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Rhizosphere bacterial interactions and impact on plant health

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The rhizosphere is a chemically complex environment that harbors a strikingly diverse microbial community. The past few decades have seen a rapid growth in the body of literature on plant–microbe–microbe interactions and plant health. Thus, the aim of this paper is to review current knowledge on plant–microbe–microbe (specifically bacteria) interactions in the rhizosphere and how these influence rhizosphere microbiomes and impact plant health. This article discusses (i) how the plant recruits beneficial rhizosphere bacteria and ii) how competition between rhizosphere bacteria and mechanisms/weapons employed in bacteria–bacteria competition shapes rhizosphere microbiome and in turn affects plant heath. The discussion mainly focuses on interference competition, characterized by production of specialized metabolites (antibacterial compounds) and exploitative competition where a bacterial strain restricts the competitor's access to nutrients such as through secretion of siderophores that could allude to cooperation. Understanding mechanisms employed in bacteria–bacteria and plant–bacteria interactions could provide insights into how to manipulate microbiomes for improved agricultural outcomes.

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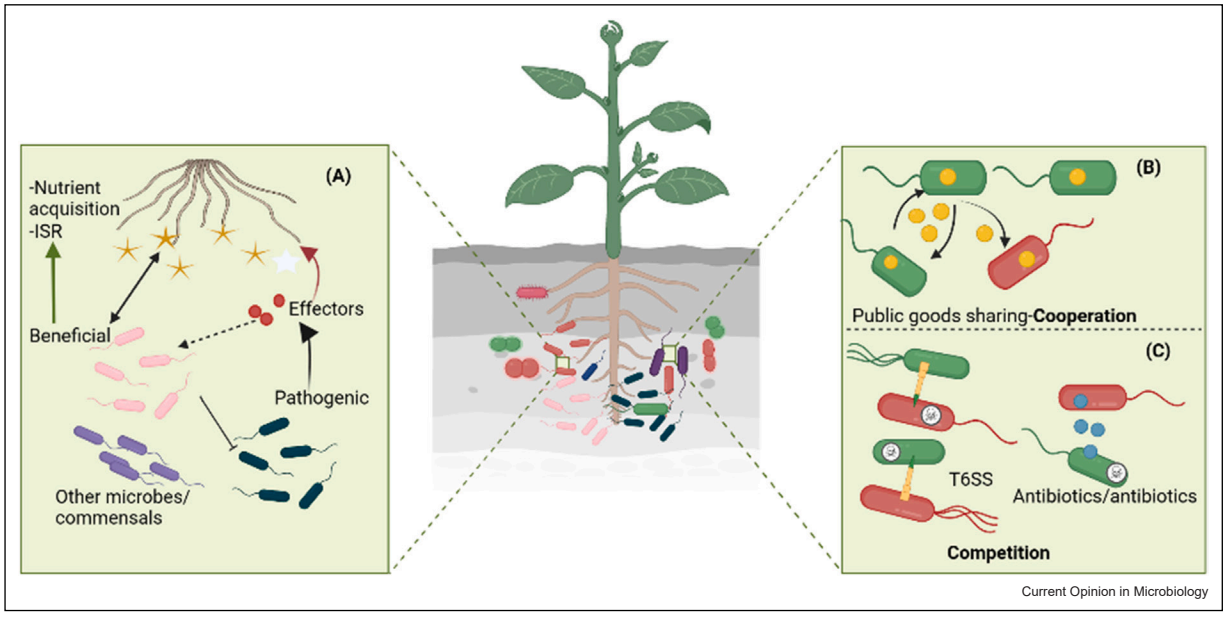
Introduction

Historically, the study of plant pathogen interactions has focused mainly on single microbes, their virulence factors, and how these enable host colonization resulting in disease. Yet, the host environment (niche) consists of complex microbial communities with dynamic interactions that can directly or indirectly impact disease development. Recent advances in sequencing technologies and availability of large 'Omics data sets' have played an important role in 'decoding' these complex interactions. Consequently, new concepts that recognize that a multicellular organism such as a plant together with its associated microbiota functions as an entity (known as a holobiont) and that microbes should be studied in the context of a microbiome or pathobiome, are emerging [1–3].

