used to identify indicator species that signal the occurrence of stress or that indicate the occurrence of random disturbance that may require human intervention. The construction of such surveillance networks could benefit humans by enabling the reconstruction of ecosystems damaged by previous anthropogenic activities. An increasing number of intelligent surveillance sensors and associated instruments have been developed that include capabilities for metabarcoding, image capture, and e-nose sensors. The application of these surveillance sensors and instruments could greatly accelerate investigations of communication networks within ecosystems and lay the foundations for further functional and theoretical studies that benefit ecosystem management.

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