Review Paper

Dynamic interplay of plants, microorganisms, and arthropods: exploring ecosystem

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ABSTRACT

Plants, microorganisms, and arthropods continuously interact within the intricate system of the environment. These interactions can often lead to significant crop damage due to diseases and pests; however, there are also circumstances where microorganisms serve as necessary symbiotic plant partners. A range of beneficial microbes in the soil support plant development and health through direct and indirect mechanisms. These beneficial microorganisms, also known as "little helpers" are vital due to their ability to colonize various niches and their ubiquitous presence. Increasingly, such microorganisms are used as biological control agents and microbial fertilizers. They are specific to pests and diseases, with a minimal negative impact on humans and the environment. Plants face numerous environmental challenges and must respond appropriately to survive. Recent studies suggest that beneficial microbial biota in the soil can affect herbivores, highlighting the importance of these biological agents. Specifically, they can reduce the harmful effects of herbivorous insect pests, which damage plants are a major factor in global yield losses. Therefore, they are expected to be essential candidates to replace chemical insecticides in the near future. This review includes recent findings on many aspects of below-ground and above-ground plant-mediated interactions.

Keywords: plant-mediated interactions, pest management, symbiosis, three-way interactions

INTRODUCTION

The world population is estimated to increase by approximately 83 million annually and is expected to reach 9.7 billion by 2050 (UN 2022). The increasing population brings along significant problems. One of the biggest challenges in this regard is how to meet the growing demand for food by the world's expanding population. Currently, one out of every nine people in the world is struggling with hunger, and Food and Agriculture Organization (FAO) estimates, food demand will increase by over 200% by 2050 (FAO 2018, 2021). On the other hand, crop losses to an average of up to 50% annually worldwide due to plant disease and pests (Fried et al. 2017; Grabka et al. 2022).

This figure is roughly equivalent to the food that could feed one billion people annually.

Intensive agriculture practices reliant on chemical inputs were heavily emphasized in the past century to feed the rapidly growing human population. This farming approach has caused significant damage to natural resources over the past fifty years. Irresponsible practices are rapidly depleting and polluting clean water, soil quality, energy, and biodiversity (IFPRI 2016; FAO 2021). This situation accelerates the disruption of the natural balance that restricts the spread of diseases, pests, and weeds, leading to even more damage (Bramble 1989; Arora and Dhaliwal 1996; Dhaliwal et al. 2010). The multifaceted problems caused by using chemical pesticides to control pests, which in turn cause economic damage, so the is a need to develop alternative methods. Thus, changes in European Union legislation (European Parliament Directive 2009/128/EC) restrict chemical pesticides and fertilizers in agricultural production processes, highlighting the apparent need to develop alternative methods to control pests while maintaining crop yields.

Plants, microorganisms, and arthropods constantly interact with each other in the ecosystems they inhabit. These interactions have a significant impact on plant growth and productivity. Harmful or pathogenic microorganisms can reduce yield, while productivity can increase through mutualistic relationships established with beneficial microorganisms (Ballhorn et al. 2017; Wilkinson et al. 2019). Unfortunately, the effects of arthropods and microorganisms on plants have been studied independently by entomologists and phytopathologists. While phytopathologists concentrate on the study of plant diseases brought by microorganisms like fungi, bacteria, and viruses, entomologists study insects and other arthropods. Researchers can better understand the elements that affect plant health and productivity by adopting a more interdisciplinary approach and considering the interactions between plants, arthropods, and microorganisms. Through the research conducted, a more apparent appreciation has been obtained regarding the significance of this matter.

Surprisingly, research on the impacts of interactions between plants, microorganisms, and arthropods (PMA) on plant production is limited. Nevertheless, all these factors coexist in the same ecosystem, interact in various ways, and can cause more benefit or harm to the plant than expected. For example, the success of the control of the invasive species "prickly pear cacti" (*Opuntia* spp.) in Australia is attributed to the South American cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera, Pyralidae), which allows pathogens to enter the plant through the wounds it creates (Courtney and Forsberg 1988; Varone et al. 2014). This example illustrates that neither the host nor the microorganism alone can control this invasive species. Instead, control of the plant is achieved through mutual interaction. A meta-analysis encompassing data from 132 records across 35 studies published between 1969 and 2011 supports this example revealing that the combined effects of herbivorous arthropods and plant diseases have a far greater impact on plant performance than the sum of their individual effects. In the meta-analysis, it was shown that arthropod herbivores and phytopathogens typically had synergistic effects on plant performance, which means that when they coexisted, the effects of each stressor were increased. Overall, these findings contribute to this understanding on how multiple stressors can interact to affect plant performance and highlight the importance of considering different types of plant traits when studying these interactions (Hauser et al. 2013). The examples presented highlight the interdependence of PMA interactions because they include complex and dynamic feedback mechanisms that significantly impact each participant's fitness and survival. These deep interdependencies highlight the tripartite interactions' integrated character, wherein the behaviors of plants, microorganisms, and insects closely influence the ecological consequences and evolutionary trajectories of one another. If interactions among PMA, such as those in the example, are fully understood and effectively utilized in agricultural production systems, this could provide a significant advantage in pest management. Furthermore, the potential application of PMA interactions in sustainable crop production has been recommended to achieve crop protection targets under the United Nations Sustainable Development Goals for 2030. This study examined the potential benefits of PMA interactions in plant production and pest management.

