Defining plant growth promoting rhizobacteria molecular and biochemical networks in beneficial plant-microbe interactions

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Abstract

Background Our knowledge of plant beneficial bacteria in the rhizosphere is rapidly expanding due to intense interest in utilizing these types of microbes in agriculture. Laboratory and field studies consistently document the growth, health and protective benefits conferred to plants by applying plant growth promoting rhizobacteria (PGPR). PGPR exert their influence on other species, including plants, in the rhizosphere by producing a wide array of extracellular molecules for communication and defense.

Scope The types of PGPR molecular products are characteristically diverse, and the mechanisms by which they are acting on the plant are only beginning to be understood. While plants may contribute to shape their microbiome, it is these bacterial products which induce beneficial responses in plants. PGPR extracellular products can directly stimulate plant genetic and molecular

pathways, leading to increases in plant growth and induction of plant resistance and tolerance. This review will discuss known PGPR-derived molecules, and how these products are implicated in inducing plant beneficial outcomes through complex plant response mechanisms.

Conclusions In order to move PGPR research to the next level, it will be important to describe and document the genetic and molecular mechanisms employed in these interactions. In this way, we will be able to restructure and harness these mechanisms in a way that allows for broad-based applications in agriculture. A greater depth of understanding of how these PGPR molecules are acting on the plant will allow more effective development of rhizobacterial applications in the field.

Keywords Agriculture · Exo-metabolite · Nutrition · Plant · Plant defense · Plant growth promoting rhizobacteria · PGPR · Resistance · Rhizosphere · Symbiosis

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Abbreviations

PGPR	Plant growth promoting rhizobacteria
NOD	Nodulation factors
NF	Nod factors
LCO	Lipo-chitooligosaccharides
LPS	Lipopolysaccharides
EPS	Exopolysaccharides
ACC	1-aminocyclopropane-1-carboxylate
deaminase	deaminase
MAMP/	Microbial/Pathogen associated molecu-
PAMP	lar patterns

MTI/PTI	MAMP/PAMP triggered immunity
ETI	Effector triggered immunity
IAA	Indole acetic acid
GA	Gibberellic acid
ET	Ethylene
ABA	Abscissic acid
JA	Jasmonic acid
SA	Salicylic acid
SAR	Systemic acquired resistance
ISR	Induced systemic resistance
VOC	Volatile organic compound
BVC	Bacterial volatile compound
QS	Quorum sensing
AHL	N-acyl homoserine lactone
CDP	Cyclodipeptide
DAPG	2,4-diacetylphloroglucinol
cLP	Cyclic lipopeptide
DMDS	Dimethyl disulfide

Introduction

With the advancements of genetic tools and technologies, the ‘black box’ analogy as applied to our knowledge of the microbial residents in the soil and rhizosphere is rapidly becoming more transparent. We are at a point in time where rhizosphere microbiome studies have the potential to be meaningfully applied. The field of rhizosphere research is awash in metagenomics and metabolomics data, identifying genes, functional taxonomic units and metabolites of microbial origin (Paterson et al. 2017). A multitude of investigations have identified specific plant growth promoting rhizobacteria (PGPR) to the species and strain level that confer observable benefits to their plant host; and there is confirmed evidence of PGPR influence on plant traits (Friesen et al. 2011). Agricultural manufacturers are investing their research efforts on developing targeted combinations of different microbes in their formulations that best provide benefits for individual crops and environment (Dessaux et al. 2016)

These examinations provide a valuable framework for understanding the taxonomy of PGPRs, as well as establishing that PGPRs are conferring measurable benefits to the plant. However, PGPR research is primed for the next step; it is time to gain a complete understanding of the mechanistic and genetic basis of microbial activities directly influencing beneficial plant genetic and physiological responses. Environmental conditions in the field are

becoming increasingly more unpredictable, exposing crops to catastrophic weather events, shifts in seasonality and increasing pest and pathogen pressures. High-throughput screening methods used for identifying, selecting and bringing the appropriate formulation of micro-organisms to market will not adequately address these inevitable challenges.

The true power in understanding the root-associated microbiome will be in detecting the chemical and genetic mechanisms by which plant-specific microbes are inducing beneficial plant outcomes. While global agricultural practitioners have been applying chemicals to crops since the Green Revolution, microbes have been exuding their own substances influencing plant biological systems from the first appearance of higher plants. Indeed, the proliferation of terrestrial plants was facilitated by their microbial partners (Vandenkoornhuysen et al. 2015). As such, we can focus our research on understanding what products rhizosphere microbes are generating, and how they induce plant genetic pathways leading to appropriate responses to environmental challenges. An overview of PGPR products and their known plant/genetic targets discussed in this review can be found in Table 1. These bacterially derived molecules are diverse in nature and activity, but are typically exo-metabolites as they function externally from the PGPR.

Through characterizing specific mechanisms, we could ‘mimic’ them, either by applying bio-manufactured bacterial products or by modifying the plant’s genetics to heterologously achieve the same results. This approach could allow for a more reliable product that may be readily deployed in response to rapidly changing environmental conditions (Timmusk et al. 2017). Rhizosphere bacteria-derived chemicals such as rhizobial NOD factors (lipochito-oligosaccharides or LCOs) have been successfully incorporated into crop protection products, enhancing plant growth in both legumes and non-legumes, as well as stimulating plant defense (Subramanian et al. 2016). PGPRs would be an invaluable resource for novel plant defense elicitors which may be more effective than synthetically derived products for crop protection (Bektas and Eulgem 2014; Wiesel et al. 2014).

The application of PGPRs provides benefits to plants through two broad aspects: 1) improving plant nutrient acquisition, and 2) inducing plant resistance. Often, the PGPR or bacterial product will provide cross-protective properties, enhancing, for example, pathogen resistance as well as abiotic resistance through influencing key plant hormone pathways, taking advantage of the natural cross-talk existing between these stress-response pathways

Table 1 PGPRs produce a wide array of molecules which positively affect plant growth and/or protection through induced systemic resistance (ISR) and abiotic tolerance mechanisms