The rhizosphere, defined as the plant root-soil interface, is home to diverse microorganisms such as bacteria, archaea, fungi, nematodes, protozoa, invertebrates, and other organisms that interact with each other [4–6]. Rhizosphere microbes can interact with their plant hosts (host–microbe) or among themselves (microbe–microbe), leading to inter- and intra-kingdom interactions [7]. These interactions can be classified into (i) negative interactions that are represented by competition (antagonism), (ii) positive interactions also known as cooperation, and (iii) neutral interactions established by commensals to take advantage of root exudates as nourishment without harming plants [8–10]. The outcome of these interactions has consequences on microbial population structure and implications on the health status of the plant host. For instance, many of the microbes in the rhizosphere serve as 'undisputed guardians' of plant health since they defend plants against pathogen invasion (by either direct activation of plant immunity to enhance disease resistance or indirectly by suppression of pathogenic microbes) as well as helping to acquire nutrients from the soil [11]. Even so, it is important to note that there are other factors that contribute to changes in rhizosphere microbial compositions that are not discussed here such as climate, plant genotype, and edaphic factors [12–14]. Understanding the complex relationships between plants and their microbiota as well as ensuing microbe–microbe interactions within the rhizosphere presents a plethora of possibilities for improving plant health without using toxic and environmentally unfriendly chemicals [14–17].

Even though we recognize the vast diversity and complexity of rhizosphere microbial compositions and interactions, due to the limited word requirements of the journal, we discuss the role of microbial interactions (limited to rhizosphere bacteria) in promoting plant

Figure 1



A graphical abstract of bacterial interactions and plant protection/health within the rhizosphere. **(a)** The plant releases root exudates (yellow stars) into the soil to either manipulate rhizosphere microbial community dynamics or recruit (double-ended arrow) beneficial bacteria (pink cells) after recognizing pathogen invasion. The recruited bacteria could suppress (blunt arrow) pathogenic bacteria (dark green) or ISR enhancing plant immunity as well as nutrient acquisition (green arrow). Successful pathogenic bacteria secrete effector proteins (red circles) to manipulate host immunity (red arrow) for their advantage (red arrow) and modulating microbiome compositions (dotted arrow). **(b)** Within the rhizosphere, where resources are deficient, bacteria cooperate to share public goods among kins (green cells). However, cheating can also occur (red cell). **(c)** The T6SS enables bacteria to outcompete other microbes (some of which maybe pathogenic) by killing or inhibiting their growth of target cells. Alternatively, bacteria produce antibiotics and/or bacteriocins to either kill or inhibit competing microbes.

health. We highlight how the plant influences or recruits beneficial bacteria in the rhizosphere. We also review how the interactions (both antagonism and cooperation) between bacteria influence rhizosphere microbial structure and in turn, how this impacts plant health.