CURRENT PERSPECTIVES ON THE INTERACTIONS AMONG PLANTS, ARTHROPODS, AND MICROORGANISMS

Recent advancements have increased the quality of products and the environment by using appropriate plant-microorganism combinations (Aneja et al. 2016; Bakker et al. 2018; Fernandez-Conradi et al. 2018; Woo and Pepe 2018; Coppola et al. 2019a; Coppola et al. 2019b; Contreras-Cornejo et al. 2020; Agbessenou et al. 2022). Indeed many countries, studies were conducted to obtain microbial fertilizer formulations containing soil-borne beneficial microorganisms. Microbial fertilizers control soil-borne diseases, decompose organic waste, improve soil structure and plant nutrition, reduce the need for chemical fertilizers as well as soil and water pollution (Bakker et al. 2018; Coppola et al. 2019a).

Historically, the effects of arthropods and microorganisms on plant health and yield have been studied independently by entomologists and phytopathologists. Beneficial microorganisms have long been used in various disease-control measures, and successful results have been reported in numerous studies. For example, *Azotobacter* spp., *Bacillus* spp., *Pseudomonas* spp., and *Trichoderma* spp. are recognized biocontrol agents that effectively control many plant diseases, including leaf spot, gray mold, soft rot, stem rot, wilt, blight, and mildew (Figueiredo et al. 2010; Kim et al. 2011; Lazebnik et al. 2014; Pieterse et al. 2014; Vinale et al. 2014; Liu et al. 2018; Bakker et al. 2018; Vaello et al. 2018; Verma et al. 2019; Metwally 2020; Oljira et al. 2020; Adeleke and Babalola 2021; El-Maraghy et al. 2021). However, information on the effects of interactions between arthropods and microorganisms on plant health and yield is limited. Furthermore, studies on the effects of these interactions on plant growth and herbivore populations have only gained momentum in recent years, and continue to be revealed. For example, Pineda et al. (2010) showed how rhizobacteria prime plants improved defense against herbivorous insects, whereas Biere and Bennett (2013) addressed the function of endophytic fungi in affecting multitrophic interactions. In the same way, Macías-Rodríguez et al. (2020) demonstrated how arbuscular mycorrhizal fungi can change the population dynamics and diets of herbivores. To provide insights into sustainable pest management strategies, Zytynska (2021) underlined the significance of comprehending plant-microbe-arthropod interactions under changing climatic conditions. While Alınç et al. (2024) reported that root inoculation with beneficial soil bacteria improved plant defenses against herbivore feeding and egg deposition, Van Dijk (2021) offered a more comprehensive view of how these interactions impact ecosystem dynamics. Mathematical models have been used to simulate the results of plant-microbe-pest interactions in an attempt to support and extend these biological findings. For instance, the positive effects of mycorrhizal fungi on the health of the potato plant have been demonstrated in the mathematic models. A model simulating the interaction between the potato plant, mycorrhizal fungi, and the Colorado potato beetle (*Leptinotarsa decemlineata* Say), an important potato pest. The Colorado potato beetle showed that although mycorrhizal fungi can improve plant productivity, reliance on these fungi may result in changes in pest populations, highlighting the requirement for balanced management strategies. By simulating these interactions with mathematical models, researchers can gain valuable insights for using these interactions in plant protection and production (Atlihan et al. 2021; Seminara et al. 2021). Some significant studies on interactions between plants, microbes, and arthropods are provided in the table below.

Table 1. Three-way interactions between plants, arthropods, and microbes reported by different researchers. An overview at the various consequences. PGPF: Plant growth-promoting fungi, PGPR: Plant growth-promoting rhizobacteria.

Pest	Microorganism	Plant	Effect	Literature
Diabrotica undecimpunctata howardi Barber and *Acalymma vittatum* Fabricius	*Pseudomonas putida* Trevisan, *Serratia marcescens* Bizio, *Pseudomonas oryzihabitans* Kodama (formerly Flavimonas) and *Bacillus pumilus* Meyer & Gottheil (PGPR)	Cucumber	Reduced pest population and enhanced plant yield	(Zehnder et al. 1997)
Plutella xylostella L.	*Acremonium alternatum* Link (PGPF)	Courgette	Negative effect on the pest feeding and development	(Raps and Vidal 1998)
Cnaphalocrocis medinalis Guenée	*Pseudomonas fluorescens* (PGPR)	Rice	51.9% reduction in the pest population and a 16.5% increase in plant yield	(Commare et al. 2002)
Amrasca biguttulla biguttulla Ishida and *Aphis gossypii* Glover	*Pseudomonas fluorescens* (PGPR)	Okra	Reduced the pest population, increased plant yield	(Gandhi et al. 2006)
Pieris rapae L. and *Spodoptera exigua* Hübner	*P. fluorescens* and *Pseudomonas syringae* van Hall (PGPR)	Arabidopsis	Negative effect on *S. exigua* development, no effect on *P. rapae*	(Van Oosten et al. 2008)
Myzus persicae Sulzer	*Bacillus subtilis* Ehrenberg and *Bacillus amyloliquefaciens* Fukumoto (PGPR)	Pepper	No effect on the pest population, positive effect on the pepper germination and development	(Herman et al. 2008)
Spodoptera littoralis Boisduval	*Rhizobium leguminosarum* Frank (PGPR)	White clover	Increased *S. littoralis* performance	(Kempel et al. 2009)

