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Article in *Frontiers in Plant Science* · October 2015

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Signaling in the phytomicrobiome: breadth and potential

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OPEN ACCESS

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Specialty section:

This article was submitted to
Plant Biotic Interactions,
a section of the journal
Frontiers in Plant Science

Received: 20 April 2015

Accepted: 24 August 2015

Published: 09 September 2015

Citation:

Smith DL, Subramanian S, Lamont JR
and Bywater-Ekegård M (2015)
Signaling in the phytomicrobiome:
breadth and potential.
Front. Plant Sci. 6:709.
doi: 10.3389/fpls.2015.00709

Higher plants have evolved intimate, complex, subtle, and relatively constant relationships with a suite of microbes, the phytomicrobiome. Over the last few decades we have learned that plants and microbes can use molecular signals to communicate. This is well-established for the legume-rhizobia nitrogen-fixing symbiosis, and reasonably elucidated for mycorrhizal associations. Bacteria within the phytomicrobiome communicate among themselves through quorum sensing and other mechanisms. Plants also detect materials produced by potential pathogens and activate pathogen-response systems. This intercommunication dictates aspects of plant development, architecture, and productivity. Understanding this signaling via biochemical, genomics, proteomics, and metabolomic studies has added valuable knowledge regarding development of effective, low-cost, eco-friendly crop inputs that reduce fossil fuel intense inputs. This knowledge underpins phytomicrobiome engineering: manipulating the beneficial consortia that manufacture signals/products that improve the ability of the plant-phytomicrobiome community to deal with various soil and climatic conditions, leading to enhanced overall crop plant productivity.

Keywords: molecular signals, plant growth promoting rhizobacteria, phytomicrobiome, holobiont, crop

Background

Most energy in the terrestrial biosphere enters it through photosynthesis (Imhoff et al., 2004) carried out by plant leaves (Luo et al., 2006). Non-photosynthetic organisms with reliable access to plant energy are in an advantaged situation. Under natural conditions higher plants are always associated with a complex and relatively constant microflora (Rout and Southworth, 2013; Turner et al., 2013a). Terrestrial plants release ~20% of photosynthetically fixed carbon as root exudates, resulting in an energy rich rhizosphere (Kuzyakov and Domanski, 2000), and a rich, generally compositionally consistent phytomicrobiome (Bulgarelli et al., 2012; Hirsch and Mauchline, 2012; Lundberg et al., 2012). These exudates vary among species, specific genotypes within species, stages of plant development and growing conditions, and influence the composition of the rhizomicrobiome (Bascom-Slack et al., 2012; Marasco et al., 2012; Badri et al., 2013a,b; Turner et al., 2013a,b; Chaparro et al., 2014).

Phytomicrobiome associations are analogous to the animal microbiome (Koenig et al., 2011); microbiome diversity, stability, and resilience play a large role in human health and disease (Cho and Blaser, 2012). Plants have likely had associated microbes since they colonized the land, almost half a billion years ago; roots of the first terrestrial plants were almost certainly less sophisticated than those that followed, making these early plants more in need of microbial assistance (Knack et al., 2015). Fossil endomycorrhizal associations occur in the early Devonian period,

demonstrating association of plant roots with fungal elements of the rhizomicrobiome (Taylor, 1995; Bonfante and Genre, 2008; Porras-Alfaro and Bayman, 2011). Mycorrhizal relationships are sophisticated and their presence >400 million years ago indicates that the phytomicrobiome had already been developing for some time; it seems likely that bacterial associations have been present for at least as long. As plants adapted to and spread through diverse terrestrial environments, evolving to grow under a range of conditions, it is probable that their associations with microbes also evolved. This community of microbes is the phytomicrobiome (Smith and Zhou, 2014), with its root associated (Hirsch and Mauchline, 2012; Lundberg et al., 2012; rhizomicrobiome), above ground associated (Rastogi et al., 2012, 2013; Badri et al., 2013b; Kembel et al., 2014; phyllosphere) and interior (Berg et al., 2014; endosphere) components. Even “lower plants” such as *Sphagnum* sp. have complex phytomicrobiomes, including highly specific associations with diazotrophs (Bragina et al., 2013).

