Review
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Implications of bacteria-bacteria interactions within plant microbiota for plant health and productivity

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Abstract: Crop production currently relies on the widespread use of agrochemicals to ensure food security. This practice is considered unsustainable, yet has no viable alternative at present. Plant microbiota can fulfil various functions in their host, some of which could be the basis for developing sustainable protection and fertilization strategies for plants without relying on chemicals. To harness such functions, a detailed understanding of plant-microbe and microbe-microbe interactions is necessary. Among interactions within the plant microbiota, those between bacteria are the most common ones; they are not only of ecological importance but also essential for maintaining the health and productivity of the host plants. This review focuses on recent literature in this field and highlights various consequences of bacteria-bacteria interactions under different agricultural settings. In addition, the molecular and genetic backgrounds of bacteria that facilitate such interactions are emphasized. Representative examples of commonly found bacterial metabolites with bioactive properties, as well as their modes of action, are given. Integrating our understanding of various binary interactions into complex models that encompass the entire microbiota will benefit future developments in agriculture and beyond, which could be further facilitated by artificial intelligence-based technologies.

Keywords: Plant microbiome; Bacteria-bacteria interactions; Plant pathogens; Crop production; Molecular interactions

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1 Introduction

Plants live in close associations with diverse microbial communities, collectively termed as plant microbiota. Recent technological advances, especially the emergence of various omics-based techniques, have allowed us to better understand the implications of a range of functions of these microbiota that are essential for their host (Berg et al., 2020). Among other roles, plant microbiomes can support the health of their hosts in various ways including the modulation of immunity, specific metabolic pathways, and direct pathogen antibiosis (Chen et al., 2018, Finkel et al., 2020, Matsumoto et al., 2021, Singh et al., 2015, Xu et al., 2022, Yang et al., 2023, Zhou et

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al., 2022). A detailed understanding of mechanisms involved in the recruitment of beneficial microorganisms by plants is of outstanding importance at times of increasing environmental concerns due to the prevalence of unsustainable agricultural practices (Munir et al., 2022). Recently, microorganisms were described that can confer holistic disease resistance to plants, which become susceptible to distinct pathogens in their absence. These have been termed as soterobionts and highlighted as a highly valuable resource for plant protection (Cernava and Berg, 2022). The discovery of further such microorganisms currently poses a significant challenge, as most of the knowledge about bacteria-bacteria/fugal and plant-bacteria/fungal interaction mechanisms has been obtained through reductionist methods, such as pure cultures (Wang and Cernava, 2023). Furthermore, it remains largely unclear which biotic or abiotic factors are determinative for the establishment of soterobionts and whether they can be supported by other microorganisms from the same community.

Specifically, bacteria-bacteria interactions are of high relevance due to the predominance of prokaryotes in most microbial communities. Different mechanisms of cell-cell interactions have been described for bacteria; however, these are mostly based on a low number of general interaction principles (Venturi and Bez, 2021). Computational approaches facilitated by high-throughput sequencing have unraveled a high diversity of bacteria that are often found as major constituents of plant microbiomes. A recently published review by Lyng and Kovác specifically addresses bacteria-bacteria interactions between different species of *Bacillus* and *Pseudomonas*, shedding light on their interplay at the taxonomic and molecular levels (Lyng and Kovács, 2023). The authors highlight the manifold interactions in which these two common constituents of the plant microbiota engage. Given the overall diversity and dynamics within bacterial communities, it is becoming evident that the number of potential binary interactions therein is enormous, which cannot be captured yet holistically despite the technological advances. Here, we compile recent insights into mechanisms related to bacteria-bacteria interactions and highlight their roles in enhancing or compromising plant health and productivity. Studies focusing on bacterial interactions are essential to understand how a unique set of microbiota establishes in different hosts, influences health or disease, and provides the basis for the development of new applications, such as synthetic communities (SynComs) or microbiome engineering (Su et al., 2024).

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2 Modes of bacteria-bacteria interactions in plants

The interspecific interactions between bacteria, which can be both positive and negative, control the establishment and/or proliferation of beneficial bacteria and potential pathogens in plants. Current research on the mechanisms of bacteria-bacteria interactions in plants mainly focuses on the following aspects: (1) contact-dependent interactions; (2) chemical substances; (3) nutrient and energy exchange; (4) quorum sensing systems; (5) biofilm formation; (6) horizontal gene transfer (Fig. 1).

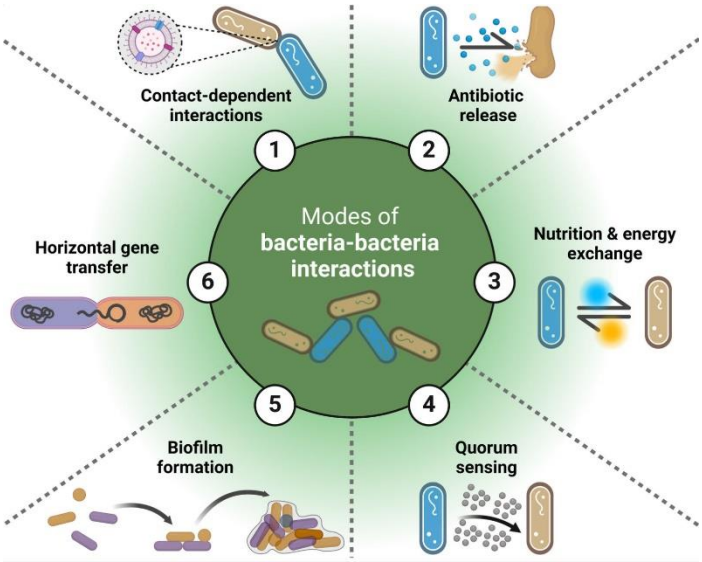

Fig. 1 Modes of bacteria-bacteria interactions. (1) Bacteria can deliver toxic proteins or DNA into cells through secretion systems that rely on cell-to-cell contact. (2) By releasing antibiotics into their surrounding environment, certain bacteria can inhibit others. (3) Nutrient exchange between different bacterial species can result in mutual benefits for both. (4) By means of quorum sensing (QS), bacteria are able to regulate gene expression, enabling the detection of signaling molecules within microbial communities. (5) In environments containing antibiotics, the development of biofilms assists bacteria in better adapting to their surroundings. (6) Bacterial DNA can be transferred to other bacteria via horizontal gene transfer, facilitating genetic diversity and adaptation.