Pest	Microorganism	Plant	Effect	Literature
			(enhanced feeding or development)	
Helicoverpa armigera Hübner	*Acremonium strictum* W. Gams (PGPF)	Broad bean	Reduced larval performance and fitness of the pest and effects carried over to the second generation	(Jaber and Vidal 2010)
Bemisia tabaci Gennadius	*B. subtilis* (PGPR)	Tomatoes	Decreased pupal development in the pest	(Valenzuela-Soto et al. 2010)
Macrosiphum euphorbiae Thomas	*Trichoderma longibrachiatum* Rifai (PGPF)	Tomatoes	Increased attraction of natural enemies to the plant	(Battaglia et al. 2013)
H. armigera	*Funneliformis mosseae* (Formerly *Glomus mosseae*) Nicolson & Gerd (PGPF)	Tomatoes	Negative effect on pest larval performance	(Song et al. 2013)
Thrips tabaci Lindeman	*Clonostachys rosea, Trichoderma* spp., *Hypocrea lixii* Patouillard, and *Fusarium* sp. (PGPF)	Onion	Reduced pest population, lower feeding punctures, and fewer eggs laid on inoculated plants.	(Muvea et al. 2014)
Leucinodes orbonalis Guenée	*T. longibrachiatum* (PGPF)	Aubergine	50% decrease in the pest population, 56% increase in plant yield	(Ghosh and Pal 2016)
M. persicae	*Bacillus velezensis* (PGPR)	Arabidopsis	Reduced pest settling, feeding, and reproduction.	(Rashid et al. 2017)
Spodoptera frugiperda Smith	*Trichoderma atroviride* Karsten (PGPF)	Maize	Decreased pest population and performance, the increased attraction of natural enemies to the inoculated plant	(Contreras-Cornejo et al. 2018)
B. tabaci	*Trichoderma harzianum* Rifai (PGPF)	Tomatoes	Approximately 35% mortality in the pest population	(Jafarbeigi et al. 2020)
S. littoralis and *Ma. euphorbiae*	*T. atroviride* and *T. harzianum* (PGPF)	Tomatoes	100% death rate on *S. littoralis* in 25 days and increased natural enemy attraction to the inoculated plant	(Coppola et al. 2019a; Coppola et al. 2019b)
Auchenorrhyncha Dumeril and *Coccoidea* spp.	*Trichoderma* spp (PGPF)	Grapevine	Increased attraction of natural enemies to the inoculated plant	(Parrilli et al. 2019)
Unaspis mabilis Lit & Barbecho	*Trichoderma* spp. (PGPF)	*Lansium domesticum* Corrêa	Reduced pest population and performance, including feeding and reproduction	(Silva et al. 2019)
Tuta absoluta Meyrick	*Trichoderma asperellum* Samuels, *Beauveria bassiana* Balsamo-Crivelli and *H. lixii* (PGPF)	Tomatoes, Nightshade	Decreased number of eggs, vitality, pupa formation, and adults of the pest	(Agbessenou et al. 2020)
S. littoralis and Ma. euphorbiae	*T. afroharzianum* Błaszczyk, *T. atroviride* (PGPF)	Tomatoes	Enhanced pest resistance at specific temperatures and induced differential defense gene expression in plants	(Di Lelio et al. 2021)
Phyllophaga vetula Horn and *Aphididae* spp.	*T. harzianum* (PGPF)	Maize	Positive effect on plant tolerance and defense responses to pests	(Contreras-Cornejo et al. 2021b)
Manduca sexta L.	*T. harzianum* and *Rhizoglomus irregulare* (formerly *Rhizophagus*	Tomatoes	Negative effect on the development of the pest	(Papantoniou et al. 2021)

Pest	Microorganism	Plant	Effect	Literature
	irregularis) Blaszk., Wubet, Renker & Buscot (PGPF)			
M. persicae and *Tetranychus urticae* Koch	*B. amyloliquefaciens*, *Pseudomonas* spp., *Trichoderma* spp. and *Cordyceps fumosorosea* (*formerly Isaria fumosorosea*) Wize (PGPR, PGPF)	Pepper	Decreased in the number of eggs laid of pest	(Pappas et al. 2021)
T. absoluta	*T. asperellum* (PGPF)	Tomatoes	Decreased larval feeding performance of the pest	(Agbessenou et al. 2022)
S. exigua	*T. harzianum* (PGPF)	Cotton, potato	Negative effect on the pest development, reproduction, survival rate, population parameters, and leaf consumption	(Risvanli 2022)
Nezara viridula L.	*T. harzianum* (PGPF)	Tomatoes	Reduction in pest growth rate	(Alınç et al. 2021)
T. urticae	*Bacillus* spp., *F. mossae*, *Pseudomonas* spp., *R. irregulare*, *Trichoderma* spp. and *C. fumosorosea* (PGPR, PGPF)	Tomatoes	Negative effects on the survival, egg production and feeding of the pest	(Samaras et al. 2023)
Diabrotica virgifera virgifera LeConte	*Trichoderma virens* Miller, Giddens & Foster and *Pseudomonas chlororaphis* Smith & Chester (PGPR, PGPF)	Maize	Suppressed pest larvae survival and development	(Huang et al. 2024)
N. viridula	*T. harzianum* (PGPF)	Tomatoes	Enhanced indirect plant defenses including natural enemy attraction to the inoculated plant	(Alınç et al. 2024)

