

Review

# Root Exudate Metabolites Alter Food Crops Microbiomes, Impacting Plant Biocontrol and Growth

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**Abstract:** Exuded plant metabolites play an important role in fostering beneficial interactions with the surrounding soil microbiota, thereby helping plants to better adjust to changing environmental conditions. These metabolites act as signals to attract or enhance the colonization of plant roots with specific groups of beneficial microbes and they modulate the dynamics of plant–microbe interactions in fulfilling plant niche-based requirements, directly and/or indirectly. This review emphasizes the expression, levels, modes of action, and net effects of the signaling metabolites that help food crop plants to become colonized by microbes that promote plant growth and development under periods of biotic stress.

**Keywords:** food crop; root exudates; signaling metabolite; PGPB; rhizosphere; microbiome

## 1. Introduction

The world’s population is currently estimated to be around eight billion people and is growing at the rate of approximately 72 million people per year (<https://www.worldometers.info/>; accessed on 27 December 2023). At the same time, it is estimated that there are nearly 900 million undernourished people in the world with ~14,000 people dying of hunger every day. With the prospect of a significantly increased global population in the next 50 years, it is essential that the worldwide availability of food crops increases dramatically.

Food availability can be significantly increased in several different ways. In the first instance, it has been estimated that “over a third of all food produced (~2.5 billion tons) is lost or wasted each year” [1]. Food wastage is not limited to richer and more developed countries; it is also a huge problem in poorer and less developed countries. Second, the genetic engineering of food crops, including genome editing using CRISPR/CAS9 technology, promises to significantly increase both the quality and the quantity of food that is currently available worldwide [2,3]. Third, the increased use of PGPB in agriculture, a technology that is currently in its early stages of development but is growing rapidly, promises to both increase crop productivity and quality as well as to decrease the use of potentially harmful chemicals in agricultural practice. Unfortunately, there is no one simple solution to the problem of insufficient global food availability. Thus, it is likely that dramatically increasing the food supply within the next 50 years will require all three of the abovementioned approaches.

Soil bacteria have interacted closely with plants for millions of years. These bacteria dramatically impact plant growth and development including increasing the ability of the plant to function in the presence of a wide range of environmental stresses, both abiotic and biotic [4].

The soil contains an enormous number, typically many thousands, of different types of microbes. Moreover, soil microbes are generally found in concentrations in the millions to hundreds of millions of organisms per gram of soil. These microbes, including various



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bacteria, fungi, cyanobacteria, archaea, and viruses, can impact the growth and development of plants positively (plant growth-promoting microbes), negatively (phytopathogenic microbes) or not at all (commensal microbes) [5,6]. Bacteria are by far the most predominant of all soil microbes and their interactions with plants have been studied to the greatest extent [4].

Soil bacteria may facilitate plant growth either directly (where bacteria and their metabolites interact directly with plants to promote their growth and development) or indirectly (where bacteria prevent various phytopathogens from inhibiting plant growth). Direct mechanisms include (i) facilitating the solubilization and uptake of minerals from the soil environment, including iron, potassium, and phosphorus; (ii) providing plants with fixed nitrogen; (iii) synthesizing the plant hormones cytokinin, gibberellin, and auxin, all of which stimulate different aspects of plant growth [7,8]; and (iv) decreasing plant ethylene using the enzyme ACC deaminase [4,9–13].