Hence, a plant growing in nature is not a single organism; it is a community: a holobiont (Hartmann et al., 2014). While a plant growing in isolation can be very useful for research purposes, it is an anomaly. Like the human microbiome, the phytomicrobiome constitutes an underappreciated biological aspect (physiology, genome, metabolome, etc.) of plants. Plants and their associated phytomicrobiome affect each other in various and subtle ways (Berendsen et al., 2012); a field-grown plant is a meta-organism (Berg et al., 2013), having a persistent and regulated relationship with its phytomicrobiome. The composition of the phytomicrobiome is regulated by numerous biotic and abiotic factors including the complex matrix of plant–microbe and microbe–microbe communications. This communication is carried out through the release of signaling compounds, the forms and functions of which are currently being elucidated. This new understanding can be exploited to: (1) develop new approaches to crop growth promotion, (2) optimize related fermentation and formulation processes, and (3) develop novel and more consistent biocontrol mechanisms for field crops (East, 2013).

The Phytomicrobiome and Plant Growth

There has been an upsurge in phytomicrobiome publications; this community of microbes is now seen as key to the growth and health of plants (Schmidt et al., 2014); there is still a great deal to be learned about the composition and nature of interactions among members of this community, and its interactions with the host plant.

Microbes associate with the phyllosphere (as both epiphytes and endophytes, of leaves and stems), rhizosphere and reproductive structures such as flowers, fruits and seeds. In grape, *Pseudomonas* and *Bacillus* spp. colonize the epidermis and xylem of the ovary and ovules, while *Bacillus* spp. colonize berries and seed cell walls (Lugtenberg and Kamilova, 2009; Compant et al., 2010a,b). Nitrogen-fixing plant growth promoting rhizobacteria (PGPR; Loiret et al., 2004; Quecine et al., 2012; e.g., *Acetobacter diazotrophicus*, *Pantoea agglomerans* 33.1) associate

with plant roots (Pisa et al., 2011), and stems of sugarcane (Velázquez et al., 2008), residing in the apoplast in a low-nitrogen, high-sucrose environment (Dong et al., 1994). Other nitrogen-fixing bacteria (*Azotobacter*, *Enterobacter*, *Bacillus*, *Klebsiella*, *Azospirillum*, *Herbaspirillum*, *Gluconacetobacter*, *Burkholderia*, *Azoarcus*) are found in grasses such as rice and maize (Von Bulow and Dobreiner, 1975; James, 2000; Baldani et al., 2002; Boddey et al., 2003; Santi et al., 2013). Phyllosphere communities influence plant development and ecosystem function, while the host controls aspects of phytomicrobiome composition and function. Environmental factors are known to alter biosynthesis of many metabolites within plants; specific members of the rhizomicrobiome also alter plant development, growth, and composition. Treatment of leaves with specific phyllosphere components suppresses feeding by insect larvae (Badri et al., 2013b). The distribution and community composition of microbes in the phyllosphere is thought to be somewhat random, whereas plants create niches in the rhizosphere and endosphere to accommodate specific microbial communities (Lebeis, 2015).

The rhizomicrobiome is comprised of diverse root endophytes (Gaiero et al., 2013), some of which are PGPRs. Compositionally the rhizomicrobiome is dynamic in time and space, in response to environmental conditions, the presence of other soil organisms, soil physical conditions, plant species and genotype and interactions between a specific microbe and a specific plant type. The best characterized microbes in the rhizomicrobiome are the PGPR. These include bacteria in the soil near plant roots, on the surface of plant root systems, in spaces between root cells or inside specialized cells of root nodules; they stimulate plant growth through a wide range of mechanisms (Gray and Smith, 2005; Mabood et al., 2014), such as: (1) nutrient solubilization (particularly phosphorus – Boddey et al., 2003; Kennedy et al., 2004; Trabelsi and Mhamdi, 2013), (2) production of metal chelating siderophores, (3) nitrogen fixation (Vessey, 2003; Bhattacharyya and Jha, 2012; Drogue et al., 2012), (4) production of phytohormones, (5) production of 1-aminocyclopropane-1-carboxylate deaminase, (6) production of volatile organic compounds, (7) induction of systemic resistance [induced systemic resistance (ISR) and systemic acquired resistance (SAR) – Jung et al., 2008b, 2011], and (8) suppression of disease through antibiosis (Bhattacharyya and Jha, 2012; Spence et al., 2014). It has also been shown that “signal” compounds produced by bacteria in the phytomicrobiome stimulate plant growth (Prithiviraj et al., 2003; Mabood et al., 2006a; Lee et al., 2009), particularly in the presence of abiotic stress (Wang et al., 2012; Subramanian, 2014; Prudent et al., 2015). In the broadest sense PGPR include legume-nodulating rhizobia. PGPR reside outside plant cells (extracellular – ePGPR) or, like rhizobia, live inside them (intracellular – iPGPR; Gray and Smith, 2005). Application of PGPR to crops, except for rhizobia, has met with mixed results in the field, causing increased growth sometimes and not others (Nelson, 2004). Elements of the phytomicrobiome also assist plants in dealing with abiotic stress. The *Arabidopsis* phytomicrobiome, for instance, can sense drought stress and help the plant maintain productivity (Zolla et al., 2013). Further, mycorrhizal associations enhance crop