Although it is known that synergistic interactions between plants, arthropods, and microorganisms are robust, the researchers' knowledge about these interactions and associated biological diversity is quite limited. In addition, there is limited data on interactions involving non-pathogenic microorganisms, and limited to commonly occurring species like *Trichoderma* spp., *Glomus* spp, *Bacillus* spp. (Verma et al. 2019; Rişvanlı and Fidan 2024). A more thorough and nuanced understanding of these intricate systems might be obtained by investigating this topic from many different perspectives, such as concentrating on less commonly recognized microbial taxa or their function in multitrophic interactions. This restricts the use of PMA interactions in pest control. However, current research has shown how many different beneficial microbes can be used to create novel, eco-friendly pest control methods. A study by Kızılkan et al. (2025) demonstrate that multiple soil-borne microorganisms could cause physiological alterations to the host plant, such as increased chlorophyll content and changed protein-to-carbohydrate ratios, which could negatively impact the population growth parameters of *Spodoptera exigua* Hübner, a major cotton pest. Utilizing such microbial variety not only fortifies plant defenses but also highlights the potential of using beneficial microorganisms to develop long-term pest management strategies.

PROMOTING PLANT GROWTH AND RESISTANCE THROUGH BENEFICIAL MICROORGANISMS: MECHANISMS AND IMPLICATIONS

Various groups of soil-borne microbes can positively affect plant development and defense activities, both directly and through plant-mediated mechanisms. These groups include mycorrhizal fungi, endophytic root fungi, rhizobium bacteria, plant growth-promoting fungi (PGPF) and plant growth-promoting rhizobacteria (PGPR) (Bezemer and van Dam 2005; Gehring and Bennett 2009). It is well established that beneficial microbes promote nutrient uptake and utilization, enhance resilience to abiotic stress, and contribute to the growth of shoots and roots. As an illustration, mycorrhizal fungi and plant roots develop symbiotic relationships that greatly increase the efficiency of water and nutrient intake, especially for nitrogen and phosphorus. Additionally, they have the ability to alter the amount of plant hormones like auxins and cytokinins, which have a direct impact on plant growth (Harman 2006; Verma et al. 2019; Macías-Rodríguez et al. 2020; Noman et al. 2020; Adeleke and Babalola 2021). In addition to these advantages, microorganisms can enhance photosynthesis by reducing oxidative stress under abiotic stress conditions, enhancing stomatal conductance, and increasing chlorophyll content (Macías-Rodríguez et al. 2020; Noman et al. 2020). Generally, the beneficial microorganisms with known positive effects are selected from *Bacillus* spp., *Azotobacter* spp., *Trichoderma* spp., *Rhizobium* spp., *Azospirillum* spp., and *Saccharomyces* spp. (Bezemer and van Dam 2005; Gehring and Bennett 2009; Lugtenberg and Kamilova 2009; Pineda et al. 2015; Woo and Pepe 2018). These microorganisms alter plant physiology through two fundamental mechanisms, which are defined as "promoting/stimulating plant growth" and "induced systemic resistance (ISR)" (Harman et al. 2004; Jafarbeigi et al. 2020; Noman et al. 2020; El-Maraghy et al. 2021; Contreras-Cornejo et al. 2021a; van Dijk 2021). The ISR has some unique features compared to other types of induced resistance because it is also induced by non-pathogenic microorganisms that colonize the plant roots. When a beneficial microorganism stimulates the plant, the plant switches to a primed state, called priming, after being attacked by a pathogen or insect. Priming refers to creating a faster and more effective defense response against possible attacks the plant may face after exposure to biotic or abiotic stress (Aranega-Bou et al. 2014). The defense generated by priming is more energy-efficient than structural defenses (Steppuhn and Baldwin 2008). In addition, the plant will specialize its response to the specific trace of the herbivore after recognizing it, making this mechanism more advantageous in inducible defense (Maffei et al. 2012; Zebelo and Maffei 2015). Therefore, resistance breeding for inducible defense features may become a significant alternative to biological control as a pest management strategy. Studies have shown that beneficial soil microorganisms can enhance plant defenses and have a negative impact on pests such as spider mites and aphids in crops such as pepper (Pappas et al. 2021), suggesting that breeding programs should take these traits into account.

Numerous beneficial microorganisms are widely used in studies to control plant pathogens because of their ability to promote plant growth and induce systemic resistance (Contreras-Cornejo et al. 2020; Noman et al. 2020). The effectiveness of ISR protects most plant species from bacteria, fungi, viruses, nematodes, and even pests (Pineda et al. 2010; Saharan and Nehra 2011; Pineda et al. 2015; Agbessenou et al. 2022).