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2.1 Cell-to-cell contact-dependent interactions

Bacteria employ two main strategies to counter invaders: the release of small molecules with antimicrobial activity into the surrounding environment and the delivery of toxic effector proteins into nearby competitors through specialized secretion systems. The latter includes type IV secretion system (T4SS), type VI secretion system (T6SS), and type VII secretion system (T7SS) secretion systems, which allow different types of cell-to-cell contact. The T4SS is a complex multi-protein structure capable of transporting DNA, effector proteins, and protein-DNA complexes either into the extracellular environment or directly into eukaryotic or prokaryotic target cells. This system facilitates bacterial conjugation transfer, DNA release and uptake, and effector protein secretion, thereby enhancing bacterial adaptability and survival capabilities. For example, *Pseudomonas putida* IsoF defends tomato plants against *Ralstonia solanacearum* using a T4BSS to deliver toxic effectors to competing bacteria in a contact-dependent manner. This strategy is supported by the *kib* gene cluster in a rare genomic island, likely acquired through horizontal gene transfer, enabling *P. putida* IsoF to eliminate bacterial competitors and penetrate biofilms for environmental persistence (Purtschert-Montenegro, et al., 2022). The T6SS is one of the most widely researched secretion systems, predominantly occurring in Proteobacteria and Bacteroidetes (Galán and Waksman, 2018). The T6SS, similar to the tail spike of T4 phage, pierces bacterial cells to deliver genetic material (Ho et al., 2014). The beneficial plant bacterium *P. putida* can kill other bacteria by secreting the toxic effector Tke2 via its K1-T6SS secretion system (Bernal, et al., 2017). The T7SS secretion system was first discovered in the pathogenic

Mycobacterium tuberculosis and is primarily found in Gram-positive bacteria. *Bacilli subtilis* can secrete the LXG antimicrobial effector YxiD through T7SS to antagonize other bacteria (Tassinari et al., 2022). Many studies have reported on the role of bacterial secretion systems in interactions between beneficial bacteria and pathogens. In addition, research into these secretion systems provides new insights into the pathogenic mechanisms of plant pathogens, offering possibilities for developing novel plant protection strategies. However, the mechanisms of bacterial secretion systems are extremely complex, involving multiple molecular and cellular interactions; a variety of advanced techniques are required to decipher the underlying mechanisms, such as molecular biology assays, proteomics, and microscopy technologies.

2.2 Interactions via chemical substances

A wide range of chemical substances have been described from bacteria-bacteria interactions, with a single one having different effects depending on the target cell. Based on their size and structure, these substances can be classified into three main groups: i) peptides, ii) non-volatile organic compounds, and iii) volatile organic compounds (VOCs; **Fig. 2**). Peptides, especially lipopeptides from interacting bacteria, can play an important role in plant health and productivity. *Bacillus* species can synthesize a diverse set of antimicrobial peptides. Iturin, bacillomycin, bacilysin, fengycin, surfactin, ericin, subtilin, mersacidin, subtilosin, and mycosubtilin are some examples reported in the literature (Chung et al., 2008, Nakkeeran et al., 2019, Özcengiz and Öğülür, 2015). A few of these have been classified as lipopeptide antibiotics (Tsuge et al., 2005). These biomolecules comprise a lipid tail linked to a cyclic or short linear oligopeptide and can contribute to plant health by antagonizing pathogens (Raaijmakers et al., 2010). The surfactant properties of putisolvin I-II produced by a plant root-associated *Pseudomonas* isolate render the molecule capable of destroying biofilms formed by other bacteria (Kuiper et al., 2003). Such compounds are not only relevant for agricultural applications but can also find use in biotechnology (Kuiper, et al., 2003).

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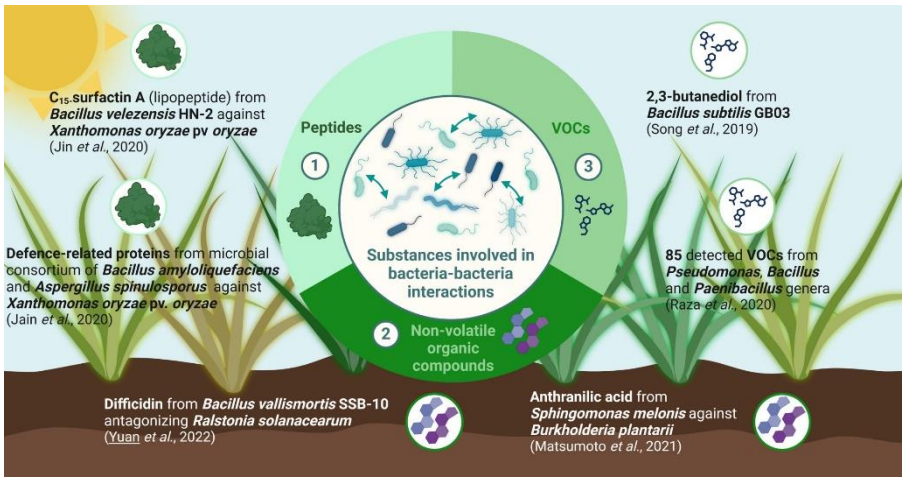

Fig. 2 Schematic illustration showing the three different substance groups commonly involved in bacteria-bacteria interactions: (1) peptides (e.g., lipopeptides, such as surfactins), (2) non-volatile organic compounds (e.g., anthranilic acid, pyrrole-derivates, and fatty acids), and (3) VOCs (e.g., 2,3-butandiol).