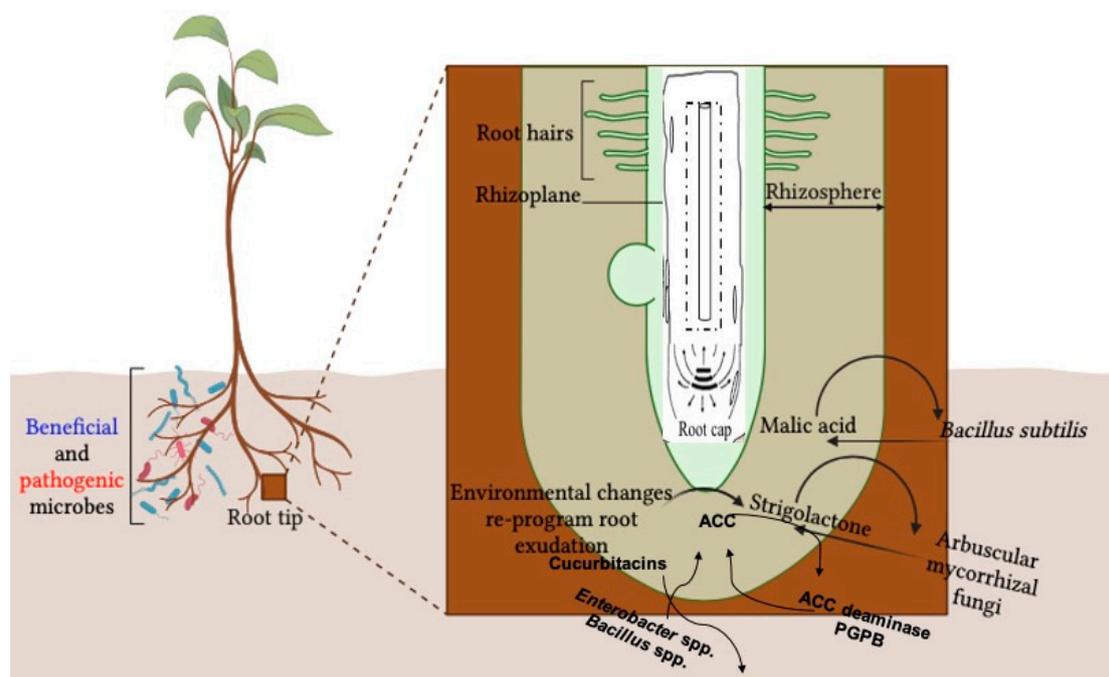
Indirect mechanisms decrease the damage or growth inhibition to the plant with various phytopathogens; these mechanisms include (i) the production of antibiotics and hydrogen cyanide which inhibit the growth of some bacterial and fungal phytopathogens; (ii) the solubilization and subsequent sequestration of iron by bacterially synthesized siderophores, thereby limiting pathogens access to iron and preventing their proliferation; (iii) the synthesis and secretion of fungal pathogen cell-wall-degrading enzymes; (iv) out-competing phytopathogens by (a) direct competition of nutrients and (b) establishing symbiosis with beneficial microorganism (e.g., arbuscular mycorrhizal fungi) [14], and as a result preventing the phytopathogens from binding extensively to plant roots; (v) the synthesis of many different volatile organic compounds that can inhibit pathogen proliferation; (vi) lowering the amount of potentially inhibitory plant ethylene concentrations by the enzyme ACC deaminase, thereby decreasing plant stress levels; and (vii) the induction of the plant's systemic resistance system, turning on the plant's defenses against various pathogens [4,11,15–18].

While the indirect mechanisms of plant growth promotion with PGPB appear to be applicable to the vast majority of plants, the bulk of the scientific literature deals with the protection afforded with PGPB to agricultural food crops [19,20]. Moreover, as of mid-2023, several dozen companies were marketing specific strains of PGPB which were purported to reduce the losses of agricultural food crops from both abiotic and biotic environmental stresses [20].

The largest numbers of bacteria are generally found in the plant rhizosphere, i.e., the portion of the soil that is present in the immediate vicinity of plant roots [5]. The reason for the high level of bacteria around plant roots is because of the exudation of a significant fraction (often 5–40%) of the carbon that is fixed by the plant through photosynthesis [21–24]. In addition to their presence in the rhizosphere, many plant growth-promoting bacteria (PGPB) are also able to colonize a plant's interior tissues (i.e., they are endophytic bacteria and are typically found in the spaces between plant cells). In addition, some bacteria form highly specific nodules on plant roots (they are symbiotic bacteria, typically including different types of Rhizobia). In the recent 10–15 years, many studies of how PGPB promote plant growth and development have been undertaken; they have focused on how groups (consortia) of bacteria, rather than individual strains, are able to act together/synergistically to positively impact plants [18]. These studies include an understanding of how the microbiomes (i.e., the groups of microbes that together influence plant behavior) of different plants attract different portions of the soil bacterial population. Each plant exudes (secretes) a unique mixture of small molecules through its roots that attracts a specific fraction of the soil bacterial community. As a result of this interaction, various plants producing different compositions of root exudate metabolites attract unique subsets of bacteria from the soil to the plant roots. Thus, the specific chemical composition of each plant's root exudates is involved in attracting from the soil the bacteria that make up a plant's root microbiome [25,26].