In general, the induction of ISR in plants occurs through activating the Jasmonic Acid (JA) and Ethylene (ET) signaling pathways. The JA and Salicylic Acid (SA) are the main components that coordinate the complex signaling pathway in the plant that provides resistance against pests and diseases. Plants can defend themselves against disease and pests by using pathways for SA and JA. When herbivores or necrotrophic pathogens damage the plant, the JA pathway is activated, causing genes to produce defense molecules. The SA pathway, on the other hand, is primarily activated in response to biotrophic pathogens and activates defense genes known as PR genes. Although these two pathways can sometimes work together, they can also act antagonistically (Pineda et al. 2013; Pieterse et al. 2014). Other hormones, such as abscisic acid, cytokinin, gibberellic acid, and auxin, play a role as the backbone of the signaling system. Upon activation of these signaling pathways, the plant tries to defend itself directly (by producing proteins that prevent feeding, such as protease inhibitors, polyphenol oxidase, and chitinase, and by producing toxins and other secondary metabolites) or indirectly (by activating defense mechanisms such as the production of volatile organic compounds to attract natural enemies). For example, SA activation leads to an effective defense against biotrophic and phloem-feeding-sucking herbivores by strengthening cell walls and producing pathogenesis-related (PR) proteins, which prevents pathogen colonization and herbivore feeding. In contrast, JA and ET activations are effective against necrotrophic pathogens and chewing insects through promoting the production of proteinase inhibitors that reduce herbivore performance and secondary metabolites like terpenoids and alkaloids (Figure 1) (Pineda et al. 2013; Pieterse et al. 2014). However, the success of induced resistance is determined by the characteristics of the pests (diet) and the interaction between the hormones involved in resistance (Pineda et al. 2013; Agbessenou et al. 2022). While promoting plant growth through beneficial microorganisms has long been known, the importance of induced defense has recently been realized. For example, rhizobacteria-induced systemic resistance, which is usually mediated through the JA and ET pathways, prepares plants for stronger and quicker reactions to subsequent herbivore or pathogen attacks (Pieterse et al. 2014; Erb and Reymond 2019). However, there is still much to be learned about the role of ISR in PMA interactions (Silva et al. 2019; Contreras-Cornejo et al. 2021a; El-Maraghy et al. 2021; Agbessenou et al. 2022)