The plant and rhizosphere bacteria

The rhizosphere microbiome plays an important role in plant health. In this regard, the plant host plays an important role in recruiting or attracting beneficial bacteria through secreted root exudates. Beneficial rhizosphere bacteria can benefit the plant directly or indirectly by 1) assisting plants to acquire nutrients from the soil, 2) suppression of plant pathogens, and 3) enhancing plant immunity through induced systemic resistance (ISR), which involves activation of plant resistance against a broad spectrum of pathogens (Figure 1a). An example of rhizosphere-facilitated nutrient uptake is iron. Under iron starvation conditions, plants secrete coumarins that modulate rhizosphere microbiota to mediate plant iron uptake and increase immunity [18–20]. Similarly, other plant root-secreted secondary metabolites such as terpenes [21] and benzoxazinoids [22–25] play a pivotal role in shaping plant rhizosphere microbe (through increasing beneficial soil microbes) and subsequently contributing to plant health. In addition to nutrient uptake, the role of rhizosphere microbiome on plant health is evidenced in disease-suppressive soils [26]. Toward this end, beneficial bacteria protect plants from diseases by suppressing pathogens through the production of antimicrobial compounds or by competing with pathogens within an ecological niche [27]. For instance, rhizosphere bacteria suppress the bacterial pathogen, *Ralstonia solanacearum*, by siderophore-mediated competition for iron [5]. In another study, [11] demonstrated that disruption of beneficial strains of ISR eliciting Firmicutes and Actinobacteria in tomato plant rhizosphere increased incidences of bacterial wilt. Similarly, wheat plants inoculated with *Rhizoctonia solani* anastomosis group 8 (AG8) were shown to recruit beneficial rhizosphere bacteria such as *Chitinophaga*, *Pseudomonas*, *Chryseobacterium*, and *Flavobacterium*, and a group of plant growth-promoting as well as nitrogen-fixing microbes that act in consortium to antagonize soil-borne pathogens [26]. In the long term, it will be important to profile bacterial communities in soils that suppress multiple diseases. A combination of metadata analysis with machine learning has recently been used to identify the general patterns of bacterial-community composition in disease-suppressive soils [27].

Other than their suppressive role in the rhizosphere, many beneficial soil-borne bacteria can boost the plant

immune system by inducing plant systemic resistance to multiple pathogens [28–30]. For instance, the plant growth-promoting rhizobacterium (PGPR) *Pseudomonas fluorescens* was shown to induce ISR in *Arabidopsis* [31]. Apart from ISR, some beneficial bacteria such as nitrogen-fixing rhizobia and PGPR can also modify plant volatiles to induce plant defense [32]. In the case of a pathogen attack, the plant cell receptors perceive a stressor issuing a 'cry for help' that is transmitted by downstream signaling networks to trigger an immune response [33,34]. This stimulates changes in plant root exudates that target and recruit selective groups of microbes to colonize their rhizosphere. It is worth noting that successful microbes secrete effectors to interfere with different host immune signaling components. For instance, pathogens encode large amounts of secreted effector proteins, however, the functions of many effectors in terms of host plant manipulation remain unknown. This might suggest the possible utilization of effectors as exquisite tools for the interaction with other microbes, potentially modulating microbiome compositions [35]. For example, [36] demonstrated that effectors such as those of the Type III secretion system (T3SS) (*R. solanacearum*) are injected into the host cell where they reprogram host cells to inhibit competitors within the same niche giving the pathogen a competitive advantage (Figure 1a). This confers an additional role of T3SS effectors to include not only in virulence but also in host–microbe–microbe interactions.

In summary, the plant plays an important role in rhizosphere bacteria selection to enhance beneficial microbes that can directly inhibit pathogens, enable the plant to acquire nutrients, or induce ISR, altogether, these promote plant health (Figure 1a) even though as demonstrated, other microbes can change the host cell and use it to reconfigure plant microbiota. Apart from plant recruitment of beneficial bacteria, important factors shaping rhizosphere microbiota likely influencing plant health are the dynamic interactions that occur between bacteria (bacteria–bacteria interactions) in the rhizosphere, discussed in the next section.

Bacteria competition influences rhizosphere microbiota

Bacteria have evolved diverse mechanisms that enable them to compete in different ecological niches. These mechanisms play a fundamental role in shaping rhizosphere microbial composition, subsequently influencing the host plant. These include exploitative competition where microbes compete for scarce resources and the winner typically limits nutrient availability from competitors (Figure 1b and 2) or interference competition mediated by production of an arsenal of antibacterial/antimicrobial compounds or weapons [8]. Interference competition can be achieved through the production of small diffusible molecules that function between physically separated bacteria or relies on secretion of lethal effector proteins to antagonize competing microbes (Figure 1c and 3). Understanding mechanisms employed by rhizosphere communities to interact opens up opportunities for engineering strategies that could be harnessed toward improvement of plant health.