## 2. How Plants Recruit Beneficial Microbes and Exclude Pathogens

The rhizosphere is a metabolically dynamic space that contains a wide range of primary and secondary metabolites that originate from both plants and microbes. Chemicals present within the rhizosphere at any given time can act as signals that connect the surrounding organisms (food crops and microbes in this case) and thereby facilitate communication. Plants program their communication according to their needs, mainly based on the environmental changes and the developmental stage of the crop by exuding these signal molecules through their root system (Figure 1). Being in a nutritionally scarce soil hub, microbes are attracted towards this valuable source of nutrition and energy [27]. The biochemical nature of root secretions ultimately determines the microbial function and diversity that host crops utilize under certain environmental conditions [28–31].



**Figure 1.** Schematic representation of how biotic stress stimulates cellular and transcriptomic levels of plants' secondary metabolites in root exudates resulting in an altered rhizomicrobiome.

Under a nitrogen-deficient environment, legume crops secrete flavonoids as a component of their root exudates [32] that attract nitrogen-fixing microbes from the surrounding soil, regulate *nod* gene expression, and help food crop proliferation through the establishment of nodulation [33,34]. Similarly, malic acid and strigolactones, which are plant signal molecules, help to recruit PGPB [35] and foster plant–mycorrhiza interactions [36] in food crops.

Under drought stress conditions, *A. thaliana* roots recruit selective bacteria (*Pseudomonas chlororaphis*) with stress remediation functions, i.e., decreased expression of ethylene and abscisic acid and increased synthesis of salicylic acid, jasmonic acid, and reactive oxygen species defense enzymes [37]. Studies by Creus et al. [38] and Molina-Favero et al. [39] have demonstrated that tomato plants can selectively recruit *Azospirillum brasilense* by secreting nitric oxide into their rhizosphere; this bacterium is a PGPB that mediates tomato root architecture by supplying IAA to its host plant. Similarly, a complex array of groundnut root exudates that contains threonine, glyoxylic oxime acid, serine, pentanoic acid, glucopyranoside, tartaric acid, and 2-pyrrolidinone enhances the selective interactions of groundnut with two PGPB, *Pseudomonas aeruginosa* RP2 and *Bacillus sonorensis* RS4 [40]. Moreover, Arabinogalactan proteins found in the root exudates of legume and non-legume food crops [41], sugars and strigolactones in non-legume food crops [42] and canavanine

from legumes [43], help host crops to establish beneficial interactions with PGPB, Rhizobia, and mycorrhizal fungi, respectively.

Root exudates not only attract plant-beneficial microbes in facilitating mutualistic symbiotic relationships from a huge variety of microbial taxa [44], but also act as a biocontrol agent of unwanted opportunistic microbes. For example, maize exudes benzoxazinoids, which are antimicrobial in nature and clear the rhizosphere of actinobacteria, proteobacteria, and all pathogenic microbial populations [45]. Similarly, coumarins, plant-based secondary metabolites, have shown antimicrobial activity and helped the model plant *A. thaliana* to shape its microbiome [46]. In addition, Badri et al. [47] demonstrated that there are at least 25 genes directly involved in *A. thaliana* root exudation and that a single gene mutation can cause a significant change to the root exudate pattern, a change that may negatively impact the plant's interaction with soil microbes. Plant root exudates may, however, cause harmful effects on plant growth and development [48]. Thus, inefficient cross-talk between plant root systems, the rhizospheric environment, and the surrounding microbial community can sometimes lead to an outbreak of soil-borne diseases, imbalance in soil physiochemical properties, disproportion in the soil microbiome [49,50], root cell death, and accumulation of phytopathogens in the root zone [47,51].