During the past few years, various lipopeptides were identified as promising agents for biological control applications. In *Arabidopsis* roots, the inhibition of *P. syringae* was shown to depend on the concentration of surfactin produced by *Bacillus* spp. (Bais et al., 2004). Moreover, C15-surfactin A, produced by *Bacillus velezensis* HN-2, displayed antibacterial activity against *Xanthomonas oryzae* pv. *oryzae (Xoo)* and effectively prevented it from infecting rice at low concentrations. Thorough assessments based on scanning electron and transmission electron microscopy showed that this compound causes significant damage to the cell wall structure of *Xoo* (Jin, et al., 2020). In parallel, C15-surfactin A exposure upregulated the expression of the plant genes *Pal*, *Pr1a* and *CatA*. C15-surfactin A could therefore be employed as a biocontrol agent due to its efficacy in inhibiting the growth of *Xoo* and effectively inducing rice resistance by triggering a hypersensitive reaction (Jin, et al., 2020). Additionally, *Bacillus amyloliquefaciens* in rice plants was identified as a promising source of new peptides with antibiotic function against plant pathogens (Jain, et al., 2020). García-Bayona and Comstock published a review focused on bacterial antagonism mediated by peptides and proteins produced by members of host-associated microbial communities (García-Bayona and Comstock, 2018). These compounds play important roles in ecosystem defence, pathogen invasion, and spatial segregation.

An exhaustive review focusing on siderophores was published by Ferreira, et al. (2019). Siderophores are low-weight molecules (500-1500 Da), possessing strong affinity and selectivity towards the binding of Fe(III) (Ahmed and Holmström, 2014). More than 500 siderophores have been reported in the literature. Among these, at least 270 have been structurally characterized (Barry and Challis, 2009). Despite this great variety, siderophores share some common moieties such as the negatively charged oxygen atoms for binding Fe(III). The following bacterial genera were described to produce such molecules: i) *Azotobacter* (Baars et al., 2016, McRose et al., 2017, Romero-Perdomo et al., 2017); ii) *Azospirillum* (Banik et al., 2016); iii) *Bacillus* (Kesaulya et al., 2018, Pourbabaee et al., 2017); iv) *Dickeya* (Sandy and Butler, 2011); v) *Klebsiella* (Bailey et al., 2018, Zhang et al., 2017); vi) *Nocardia* (Hoshino et al., 2011); vii) *Pantoea* (Burbank et al., 2015, Soutar and Stavrinides, 2018); viii) *Paenibacillus* (Liu et al., 2017); ix) *Pseudomonas* (Baune et al., 2017, Deori et al., 2017, Pourbabaee, et al., 2017); x) *Serratia* (Gerc et al., 2014); and xi) *Streptomyces* (Gáll et al., 2016, Goudjal et al., 2015, Schütze et al., 2014). These molecules are often involved in bacteria-bacteria interactions and therefore of high importance for the development of biological control agents.

Comparative analyses of experimental data have shown that volatile metabolites have a greater contribution to microbial interactions than non-volatile ones (Kanchiswamy et al., 2015). Volatile organic compounds (VOCs) are a broad group of lipophilic compounds with high vapour pressure, low boiling point, and typically 100-500 Da molecular weight (Raza et al., 2020, Schulz-Bohm et al., 2018). Bacterial VOCs have been reported to affect different organisms, such as bacteria, fungi, plants, and animals. Among them, many have inhibitory effects towards plant pests and pathogens (Garbeva and Weisskopf, 2019). Over the last 15 years, the significance of VOCs as mediators of mutualistic interactions between plant-associated bacteria and their hosts has become evident. Garbeva and Weisskopf summarized the current knowledge concerning bacterial VOC-mediated plant protection against biotic and abiotic stresses in a detailed review

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(Garbeva and Weisskopf, 2019). They also highlighted the scientific gaps that need to be answered to better understand molecular mechanisms, such as factors underlying the i) biosynthesis of bacterial volatiles, ii) the complex regulation of their emission in natural communities, iii) the perception of bacterial volatiles by plants, and iv) their modes of actions (Garbeva and Weisskopf, 2019). Song et al. investigated the plant protection efficiency of 2,3-butanediol using filter paper soaked with this substance or a culture of *B. subtilis* GB03. In both cases, continuous exposure to an atmosphere enriched in volatiles led to a decrease in the leaf spot symptoms of cucumber (Song et al., 2019). Raza et al. demonstrated in a model plant system that bacterial community richness and composition are important for VOC production, pathogen suppression, and plant growth-promotion (Raza, et al., 2020). VOC-producing bacterial communities with different richness levels were assembled, varying from 1 to 12 strains and with three soil-dwelling genera (*Paenibacillus*, *Bacillus*, and *Pseudomonas*). Their VOC production correlated positively with the suppression of pathogens and plant growth promotion. All bacteria produced a diverse set of VOCs. However, the pathogen suppression effect reached its maximum at intermediate community richness levels. Based on the results, they proposed that both the number of interacting bacterial species and the structure of the rhizosphere microbiome affect the balance between VOC-mediated microbe-pathogen and microbe–plant interactions, regulating plant disease occurrence in agricultural ecosystems (Raza, et al., 2020).

Revealing the chemical communication between bacteria provides valuable insights into understanding how a certain plant microbiome is shaped. The current research on bacterial communication mainly focuses on culturable bacteria; however, these represent only a small part of the entire microbiota. Future research requires a more diverse set of methods to better describe chemical interactions in complex communities.

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2.3 Nutrient and energy exchange

Antagonistic interactions are commonly observed in natural microbial communities. However, in recent years, it was increasingly observed that bacteria also engage in a wide range of cooperative behaviours. For instance, they use substantial resources to produce metabolic by-products for utilization by other bacteria, thereby assisting them. In most cases, cooperating bacteria are related, and by aiding their kin, they can increase the chances of their own genes being indirectly propagated (D'Souza et al., 2018). However, associations between non-related bacteria have also been observed. The rhizobacterium *Bacillus cereus* UW85 stimulates the growth of bacteria from the *Cytophaga-Flavobacterium* group (Bacteroidetes) in the soybean rhizosphere. The growth-promoting mechanism likely involves bacterial cell wall components, because peptidoglycan isolated from *B. cereus* cultures stimulated the growth of *Flavobacterium johnsoniae in vitro*. In another study, *Bacillus velezensis* SQR9 was able to induce the enrichment of *Pseudomonas stutzeri* in the cucumber rhizosphere. These two microorganisms formed robust biofilms both *in vitro* and on the surface of plant roots. Metabolomic and transcriptomic analyses showed that SQR9 facilitates the growth of *P. stutzeri* through metabolic cross-feeding (Sun et al., 2022).