'An offensive operation': exploitative competition

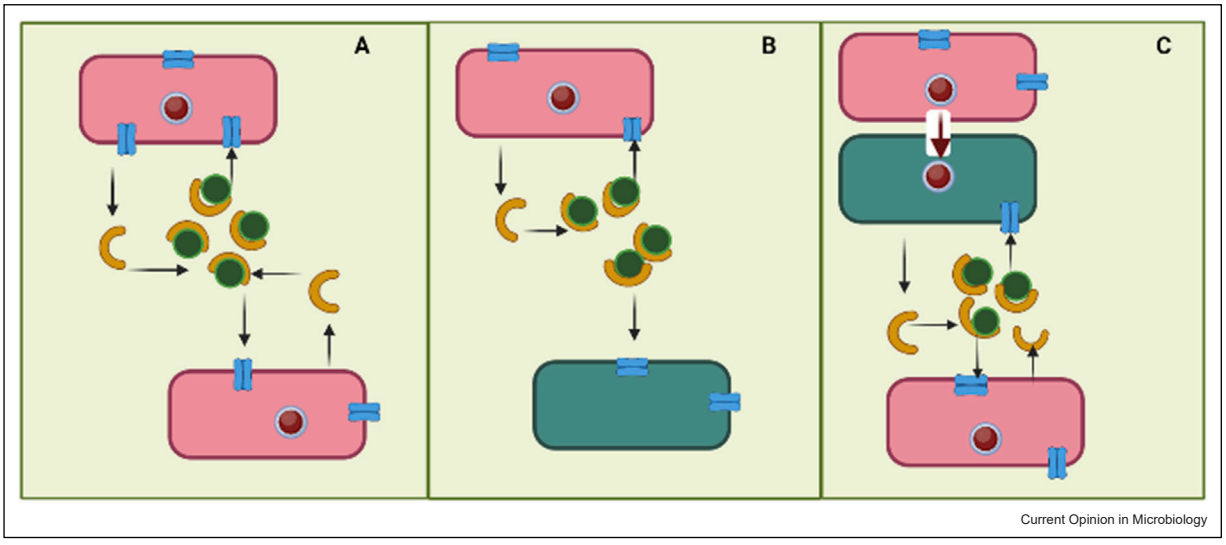
Exploitative competition occurs due to high demand of the same nutrients by members of a microbial community. Here, one organism indirectly outcompetes its rivals by utilizing limiting resources or nutrients, such as carbon, phosphorus, iron, and nitrogen, which are essential for bacterial growth. Iron is seen as the 'gold' that drives exploitative competition (Figure 1b). To overcome iron depletion, bacteria produce siderophores (public goods), chelated compounds that bind trivalent iron ions and play an important role in pathogenesis (Figure 2). Siderophores can lock iron away from competitors that do not have matching receptors. In this regard, siderophore production has been observed to be a major way that plant growth-promoting bacteria (PGPB) deprive plant pathogenic bacteria of iron [5]. Nonetheless, successful pathogenic bacteria such as *Xanthomonas oryzae* pv. *oryzicola* can improve their competition for iron uptake through gene editing in a ferric siderophore receptor [37]. Siderophores carry two conflicting social effects on community members, either as 'public goods' or 'public bads' [5,38,39]. Siderophore as 'public goods' is often considered a form of cooperation since the secreted molecules can be shared between closely related cells or kin selection [40].

Cooperation is an 'expensive affair' due to exploitation by noncooperators or 'cheaters' and with time, the 'cheaters' outcompete producers in the population, an event that undermines cooperation in the population. This raises the question why would a microbe be willing to 'dig deeper into its pocket' just to benefit another over self? Horizontal gene transfer is associated with production of cooperative public goods including siderophores [41,42]. Precisely, siderophore nonproducers have been shown to evolve receptors that match the modified siderophores, or by acquiring a matching receptor via horizontal gene transfer as portrayed by *Pseudomonas* spp. isolates from soil and freshwater habitats [43].

Therefore, gene coding for the production of a public good can allow 'cheaters' to acquire the 'cooperative gene', hence turning them turned into 'cooperators' (Figure 2).