salinity tolerance (Porcel et al., 2012; Ruiz-Lozano et al., 2012). At a time when we are looking to crop plants to provide biofuels and other bioproducts while still feeding the world's growing population, against a background of climate change, understanding and developing technologies that can increase overall plant productivity is imperative (Ragauskas et al., 2006; Babalola, 2010; Dutta and Podile, 2010; Beneduzi et al., 2012; Orrell and Bennett, 2013).

Newer deployments of PGPR and/or arbuscular mycorrhizal fungi (AMF) consortia that promote crop productivity by mimicking, or partially reconstructing, the phytomicrobiome are being developed. Application of a PGPR consortium (*Bacillus amyloliquefaciens* IN937a, *Bacillus pumilus* T4, AMF *Glomus intraradices*) to greenhouse tomato resulted in full yield with 30% less fertilizer (Adesemoye et al., 2009). Co-inoculation of *B. japonicum* 532C, RCR3407 and *B. subtilis* MIB600 increased biomass for two soybean cultivars (Atieno et al., 2012). Co-inoculation of *B. japonicum* E109 and *Bacillus amyloliquefaciens* LL2012 improved soybean nodulation efficiency. Phytohormone production by *B. amyloliquefaciens* LL2012 improved nodulation efficiency for *B. japonicum* E109 (Masciarelli et al., 2014). A consortium of *B. megaterium*, *Enterobacter* sp., *B. thuringiensis* and *Bacillus* sp., plus composted sugar beet residue, on *Lavandula dentata* L. helped restore soils by increasing phosphorus availability, soil nitrogen fixation and foliar NPK content (Mengual et al., 2014).

Signaling in the Phytomicrobiome

The complex community formed by the plant and its phytomicrobiome is carefully orchestrated; there is signal exchange among the various microbes involved, and also between the host plant and the microbe community (Engelmoer et al., 2014). These signals regulate aspects of each other's activities and the community overall. Microbial chemical signals can help plants initiate immune responses to harmful pathogens or allow the entry of beneficial endophytes (Hartmann et al., 2014). Microbe associated molecular patterns (MAMPs) play a key role in plant immune response and antibiotic secretion in microbes. Plant associated *Bacillus* strains have been shown to down-regulate MAMP-regulated immune response including antibiotic secretion in the presence of plant root exudates to better facilitate root infection (Lakshmanan et al., 2012). Bacteria can also interfere with signaling between plants and other microbial strains. LCOs are similar in structure to chitin and can be cleaved by bacterially produced chitinases, thus interfering with plant microbe symbioses (Jung et al., 2008a). Other aspects plant-microbe symbiosis follow pathways similar to pathogen infection (Barea, 2015).

Signaling compounds produced by plants include a variety of root exudates such as primary metabolites (carbohydrates, proteins, organic acids, etc.) and secondary metabolites (flavonoids, phenol, phytohormones, etc.). Plants often excrete more of these signaling compounds in response to stress. PGPR-to-plant signaling compounds include phytohormones,

acyl homoserine lactones, phenols and peptides and can also act as microbe to microbe signals (Barea, 2015). Root exudates signal and recruit specific microbial communities. Secretion of malic acid in *Arabidopsis thaliana* in response to foliage pathogen attack stimulates the formation of beneficial biofilms in the rhizosphere (Rudrappa et al., 2008).