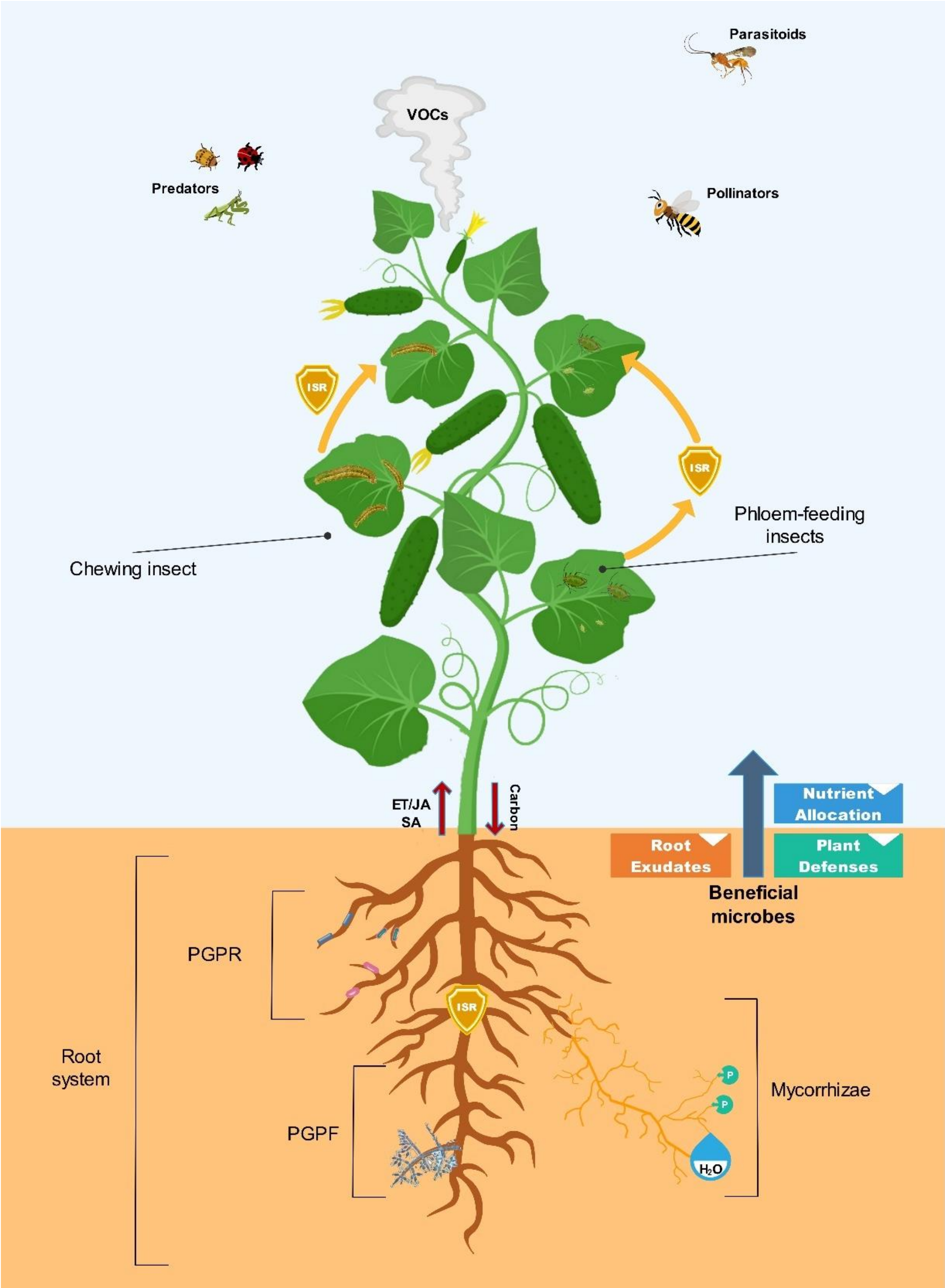

Figure 1. Below-ground and above-ground interactions in plants, microorganisms, and arthropods. Beneficial microorganisms interact with the plant's above-ground and below-ground parts, activating various defense mechanisms. ISR is triggered through these interactions, increasing resistance against diseases and pests. Changes in plant nutrition and defense result in a decrease in the population of harmful herbivores. While the population of piercing-sucking insects may appear to increase in the short term, the density of populations decreases due to the increased attraction of natural enemies to the plant. Increased pollinator visitation and richness of nutrients also lead to an increase in yield. (*VOCs: Volatile organic compounds, PGPF: Plant growth-promoting fungi, PGPR: Plant growth-promoting rhizobacteria).

THE EFFECT OF SOIL-BORNE MICROBES ON ABOVE-GROUND HERBIVORES

Certain microorganisms that form a symbiotic relationship with plants can influence the performance, population dynamics, and community structure of herbivorous insects that feed on them by altering the phenology, morphology, physiology, and biochemistry of plants. For example, positive effects of *Trichoderma* spp., arbuscular mycorrhizal fungi, and other endophytic fungi in the biological control of herbivorous insects have been reported (see Table 1). Furthermore, it is known that these beneficial microorganisms trigger plant defense against herbivores.

Beneficial soil-borne microorganisms can enhance plant resistance against above-ground herbivorous insects. However, this can also make the plant more nutritious and attractive to some herbivores, and the overall impact on insect performance is determined by the beneficial effects of enhanced plant growth and the detrimental effects of plant resistance combine. For instance, it was shown that applying plant growth-promoting rhizobacteria (PGPR) to tomato plants (*Solanum lycopersicum* L.) increased their biomass and nutrient content, which in turn made them more attractive to whiteflies (*Bemisia tabaci* Gennadius). Similarly, arbuscular mycorrhizal fungi (AMF) improved nitrogen acquisition in plants such as *Medicago truncatula* Gaertn., increasing the plants' nutritional value for aphids that feed on phloem (Wilkinson et al. 2019; Noman et al. 2020). These plant-mediated effects can be modulated by a variety of biotic and abiotic factors. For example, a specific type of microorganisms that promotes plant growth (e.g. mycorrhizal fungi or rhizobacteria), plant species and the feeding type of the herbivorous pest (e.g. phloem feeders or chewing insects) are significant biological factors that affect the result. Among abiotic factors, temperature, humidity, and the availability of nutrients in the soil are important determinants of these interactions (Silva et al. 2019; Noman et al. 2020). Therefore, the impact on above-ground herbivorous insects can be positive, negative, or neutral. But even with advancements in this field, there is still much to be explored, such as how microbial diversity affects defense responses and how multiple stressors interact with each other.

Although it is known that microorganisms can respond differently to herbivores under certain conditions, this situation also depends on the interactions between the microorganisms and the surrounding community of organisms, including other microorganisms, plants, and herbivores. For example, three different combinations of the mycorrhizal fungus species have shown different effects on host selection by leaf-miner fly (*Chromatomyia syngenesiae* Hardy) and seed-feeding insects (*Tephritis neesii* Meigen and *Ozirhincus leucanthemi* Vallot) (Gange et al. 2005). In addition, different combinations of PGPR strains in rice (*Oryza sativa* L.) also have a strong negative effect on leaf-folder caterpillars (*Cnaphalocrocis medinalis* Guenée) (Saravanakumar et al. 2007). Furthermore, enzymes involved in plant defense, such as chitinase, trypsin inhibitors, polyphenol oxidase, and lipoxygenase, are also present in similar species (Commare et al. 2002; Gange et al. 2003; Saravanakumar et al. 2007; Saravanakumar et al. 2008). There is a need for more realistic studies of these relationships, as different species and combinations of beneficial microorganisms may have different effects on herbivores and even higher trophic levels.