Other than competing for nutrients in the rhizosphere, bacteria can also compete to colonize a niche/enhance

Figure 2

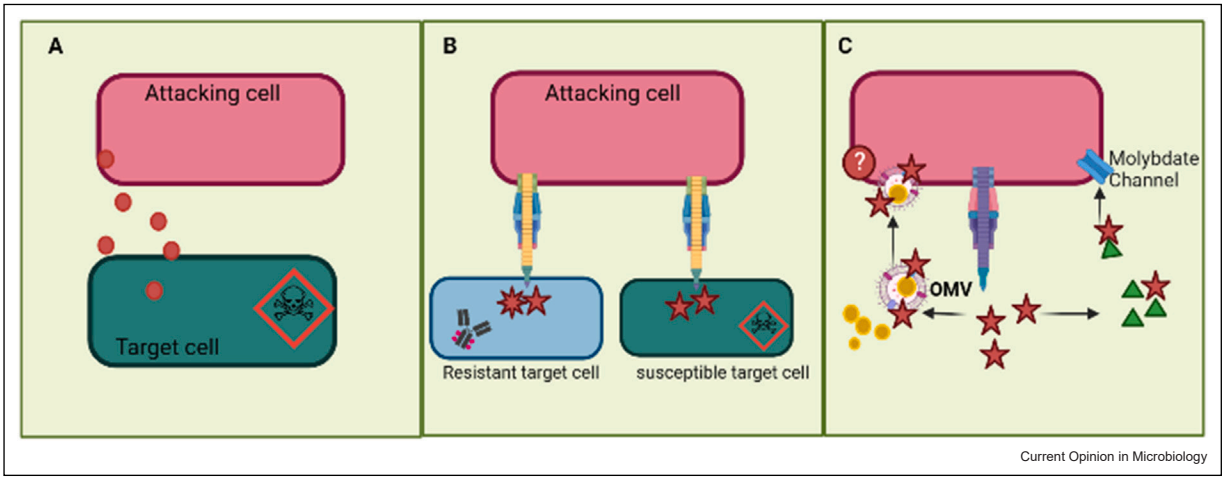


Siderophore-mediated iron uptake by bacteria in the rhizosphere. **(a)** Under an iron-limited environment, competitive bacteria (red) produce specific low-molecular-weight chelators, siderophores (yellow crescent) to sequester and solubilize insoluble iron (green circle) that can be shared among cells. **(b)** Cheating happens when siderophore nonproducers (turquoise) have the matching receptors (light-blue channels) for iron uptake and exploit the 'public goods' produced by others while not contributing themselves. **(c)** Through horizontal gene transfer, 'cheaters' can acquire a gene (red arrow) for siderophore receptor (red circle), thus transforming them into 'noncheaters'.

access to a given space. Another strategy to occupy an ecological niche is through the formation of a biofilm. Biofilm-forming bacteria can survive under environmental stresses [44,45]. Biofilms formed by some bacteria produce volatile compounds that inhibit development of competing biofilm colonies [46].

Generally, there is a lack of understanding of how sharing of public goods between plant- associated bacteria influences microbial community and improves plant health [2]. Nonetheless, cooperation in microbial communities can be harnessed for development of better consortia of plant-beneficial microbes (reviewed

Figure 3



Interference competition of bacteria. **(a)** Bacteriocin/antibiotics (red circles) production to facilitate competition. **(b)** The T6SS nanomachine delivers toxic effector proteins (red stars) from an attacking cell to nearby target cells. Susceptible target cells are subject to the noxious actions of the delivered T6SS effectors, while resistant target cells possess cognate immunity proteins (black with pink stars) that bind to the incoming effectors to neutralize them. **(c)** Effectors secreted by the T6SS (red stars) can sequester nutrients present in the environment. Under an iron- (yellow circles) limited environment, T6SS effectors recruit OMV to facilitate iron acquisition. The mechanism of T6SS–OMV–iron uptake is still unknown (?). In the absence of oxygen, T6SS effectors are secreted to enhance molybdate (green triangles) acquisition.