Type of PGPR Product	PGPR Strain	Exogenous Molecule	Benefit Conferred	Gene/Plant Target	Reference
Phytohormone	<i>Bacillus amyloliquefaciens</i>	Indole acetic acid (IAA)	Increased plant fresh weight	Auxin pathway	Idris et al., 2007
Phytohormone	<i>Paenibacillus polymyxa</i> BFKC01	IAA	Increased lateral roots and plant biomass	Auxin pathway	Zhou et al. 2016
Phytohormone	<i>Pseudomonas</i> spp.	Salicylic acid (SA)	SAR (Systemic acquired resistance) *	Exogenous SA accumulation*	Maurhofer et al. 1998, Bakker et al. 2014
Symbiotic molecule	<i>Rhizobia</i>	LCO (Nod factor)	Nitrogen fixation	Symbiotic Pathway	Oldroyd 2013
Symbiotic molecule	<i>Rhizobia</i>	LCO (Nod factor)	Increases in root growth	LysM receptors, unknown plant hormone pathway(s)	Oláh et al., 2005, Khan et al. 2011, Tanaka et al. 2015
Symbiotic molecule	<i>Rhizobia</i>	NopL (T3SS)	Defense suppression, nodule development	MAP kinase	Zhang et al. 2011, Ge et al. 2016
Bacterial volatile compounds (BVCs)	<i>Bacillus subtilis</i> GB03	Undefined BVCs	Increased iron transport	<i>FTT1</i> (Fe-deficiency-induced transcription factor 1)	Zhang et al. 2009
BVC	<i>Bacillus subtilis</i> GB03	Acetoin	ISR (Induced systemic resistance)	Ethylene (ET) pathway	Ryu et al. 2004
BVC	<i>Bacillus amyloliquefaciens</i> IN937a	2-pentanol	ISR	SA and Jasmonic acid (JA) pathway	Choi et al. 2014
BVC	<i>Bacillus subtilis</i> FB17	Acetoin	ISR	SA and ET pathway	Rudrappa et al. 2010
BVC	<i>Paenibacillus polymyxa</i> E681	Acetoin, tridecane, others	ISR	ET pathway	Lee et al. 2012
BVC	<i>Pseudomonas</i> spp., <i>Burkholderia</i> spp.	Indole	Increased lateral root/primordia	Auxin root developmental pathway	Bailey et al. 2014
BVC	<i>Paraburkholderia phytofirmans</i> PsJN	Dimethyl disulfide (DMDS)	Positive plant growth in salt-stress	Undetermined	Ledger et al. 2016
BVC	<i>Bacillus cereus</i> C1L	Dimethyl disulfide (DMDS)	ISR	Undetermined	Huang et al. 2012
Quorum sensing (QS)	<i>Pseudomonas</i> spp.	AHL (N-acyl homoserine lactone)	Root elongation, lateral root growth	<i>AtCaM</i> , <i>AtMYB44</i> , <i>GCR1</i> & <i>GPA1</i>	Liu et al., 2012, Zhao et al. 2014, Zhao et al. 2016
QS	<i>Rhizobia</i> spp.	AHL	SAR	SA accumulation	Schuhegger et al. 2006, Schikora et al. 2011, Zarkani et al. 2013
QS	<i>Rhizobia</i> spp. (long chain)	AHL	Increased lateral root hair primordia	Auxin pathway	Ortiz-Castro et al., 2008, Bai et al. 2012
QS	<i>Pseudomonas</i> spp.	Cyclodipeptides (CDPs)	Increase lateral roots	Auxin mimic and QS	Ortiz -Castro et al. 2011, González et al. 2017
Antibiotic	<i>Bacillus subtilis</i>	Surfactin	ISR	Oxylipin pathway	Ongena et al. 2007
Antibiotic	<i>Pseudomonas</i> spp.	2,4-diacetylphloroglucinol (DAPG)	Increased root branching	Auxin pathway	Brazelton et al. 2008
Antibiotic	<i>Pseudomonas</i> spp.	(DAPG)	ISR	ET pathway	Iavicoli et al. 2003

Table 1 (continued)

Type of PGPR Product	PGPR Strain	Exogenous Molecule	Benefit Conferred	Gene/Plant Target	Reference
Siderophore	<i>Pseudomonas fluorescens</i> C7R12	Pyoverdine	Uptake of Fe	Undetermined	Vansuyt et al. 2007, Trapet et al. 2016
Siderophore	<i>Pseudomonas fluorescens</i> C7R12	Pyoverdine	ISR	Undetermined	Meziane et al. 2005
Protein	<i>Bacillus amyloliquefaciens</i> NC6	PeBA1	ISR	SA- and JA/ET-dependent pathways	Wang et al. 2016
Protein	<i>Brevibacillus laterosporus</i> A60	PeBL1	ISR	SA- and JA/ET-dependent pathways	Wang et al. 2015
Antimicrobial	<i>Azospirillum brasilense</i>	Phenylacetic acid (PAA)	Auxin-like	Auxin pathway	Somers et al. 2005
Antimicrobial	<i>Bacillus fortis</i> IAGS162	Phenylacetic acid (PAA)	ISR	Phenylpropenoid pathway	Akram et al. 2016
Benzene-containing molecule (Anti-fungal/Anti-microbial)	<i>Pseudomonas aeruginosa</i> PM12	3-hydroxy-5-methoxy benzene methanol (HMB)	ISR	SA and Phenylpropenoid pathways	Fatima and Anjum 2017
Antimicrobial peptide	<i>Bacillus thuringiensis</i> NEB17	Thuricin 17 (Th17)	Reduction of salt-stress	Upregulation of chloroplasts	Subramanian et al. 2016

*The role of PGPR SA production in plant defense is debated

(Fujita et al. 2006). Moreover, PGPR effects on nutrient acquisition can overlap with plant defense pathways through as yet poorly understood crosstalk, often resulting in trade-offs between growth/nutrition and immunity. In two recent studies conducted in nutrient limited conditions, the presence of rhizosphere bacteria (synthetic community ‘SynCom’) or the product of a PGPR (the siderophore pyoverdine) influenced the plant response, seeming to tip the scales toward nutrient acquisition (phosphate and iron, respectively) rather than pathogen defense (Castrillo et al. 2017; Trapet et al. 2016). In light of this, similar PGPR products will be discussed in the separate aspects in which they influence the plant.

This review will not be covering the multitude of PGPR influences on the soil surrounding the plant root such as phosphorous solubilization (Alori et al. 2017) and assorted means of altering local pH and physical properties of the rhizosphere (Olanrewaju et al. 2017). The vast collection of bacterial products dictates the limits of this review: it is impossible to cover every molecule that has been reported. Some are already well reviewed such as LPS (Pel and Pieterse 2013), EPS (Gauri et al. 2012), phenazine (Chin-A-Woeng et al. 2003), and ACC deaminase (Glick 2014) and will not be comprehensively addressed in this review. Many beneficial mechanisms of PGPRs also involve influencing the plant to exude a variety of products into the rhizosphere, which indirectly serve to benefit the plant such as recruiting more PGPRs (Rudrappa et al. 2010) or increasing plant release of nutrient scavenging molecules (Zhou et al. 2016). PGPR also engage in a plethora of inter-species anti-microbial, predatory or communal activities that ultimately influence the plant in a beneficial manner, but will not be considered here as direct microbe-plant interactions.

Bacteria enhance plant nutrient acquisition and growth

Plants co-evolved with microorganisms in symbiotic relationships to successfully colonize terrestrial ecosystems (Werner et al. 2014; Zilber-Rosenberg and Rosenberg 2008). Understanding naturally occurring PGPR beneficial features and interactions could foster the design of agro-systems with decreased fertilizer inputs and sustained or improved plant yields. The most widely explored plant beneficial trait is the mutual symbiotic biological nitrogen fixation by *Rhizobia* (Udvardi and Poole 2013), but numerous other nutrient acquisition

machineries have been observed which facilitate plant access to macro-nutrients, micro-nutrients, and carbon allocation.

Nod factors (lipo-chitooligosaccharides (LCOs))

The mutualistic symbiosis that occurs between rhizobia and their legume hosts is well described, and many genetic and molecular determinants have been uncovered through various model legume-rhizobia systems (Oldroyd 2013). Compounds known as flavonoids are released from legume roots and induce the transcription of rhizobia Nod factors (NF) (Kondorosi et al. 1989). The nod factors (NFs) produced by rhizobia in response to flavonoids are lipo-chitooligosaccharides (LCO), consisting of a chitin core of β 1, 4 linked polymers of N-acetylglucosamine (GlcNAc). The key feature that sets LCOs apart from chitin (an ancient molecule associated with fungi and insect exoskeletons) is the N-acyl moiety consisting of a fatty acid chain varying in length, saturation and substitution groups. These ‘decorated’ side chains are most likely the primary causal agent conferring specificity between rhizobial strains and plant host targets (Oldroyd 2013).