THE EFFECT OF ABOVE-GROUND HERBIVORES ON SOIL-BORNE MICROBES

There are studies on the effects of beneficial microorganisms on herbivorous insects; however, studies on their effects on beneficial microorganisms are limited. Recently, with the beginning of understanding these interactions, interest in this subject has increased. Herbivorous insects can cause a decrease, increase, or no effect on soil-borne microorganisms. For example, Gehring and Bennett (2009) reported that herbivory by *Neoclytus acuminatus* Fabricius reduced the number of AMF in *Pinus edulis* Engelm. Conversely, Friman et al. (2021) found that herbivory by *Helicoverpa armigera* Hübner larvae increased the activity of beneficial soil bacteria, possibly through root exudate-mediated signaling. Although the underlying mechanisms of these interactions have not been revealed much, it is assumed that the primary factor here is related to the amount of carbon compounds, such as sugars, amino acids, and organic acids shared by plants' roots (Gehring and Bennett 2009). Insect larvae's root herbivory can affect soil carbon and nutrient changes, including alterations in soil pH, moisture, and microbial biomass (Grayston et al. 2001). For example, Grayston et al. (2001) noticed that by increasing the amount of root exudates, which act as a carbon source for soil microbes, *Diabrotica virgifera* LeConte larvae's root herbivory decreased soil pH and changed nutrient availability. In the same way, Erb et al. (2009) showed that plants damaged by herbivores allocated more carbon and nitrogen resources to their roots, which affected the activity and composition of the soil microbial community. Plants increase the transfer of carbon compounds to their roots to tolerate damage from herbivores (Erb et al. 2009; Johnson et al. 2009). It is expected that this scenario will have an impact on the rhizosphere microbiomes. In addition to this factor, the microbiome can be altered by herbivore feeding behavior because of altered plant root exudation. In the rhizosphere, root exudates are crucial to plant-microorganism interactions. Plant hormones impact root exudates, affecting the microbiome around the plant root (Eichmann et al. 2021). However, above-ground herbivores can alter the composition and quantity of root exudates, thereby affecting below-ground microorganisms (Kostenko and Bezemer 2020; Delory et al. 2021). Organic acids (e.g. including malic acid, citric acid, fumaric acid) and carbohydrates (e.g. glucose, fructose) are among the metabolites found in root exudates that trigger bacterial mobility and microorganism attraction to roots (Tahir et al. 2015; Eichmann et al. 2021; Chen and Liu 2024). For example, Arabidopsis contains high levels of malic acid in its root exudates after being infected with the bacterial leaf pathogen *Pseudomonas syringae* pv. tomato Okabe. This situation leads to the increased attraction of the ISR-stimulated microorganism *Bacillus subtilis* Ehrenberg to roots (Bais et al. 2006; Rudrappa et al. 2008). The underlying mechanisms become more complex with the plant defense mechanisms and synthesis of secondary metabolites created for herbivores (Soler et al. 2007; Erb et al. 2009). On the other hand, the primary plant defense mechanism stimulated by herbivore attacks can affect these microorganisms (van Dam and Heil 2011; Sánchez-Sánchez and Morquecho-Contreras 2017; Bernaola and Stout 2019).

These findings demonstrate how insects can impact beneficial microorganisms living in plant roots, and interactions between above-ground and below-ground environments should be considered in future research. Experimental evidence of these mechanisms is needed.

THE EFFECT OF SOIL-BORNE MICROBES ON NATURAL ENEMIES

Plants emit some volatile organic compounds (VOCs) when under herbivore attack to attract natural enemies of herbivores as part of a defense mechanism (Dicke et al. 2009). Emitting volatile organic compounds is a highly effective strategy for plants to survive. Low molecular weight terpenes such as methyl salicylate (MeSA), methyl jasmonate (MeJA), green leaf volatiles (GLVs), and monoterpenes (C_{10}) and sesquiterpenes (C_{15}) have been reported as solid chemical weapons of plants against pathogens or herbivores (Arimura et al. 2004; Clavijo Mccormick et al. 2014; Heil 2014). For instance, in response to herbivore damage, *Arabidopsis thaliana* L. and *Brassica oleracea* L. emit GLVs such as (Z)-3-hexenal and (E)-2-hexenal, which attract parasitic wasps like *Cotesia glomerata* L. (Dicke et al., 2009). Similarly, plants like *Cucumis sativus* L. emit sesquiterpenes like β-caryophyllene (C15) in response to herbivory by *Tetranychus urticae* Koch, which attract predatory mites like *Phytoseiulus persimilis* Athias-Henriot (Arimura et al. 2004). This is one of the main ways that plants defend themselves indirectly. The most important signaling pathway for the emission of these volatiles is the JA signaling pathway. Due to multitrophic effects, changes in the JA signaling pathway lead to changes in the volatile composition (Dicke et al. 2009; Snoeren et al. 2009; Soler et al. 2012). Therefore, it is also expected that the activation of the JA pathway by beneficial microorganisms, such as *Rhizobium* spp. or *Trichoderma* spp., affects the emission rate or composition of volatiles. A study investigating the changes in volatile emission due to microorganisms found that the sesquiterpenes emitted from *Glomus* spp. –inoculated mycorrhizal plants in response to herbivore attacks were more than those emitted from non-mycorrhizal plants (Fontana et al. 2009). Investigations have shown that soil-borne beneficial microorganisms, including *Pseudomonas* spp. and *Bacillus* spp., can mediate indirect defense against herbivores and alter their natural enemies' effectiveness. Research on how helpful bacteria affect indirect defense has revealed that variations in volatile organic compounds attract parasitoids like *Cotesia* spp. (Guerrieri et al. 2004; Hempel et al. 2009). Even when the number of plants colonized by beneficial microorganisms in an area is lower than that of non-colonized plants, they can increase the parasitoid attack rate, performance, and attraction like *Diaeretiella rapae* M'Intosh (Pineda et al. 2013; Coppola et al. 2017; Verma et al. 2019).