Table 1

Summary of recent antibacterial T6SS effector proteins involved in contact-dependent interbacterial antagonism as well as nutrient acquisition from the environment.

Effector class	Effector name	Biochemical activity	Organism	Ref	Comment
Membrane-associated	valine-glycine repeat protein G2b (VgrG2b)	Membrane blebbing to inhibit growth	*P. aeruginosa*	[84]	The activity of some T6SS effector mimics known antibiotics such as β-lactam. In addition, VgrG2 group could be trans-kingdom effectors
	Small secreted protein 6 (Ssp6) type VI (p)ppApp synthetase 1 (Tas1)	Depolarization of the inner membrane	*Serratia marcescens*	[85]	SsP6 is a new family of T6SS-delivered antibacterial effector that can form cation-selective pores
Nuclease	The restriction endonuclease (Tox-REase-5) domain-containing nuclease effector (TseTBg)	RNase and DNase activity	*Burkholderia gladioli*	[86]	T6SS effectors have evolved to exhibit dual- nuclease activity with cognate immunity proteins that exert transcription repression activity, analogous to type-II antitoxins
	Tas1	DNase activity	*P. aeruginosa*	[87]	Various T6SS effectors are involved in cell growth rate as well as in bacterial physiology
	Type six DNase effector (Tde)	Cell elongation and DNA degradation	*A. tumefaciens*	[88]	Environment determines Tde activity. For instance, carbon starvation promotes killing
	Rearrangement hotspot B effector (RhsB)	DNase activity	*Acidovorax citrulli*	[89]	T6SS effectors can kill not only Gram-negative but also Gram-positive bacteria
	Rearrangement hotspot A effector (RhsA)	Possesses NAD(P)+ hydrolase activity	*P. protegens*	[90]	T6SS effectors from commensal bacterium can inhibit the growth of its bacterial competitors
Cell wall-disrupting effectors	Type-six secretion systems amidase effector (Tae1)	Mediates *in vivo* degradation of cell walls	*P. aeruginosa*	[91]	The function of Tae1 can vary depending on the composition of peptidoglycan
	Lysozyme-like effector	Induces peptidoglycan degradation leading to cell lysis	*Pantoea agglomerans*	[92]	With use of computational analysis, novel T6SS effectors can be identified
	Type-VI amidase effector (Tae)	Cleaves D-Ala-meso-diaminopimelic acid and D-Glu bonds in peptidoglycan	*A. tumefaciens*	[88]	Some T6SS effectors could be dominant only when the environment is nutrient-rich. However, when there are limited nutrients, they are likely to promote efficiency of other effectors
Other functions	LPS-binding effector (TeoL)	Acquisition of iron from Outer membrane vesicles (OMVs)	*Cupriavidus necator*	[74]	T6SS effectors are not only involved in bacterial killing. but also implicated in 'nonkilling' activity such as nutrient acquisition
	Hcp2 and HsiA2	Molybdate acquisition through secretion of molybdate-binding protein	*P. aeruginosa*	[75]	

Based on their biochemical activities, T6SS effectors target cell membrane, nucleases, and cell wall. T6SS-secreted proteins are also involved in nutrient acquisition from the environment and thus enabling bacteria to survive better within the rhizosphere and in niches that are typically nutrient-deficient.

in [47]). For example, maize plants were shown to favor recruitment of bacteria with fewer beneficial properties than those with many [48]. This could suggest that a bacterium with fewer beneficial functions in a consortium is likely to be more productive for those given functions and a bacterium with many functions might be less efficient in performing all of them.

Shoot to kill or disable: interference competition

Antibiotic and bacteriocin production

The plant rhizosphere is highly populated with plant pathogenic, beneficial, and commensal bacteria. To survive in this highly competitive environment, bacteria aggressively compete with other bacterial cells by employing a variety of sophisticated offensive weapons to tackle intra- and interspecific competition. This includes the production of antibiotics, bacteriolytic enzymes against phytopathogenic fungi [49], and proteinaceous antibiotics known as bacteriocins [50]. Since the focus of this review is on bacterial interactions, we will focus on antibiotics as well bacteriocins. In contrast to antibiotics that are broad-spectrum metabolites produced by multienzyme complexes, bacteriocins are ribosomally synthesized narrow-spectrum proteinaceous substances produced by a wide range of bacterial species [51,52]. Owing to target specificity of bacteriocins (no collateral damage), they present an exciting possibility of being used as plantibiotics (biological agents, which selectively kill plant pathogens) [53].