In order to inhabit a plant's rhizosphere or colonize a plant's interior, a microbe must be able to live on the carbon sources that the host plant offers and bypass the host plant's defense mechanisms. Similarly, plants must have the ability to decide whether to allow a microbe to be the part of its microbiome and have it involved in mutualistic interactions or combat it through its defense systems [52]. Food crops, like most other plants, present multiple layers of scrutiny checkpoints for a foreign microbe (not native to the plant) to pass through and become resident on or in the plant. For example, the host-microbe interactions are highly dependent on the genetics and the growth stage of the participants, which is largely triggered by environmental biotic and abiotic factors [53]. Plants' cell membranes are equipped with hundreds of pattern recognition receptors (PRRs) and Nod-like receptors (NLRs) [52,54,55]. These receptors recognize a variety of conserved microbe-associated molecular patterns—MAMPs (e.g., chitin, flagellin, peptidoglycan, etc.)—and distinguish between a potential symbiont and a pathogen, the latter of which is eventually dealt with by the activation of pattern-triggered immunity (PTI) responses. NLRs are believed to be involved in fostering beneficial plant-microbe interactions such as nitrogen-fixing bacteria with legumes. Nod factors secreted by nitrogen-fixing bacteria are recognized by a variety of LysM receptors (LysM is a small widespread globular protein domain involved in binding bacterial peptidoglycan moieties) situated on the plasma membranes of legume crops [56] and establish a symbiotic relationship with host plants.

Since many microorganisms (both pathogenic and non-pathogenic) share the conserved core of MAMPs, and only a weak immune response is generated when a PRR recognizes a microbe-associated molecular pattern; therefore, the recognition of microbial antigenic entities by multiple receptors is required to implement an intense immune response [57]. Perception of a microbe-associated molecular pattern at the same time by multiple receptors on the membrane can be validated by the simultaneous recognition of an effector [57] and damage-associated molecular pattern [58,59], thereby leading to a significantly more rigorous immune response via the increased expression of genes involved in the plant host defense mechanism [52,58]. Unfortunately, not all of the members of the rhizospheric microbiota exhibit and follow clear signaling patterns with the host plant. Ultimately, it is the choice that a host plant makes to allow a particular microbe to be a part of its microbiome, depending on the potentially host beneficial activities that the microbe offers. Nevertheless, being sessile in nature, plants have to make endless critical decisions throughout their life regarding what to keep and what to fight, considering the resources that they possess and the environmental challenges that they face at any given time. The exact mechanism(s) regarding how plants chose one or the other still remains to be uncovered [52].

### 3. Plant Root Exudates

Root exudates are a chemically diverse class of substances that plants, throughout their lifetime, secrete into their surrounding environment (rhizosphere) via their root system. It is estimated that plant roots secrete about 5–40% of their photosynthetic assimilated carbon as root exudates [21,24]. Plant root exudates are comprised of high- and low-molecular-weight compounds belonging to organic acids, sugars, phenols, amino acids, hormones, flavonoids, and growth regulators [60].

Root exudates affect soil microflora differentially; they exhibit both stimulatory and inhibitory activities toward a variety of soil microorganisms [60]. There is a large body of literature indicating that plants utilize their root exudates to shape their microbiome [60–62]. Root exudates play important roles in plant growth and development by regulating micro-niches within the rhizosphere, recruiting and harboring selective microbiota, and communicating to soil microbes under various environmental conditions [62].

Root exudates are dynamic in nature; the composition, concentration, and balance between these two variables changes at different time points. For example, the levels of sugars and secondary metabolites in the root exudates of the model plant *Arabidopsis thaliana*, which were collected at various developmental stages over time, were found to be significantly different from each other and attracted different consortia of microbes that contained a diverse range of functions, and were able to help the plant respond to a range of environmental changes [63–65].