EFFECT OF SOIL-BORNE MICROBES ON POLLINATORS

Natural and agricultural ecosystems rely heavily on pollinators. It is known that plant-mediated interactions occur between soil microorganisms and pollinating insects; however, there is limited research on this topic. Current studies indicate that plants colonized by beneficial microorganisms, such as AMF, perform better in flower and seed production than non-colonized plants. This interaction increases the number of flowers, flowering amount, and nectar production. For instance, it has been noted that AMF colonization enhances flower production in a variety of vascular plants, including *A. thaliana*, *Chamerion angustifolium* L. (fireweed) and *Medicago sativa* L. (alfalfa) (Gange and Smith 2005; Cahill et al. 2008; Kessler and Halitschke 2009; Barber et al. 2012). As a result, it is expected to positively affect yield as plants with more flowers and nectar production when visited more by pollinators. Indeed, Chen et al. (2022) demonstrated that the application of AMF increased the number of flowers and fruits in Raspberry plants

(*Rubus idaeus* L.) by 33% and 35%, respectively. By increasing the number of flowers and fruit, pollinators were more likely to visit, indirectly increasing raspberry production. In addition, the synergistic effect of AMF and pollination led to a 43% increase in yield. There is ample evidence that plant-insect interactions are significantly influenced by the existing microbiomes of host plants, such as many flowering species that attract pollinators, including *R. idaeus* (Ushio et al. 2015; Shikano et al. 2017; Singh et al. 2020; Cusumano et al. 2022). For example, Barber et al. (2015) reported that *Acalymma vittatum* Fabricius, a harmful insect species in cucumber roots, caused a 34% reduction in leaf and fruit production and reduced pollinator visitation by 39%. Beneficial microorganisms are thought to impact this harmful species negatively and could, therefore, increase yield and pollination. Recent studies in pollination biology have focused on the role of the plant microbiome in plant-insect interactions (Good et al. 2014; Schaeffer et al. 2014; Mogren and Shikano 2021). Some microorganisms, such as bacteria, produce volatile compounds that act as semiochemicals, facilitating communication between plants and other organisms. These compounds function as pheromones, allomones, kairomones, attractants, or repellents, playing key roles in inter- and intra-species interactions. Typically, they are formed through the microbial transformation of fatty acids, amino acids, or carbohydrates. These volatiles convey critical information, such as the presence and quality of floral resources (nectar, pollen, oils), similar to plant volatiles (Nordlund and Lewis 1976; Leroy et al. 2011). For example, microbial volatiles can influence pollinator visitation rates and enhance yield by signaling the availability of high-quality nectar in the environment (Pineda et al. 2010; Knauer and Schiestl 2015; Pozo et al. 2015; Saini et al. 2019; Chen et al. 2022). While the direct effects of soil-borne microorganisms on pollinators are still unclear, yet it is clear that healthy soil and diverse microbial communities are important for supporting healthy plant communities and the ecosystem services they provide, including pollinator support.

In conclusion, soil-borne microorganisms can significantly affect plant-pollinator interactions positively and negatively and should be considered in developing sustainable agricultural practices. Studies highlight the importance of understanding the complex interactions between soil-borne microorganisms and pollinators to promote healthy pollinator populations and sustainable crop production.

RESULT AND FUTURE EXPECTATIONS

Interest in plants, microorganisms, and arthropods interactions has increased in recent years due to a growing recognition of the importance of these interactions for sustainable agriculture. These interactions can significantly impact plant growth and productivity and can be harnessed to improve crop yields and reduce the use of harmful chemical inputs.

An important reason for the increased interest in these interactions is the growing problem of pesticide resistance. Pests can evolve resistance to commonly used chemical pesticides, reducing their efficacy and increasing pest populations. Microorganism-based products such as biopesticides can provide an alternative mode of action to chemical pesticides, reducing the selection pressures for resistance to these chemicals. By using combinations of chemical and microorganism-based products with different modes of action, it may be possible to delay or prevent the development of pesticide resistance. In addition to their potential role in managing pesticide resistance, microorganism-based products can also provide other benefits. For example, they can have lower environmental impact than chemical pesticides and be part of an integrated pest management strategy that incorporates multiple tactics for pest control.

There has been limited use of microorganism-derived products, such as biopesticides and biofertilizers, because of concerns about their effectiveness, which is considered low and variable when used in field conditions. Although these products have shown to be effective against pests and can improve plant growth in laboratory studies, results obtained under field conditions can sometimes be inconsistent. Farmers and growers are often reluctant to use these products as they may not deliver the expected results. Overall, there is a growing recognition of the potential benefits of microbial-based products for sustainable agriculture, and efforts are underway to improve their efficacy and increase their adoption by farmers and growers. To encourage farmers to use biocontrol agents and biofertilizers, it is essential to highlight the advantages of beneficial microorganisms and the ecological problems caused by chemical pesticides and fertilizers. Microbial-based products have the potential to play an important role in achieving these goals. It is worth noting, however, that research in this area is ongoing, and there is hope that improvements can be made to the efficacy of microbial-based products. As such, these products may become more widely used in the future as their potential benefits become more widely recognized.

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ETHICAL CONSIDERATIONS

No human or animals were harmed in the conduct of this study.

DECLARATION OF COMPETING INTEREST

The authors declare that there is no competing interests to any authors.

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