LCOs are implicated in plant growth promotional activities that span from the classic instigation of mutualistic symbiosis, to altering plant hormone regimes leading to improved photosynthesis and increased resistance to biotic and abiotic challenges (Khan et al. 2008; Mitra and Long 2004; Rey et al. 2013). The touchstone of this intimate relationship between rhizobial LCOs and plants lies in the direct plant perception of the bacterial signal molecule. Plant receptors for LCOs found in legumes are classified in the lysin motif containing receptor-like kinase family (Liang et al. 2014). LysM receptors, found across all domains except Archaea (Gust et al. 2012), bind and respond to microbial associated molecular patterns (MAMPs) including chitin (Antolín-Llovera et al. 2012).

This similarity between plant receptor structure and activity across plant species suggests that the symbiotic pathway evolved from plant defense response pathways, and indeed, LCO - LysM binding has been found to be part of the plant immune response pathway (Rey et al. 2013). The NF receptor in the legume root hair epidermal plasma membrane has an extracellular LysM receptor-like kinase that binds with its cognate NF (Broghammer et al. 2012). This binding sets off a cascade of signaling events, including accumulation of cytokinins and calcium spiking, to initiate root hair curling, development of an infection thread and

subsequent rhizobial infection (Oldroyd et al. 2011; Rose et al. 2012; van Zeijl et al. 2015). The subsequent mutual symbiotic infection occurs in plant-derived structures called nodules, where the bacteria fix atmospheric N in exchange for photosynthetically derived C. Many thorough reviews detailing the primary research on plant LysM receptor evolution, mechanisms and function in both immunity and symbiosis have been published in the past 5 years (Antolín-Llovera et al. 2012; Gust et al. 2012; Limpens et al. 2015).

Due to the ubiquitous nature of plant LysM receptors, LCOs are important signal molecules in the rhizosphere and have also been shown to trigger plant growth enhancement effects in legumes and non-legumes alike. Many studies from the past two decades have observed increases in growth and germination of many different types of plants in response to application of rhizobial LCOs (Gautam et al. 2016; Marks et al. 2015; Prithiviraj et al. 2003; Souleimanov et al. 2002). However, few have sought to elucidate specific mechanisms or genetic pathways involved in the plant – microbe derived LCO signal molecule in order to understand the direct influence on improved plant nutrition. Candidates include the LysM receptor pathway, calcium signaling and influence on phytohormone pathways such as auxin.

LCOs can influence plant nutrition through alteration of root architecture. Changes in plant root architecture induced by bacteria in the rhizosphere have significant implications in plant health. Enhanced root surface and expansion of plant root systems increase the plant’s ability to acquire nutrients. Application of LCO to *M. truncatula* was shown to increase lateral root branching via the same pathway required for symbiosis, the most notable component being the LysM nod factor receptors (Oláh et al. 2005). In the non-legume *Arabidopsis thaliana* (L.) grown in media containing the biologically relevant concentration of 10 nM LCO from *Bradyrhizobium japonicum*, root tip numbers increased by 33%, root length increased by 33%, and root surface area increased 76% (Khan et al. 2011). Treatments containing various concentrations of chitin oligomers at similar concentrations did not result in any significant changes in root phenotype, indicating that the acylated moiety may be required for the growth response of *Arabidopsis*.

Further evidence of LCOs acting as generalized positive regulators of growth was demonstrated when seedlings of the C4 monocot *Zea mays* (maize) treated with 10 nM LCO showed significant increases in lateral root

lengths (Tanaka et al. 2015). Transcriptional expression analysis revealed changes in gene expression in response to LCO; genes involved in transcriptional regulation and secondary metabolism were upregulated and stress response genes were down-regulated. Four genes with strong positive responses to induction by LCO were further analyzed with promoter fusion reporters in transgenic maize roots. One of which, the gene encoding the calmodulin-binding protein *CaMB*, had a 3-fold increase in expression and primarily localized to the root epidermis, could have a role in affecting hormone ABA hormone signaling, and thus altering root growth and development.

Nop effectors of rhizobia type III secretion system (T3SS)

Plant hormone signaling directs both plant immunity (Pieterse et al. 2012) and plant growth and nutrition (Rubio et al. 2009). As such, shared components of these pathways result in a high level of crosstalk and trade-offs between defense and fitness (Denancé et al. 2013; Karasov et al. 2017; Takatsuji 2017). A critical component of rhizobia nodulation of its legume host is the requirement for the bacteria to suppress the plant's immune response, allowing for entry and infection to establish the symbiosis. LCO are shown to cause suppression of plant immunity; treatment with LCOs suppressed expression of the pathogenesis-related protein MtBGLU1 in *M. truncatula* (Mitra and Long 2004). In the non-legume *Arabidopsis*, LCOs suppressed FLS2 MAMP receptor based immunity, possibly through degradation of the FLS2 protein (Liang et al. 2013). Concomitant with this suppression is a positive growth response.

Other rhizobial molecules such as lipopolysaccharides (LPS) and exopolysaccharides (EPS) are implicated in the suppression of plant immunity to induce and maintain a successful infection (Aslam et al. 2008; Jones et al. 2008). While these carbohydrate signal molecules presumably interact at the plant cell membrane, an interesting mode of rhizobia-legume interaction occurs via rhizobia type III secretion systems (T3SS). T3SS are a mechanism to directly deliver effector proteins into the cell and are well studied in pathogenic bacteria (Ji and Dong 2015). Though not all rhizobia have T3SS, many genera have so far been described such as *Sinorhizobium* and *Bradyrhizobium* (Stachelin and Krishnan 2015). Nodulating outer proteins (Nops) are the effector proteins transported

through T3SS and can be secreted from rhizobia in response to flavonoids (de Campos et al. 2011).

Nops are important in the recognition and formation of nodules independent of the presence of NFs. T3SS in *B. elkanii* was found to be able to bypass the Nod factor receptor (NFR) and NF requirement to form nodules in soybean (Okazaki et al. 2013). The T3SS effector NopL from *Rhizobium* sp. strain NGR234 was found to prevent early nodule senescence in *Phaseolus vulgaris* (cv. Tendergreen) through interacting with the MAPK pathway (Zhang et al. 2011). In light of this, Nops are likely involved in suppressing the legume immune response. For further illustration, NopL is recognized as acting to block transcription of the PR proteins glucanases and chitinases regulated by the MAP kinase pathway (Bartsev et al. 2004), and has recently been found to be a substrate of plant defense-related MAP kinase involved in host defense suppression (Ge et al. 2016). Rhizobial products that suppress plant immunity are generally understood to be acting to allow sustained infection in the plant, but they may also be contributing to plant growth benefits by influencing these complex pathways and modulating trade-offs with fitness.

The substantial body of research in symbiotic factors in association with their legume host provides a strong model for the direction of studies that may be performed with these molecules to understand other PGPR-plant interactions to the same extent. Molecules produced by PGPRs in the rhizosphere range from simple amino acids to large polysaccharides and proteins, and as such, a wide variety of impacts on plant physiology are possible. Understanding the genetic basis of these relations may allow manipulation of the rhizospheres of crops to encourage and induce plant growth and nutrition.

Non-symbiotic bacterial molecules influencing plant growth and nutrition

Many rhizobacterial exo-metabolites also serve as MAMPs, eliciting a positive plant response through systemic defense priming (Wiesel et al. 2014), which will be discussed in the following section. Rhizobacterial chemicals can also directly influence plant nutrition and growth through alterations in plant physiological responses; the molecular pathways are not entirely resolved, and may overlap with known plant defense and symbiotic factors. Some studies have isolated a bacterial metabolite and observed a positive plant response, but the specific response pathway is unknown, while other

work narrows down the PGPR organism and the transcriptional responses, without identifying the specific exo-metabolite inducer. It is clear that bacteria in the rhizosphere can influence plants directly through exudation of a multitude of chemical compounds such as secondary metabolites, and small signaling molecules.