Many factors influence the composition of root exudates and shifts in root exudate patterns, with changes in climatic conditions being the most pivotal. Other factors that have been reported to change root exudation patterns include soil pH, soil type, soil temperature, soil oxygen content (aeration), soil physio-chemical properties, plant developmental stage, and plant genotype [24,64,66–68]. Intercropping has also been reported to alter the pattern of root exudates and to help food crops (e.g., tomato) to recruit beneficial microbiota to the rhizosphere [69]. Many mechanisms are employed to secrete root exudates into the surrounding soil medium; that is, low-molecular-weight compounds are secreted by passive transport (diffusion, ion channels, vesicular transport), whereas high-molecular-weight compounds are transported via active transport (membrane transport of proteins at the expense of energy driven by ATP hydrolysis) [70]. The level of root exudates is highest at the tip and the lateral branches of roots, and it becomes diluted as the root system proliferates [21]. The root system architecture is the first point at the plant–soil interface that becomes affected by climatic change due to any stress stimuli [24]. The nature and amount of root exudates are therefore primarily determined by the variations that occur in the root system under changing environments [71,72]. Moreover, it has also been shown that different structures serve as specialized locations to secrete specific root chemistries. For example, asparagine and threonine are exudated from the root meristematic and elongation zones; amino acids like glutamic acid, valine, leucine, and phenylalanine are secreted from the root hairs; and aspartic acid can be secreted from any part of the whole root system [24,73].

### 4. Overview of How Food Crop Root Exudates Facilitate Plant Biocontrol

Biocontrol in food crops begins at the plant's root–soil interface. It is neither energy efficient nor genetically possible for a plant to synthesize tailored antimicrobial weapons for each pathogen they might encounter during their life span. Rather, they have evolved ways to attract and recruit a microbial army with weapons (biocidal functions) to fight for them at the expense of a small portion of their atmospherically fixed carbon [10,20,25,74–79]. Thus, many PGPB have evolved together with their hosts to continue to offer them the functions necessary for the survival of the host plant in challenging environmental conditions.

Available knowledge of the molecular mechanisms and changes that occur within plants during biocontrol by soil microbes at transcriptomic and metabolomic levels are somewhat limited, although this research area is still growing. Fortunately, a few reports have discussed the role of some known biomolecules that have been identified in root

exudates of food crops and have been suggested to shape the microbiome of a host plant's rhizosphere and help it to better cope with various sorts of biotic stresses (phytopathogens). Table 1 presents such information and includes the food crop, the chemical signal found in root exudates, the changes to the microbiome as a result of adding this chemical signal, and the effects of such interactions on the biocontrol of known phytopathogens.