2.4 Quorum sensing systems

Quorum sensing (QS), a critical determinant of microbial interactions, enables cells in a microbial community to detect signaling molecules, leading to a cascade of reactions and regulating gene expression. In this way, QS affects nutrient absorption, material transport and energy metabolism, and orchestrates microbial interactions that define the community structure, facilitating swift adaptation to changing environmental conditions (Zeng et al., 2023). QS systems differ between Gram-negative and Gram-positive bacteria. In the former, signal molecules are typically acyl-homoserine lactone (AHL) or cis-11-methyl-2-dodecenoic acid (also known as Diffusible Signal Factor-DSF), mainly found in genera like *Pseudomonas* and *Xanthomonas*. Conversely, in Gram-positive bacteria, these molecules are generally peptides (Danhorn and Fuqua, 2007, Lazdunski et al., 2004). Notably, in species such as *B. subtilis* and *Streptococcus pneumoniae*, these peptide signals play a crucial role in triggering sporulation and the development of competence.

Pathogens can utilize QS molecules to regulate the expression of virulence factors. For instance, the plant pathogen *Pantoea stewartii* regulates its biofilm formation and colonization abilities through the EsaI/EsaR QS system, leading to its pathogenicity. QS mutants of *P. stewartii* are unable to disperse and migrate in the vascular system, thereby reducing disease severity (Koutsoudis et al., 2006). Some bacteria possess the ability to release compounds that disrupt the production and dispersal of autoinducers, hence meddling with the quorum sensing systems of specific microbial species. This interference hampers microbial communication, diminishing the levels of harmful factor expression, and thus modulates bacterial growth and reproduction mechanisms. This process is identified as quorum sensing quenching, with the involved compounds referred to as quorum sensing inhibitors. The *Lysobacter enzymogenes* OH11 strain, which lacks AHL synthesis capability, can utilize the T4SS to inject the effector protein Le1288 (LqqE1) into the cytoplasm of another soil bacterium, *Pseudomonas fluorescens* 2P24 (2P24), which possesses an AHL communication system. Unlike typical AHL quenching proteins, LqqE1 does not degrade AHL but inhibits AHL synthesis by directly binding to the AHL synthase PcoI in 2P24 (Liao et al., 2023). With more in-depth research into QS mechanisms, we will better understand bacterial communication and develop new strategies to control bacterial plant diseases.

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2.5 Biofilm formation

Biofilms, often harboring complex microbial communities, represent a collective behaviour of bacteria adapting to specific and often extreme surface environments. It is well-known that the formation of biofilms involves various collective behaviours and depends on the complex regulation of quorum sensing (QS). In the development of biofilms, synergistic and antagonistic interactions both exist between bacteria. *Pseudoalteromonas* sp. MEBiC 03485 boosts the extracellular polymeric substance (EPS) production of *Porphyridium cruentum* UTEX 161 (Han et al., 2020). This expansion in EPS productivity occurs because of specific chemical compounds discharged by bacteria. Using rheology and microscopy-based approaches, Yannarell et al. recently explored a dual-species biofilm consisting of *B. subtilis* and *Pantoea agglomerans* (Yannarell et al., 2019). Several features of the mixed-community biofilm appeared to be distinct from those identified in monocultures, highlighting the importance of characterizing multispecies consortia for a better understanding of naturally occurring bacterial interactions. The formation of biofilms

can also serve as a physical barrier to help bacteria adapt to the presence of other bacteria. Molina-Santiago et al. explored the interaction between *B. subtilis* 3610 and *Pseudomonas chlororaphis* PCL1606, and revealed that the extracellular matrix of *B. subtilis* protects colonies from *P. chlororaphis*. *B. subtilis* is a soil-dwelling bacterium engaging in mutualistic interactions with plants, frequently used as a model of biofilm formation (Beauregard et al., 2013). The absence of extracellular matrix from *B. subtilis* resulted in its increased fluidity and loss of colony structure. The *P. chlororaphis* type VI secretion system was activated upon contact with *B. subtilis*, stimulating sporulation mediated by histidine kinases KinA and KinB. The authors also demonstrated the importance of the extracellular matrix and the *P. chlororaphis* type VI secretion system in modulating the coexistence of these two species on melon leaves and seeds (Molina-Santiago, et al., 2019). Microorganisms in biofilms engage in complex interactions, involving both known and obscure mechanisms. Although our understanding of these interactions has significantly deepened, there are still unresolved questions about biofilm maintenance and stability, creating space for new discoveries.

2.6 Horizontal gene transfer

Bacteria acquire new DNA through horizontal gene transfer (HGT), enabling them to adapt to constantly changing environments. This exogenous DNA may contain elements that can expand the bacterial habitat range, alter the relationship between bacteria and their hosts, or provide advantages in competition with other organisms. DNA can be transferred in multiple ways, with conjugation, transposition, and transformation being the most studied mechanisms. However, additional mechanisms are gradually being discovered, such as acquisition through outer membrane vesicles and transfer via virus-like particles (Brito, 2021). By combining theoretical deduction and numerical simulations, researchers have found that HGT unexpectedly exceeds the scale of biodiversity predicted by classical models. HGT is achieved by facilitating dynamic neutrality among competing species, thus permitting the coexistence of multiple competitive species (Zhu et al., 2024).

HGT within microbial communities aids bacterial adaptation to diverse environmental stimuli. This process is critically important in the context of the spread of antibiotic resistance genes, a phenomenon further amplified by the formation of biofilms. As improved detection methods and innovative theoretical and computational approaches are increasingly being implemented in relevant studies, our understanding of bacterial HGT has significantly widened. In the future, in-depth sequencing of metagenomes will allow the recovery of complete genomes to reveal a multitude of co-existing species, including those that are unculturable in the laboratory. These data will greatly enhance our knowledge of the complex microbial dynamics facilitated by HGT.