Phytohormones

Both pathogenic and beneficial bacteria can produce phytohormones (Costacurta and Vanderleyden 1995; Jones and Dangel 2006; Spaepen 2015). In the rhizosphere, many PGPRs are known to promote plant growth, in part, due to the activity of substances that are also plant hormones, or that are structurally similar. These bacterially derived chemicals tend to be in the category of plant growth regulators such as auxin (IAA), gibberellic acid (GA) and ethylene (ET) (Gamalero and Glick 2011). Three strains of *Bradyrhizobium japonicum* were reported to produce significant levels of the hormones IAA, GA, zeatin, ethylene, and ABA (Boiero et al. 2007).

Auxin is a major regulator of plant growth, development and stress response (Liu et al. 2014). It is well known for its role in lateral root formation, and it is also a major player in nodule meristem elongation (Oldroyd et al. 2011). IAA production is widespread among both pathogens and PGPR in the soil and rhizosphere (Costacurta and Vanderleyden 1995). In pathogens, IAA production can be associated with their mode of virulence. For example, in *R. solanacearum* and *Erwinia chrysanthemi*, IAA synthesis occurs along with Type III secretion system expression, and *A. tumefaciens* transfers T-DNA encoding genes for the constitutive expression of IAA to produce undifferentiated tissue (tumors) in the plant (Spaepen and Vanderleyden 2011).

The PGPR *B. amyloliquefaciens* FZB42 produces IAA, which was found to be essential in its ability to promote plant growth (Idris et al. 2007). FZB42 grown with *Lemna minor* ST (duckweed) significantly increased fresh weight, while FZB42 mutants deficient in tryptophan (precursor to IAA) had no difference in fresh weight from controls. Earlier work by Kamilova et al. (2006) described the relatively high content of L-tryptophan in plant exudate from tomato, cucumber and radish, leading to the suggestion that auxin production by some PGPRs may be dependent on tryptophan substrate provided by the host. In that study, the researchers found that radish had the highest amount of tryptophan in its exudates, and that the PGPR *P. fluorescens* strain

WCS365 known to produce auxin in the presence of tryptophan provided the greatest amount of growth promotion in this plant (Kamilova et al. 2006).

Paenibacillus polymyxa strain BFKC01 is an example of a PGPR found to provide benefits spanning the major modes of improving plant nutrition, and enhancing biotic and abiotic resistance. In recent work by Zhou et al. (2016), BFKC01 produced measurable concentrations of IAA in culture (supplemented with tryptophan) and *Arabidopsis* inoculated with this strain had increased levels of IAA as measured by DR5:GUS reporter lines and gas chromatography. *Arabidopsis* Col0 inoculated with BFKC01 grown in Fe deficient medium produced significantly more lateral roots and higher plant biomass than control plants. The authors attribute the improved plant growth, in part, to the increased density of lateral roots which likely resulted from the presence of bacterially derived IAA.

Bacterial volatiles

Volatile organic compounds (VOC) are typically aromatic molecules produced by both plants and bacteria. In recent reviews, authors Chung et al. (2016) and Audrain et al. (2015) propose more specific terminology in reference to the suite of low molecular weight chemicals released by bacteria to reflect the presence of organic and inorganic compounds. The term ‘bacterial volatile compound’ (BVC) will be used in this review to align with this more recent viewpoint. BVCs are well documented to promote plant growth and induce plant defense responses (Farag et al. 2013). In a large scale screening study evaluating 42 rhizosphere bacteria and 4 different growth media, Blom et al. (2011) found that indole from *Pseudomonas* and *Burkholderia* species suppressed ethylene responses to the MAMP elicitor flg22. More recently, the same group described positive growth effects on *Arabidopsis* through the auxin root development pathway. When 10 nM of indole was added to the growth media, *A. thaliana* seedlings lateral roots increased by 300%. An intact polar auxin transport system was required, but it is not yet clear whether indole is the signal molecule or if it is used as a precursor for the IAA molecule causing the proliferation of lateral root primordia (Bailly et al. 2014).

Rhizosphere BVCs have also been shown to directly induce plant expression of nutrient ion transporters. The beneficial bacterium *Bacillus subtilis* GB03 enhances *Arabidopsis* iron accumulation via activation of the plant’s

own iron acquisition machinery (Zhang et al. 2009). Upon exposure to bacterial BVC, *A. thaliana* plants up-regulate the Fe-deficiency-induced transcription factor 1 (FIT1) that is necessary for GB03 BVC-induction of ferric reductase FRO2 and the iron transporter IRT1 expression (Zhang et al. 2009). The iron accumulation feature by this bacterium can also be triggered by direct application of GB03 bacterium, promoting iron acquisition in non-model plants. In cassava (*Manihot esculenta*), GB03 treatment of stem cuttings prior to planting promoted iron increase in the leaf by 400% (Freitas et al. 2015) and a 200% increase in root iron content in the field over a two year field trial (Freitas, unpublished), compared to untreated control. The increased iron uptake was accompanied not only by an increase in the photosynthetic rate but also a delay in leaf senescence. Interestingly, the PGPR *P. polymyxa* BFKC01 also increased the expression of *AtFIT1* and *IRT1* in inoculated *Arabidopsis* plants, though the bacterial elicitor was not investigated in this study, but it is intriguing to speculate to the role of BVC in this system (Zhou et al. 2016),

Bacterial N-acyl homoserine lactones (AHLs)

Many survival and infection activities of rhizosphere bacteria are under the control of the density-dependent communication system known as quorum sensing (QS). QS communication of bacteria in the rhizosphere most likely underlies a significant portion of intra- and inter-species interactions occurring in the rhizo-microbiome (Lowery et al. 2008). Both gram negative and gram positive bacteria participate in this mode of interaction, but with quite distinct differences in signal molecule structure and transcriptional response machinery. The most well studied QS system of Gram negative bacteria is composed of an extracellular signal molecule called an auto-inducer (AI), produced by an AI synthase, and a transcriptional response regulator protein to which the AI binds and upregulates expression of downstream operons involved in QS. Synthesis of the AI can be triggered initially by environmental conditions and as the population increases, the concentration of the signal builds in the environment, and a positive feedback loop can be enacted amongst the community of bacterial cells (Bassler and Miller 2013).

Numerous rhizosphere bacterial species are known to have QS control over functions related to their survival and activities in this environment (Pierson et al. 1998; Venturi and Fuqua 2013). QS regulation of bacterial activities can be tightly synchronized through AI structure and concentration, and through response regulator

specificity; however, there is an abundance of evidence that QS is involved in inter-species crosstalk (Tashiro et al. 2013). Gram negative bacterial AI signals are N-acyl homoserine lactones (AHL), which consist of an invariant lactone ring and an acyl side-chain of varying lengths, saturation, and hydroxyl groups (Chernin 2011; Czajkowski and Jafra 2009). *Rhizobia* species seem to produce acyl chains with lengths ranging from C6 to C18, with a greater abundance of the long chain variants (Marketon et al. 2002; Teplitski et al. 2003). Rhizospheric *Pseudomonas* spp. AHL side chains can range from C6 to C12 (Ortiz-Castro et al. 2008).