**Table 1.** Effect of root exudate metabolite on plant microbiome overcoming biotic stress.

Food Crop	Root Exudate	Affected Microbiome (↑ * or ↓ *)	Biocontrol/Outcome	Reference
Arabidopsis #	Malic acid	<i>Bacillus subtilis</i> FB17 ↑	<i>Pseudomonas syringae</i> pv tomato	[80–82]
Arabidopsis #	Amino acids and long-chain fatty acids	<i>Pseudomonas</i> sp. ↑	<i>Pseudomonas syringae</i> pv tomato	[83]
Barley	Phenolic compound	<i>Pseudomonas fluorescens</i> ↑	<i>Pythium ultimum</i>	[84]
Barley	Phenolic compounds	Beneficial rhizosphere community	<i>Fusarium graminearum</i>	[85,86]
Bayberry	Humic acid	<i>Mycobacterium</i> and <i>Crossiella</i> ↑ <i>Acidothermus</i> , <i>Bryobacter</i> , <i>Acidibacter</i> <i>Geminibasidium</i> , and <i>Mycena</i> ↓	Plant growth promotion and enhance disease resistance	[87]
Carex	Volatile organic compound (Monoterpene (Z)-limonene-oxide)	<i>Janthinobacterium</i> , <i>Collimonas</i> , and <i>Paenibacillus</i> ↑	<i>Fusarium culmorum</i>	[88]
Pepper	L-Malic acid	<i>B. subtilis</i> GB03 ↑	Aphids and <i>Ralstonia solanacearum</i> SL1931 control	[72,89]
Cucumber	Fumaric acid and citric acid	<i>Bacillus amyloliquefaciens</i> ↑	<i>Fusarium oxysporum</i> f. sp. Cucumerinum	[82]
Ginseng	Organic acids, sugars, and amino acids	PGPB ↑	<i>Alternaria panax</i>	[90]
Maize	Benzoxazinoids	Flavobacteriaceae and <i>Comamonadacea</i> ↓	Increased plant growth and disease resistance	[91]
Maize	Sesquiterpene (E)- $\beta$ -caryophyllene (Ebc)	Soil-borne entomopathogenic nematode ↑	<i>Diabrotica virgifera</i> larvae	[92,93]
Maize	Phenolic compounds	<i>Acinetobacter calcoaceticus</i> ↑	Larvae of western corn rootworms	[94]
Melon and watermelon	Cucurbitacins	<i>Enterobacter</i> and <i>Bacillus</i> ↑	Increased resistance to fungal pathogens	[95]
Canola	Trehalose, indolyl, glucosinolates, and sulfur	<i>Gammaproteobacteria</i> , <i>Firmicutes</i> , <i>Bacillus</i> , <i>Paenibacillus</i> , <i>Pseudomonas</i> , and <i>Stenotrophomonas</i> ↑	Biocontrol of cabbage root fly ( <i>Delia radicum</i> )	[96]
Peanut	Ethylene	<i>Actinobacterial species</i> ↑	Cassava ( <i>Manihot esculenta</i> )	[97]
Potato	Volatile compounds	<i>Phytophthora infestans</i> ↓	Biotic and abiotic stress reduction	[98]
Sorghum	Strigolactone	AMF colonization ↑	<i>Striga hermonthica</i>	[99]
Sweet wormwood	Artemisinin	<i>Sphingomonas</i> and <i>Sphingobium</i> ↑	Enhanced plant environmental fitness	[100]
Tomato	$\beta$ -Aldehyde	<i>Lysobacter</i> sp. ↑	Plant growth and defense enhancement	[101]
Tomato	$\beta$ -Caryophyllene	<i>B. amyloliquefaciens</i> ↑ and <i>Pseudomonas aeruginosa</i> ↓	Disease reduction and plant growth-promotion	[102]
Tomato	Strigolactone	AMF colonization ↑	<i>Meloidogyne incognita</i>	[103]
Tomato	Volatile organic compound	<i>Bacillus</i> sp. ↑	<i>Fusarium oxysporum</i>	[104]
Watermelon	Trans-chlorogenic acid, caffeic acid, and trans-cinnamic acid	PGPB ↑	<i>Fusarium oxysporum</i>	[105]

\* ↑ increased abundance; ↓ decreased abundance; # a model plant but not a food crop.

## 5. Bioengineering of Rhizospheric Soils for Disease Suppression

Production of food crops mainly relies on the soil's overall health and productivity. Yield loss due to biotic stress varies depending on the extent, spread, time of disease incidence, and nature of the pathogen(s) in the field; unfortunately, complete crop losses have been reported for many economically important food crops due to pathogen attacks [106,107]. Disease incidence is not a normal physiological state, and it prevails

when the symbiotic homeostasis between a plant and its ecological niche is disturbed. Plants continuously send chemical signals into the surrounding soils, via root exudates, as communication measures. These messages keep changing in response to changes in the environment and are primarily aimed at facilitating a quick and smooth plant adaptation to the new environment.