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3 Agricultural relevance of bacteria-bacteria interactions

3.1 Harnessing bacteria-bacteria interactions to enhance plant health and disease resistance

Plant health is often compromized by resistant phytopathogens that cannot be controlled by conventional strategies. While the most prevalent diseases are caused by fungi, phytopathogenic bacteria also account for substantial yield losses (Elshafie et al., 2012, Molina-Santiago et al., 2019, Purtschert-Montenegro et al., 2022, Weise et al., 2012, Yin et al., 2011). Alternatives to conventional agrochemical-based protection strategies can emerge from observations of specific bacteria-bacteria interactions. Specifically, beneficial bacteria can engage in interactions that are detrimental for their pathogenic counterparts, thus protecting different plant species from the seedling stage onwards (Venturi and Bez, 2021). A conceptual framework on this phenomenon was provided by Hassani et al., illustrating that interactions within the microbiota are critical for the establishment and maintenance of host health (Hassani et al., 2018). During the past decades, manifold bacteria-bacteria interactions were regarded as crucial to maintain plant health under laboratory, field or greenhouse conditions. Members of the bacterial genera *i) Pseudomonas, ii) Bacillus*, *iii) Rhizobium*, *iv) Pantoea*, *v) Azospirillum*, and *vi) Azotobacter* have been considered as highly promising for agricultural applications (Ferreira et al., 2019). Among these, *Pseudomonas* spp. and *Bacillus* spp. are the most frequently described plant-beneficial bacteria. The ability of beneficial bacteria to protect plants against pathogens (Bernal et al., 2017, Combes-Meynet et al., 2011, Gu et al., 2017, Molina-Santiago, et al., 2019, Purtschert-Montenegro, et al., 2022, Zeriouh et al., 2011) and to promote their growth has been widely acknowledged (Combes-Meynet, et al., 2011, Lally et al., 2017, Roca et al., 2012). A representative set of interaction types as well as their consequences for host plant health are provided in **Table 1**. Typical plant characteristics that can be improved by bacteria-bacteria interactions are schematically visualized in **Fig. 3A**. In general, many natural products formed by *Pseudomonads*-like soil-dwelling microorganisms are a consistent source of potential antimicrobial metabolites and biopesticides. Yang et al. successfully isolated a *Pseudomonas mosselii* strain from the rice rhizosphere that specifically inhibited the growth of plant-pathogenic *Xanthomonas* species (Yang, et al., 2023). The bioactive compound produced by *P. mosselii* was identified as pseudoiodinine. An approximately 20-fold increase in the production of pseudoiodinine was achieved by optimizing the growth medium, via overexpressing the biosynthetic operon and removing the *CsrA* (a carbon storage regulator) binding sites. *P. mosselii* as well as purified pseudoiodinine inhibited the pathogen without affecting the rice host, suggesting the applicability of this compound in controlling certain diseases (Yang, et al., 2023).

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1 **Table 1 Examples of different bacteria-bacteria interactions and their consequences for the health and productivity of plants**

Bacteria-bacteria interaction	Description of the interaction	Category	Consequence on the plant	Reference
Pseudomonas mosselii 923 against *Xanthomonas* species	*Xanthomonas* species are inhibited by pseudoiodinine from *P*: *mosselii* 923	Negative, amensalism	Rice plants are protected against bacterial and fungal pathogens	Yang, et al., 2023
Pseudomonas putida IsoF against *Ralstonia solanacearum*	Delivery of toxic effector to *R. solanacearum* via type IVB secretion system	Negative, amensalism	Tomato plants are protected against the pathogen *R. solanacearum*	Purtschert-Montenegro, et al., 2022
Aeromicrobium Leaf245 against *Nocardioides* Leaf374	*Nocardioides* is lysed by an antimicrobial peptidase from *Aeromicrobium*	Negative, amensalism	Potential growth-promotion and disease-suppression	Schäfer, et al., 2022
Sphingomonas melonis against *Burkholderia plantarii*.	*S. melonis* produces anthranilic acid that interferes with the sigma factor RpoS of *B.plantarii*, likely causing impairment of upstream cascades required for virulence factor biosynthesis	Negative, amensalism	Rice becomes disease-resistant against *B.plantarii*	Matsumoto, et al., 2021
Bacillus velezensis HN-2 against *Xanthomonas oryzae* pv. *oryzae*	C_{15}-surfactin A produced by *B. velezensis* HN-2 shows antibacterial activity against *Xoo*	Negative, amensalism	*Xoo* infection in rice is inhibited	Jin et al., 2020
B. subtilis 3610 against *Pseudomonas chlororaphis* PCL1606	*B. subtilis* protects itself with extracellular matrix from *P. chlororaphis*	Negative, amensalism	Establishment of mutualistic interactions with *B. subtilis*	Molina-Santiago, et al., 2019
P. fluorescens F113 and endophytic microbial consortium (*P. fluorescens* L111, L228, and L321; *Pseudomonas* sp. L117, L130, L132, and Rt03; *Serratia* sp. R324 and S120; *Enterobacter* sp. R232)	Plant associated bacteria with PGP properties	Positive, mutualism	Significant increment in crop height and pod biomass	Lally, et al., 2017
B. subtilis UMAF6614 and UMAF6639 against *Xanthomonas campestris* pv. *cucurbitae* and *Pectobacterium carotovorum* subsp. *carotovorum*	Antibiotics (iturin A and bacillomycin) from *Bacillus* have cytotoxic effect on phytopathogens	Negative, amensalism	Control of the bacterial leaf spot and soft rot pathogens of cucurbits	Zeriouh, et al., 2011

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P. fluorescens F113 and *Azospirillum brasilense* Sp245-Rif	DAPG-producing *Pseudomonas* enhances *Azospirillum´*s cell motility, biofilm formation, production of PBH and auxin	Positive, mutualism	Enhanced phytostimulation effects	Combes-Meynet, et al., 2011