That plants and microbes use signal compounds to communicate during establishment of beneficial plant-microbe interactions (Desbrosses and Stougaard, 2011), is well-described for the legume-rhizobia nitrogen fixing symbiosis (Oldroyd et al., 2010; Giles et al., 2011; Oldroyd, 2013), and somewhat elucidated for mycorrhizal associations (Gough and Cullimore, 2011). In the legume-rhizobia relationship the plant releases flavonoid signals to rhizobia (Hassan and Mathesius, 2012) or, in some cases, jasmonate signals (Mabood et al., 2006a,b; Mabood et al., 2014), followed by rhizobial production of lipo-chitooligosaccharides (LCOs) as return signals (Oldroyd, 2013). The LCOs are bound by LysM receptors, which have kinase activity (Antolin-Llovera et al., 2012), changing root hormone profile (Zamioudis et al., 2013) and triggering development of root nodules. Plants also communicate with, or otherwise influence the phytomicrobiome, affecting its composition and structure (Delaux et al., 2012; Badri et al., 2013a; Bálint et al., 2013; Peiffer et al., 2013; Turner et al., 2013b; Venkateshwaran et al., 2013; Chaparro et al., 2014; Evangelisti et al., 2014). Bacteria also communicate among themselves (Cretoiu et al., 2013); quorum sensing via *N*-acyl homoserine lactone (Teplitski et al., 2000) is well-characterized, and there are likely other, as of yet unknown, mechanisms (Lv et al., 2013). Quorum sensing signals can trigger immune responses and changes in hormone profiles in plants, leading to growth responses (Hartmann and Schikora, 2012). Quorum sensing in the phytomicrobiome will be the subject of an upcoming *Frontiers in Plant Science* theme volume (Plant responses to bacterial quorum sensing signal molecules, topic editors Schikora A, Hartmann A, and Munchen HZ). This sort of signaling almost certainly occurs in the phytomicrobiome. Plants also detect materials produced by potential pathogens and respond by activating response systems (Tena et al., 2011). Phytomicrobiome intercommunication in the rhizosphere dictates aspects of above-ground plant architecture and above-ground symbiotic/pathogenic microbial communities (Segonzac and Zipfel, 2011; Tena et al., 2011). Similarly, pathogen or herbivore attacks above ground can effect microbial community composition in the rhizosphere. Above ground injury has been shown to stimulate the production of signaling compounds in plant roots (Lakshmanan et al., 2012). Greater photosynthetic rates under elevated CO₂ conditions have been shown to change microbial community composition in the rhizosphere (Berlec, 2012; He et al., 2012). Understanding plant responses to microbial signals via proteomics (Elmore et al., 2012; Nguyen et al., 2012; Rose et al., 2012) and metabolomics (Watrous et al., 2012; Zhang et al., 2012) studies has added valuable knowledge toward developing effective low-cost and eco-friendly practices to reduce fossil-fuel dependent crop inputs, leading to interest in phytomicrobiomes engineered to enhanced plant growth under

variable soil and climatic conditions, improving global crop productivity.

Surprisingly, LCOs are also able to stimulate plant growth directly (Souleimanov et al., 2002; Prithiviraj et al., 2003; Almaraz et al., 2007; Khan et al., 2008; Wang et al., 2012); confirmed by Oláh et al. (2005) for root growth in *Medicago truncatula*, Chen et al. (2007) for accelerated flowering (a typical response to stress) and increased yield in tomato, and stimulation of early somatic embryo development in Norway spruce (Dyachok et al., 2002). Enhanced germination and seedling growth, along with the mitogenic nature of LCOs, suggest accelerated meristem activity. Products based on LCOs are now used to treat seed sown into several 10s of million ha of crop land each year, largely corn and soybean. A similar jasmonate product is now available. The effects of LCOs are much greater when stress (salt, drought, cold) is present than under optimum conditions (Smith, 2009, 2010; Subramanian et al., 2009, 2010, 2011; Schwinghamer et al., 2014; Subramanian, 2014; Prudent et al., 2015). Thuricin 17, a bacteriocin produced by *Bacillus thuringiensis* NEB17 isolated from soybean roots, improves plant growth and resilience to stress (Schwinghamer et al., 2014; Subramanian, 2014). Inhibition of legume nodulation, and of overall plant growth, by stressful conditions can be overcome by LCOs (nodulation – Zhang and Smith, 1995, 2002; plant growth – Schwinghamer et al., 2014; Prudent et al., 2015); Estévez et al. (2009) showed that at least one rhizobial strain produce different LCOs when grown under salt stress, and that salt stress itself can induce the *nod* genes of this strain (Guasch-Vidal et al., 2013).