Bacterial AHLs in the rhizosphere induce distinct responses in plants (Götz-Rösch et al. 2015; Schikora et al. 2016). Joseph and Phillips (2003) observed a significant increase of stomatal conductance and transpiration in *Phaseolus vulgaris* L. (bean) when 10 nM AHL was applied to the roots (Joseph and Phillips 2003). In the legume *M. truncatula*, an increase in nodule number was found when *S. meliloti*-specific 3-oxo-C14-HL was applied to the roots (Veliz-Vallejos et al. 2014). Specific plant responses were demonstrated in the landmark work by Mathesius et al. (2003), who generated thorough protein expression data from *M. truncatula* exposed to AHL from its symbiont *S. meliloti* (3-oxo-C16:1-HL) and from the plant pathogen *P. aeruginosa* (3-oxo-C12-HL). The group found 154 proteins that were altered in accumulation, and identified 99 with homologs; two thirds of these proteins were the same for both AHLs, but 1/3 of the proteins were altered between the AHL treatments. Roughly 23% of proteins with known homologies were related to plant defense, while 5% were involved in flavonoid synthesis and another 5% were related to hormone synthesis such as auxin.

Similar to the Mathesius et al. (2003) work, Miao et al. (2012) profiled the proteome of *A. thaliana* exposed to 3-oxo-C8-HL and found changes in accumulation of proteins related to defense response, protein biosynthesis, phyto-hormone response, metabolism and cytoskeleton remodeling (Miao et al. 2012). In alignment with these observations, many studies have described changes in root growth elicited by the application of AHL. von Rad et al. (2008) found transcriptional changes related to cell growth and growth hormones as well as root elongation in *A. thaliana* exposed to C6-HL (von Rad et al. 2008). Elongation of *A. thaliana* roots by 3-oxo-C6-HL and 3-oxo-C8-HL is proposed to be mediated through G-protein-coupled receptors GCR1 and GPA1 which are responsive to key plant hormones and

play a role in root development (Liu et al. 2012). More recent work from this group has shown that the *Arabidopsis* growth and developmental protein AtCaM and the transcription factor AtMYB44 are key in the root elongation response to 3OC6-HSL (Zhao et al. 2014, 2016). Ortiz-Castro et al. (2008) found root architecture changes such as increased branching, lateral root hair primordia and root hair formation with the longer chain C10-HL (Ortiz-Castro et al. 2008). The application of 3-oxo-C10-HL induced adventitious root formation and auxin response gene expression in legume *Vigna radiata* (mung bean) seedlings (Bai et al. 2012).

More PGPR derived signaling molecules are sure to be identified as activating plant growth and nutrition pathways. An example of a potential inter-kingdom signaling molecule affecting both PGPR QS and plant growth are the cyclodipeptides (CDPs). Several different CDPs from *P. aeruginosa* were found to stimulate lateral growth, likely through acting as an auxin-like signal (Ortiz-Castro et al. 2011). Interestingly, the CDPs from *P. aeruginosa* may have multiple significant functions involved in plant beneficial interactions. Certain CDPs were found to act directly on the LasR AHL QS system to negatively control their own synthesis, which is important as larger concentrations of CDP are required to stimulate lateral root growth as compared to auxin (González et al. 2017). The same study used a bioinformatics approach to identify possible non ribosomal peptide synthases responsible for CDP production, and found highly homologous protein sequences associated with the production of the bacterial iron scavenging siderophore pyoverdine. The matching sequence encodes PvdD, a synthase for pyoverdine and is under the regulatory control of LasR AHL QS regulation which is upregulated in iron starvation conditions (Stintzi et al. 1998). Intriguing recent research has re-iterated some known PGPR activities of pyoverdine, as well as illuminating more details of the plant responses to this siderophore.

Siderophores

As will be reviewed in the following sections, many bacterial products play a dual role in stimulating plant nutrition and in eliciting plant defense responses. Many of these products and mechanisms of PGPRs seem to influence the nexus of the plant pathways modulating the direction or ‘choice’ between the two, particularly during nutrient limiting conditions. One such example is the activity of the PGPR *P. fluorescens* C7R12 siderophore

pyoverdine (Trapet et al. 2016). As is discussed in the publication of this study, PGPR siderophores can be assimilated by plants to scavenge for iron (Vansuyt et al. 2007) and also may be elicitors of plant resistance to pathogens as exogenous pyoverdine promoted ISR in bean and tomato (Meziane et al. 2005). *Arabidopsis* in iron-deficient conditions and in the presence of the uncomplexed iron siderophore pyoverdine experienced growth promotion at the expense of increased susceptibility to *Botrytis cinerea*. Furthermore, the researchers identified the *HBII* transcription factor as the node between plant growth and immunity (Trapet et al. 2016).

PGPRs induce plant resistance

Biotic stresses caused by pathogenic bacteria, fungus, virus and pests are significant limiting factors for crop yield and productivity. The limitations associated with the conventional breeding practices often lead to development of new techniques to enhance resistance against biotic stressors. Over the last several decades genetic engineering by transforming crop plants with resistance genes against various different biotic stress agents has led to some progress in increasing plant and crop resistance (Dangl et al. 2013). The ability of pests and pathogens to develop counter-resistance against both conventional breeding practices and genetic engineering approaches has led to major road blocks to boosting yields (Dively et al. 2016; Tabashnik et al. 2013). Utilization of synthetic chemicals to mitigate biotic stressors has turned out to be an effective strategy, but raises several other concerns such as shelf life and other non-target toxic residual effects to other benign organisms (Glick 2012). Harnessing benign microbes or “biologicals” for crop protection is an increasingly popular approach. However, the lack of reproducibility or mechanistic explanation for the biological controls can lead to reluctance in applying them at a large-scale for crop protection. Over the last several years, the impact of the plant-associated microbiome has led to an understanding that it plays a critical role in plant fitness and survival (Busby et al. 2017). The current knowledge of the beneficial microbiome and host interaction lacks key information pertaining to the signaling events and the components of innate immune responses that govern the interaction of plants with beneficial microbes.

Plants use a multitude of systemic signaling molecules, termed ‘phytohormones’, to regulate various stages of their

development and to coordinate defense responses. These plant hormones are necessarily specific to the function they control, and much cross-talk exists between hormone pathways (Thaler et al. 2012). Phytohormones such as salicylic acid (SA), ethylene (ET), and jasmonic acid (JA) are tightly involved in plant defense response networks such as systemic acquired resistance (SAR), and induced systemic resistance (ISR) (Glazebrook 2005; Heil and Bostock 2002). SAR is induced by microbial associated molecular patterns (MAMPs). When the plant recognizes a microbial compound such as flagella or chitin through membrane bound pattern recognition receptors (PRRs), the plant marshals its first line of defense, MAMP triggered immunity (MTI). If this fails, the next line of defense is microbial effector triggered immunity (ETI) which includes programmed cell death. SAR occurs after PTI and/or ETI, and involves long-distance signaling via the plant phytohormone salicylic acid (SA) to upregulate *PATHOGENESIS-RELATED* (PR) genes encoding antimicrobial proteins (Fu and Dong 2013; Jones and Dangl 2006).

ISR is an inducible plant defense response triggered by non-pathogenic rhizobacteria, and it increases the plant's systemic resistance to subsequent pathogen challenge (Ongena and Jacques 2008). Unlike SAR, ISR has been found to act through a SA-independent pathway to confer systemic protection after exposure to beneficial microbes (Pieterse et al. 2014). Rather, ISR signaling pathways are thought to be based on the phytohormones ethylene (ET) and jasmonic acid (JA) (Verhagen et al. 2004). ISR essentially allows the plant to more quickly activate its above-ground defenses against pathogens, which is known as 'priming' (Conrath et al. 2006) with a mobile signal in a root to shoot manner (Pieterse et al. 2014). These plant defense mechanisms are found plant-wide; distinct MAMP responses having been demonstrated in *A. thaliana* roots where they seem to be ET dependent (Millet et al. 2010). The phenomenon of plant priming is widespread among known PGPRs and its distinct advantage is that fitness costs to the plant remain relatively low as compared to plant defense responses to triggering stress (Martinez-Medina et al. 2016).