2 DAPG: 2,4-diacetylphloroglucinol; PGPR: plant-growth-promoting rhizobacteria. PGP: plant growth promoting. PBH: poly-β-hydroxybutyrate. *Xoo*: *Xanthomonas oryzae* pv.
3 *oryzae*

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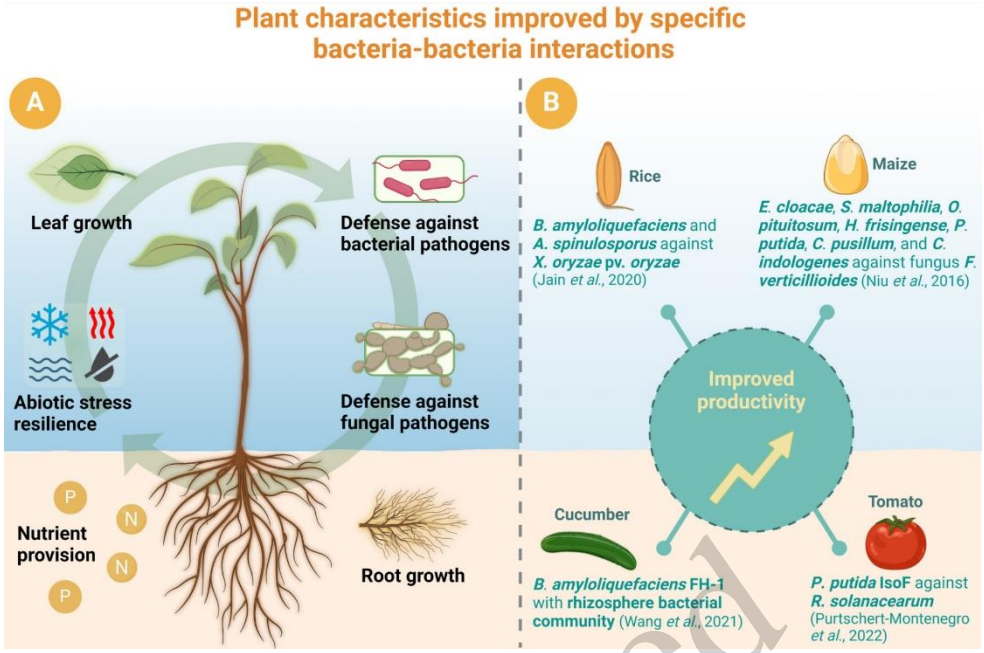

Fig. 3 Schematic representation of various scenarios where plant fitness and/or productivity are improved by specific bacteria-bacteria interactions. Such interactions can result in improved root and leaf growth, defence against fungal and bacterial pathogens, abiotic stress resilience, and nutrient provision (A). The productivity of different plants (e.g., rice, maize, tomato, and cucumber) can also be enhanced by different bacteria-bacteria interactions (B).

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A study on the core bacterial endophytes of rice revealed 14 prevailing amplicon sequence variants (Zhang, et al., 2022). Especially, *Pantoea* and *Xanthomonas* were identified as potentially vertically transmitted taxa. They exhibited cellulase activity and were found to produce indole-3-acetic acid. Five *Pantoea* strains showed moderate antagonism against major pathogens of rice diseases like *Magnaporthe oryzae* and *X. oryzae* pv. *oryzae*. These data provide an important basis for harnessing functions of naturally occurring members of the plant microbiota for crop protection. Matsumoto et al. observed that rice plants of the same genotype under the same pathogen pressure can be differentiated into disease-resistant and susceptible phenotypes (Matsumoto, et al., 2021). After the identification of a seed-endophytic bacterium (*Sphingomonas melonis*) as the resistance-conferring agent against the seed-borne pathogen *Burkholderia plantarii*, the integration of high-throughput data, gene mutagenesis and molecular interaction assays was performed, facilitating the discovery of the mode of action. *Sphingomonas melonis*, accumulated and transmitted across generations in disease-resistant rice seeds, confers resistance to disease-susceptible phenotypes producing anthranilic acid. This compound interferes with the sigma factor RpoS of rice-pathogenic *B. plantarii*, likely causing the impairment of upstream cascades required for virulence factor biosynthesis (Matsumoto, et al., 2021). In another study focusing on rice plants, *X. oryzae* pv. *oryzae* was found to be antagonized by *B. velezensis* HN-2 (Jin, et al., 2020). This study highlighted the importance of identifying core endophytes, vertically

transmitted microbiota, and network hubs, which can be crucial for the development of an effective strategy for the targeted manipulation of microbiomes towards improving plant health.

Currently, the use of numerous biological control agents is hindered by various factors. These include the poor survival rate and colonization capacity of the introduced biocontrol strains, along with a reduction in the expression of essential antagonistic traits in field application. Thus, it is critical to comprehensively understand the dynamic interactions among pathogens, antagonistic microorganisms, and the environment to formulate effective biological control strategies.

3.2 Plant fitness and productivity can be improved by bacteria-bacteria interactions

Heat, drought, flood, and cold weather are among the most frequent abiotic stresses faced by agricultural plants, reducing their productivity. Due to climate change, the impact and intensity of these stresses have gradually increased during recent decades (Chaudhry and Sidhu, 2021). Many microorganisms can produce secondary and primary metabolites, which help plants mitigate these stresses (Biró et al., 2006, Garcia et al., 2022, Munir, et al., 2022, Rajkumar et al., 2013). When bacteria interact within microbiomes, the outcome can coincide with a better productivity of the host plant, improved growth, or higher fitness (Hawkes et al., 2021, Niu, et al., 2017, Wang et al., 2021, Yuan et al., 2016). Various studies have shown that the productivity of rice, maize, tomato, cucumber, and other agricultural plants can be enhanced by bacteria-bacteria interactions **(Fig. 3B)**. A recent review by Munir et al. summarized the impacts of abiotic stressors on agricultural productivity and the role of beneficial microorganisms in alleviating negative effects (Munir, et al., 2022). Targeted inoculation with beneficial microbes can also reduce the effects of different biotic stresses enhancing plant fitness (Ansari and Ahmad, 2019, Jain et al., 2020, Niu, et al., 2017, Tan et al., 2021, Wang, et al., 2021, Wei et al., 2015). To this end, Liu et al. proposed the "DefenseBiome" concept, providing a framework for the design and construction of beneficial microbial synthetic communities to improve the fundamental understanding of plant-microbial interactions and the development of related products for agriculture (Liu et al., 2020).