Future Directions

We now understand that the phytomicrobiome is a complex, structured and dynamic community with a relatively constant set of potential members, whose relative abundances can shift within plant species and their genotypes, and in response to both abiotic conditions and plant development, leading to dynamism in the communications among the microbial community and the host plants. Methods, such as high throughput genotyping, are allowing us to determine the taxonomic diversity of the phytomicrobiome (Hirsch and Mauchline, 2012; Peiffer et al., 2013; Turner et al., 2013b). A better understanding of plant signaling may also become a tool for investigating community composition of the phytomicrobiome. Root exudates play an important role in the formation of microbial communities in the rhizosphere and can be useful in predicting community compositions (Berg et al., 2014). Correlations between phytomicrobiome bacterial diversity and host growth, mortality, and function suggest that incorporating information on plant–microbe associations will improve our ability to understand plant functional biogeography and drivers of variation in plant and ecosystem function (Kembel et al., 2014). It has even been suggested that beneficial effects of the phytomicrobiome could be enhanced through plant breeding, developing genotypes that encourage best membership in the phytomicrobiome

(Bakker et al., 2012). More effective methods to study plant MAMP receptors are being developed (Wittulsky et al., 2014) and could lead to ways to engineer plant recognition receptors.

Novel methods of manipulating signaling in the phytomicrobiome could lead to crop production practices that are less reliant on non-renewable resources and crops more resilient in the face of stresses (Marasco et al., 2012), most crucially, those associated with climate change. Plant stress response seems to play an important role in the release of signaling compounds in the rhizosphere but the specifics of this interaction are still unclear. A better understanding of the relationship between environmental plant stress and signaling could help in developing technologies that utilize plant signaling in crop stress alleviation (Barea, 2015).

Recent developments have shown that temperature (Schwinghamer et al., 2014) and water stress (Prudent et al., 2015) can influence plant microbe communication. Environmental factors likely play an important and underdescribed role in signaling in the phytomicrobiome. Variable environmental factors may account for some of the inconsistency observed in field trials of microbial products that previously yielded favorable results in laboratory conditions. A more complete understanding of how plant–microbe communication is influenced by environmental factors will likely be useful in achieving more consistent results with agricultural microbial products.

Despite being at an early stage in understanding these communities, it is clear that there is considerable potential for application of coordinated microbial consortia to crop agriculture and, thus, to enhancing global food security. While advances in methods and technologies in microbiology used to investigate non-culturable microbial strains have led to a stronger focus on a community level approach to plant–microbe interaction research (Berlec, 2012; Rastogi et al., 2013), isolated, culturable microbial strains are still required for most plant–microbe signaling research, particularly if the research is aimed at developing commercial microbial products. Culturable strains are needed both to produce a consistent product and to verify growth promotion through plant growth trials. There are clear opportunities for development of products for more sustainable agronomic production systems (Kloepper et al., 2004; De-la-Peña and Loyola-Vargas, 2014). A range of PGPR have been identified, and even developed into products utilized in crop production. Signaling compounds that directly stimulate plant growth or improve stress tolerance have great potential because they can be produced by microbes in a controlled bioreactor rather than in variable field conditions as with inoculants. The global market for biostimulants has been projected to reach \$2.241 billion by 2018 and to have a compounded annual growth rate of 12.5% from 2013 to 2018 (Calvo et al., 2014). Products based on multispecies consortia may address consistency in performance observed in single species inoculants. Industry is working to harness the knowledge surrounding the phytomicrobiome, to quickly bring sustainable, consortia-based products to production agriculture.

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Conflict of Interest Statement: The fourth author is Executive Vice President of Technology and Innovation at Inocucor Technologies, a company that manufactures and sells microbial consortia for plants; the first author conducts research in collaboration with this company, where the research is funded through a Canadian Federal Government program (Mitacs) which leverages industrial funding.

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