Notably, several plant associated bacteria are reported to produce SA (Bakker et al. 2014). While these strains are confirmed to produce SA in culture, some doubt is cast as to whether the reports of elevated SA in the rhizospheres of inoculated plants are the result of an artifact in measurements. There seems to be no consensus as to whether SA from PGPR strains contributes to ISR induction. Through heterologous expression of SA

production genes, it was demonstrated that the presence of bacteria-produced SA in some patho-systems indeed correlates to improved induction of ISR (Maurhofer et al. 1998). Others dispute as to whether measurements of PGPR-SA released into the rhizosphere may be plant derived or siderophores containing an SA-like derivative, and neither likely has an additional impact on the plants SA-dependent immune response (Bakker et al. 2014). Bacterial SA may not be playing a direct role, rather it is known to be a precursor to pyochelin (Pch) which, along with the phenazine pyocyanin, may be the true elicitor from *P. aeruginosa* 7NSK2 inducing ISR on tomato against *B. cinerea* (Audenaert et al. 2002).

Bacterial antibiotics can induce plant defense responses

Plant interactions with PGPR can be provoked via extracellular factors produced by the bacteria such as antibiotics. The most widely accepted definition of antibiotics is that they are chemically diverse, organic, low-molecular weight compounds produced by microorganisms that are deleterious to the growth or metabolic activities of other microorganisms (Thomashow and Weller 1996). Soil bacterial communities have been a resource of discoverable antibiotics for human use, especially during the "Golden Age" of antibiotic isolation spanning from the 1940's to the 1960's (Lewis 2013). A resurgent interest has emerged in isolating these soil and plant associated microbe products for curative use in agriculture in hopes of remedying microbial pathogen-caused diseases (Mendes et al. 2011). Many antibiotics found to be produced by PGPRs act to benefit the plant indirectly through the traditional antibiotic context of killing plant pathogens (antagonism). In the following examples of this review, however, will be descriptions of direct plant responses to PGPR antibiotics.

One of the most studied PGPR antibiotics, 2,4-diacetylphloroglucinol (DAPG), has been found in concentrations of 2.1 µg per gram of soil associated with wheat roots (Bonsall et al. 1997) and is well-established to promote plant growth through its antibiotic activities toward plant fungal and bacterial pathogens (Weller et al. 2007). As with many other PGPR products, DAPG also may stimulate plant growth in some systems through increasing plant production of auxin and altering root architecture (Brazelton et al. 2008). DAPG is copiously produced by many rhizosphere strains of *P. fluorescens*, and is considered the primary attribute responsible for this family of PGPR to be so broadly effective (Weller et al.

2012). Many strains of *P. fluorescens* also produce another class of antibiotics, phenazines, that have been recently implicated in inducing ISR in rice challenged with *Magnaporthe oryzae* (Ma et al. 2016).

Early on in the investigations of DAPG plant growth promotional activity, this antibiotic was discovered to also act as an elicitor of ISR. Iavicoli et al. (2003), using the pathosystem of *Arabidopsis*, the PGPR *Pseudomonas fluorescens* CHA0r and the oomycete *Peronospora parasitica*, reported that CHA0r inoculation reduced sporulation and colonization of the leaf parasite through a DAPG-dependent induction of ISR. Direct applications of DAPG (10–100 μ M) mimicked the ISR protective qualities of CHA0r and DAPG-production mutants of the PGPR were unable to induce the ISR response in *Arabidopsis*. Further investigation using *Arabidopsis* defense pathway mutants revealed the requirement for NPR1–1, JAR1 and EIR1 for the DAPG-induced ISR response. Intriguingly, the investigators found through other mutant, gene expression and phytohormone assays that SA and JA are not likely to be involved directly in the DAPG-ISR pathway, noting that the mutation in EIR1 may act independently of the ET pathway and that it would be difficult to assign a definitive pathway in this system (Iavicoli et al. 2003). Though Iavicoli et al. 2003 found no ISR protection using CHA0r and the pathogens *Botrytis cinerea* and *P. syringae* pv. *tomato* DC3000, other strains of *P. fluorescens* such as WCS417r have been found to elicit ISR protection from *Pst* DC3000 and *Fusarium oxysporum* f. sp. *raphanin* (Pieterse et al. 1998).

Another powerful class of antibiotics isolated from rhizobacteria is the lipopeptides (LP), which can be linear or cyclic oligopeptides of various sizes and having a lipid tail of various lengths. The majority are cyclic lipopeptides (cLPs); defined as a heptapeptide interlinked with a β -hydroxy fatty acid to form a cyclic lactone ring structure (Ongena and Jacques 2008). cLPs known to date have been isolated primarily from *Pseudomonas* and *Bacillus* species, each having their own assortment of unique cLP configurations (Raaijmakers et al. 2010). The well-studied cLPs from *Bacillus* spp. include surfactin, iturin and fengycin. Surfactin is produced in significant quantities by *Bacillus* spp. (Nihorimbere et al. 2012), and is considered one of the most potent natural surfactants known, acting through disrupting biological membranes (Carrillo et al. 2003). Due to their amphiphilic structures, cLPs are able to intercalate into lipid bilayers, forming pores and disrupting the

membrane structure depending on the concentration of the cLP (Ongena and Jacques 2008).

Cyclic lipopeptide bacterial antibiotics, particularly surfactin, are copiously produced by *Bacillus* spp. (Ongena and Jacques 2008). The *Bacillus* group is well represented in the rhizosphere and is estimated to make up 95% of the gram positive bacteria found there (Prashar et al. 2013). Surfactin serves many roles in the rhizosphere, such as antibiosis, and has also been found to be required for attachment to the plant root (Bais et al. 2004; Ongena and Jacques 2008). Importantly, surfactin is able to stimulate direct plant responses at the root in the form of induced systemic resistance (ISR) (Ongena et al. 2007). Known bacterial elicitors of ISR are MAMPs such as flagella and lipo-polysaccharides (LPS) (De Vleeschauwer and Höfte 2009), but more recently, other bacterially derived substances such as cLPs have been found to induce ISR. Not only do a broad range of plants have an ISR response to surfactin, but many members of *B. subtilis* and *B. amyloliquefaciens* groups produce sufficient surfactin to provide disease protection via ISR (Cawoy et al. 2014).

In experiments with bean and tomato plants Ongena et al. (2007) found that inoculation with the surfactin-producing *B. subtilis* 499 increased disease suppression by 33% against the challenging pathogen *Botrytis cinerea*. Application of purified surfactin increased disease control by 28%. The stimulation of ISR was demonstrated by using surfactin overproducing strains of *Bacillus* spp. and surveying a key ISR indicator, the Lipoxygenase (LOX) enzyme. Three-fold increases in LOX activity were observed in *Botrytis*-challenged tomato plants inoculated with the *Bacillus* spp. surfactin overproducer (Ongena et al. 2007). ISR defense responses were revealed in a study on *Lolium perenne* (perennial ryegrass) challenged with *Magnaporthe oryzae*. When inoculated with surfactin and with live cells of *B. amyloliquefaciens* FZB42-AK3, ryegrass presented with enhanced accumulation of hydrogen peroxide, higher peroxidase activity, deposition of callose and the hypersensitive response (HR) response; all indicators of ISR (Rahman et al. 2015).