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Jain et al. evaluated the defense network provided by beneficial microorganisms in the rice rhizosphere and observed reduced plant mortality as well as an increase in dry biomass and chlorophyll content in the presence of this network (Jain, et al., 2020). Another study focused on the beneficial functions of *P. fuorescens* FAP2 and *Bacillus licheniformis* B642, two well-characterized PGPR strains (Ansari and Ahmad, 2019). Rhizosphere and rhizoplane colonization of wheat seedlings by both isolates resulted in the production of indole acetic acid (IAA), siderophores, ammonia, and phosphate solubilization, as well as some biofilm-related functions (e.g., production of exopolysaccharides, alginate, and cell surface hydrophobicity). The effects of co-inoculation revealed the significant enhancement of vegetative growth, photosynthetic parameters (e.g., chlorophyll content, transpiration rate, internal CO_2 concentration, stomatal conductance, and net photosynthetic rate), and leaf water potential, in comparison with single inoculation and the uninoculated control. Combes-Meynet et al. have shown that the *Pseudomonas*-produced secondary metabolite 2,4-diacetylphloroglucinol (DAPG) can act as a signal molecule for plant-growth-promoting rhizobacteria (PGPR), enhancing their phytostimulation effects (Combes-Meynet, et al., 2011). In wheat, DAPG-producing *P. fluorescens* F113 can enhance cell motility, biofilm formation and the production of poly-β-hydroxybutyrate and auxin of *Azospi-*

rillum brasilense Sp245-Rif (Sp245-Rif). A differential fluorescence induction promoter-trapping approach was used to confirm the high expression of Sp245s-Rif gene in the presence of DAPG. Compared with its *phl*-negative mutant, the expression of four genes (*nirK*, *nifX-nifB*, *ppdC*, and *flgE*) was upregulated in the presence of *P. fluorescens* F113 (Combes-Meynet, et al., 2011). In a different study, Tan et al. demonstrated that the fitness of *Lemna minor* is modified due to interactions between the microbiome and *P. fluorescens* (Tan, et al., 2021). The microbiome promoted the rapid evolution of *P. fluorescens*, which reciprocally altered the microbiome, and these eco-evolutionary dynamics subsequently modified the fitness of the host. The results suggested that the microbial effects probably occur through changes in the production of the plant growth hormone auxin by the microbiome (Tan, et al., 2021). Wang et al. aimed to explore the ecological roles of *B. amyloliquefaciens* FH-1 (FH) on rhizosphere properties, cucumber seedlings, and the bacterial community (Wang, et al., 2021). FH was shown to *i*) promote cucumber seedling growth, *ii*) reduce the rhizosphere bacterial diversity, *iii*) increase Proteobacteria abundance, and *iv*) decrease Acidobacteria abundance. The weight, height and length of cucumber seedlings were significantly correlated with 18 inhibited taxa and the enrichment of *Nannocystaceae*. FH might therefore promote cucumber seedling growth via the enrichment of *Nannocystaceae* and the inhibition of various taxa belonging to Acidobacteria, Actinobacteria, Chlorofexi, Plantctomycetes and Verrucomicrobia (Wang, et al., 2021).

In order to study bacterial dynamics under soil nitrogen limitation, Garcia et al. recently applied selection pressure for the microbiome-driven enhancement of *Brassica rapa* biomass (Garcia, et al., 2022). The selection pressure enhanced the seed yield of *B. rapa* and the utilization efficiency of nitrogen. Among specific bacterial phyla such as Proteobacteria and Bacteroidetes, distinct interactions emerged in response to selection, and without selection, the bacterial communities showed less complex interactions. These results suggested that group-level bacterial synergies can modify microbiome functions, thereby affecting the growth of the host plant under soil nitrogen limitation (Garcia, et al., 2022). Zhang et al. found that the stem xylem selectively recruits highly conserved microbes dominated by Gammaproteobacteria, and assessed the assembly and functions of maize microbiomes across soil types, climate zones, and genotypes (Zhang, et al., 2022). The authors revealed that the proportion of bacterial taxa carrying the nitrogenase gene (*nifH*) in stem xylem was higher than in the root and leaf endosphere. They constructed synthetic communities consisting of two core diazotrophs and two helpers. By utilizing GFP-tagged strains and ^{15}N isotopes, it was demonstrated that these strains contributed to biological nitrogen fixation in maize stems (Zhang, et al., 2022). In a different study related to abiotic stress, Mueller et al. developed a method to select for rhizosphere microbiomes that confer tolerance to the model grass *Brachypodium distachyon* under sodium or aluminium salt stress (Mueller et al., 2021). The proposed selection generated microbiomes that were able to enhance plant fitness. Yuan et al. hypothesized that the high halo-tolerance of the seepweed *Suaeda salsa* is due to a specialized belowground microbiome interplay (Yuan, et al., 2016). To test this hypothesis, they performed a phylogenetic trait-based analysis. Rhizospheric and endophytic bacteria associated with *S. salsa* were shown to contribute to salt stress acclimatization, nutrient solubilization, and competitive root colonization (Yuan, et al., 2016). Plant growth was shown to in-

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crease linearly with the inoculation of different species, with *Klebsiella pneumoniae* and *Brevibacillus agri* playing important roles in improving fitness in monocultures (Singh, et al., 2015).