Production of antibiotics and bacteriocins is tightly regulated [54]. For instance, antibiotic production is enhanced only when (i) competing against phylogenetically distant species and (ii) the rival cells are sensitive to a specific class of antibiotics [55]. On the other hand, production of bacteriocins is also favored by specific conditions such as UV irradiation, nutrient limitation, and production of antimicrobial compounds by other bacteria [51,56]. Studies have shown that bacteriocins are capable of killing closely related rival bacteria without affecting the bacteriocin-producing strain due to post-transcriptional modification and/or specific immunity mechanisms [57,58]. Similarly, some antibiotics producing bacteria such as *Bacillus subtilis* can discriminate self from nonself when self-produced antibiotics are involved in self-recognition [59,60].

Different types of bacteriocins: R-, F-, S-, and M-type pyocins have been identified in rhizosphere -associated bacteria where they differ in their morphology as well as mode of killing [61,62]. Their mode of activity ranges from pore formation in the cell membrane to nonspecific degradation of cellular DNA, cleavage of rRNA 16S or tRNA, or inhibition of peptidoglycan synthesis resulting in cell death [63]. Bacteria produce nonribosomal peptides as well as polyketide antibiotics.

Type-six secretion systems

To effectively compete for space and resources, bacteria employ various contact-dependent systems such as Type zero secretion system (T0SS) (also known as OMV) [64], T4SS [65], and type-six secretion systems (T6SS) [66–68], which have been linked to bacterial competition. For the purpose of this review, we focus on the T6SS. The T6SS is a well-studied double-tubular nanomachine widely found in Gram-negative bacteria capable of penetrating neighboring cells to deliver effectors (Figure 1c and 3). Owing to the short range between the attacking and target cells, it is predicted that dead cells accumulate to form 'corpse barriers' that block further attacks of T6SS-sensitive cells [67]. Interestingly, the solution to this barrier lies on the ability of T6SS to deliver lytic toxins that not only kill but also disintegrate target cells. T6SS effectors have been reported to function as peptidoglycan hydrolases, phospholipases, RNA, and DNases, pore-forming proteins among other functions as shown in Table 1. One thing to note is that crucial genes that encode antibacterial toxic effectors are accompanied by genes that encode immunity proteins able to bind to their cognate effector, neutralizing its action as seen in Figure 3. This protects the toxin-secreting cell from the noxious effects of its own antibacterial effectors and from those that may be delivered by the T6SS of neighboring sibling cells [69,70].

Over the last decade, the T6SS has emerged as a key player in interkingdom interactions and a critical determinant of interbacterial competition (as reviewed in [3,70–72]). Hence, T6SS effectors can impact plant health by either targeting and undermining plant immunity (antieukaryotic) or conferring competitive advantage to the producer [3,72]. It must be noted though that currently, T6SS effectors of plant-associated bacteria are shown to be mostly recruited for competition. However, there is some indication that the T6SS of plant-related bacteria do attenuate host immunity even though there is no clear understanding of the mechanism or effectors associated with this attenuation [73]. Many PGPB make use of their T6SS to deliver weapons against other rhizosphere competitors. For instance, the T6SS has also been shown to protect *Pseudomonas chlororaphis*, a PGPB strain, against both prokaryotic and eukaryotic rhizosphere colonizers [16]. Of importance though is that some effectors secreted by the T6SS do not need to be delivered into rival cells to execute killings. For instance, under iron-deficient conditions, the T6SS of bacterial cells secrete lipopolysaccharide (LPS)-binding effector to recruit OMVs to confer competitive advantage over rival cells [74]. Furthermore,

under anaerobic conditions, the T6SS provide a fitness advantage to *P. aeruginosa* for molybdate acquisition [75].