Also of note, *B. subtilis* surfactin production is under the control of the QS regulon *comQXPA*, wherein the signal molecule secreted from the cell is a short, ribosomally synthesized, peptide called ComX (Dogsda et al. 2014). The work of Oslizlo et al. (2015) evaluated the diversity of QS ‘phenotypes’ (correlated to polymorphisms in the *comQXPA* QS system) and the relationship

to plant beneficial activities (primarily surfactin production) in *B. subtilis* isolated from the rhizoplane of tomato. The *comQXPA* QS and other QS systems in Gram-positive bacteria have unique and diverse extracellular signaling molecules.

Quorum sensing signals induce plant defense responses

Plants have been shown to up-regulate defense and immune response systems when treated with AHLs, the Gram-negative QS signal molecule. *Arabidopsis* had greater resistance to *P. syringae* pv *tomato* (*Pst*) when inoculated with 3-oxo-C14-HL-producing *S. meliloti* (Zarkani et al. 2013). Direct application of AHLs and inoculation of tomato with AHL-producing bacteria *S. liquefaciens* MG1 and *P. putida* IsoF increased the resistance to the pathogen *A. alternata*, increased SA levels in the plant and upregulated PR1, indicating that the AHL induced ISR (Schuhegger et al. 2006). Schikora et al. (2011) also found increased PR1 expression in *A. thaliana* challenged with the pathogen-associated molecular pattern (PAMP), flg22 when roots were treated with oxo-C14-HL. Systemic resistance was also induced by the AHL when *A. thaliana* was challenged with the fungal pathogen *Golovinomyces orontii* and the bacterial pathogen *P. syringae* pv *tomato* DC3000 (Schikora et al. 2011). Further evidence of AHL defense priming was revealed when oxo-C14-HL caused hallmark defense responses such as increased callose deposition, cell wall lignification and accumulation of phenolic substances, as well as increased SA, leading to stomatal closure in *A. thaliana* when challenged with *P. syringae* (Schenk et al. 2014).

The ‘universal’ QS signal molecule, AI-2 is a cyclic structure containing boron encoded by the *luxS* gene (Chen et al. 2002). It is found in a wide variety of both Gram-positive and Gram-negative bacteria. The broad distribution of AI-2 implicates it as being involved in inter-kingdom signaling (Schauder et al. 2001), and this suggests that it could have an impact on plant growth or immunity. AI-2 responses have been observed in *S. meliloti* which doesn’t produce AI-2 signals (Pereira et al. 2008) and certain strains of *B. subtilis* found in dairies are known to have intact *luxS* AI-2 QS systems (Duanis-Assaf et al. 2015); both bacteria species are represented in the rhizosphere. Recently, through the use of AI-2 receptor *LuxP/LsrB* reporter strains, mammalian epithelial cells were found to produce AI-2 ‘mimic’ molecules in response to co-culture with bacteria. The

authors proposed that the utility of the AI-2 signal could be in establishing inter-kingdom symbiosis (Ismail et al. 2016). However, unlike the Gram-negative AHL QS signal molecule, no work to date has investigated the direct plant responses to other QS signals such as AI-2 or the *comQXPA* QS system signal ComX.

Rhizosphere BVCs induce plant systemic priming defenses

The release of BVCs in the rhizosphere stimulate diverse responses in plants, enhancing both nutrition/biomass and defense (Chung et al. 2016). Seminal work by Ryu et al. (2004) established the role of BVC in the induction of plant ISR through the implementation of elegant ‘split-plate’ studies of *Arabidopsis* seedlings challenged with *Erwinia carotovora* subsp. *carotovora* SCC1. The PGPR bacteria were grown in the same plate on the opposite side of the barrier (Ryu et al. 2004). The ISR-eliciting compounds 2, 3-butanediol and 3-hydroxy-2-butanone (collectively termed ‘acetoin’) were identified from *B. subtilis* GB03 and *B. amyloliquefaciens* IN937a, and the ISR protection was found to act primarily through the ET dependent pathway. Subsequent studies by Ryu and other groups have further identified specific BVCs and other pathosystems in which they and their PGPR producer effectively promote ISR.

For example, acetoin was also the active BVC from *B. subtilis* FB17 in the *Arabidopsis* - *Pseudomonas syringae* pv. *tomato* DC3000 system; this ISR was found to be dependent on SA and ET (Rudrappa et al. 2010). Other examples are: 2-pentanol from *Bacillus amyloliquefaciens* strain IN937a promotes effective ISR in pepper against *Xanthomonas axonopodis* pv. *vesicatoria* in an SA and JA dependent pathway (Choi et al. 2014), and the PGPR *Bacillus cereus* C1L produces dimethyl disulfide (DMDS) which induces ISR in tobacco and corn challenged with fungal pathogens (Huang et al. 2012).

Zamioudis et al. 2015 has demonstrated that volatiles from the PGPR *P. simiae* WCS417 induced ISR in *Arabidopsis* in a *MYB72*-dependent manner. Moreover, the BVCs from WCS417 upregulated *MYB72* expression concomitant with iron starvation response genes including *FIT1* (Zamioudis et al. 2015). The BVC-induced upregulation of *MYB72* was independent of iron availability and the ability of the plant to acquire Fe was enhanced through upregulation of Fe-deficiency genes. The jack-of-all-trades PGPR *P. polymyxa* strain BFKC01, which was noted in the above section for its

ability to improve plant nutrition through IAA production, was also found to induce ISR in *Arabidopsis* through increasing the transcription of *MYB72*. As might be expected, this PGPR also improved Fe uptake through upregulating the Fe deficiency transcription factor *FIT1* (Zhou et al. 2016). Though an elicitor was not investigated in this work, other strains of *P. polymyxa* such as E681 have been found to induce ISR in *Arabidopsis* through production of a multitude of BVCs, including methanethiol, isoprene, acetic acid-butyl ester, acetoin, and in this case, the unique low molecular weight compound tridecane (Lee et al. 2012). Other recent work invokes the tight connection between microbial-mediated plant defense hormone pathways and the plant nutrient deficiency sensing networks such as phosphate (Castrillo et al. 2017), and highlights the cross-connectivity of PGPR-induced plant responses to multifaceted challenges.

Diverse PGPR molecules elicit plant defense

A selection of various proteins and small molecules from PGPRs have been found that seem to act by promoting plant defense pathways, but due to space and in some cases, a dearth of research, will only be mentioned in brief. Several bacterial proteins found to be salient in PGPR activities will not be comprehensively assessed in this review. Several uncharacterized proteins, one from *Bacillus amyloliquefaciens* NC6 (protein ‘PeBA1’) and the other from *Brevibacillus laterosporus* strain A60 (protein ‘PeBL1’) activate ISR responses in tobacco against TMV and *P. syringae* pv. tabaci, and *B. cinerea* (Wang et al. 2015, 2016), but further investigations have not yet been published. The small molecule phenylacetic acid (PAA) is classified as an antimicrobial, but PAA isolated from *Azospirillum brasilense* was found to be similar to auxin (Somers et al. 2005). More recently, PAA from *Bacillus fortis* IAGS162 was shown to be the elicitor of ISR in tomato against *F. oxysporum* f.sp. lycopersici (Akram et al. 2016). Through metabolomics techniques, the PGPR *Pseudomonas aeruginosa* PM12 was found to promote ISR in tomato challenged with *F. oxysporum* via 3-hydroxy-5-methoxy benzene methanol (HMB). A soil drench of 1.0 mM and 10.0 mM HMB significantly reduced the disease index.