Under biotic stress conditions, plants undergo a complex array of physiological events, including altered gene expression and excessive secretion of root exudates; the increased root exudation attracts and recruits more beneficial bacteria from the soil, a situation termed as a “cry for help” [108]. If the newly recruited microbial army works as needed, plants overcome the stress, the microbiome is shifted, and a new symbiotic homeostasis is obtained. However, if the stress stimuli overcome the plant and its microbiome combined defense mechanisms, disease incidence and severity increase, and the entire homeostasis is challenged by the intruder phytopathogens, eventually leading to plant death. The rhizosphere soil microbiome of a plant works in harmony with the host defense system and provides valuable services to the ecological niches by enhancing disease resilience [64]. A large number of studies have shown the potential capabilities of microorganisms to mitigate biotic stress *in planta*. Table 1 provides research-based evidence of hosts’ needs-based microbial help to ameliorate biotic stress, i.e., how plants through the use of root exudates call for help and gather the required functions in close proximity to stave off phytopathogens. Considering the interactions of plants with their microbiomes and the dynamics of such interactions, a plant’s rhizosphere can be engineered to achieve an optimized balance in chemical signals, the introduction of microbes that could respond and utilize such signals, and the optimization of the microbial-pesticidal functions to overcome present or future disease incidences. When it comes to the decision of which microbe(s) should be part of the synthetic community, there are certain parameters to be considered: bio-compatibility of microbial members of the community within and with their plant host, a stable pool of desired functions (pesticides in this case), and an overall congruence of functions to be fit into various environmental conditions. One study showed that species-rich synthetic communities of similar genera seem to be more efficient and highly stable compared to species-poor (genera-rich) communities in controlling *Rhizoctonia solanacearum* densities in the rhizosphere of tomato plants [109]. Moreover, a synthetic community of distantly related bacterial and fungal genera could be useful in obtaining fitness over various plant genotypes and/or diverse environmental conditions [27]. Several attempts at microbial synthetic community formulations based on plants’ “cry for help” have been documented [110,111]. A machine learning computational technique was used to compose a synthetic community using root exudates from plants growing in phosphate-deficient soil. A pool of bacterial strains was grown in root exudates collected from *A. thaliana* growing under Pi-deficient conditions and monitored individually for their effects on the phosphate contents in plant shoots, which helped to design a synthetic community for a consistent predictable plant phenotype [110]. Similarly, under conditions of a downy mildew pathogen attack, *A. thaliana* plants selected bacterial consortia that worked synergistically with plant defense systems, resulting in phenotypically healthier plants [111].

Moreover, such knowledge can be used to create functionally reliable synthetic microbial communities that improve plant fitness. The right plant, the right time, and most importantly, the right microbe in the right formulation is what will make these bio-based-control systems a success story. Taking the complexity of plant–microbe interactions into consideration, agricultural biologicals do not appear to be stand-alone solutions [111,112]; plants need to be fostered and the desired microbial populations need to be promulgated. Therefore, it is suggested to combine a synthetic beneficial microbial community with the traces of chemicals previously proven to establish specific microbial populations in the rhizosphere. Such combinations could enhance the survival chances of the target microbes and offer them a competitive advantage for colonizing plants over their unwanted and potentially deleterious counterparts.

Bioengineering of rhizospheric soil for disease suppression and to promote plant fitness is an emerging field, offering great promise towards achieving agricultural sustainability, but also requires extreme care in selecting what is working under controlled conditions with the understanding that things may behave differently in the natural environment. Microbial consortia have often been demonstrated to be better options compared to single microbial inoculants in protecting plants from environmental stresses [79] but care should be taken in increasing complexities in the design of functionally reliable synthetic communities, as this may decrease the overall feasibility of the large-scale production and application of such biological tools.

## 6. Conclusions and Future Perspectives

One of the biggest challenges that the agriculture sector is facing is to feed the ever-increasing population of the world. As many strategies have been discussed earlier, the use of PGPB has shown promise in many facets. While individual strains of PGPB are highly effective in laboratory conditions, they are often found to be much less effective in the field. However, one way to make PGPB more effective, especially in addressing crop plant biotic stresses, is to first develop an understanding of the elements of crop plant root exudates which attract the microbes that select for a beneficial root microbiome. This information might then be used to develop microbial consortia with which to beneficially treat crop plant seeds and seedlings, thereby increasing the reliability of PGPB use in the field.

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