Phytoremediation can serve as a sustainable and effective technology for cadmium remediation, especially in agricultural soil. To this end, the rhizosphere microbiome can promote the growth and cadmium accumulation in hyperaccumulator plants. A recent study by Fan et al. used accumulating and non-accumulating ecotypes of *Sedum alfredii* as model plants to investigate the assembly and influence of the rhizosphere microbiome on plant growth under high cadmium conditions (Fan et al., 2022). Their results showed that distinct root microbiomes assembled in both ecotypes of *S. alfredii*. The bacterial genera *Sphingomonas*, *Lysobacter*, *Afipia*, *Hydrogenispora*, *Luedemannella*, *Adhaeribacter*, and *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* were enriched in cadmium-contaminated soils. The rhizosphere microbiome, assembled in the accumulating ecotype, contributed to plant fitness via nitrogen fixation, phosphorus solubilization, siderophore metabolism, and IAA synthesis, as well as cadmium uptake (Fan, et al., 2022).

3.3 Understanding bacteria-bacteria interactions can guide the design of synthetic communities

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Synthetic microbial communities are composed of two or more defined microorganisms. Within such communities, members can engage in complex communication via exchanging, detecting, and responding to signaling molecules. They can perform different tasks in this setting, thereby achieving complex functions that a single microbial strain cannot accomplish. In natural systems, microbial communities play important roles in various environments, which often inspires the construction of synthetic microbial communities. Niu et al. constructed a synthetic bacterial community consisting of seven bacterial species: *Enterobacter cloacae*, *Stenotrophomonas maltophilia*, *Ochrobactrum pituitosum*, *Herbaspirillum frisingense*, *Pseudomonas putida*, *Curtobacterium pusillum*, and *Chryseobacterium indologenes* (Niu et al., 2017). These represent three of the four most dominant bacterial phyla typically found on maize roots. The findings suggested that *E. cloacae* plays a key role in this model ecosystem; this synthetic community synergistically inhibited the phytopathogenic fungus *Fusarium verticillioides in planta* and *in vitro* (Niu, et al., 2017).

By selectively removing or replacing individual species to test their impact on synthetic microbial communities, insights into microbial interactions can be obtained. Schäfer et al. recently studied bacterial interactions in the phyllosphere microbiota (Schäfer et al., 2022). They screened microbial interactions in the model plant *Arabidopsis* by individually adding 200 endogenous strains to a synthetic community composed of 15 bacterial strains, and tracked changes in microbial community composition after colonization. It was found that 90% of the bacterial interactions were negative, and strains that were phylogenetically more related had more consistent effects on the synthetic community (Schäfer, et al., 2022). Finkel et al. used a bacterial synthetic community consisting of 185 isolates for inoculation experiments (Finkel, et al., 2020). They constructed the synthetic community based on four classified modules of co-occurring bacteria and identified interactions between microorganisms that determine the root phenotype. The interactions were shown to mainly involve the bacterial genus *Variovorax*, which reversed the

inhibition of root growth induced by a wide diversity of other bacteria. Furthermore, *Variovorax* was shown to manipulate the levels of plant hormones, balancing the effects of the synthetic community on root growth.

Combining knowledge from synthetic biology and ecology can inform the construction of synthetic microbial communities. However, in natural environments, even a simple microbial ecosystem typically contains at least ten interwoven species, which can yield combinations of hundreds or even thousands of interactions (Shuyao L, 2021). Thus far, unravelling and studying the vast number of interactions in microbial ecosystems has been a challenging task, partly due to the lack of feasible and manageable tools to decipher species interactions in complex communities. However, a detailed understanding of such interactions will be required for the design of more reliable synthetic communities applicable for plant protection.

4 Concluding remarks and perspectives

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The potential of bacteria-bacteria interactions to improve agricultural practices, especially the reduction of pesticide use, has been explored intensively during recent years. Many of these findings could be translated into sustainable applications during the next decade. However, viable solutions will require a deeper understanding of soil and plant microbiomes as well as key interactions therein. The development of biological control applications can profit from microbiome analyses at various stages (Cernava, 2021). Such analyses can support the identification of synergistic as well as antagonistic interactions between biological control agents and members of naturally occurring bacterial communities. Future developments will also need to rely on the efficient production of living microorganisms, especially bacteria, for agricultural use. For this purpose, the industrial-scale fermentation of mixed bacterial communities could provide viable means not only to reduce production costs but also to increase their efficacy under field conditions (Rändler-Kleine et al., 2020). To identify microorganisms that are suitable for such approaches, the large-scale profiling of various microbiomes is necessary to identify prevailing synergistic interactions between bacteria under distinct environmental conditions.

The advent of artificial intelligence (AI) technologies has allowed us to significantly enhance our understanding of complex microbial interactions. AI algorithms are capable of processing and analyzing large volumes of biological data, including genomics, transcriptomics and proteomics, supporting the identification of patterns and correlations in microbial interactions. Moreover, machine-learning models can be used to predict the behavior of microbes under various environmental conditions and how they interact with each other. Specifically developed models can forecast microbial responses to environmental changes based on historical data. Overall, AI provides a vital basis for a range of powerful tools and methods that can accelerate discovery processes and enhance the precision and efficiency of research towards a comprehensive understanding of microbial interactions (Hernández Medina et al., 2022).

A deeper knowledge of bacteria-bacteria interactions will also facilitate the development of microbiome engineering approaches. In the past, the modulatory effects of microbiome was often observed when plants were inoculated with various beneficial bacteria (Berg et al., 2021). It is highly probable that we will able to engineer plant and soil microbiomes with great precision in the near future not only to increase sustainability in agriculture but also to boost plant health and productivity to a level unachievable by applying conventional agrochemicals.

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Author contributions

Yun CHEN and Tomislav CERNAVA contributed to the manuscript's conceptualization, review and editing. Zhonghua MA contributed to the manuscript's editing. Giovanni Davide BARONE and Yaqi ZHOU compiled the data and wrote the manuscript. Hongkai WANG and Sunde XU contributed to the figure and table design. All authors have read and approved the final manuscript.

Compliance with ethics guidelines

Giovanni Davide BARONE, Yaqi ZHOU, Hongkai WANG, Sunde XU, Zhonghua MA, Tomislav CERNAVA and Yun CHEN declare that they have no conflict of interest.

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