HMB (Fatima and Anjum 2017). The bacteriocin peptide Thuricin 17 (Th17) from the PGPR *Bacillus thuringiensis* strain NEB17, has long been known to have antimicrobial activities (Gray et al. 2006), but

recent proteomic analysis of salt-stress *Arabidopsis* suggests that it may alleviate the deleterious effect of the abiotic stress on photosystems I and II through upregulation of chloroplast proteins (Subramanian et al. 2016).

PGPR also function to elicit plant abiotic defense responses

Abiotic challenges to plants are particularly pernicious, as plants must manifest their responses by utilizing the limited genetic plasticity gained through evolution. Plants may be exposed to transient or long term environmental stresses such as drought, flooding, extreme heat, freezing, or excessive salt (Mickelbart et al. 2015). Similar to plant biotic resistance, plant abiotic resistance relies on genetic regulatory mechanisms induced by changes in key phytohormone pathways that intersect in a complex manner (Verma et al. 2016). Abscisic acid (ABA) is most often associated with the plant’s abiotic stress response strategy, especially in an antagonistic continuum with cytokinin (Yang et al. 2009). Classical defense response pathway genes such as the widespread plant transcription factor *WRKY* and the ABA responsive *MYB* factor are often used as signifiers of an abiotic resistance response, most commonly drought and salt stress challenges (Agarwal et al. 2011; Yanhui et al. 2006).

Many studies have observed increased ABA accumulation in PGPR-inoculated plants under various abiotic stress conditions. *Bacillus licheniformis* SA03-treated *Chrysanthemum morifolium* in saline-alkaline conditions had nearly double the level of ABA in leaves than the control as detected by ELISA (Zhou et al. 2017). Plants inoculated with SA03 and exposed to saline-alkaline stress conditions showed fewer symptoms and had higher fresh and dry shoot weights, whereas inoculated plants treated with the ABA inhibitor FLU exhibited no tolerance to the stress. The PGPR *Bacillus aryabhatai* strain SRB02 enhanced levels of ABA in soybean under control and heat stress (again, nearly double that of controls) and the inoculated plants were observed to have ABA-mediated stomatal closure during heat stress (Park et al. 2017). Inoculation of *Vitis vinifera* with *Bacillus licheniformis* Rt4M10 increased ABA concentrations in leaves (fresh weight) by 76-fold and inoculation with *Pseudomonas fluorescens* Rt6M10 resulted in ABA increasing by 40-fold; rates of water loss were also reduced in correlation with the increases of ABA in PGPR-inoculated *V. vinifera* (Salomon et al. 2014)

The products of PGPRs which specifically induce abiotic resistance or tolerance are not as well described in the literature as those known to be involved in defense priming, but likely overlap with those found to promote plant nutrition and biotic resistance. Indeed, reported examples of abiotic resistance elicitors include PGPR products such as ACC deaminase (Glick et al. 2007), phytohormones such as IAA (Marulanda et al. 2009), signal molecules such as LCOs (Subramanian et al. 2016) and AHLs (Ding et al. 2016), and BVCs (Liu and Zhang 2015). Promising recent research into the role of PGPR BVCs on *Arabidopsis* salinity tolerance has shown that the *Paraburkholderia phytofirmans* PsJN BVCs 2-undecanone, 7-hexanol, 3-methylbutanol and dimethyl disulfide (DMDS) stimulated positive plant growth under both normal and saline-stress conditions (Ledger et al. 2016).

The PGPR *Dietzia natronolimnaea* strain STR1 confers salt tolerance to wheat (*Triticum aestivum* L.). STR1-inoculated plants had increased expression of the *SOS4* pyridoxal kinase, which controls N^+ and K^+ balance through adjusting ion transporter activity, and modulated *TaMYB* and *TaWRKY* transcription factor expression. However, this strain does not have commonly known plant beneficial traits such as IAA production and ACC deaminase activity (Bharti et al. 2016). *D. natronolimnaea* STR1 is known in other environmental contexts to produce high levels of carotenoids, which could be an intriguing new PGPR metabolite to investigate (Gharibzadeh et al. 2014).

An example of a bacterially-mediated sodium tolerance mechanism is from work that specifically investigated the *Arabidopsis* *HKT1* gene encoding a high affinity potassium transporter involved in Na^+ import into the plant root.

Fig. 1 Plant benefits conferred by PGPR and their products can be viewed in two broad categories. **A.** PGPRs and associated molecules improve plant nutrition and growth. **B.** PGPR molecules can also act to increase plant resistance and tolerance to biotic and

abiotic challenges. **C.** Many PGPR molecules can positively affect both plant growth and plant resistance through overlapping mechanisms

Treatment with the PGPR *B. subtilis* GB03 resulted in an orchestrated down-regulation in the roots and up-regulation in the shoots of *HKT1*. Plants in these treatments had lower levels of sodium uptake overall. This response is particularly intriguing considering that *HKT1* overexpression in *Arabidopsis* does not increase salt tolerance. Also, salt tolerance in *htk1* mutants could not be restored by *B. subtilis* GB03 treatment (Zhang et al. 2008). More in-depth investigations will be helpful in determining the additional factors and mechanisms that the PGPR is implementing in conferring salt tolerance to plants.

Furthermore, drought tolerance in plants is associated with tolerance to vessel clogging or destruction-related diseases such as *Fusarium oxysporum* in an abiotic-related manner (Dowd et al. 2004). In cotton, an up-regulation of P5CS gene and proline abundance in stems are enhanced in PGPR-treated plants compared to control plants both inoculated with *Rhizoctonia solani* (Medeiros et al. 2011). The specific role of such induced drought-related tolerance on the disease control is yet to be determined.

This is an enticing glimpse into the potential direct genetic and transcriptional mechanisms of PGPR on the plant. However, at this juncture, the field is still somewhat intractable due to the complexity of plant hormone signaling pathways and their control over multiple plant growth, development and defense regimes. Despite the challenging nature of these interactions, it is clearly worthwhile to consider the promising examples of PGPR amelioration of abiotic challenges to plants. Unraveling the inter-relationships between PGPR and plant genetic mechanisms is imperative considering the urgent need to address these issues in our agroecosystems.

Conclusion

Clearly, PGPR are influencing plant growth and nutrition in very specific ways involving bacterial components inducing plant responses. Molecules from PGPRs can affect the plant in complex and overlapping mechanisms; sometimes influencing both plant growth and nutrition and resistance concomitantly. In other instances, the same PGPR product will promote plant health in only one specific way dependent on the type of plant host as well as the biotic and abiotic challenges present (see Fig. 1).

Many PGPR studies are focused on screening and identifying the species and strains of PGPRs associated

with specific plant hosts (Finkel et al. 2017). At this juncture, the field is primed to move beyond correlation, and make great strides in understanding plant beneficial mechanisms. PGPR research should begin to focus on understanding not only the genetic factors, but also the context of the genetic mechanisms underlying plant beneficial microbial activities. The ability to ‘engineer’ the rhizosphere (Dessaux et al. 2016) will be more effective as we move away from the current paradigm of species-based consortia and microbiome cataloguing (Maymon et al. 2015; Schlaeppi and Bulgarelli 2015). The functions conferred by the changes in plant expression induced by the microbiome as a whole may prove to be more relevant than the specific microbe species enacting those changes, and the mechanisms by which the microbes act could be key in future applied PGPR development. With this in mind, concomitant explorations of microbial genetic manipulation of the plant, and chemical genomics approaches (Stokes and McCourt 2014) to evaluate key microbial molecular components inducing plant beneficial responses could allow for significant progress in understanding and implementing PGPR in the field. By identifying and elucidating the specific mechanisms of microbial-plant beneficial activity, safer, more effective and sustainable PGPR applications may be developed for agricultural and horticultural management practices.

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Asterisks (*) denote the work is a review article.

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