Similar to bacteriocin production, the assembly and firing actions of T6SS are costly, therefore, the system is tightly regulated. Accumulating evidence suggests that T6SS is regulated by many factors such as the quorum sensing system (QS), response to different environmental cues, such as reactive oxygen species, metal scarcity, temperature, and pH, and membrane damage caused by the attack of competitor bacteria [76–78]. Some phytopathogenic bacteria have more than one T6SS with possible roles in antibacterial or anti-eukaryotic activities [79,80]. This begs the question, how are these different systems regulated?

Future perspectives: implication of plant–microbe–microbe virulence mechanisms in disease control

Although plants can be protected from phytopathogens through various management strategies, including the use of chemicals, this leads to inflated costs of production and adverse environmental effects. Deployment of resistance genes (*R*-genes) is the most effective, environmentally sound, and widely used strategy for providing disease resistance to crop plants. Nonetheless, *R*-genes have been overpowered due to the evolution of new virulence traits within pathogen populations. Advances that allow integration of microbiomics and quantitative plant genetics show promise toward a new generation of microbiome-assisted breeding programs and crops [81]. Biological control of phytopathogen attack involving microbial communities, single strains, or microbial secondary metabolites offers a sustainable alternative approach to disease control in agriculture. For biological control of plant root pathogens to be in operation, there is a need to deeply understand molecular mechanisms that mediate host–microbe–microbe interactions within the rhizosphere. This realization of the complexity of microbial interactions has led to the use of synthetically designed concoctions of beneficial microbes (SynComs) that better mimic host–microbe–microbe interactions [17]. To develop SynComs as biocontrol products with increased versatility, combining compatible beneficial microorganisms with complementary effects on different targets is highly encouraged. In addition, for SynComs to be commercial products, consistency of the outcomes needs to be tested and further validated across multiple field trials in regions where it is aimed to be used.

Bacteriocins, which show a high degree of selectivity toward their targets with no off-target effects, can be produced at a large scale and applied as antibiotic agents. This begins by employing advanced techniques for identification and functional characterization of bacteriocins to be exploited for disease control in plants. This is then followed by large-scale production in a biofactory, from which bacteriocin-containing extracts can be obtained and applied to crops as biopesticides. In addition, since plants can express these bacteriocins [53,82], transgenic plants can be produced for effective control of targeted bacterial pathogens. An alternative non-GMO (genetically modified organism) approach is the application of nonpathogenic bacteriocin-producing strains directly on crops.

T6SS have been identified in both pathogenic and nonpathogenic Gram-negative bacteria. This can be exploited in biocontrol of plant pathogens. For instance, nonpathogenic bacteria with a T6SS have been proposed as possible biocontrol agents based on their ability to outcompete and inhibit plant pathogens [83]. Another promising agricultural strategy to controlling plant pathogens is by disruption of QS systems that regulate T6SS. Therefore, understanding of the molecular mechanisms and regulation of the T6SS should ultimately allow for its application in biocontrol of plant pathogens. Despite this potential, it is important to note that the role of T6SS in inhibition has mostly been studied using limited competition approaches that use only two bacterial strains per experiment. To fully comprehend the potential role of T6SS in disease control, modeling studies coupled with experimental studies need to be conducted. Another interesting possibility is the complementing strategies of the T6SS and OMV. Since the T6SS kill in a contact-dependent manner, it could be directed at killing bacterial cells in close proximity, while OMVs could be used to target distant cells. However, since both systems are relatively newly discovered, there is still much we do not understand. For example, regulation, assemblage, and cues that lead to their activation.

Overall, we anticipate that studies on virulence mechanisms that mediate microbe interactions will undergo a great deal of new and intriguing advancements in the coming years. This will help us expand our understanding of these mechanisms and find more effective ways to control plant diseases.

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Conflict of interest statement

None.

Data Availability

No data were used for the research described in the article.

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- • of special interest
- •• of outstanding interest

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