Biotic Interactions in the Rhizosphere: A Diverse Cooperative Enterprise for Plant Productivity[1][C]

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Microbes and plants have evolved biochemical mechanisms to communicate with each other. The molecules responsible for such communication are secreted during beneficial or harmful interactions. Hundreds of these molecules secreted into the rhizosphere have been identified, and their functions are being studied in order to understand the mechanisms of interaction and communication among the different members of the rhizosphere community. The importance of root and microbe secretion to the underground habitat in improving crop productivity is increasingly recognized, with the discovery and characterization of new secreting compounds found in the rhizosphere. Different omic approaches, such as genomics, transcriptomics, proteomics, and metabolomics, have expanded our understanding of the first signals between microbes and plants. In this review, we highlight the more recent discoveries related to molecules secreted into the rhizosphere and how they affect plant productivity, either negatively or positively. In addition, we include a survey of novel approaches to studying the rhizosphere and emerging opportunities to direct future studies.

Due to the increasing human population, the continued production of food and energy is a basic challenge today (Edgerton, 2009; Ray et al., 2013). With more than seven billion people to feed, the productive yield of crops needs to be higher, more sustainable, and more efficient worldwide. Productivity is not only the plant growth per hectare in the field. It is also defined by the fitness, food production, and healthy development of plants (Boyer, 1982; Edgerton, 2009). Most losses in food production are due to diseases caused by different pathogens and pests, the effect of which is augmented by abiotic stresses such as heat and drought. Although some microorganisms responsible for plant diseases colonize the upper part of the plant, many more are found in the soil and are capable of either destroying a vast number of cultivars (Borneman and Becker, 2007; Berendsen et al., 2012) or building useful symbiotic relationships (Venkateshwaran et al., 2013).

The criticality of the interaction between roots and microorganisms to agricultural output is increasingly recognized. There are many chemicals secreted from microorganisms and roots, such as amino acids, organic acids, flavonols, glucosinolates, indole compounds, fatty acids, polysaccharides, and proteins in the rhizosphere (De-la-Peña et al., 2012a; Nguema-Ona et al., 2013; Weston et al., 2013; Li et al., 2014; Talboys et al., 2014; Zhang et al., 2014), that act as signals; once the recipient organisms recognize them, the process of communication and interaction begins. The type and composition of root secretion can alter the microbial dynamic and diversity of the soil, favoring the growth of microorganisms that can benefit plant health and crop productivity, while, in other cases, root-exuded compounds prevent the growth of harmful microbes (Bais et al., 2006; Chaparro et al., 2012; Dutta et al., 2013; Li et al., 2013). Phytochemicals collected from the root exudates of Arabidopsis (*Arabidopsis thaliana*) added into the soil have shown how important these compounds are to the modulation of microbe composition (Badri et al., 2013).

Although soil microorganisms are associated with plant disease and productivity losses, numerous bacteria and fungi species are beneficial for plant productivity (van der Heijden et al., 2008; Pérez-García et al., 2011; Venkateshwaran et al., 2013). For instance, the rhizobia bacteria build a social network with legumes in a symbiotic structure called a nodule, where atmospheric nitrogen is fixed and transferred to a plant for its use (Spaink, 2000). To overcome nitrogen deficiency, legumes release specific flavonoids that attract and initiate these symbiotic relationships with rhizobia (Zhang et al., 2009), which secrete exopolysaccharides needed for symbiosis (Cheng and Walker, 1998; Berge et al., 2009). This symbiosis introduces 50 to 70 × 10^6 tons of nitrogen annually into the soil of agricultural systems (Herridge et al., 2008), which reduces the use of fertilizers that, depending on the dose and type, can have a detrimental environmental impact. On the other hand, arbuscular mycorrhizal fungi (AMF) also benefit plant productivity by spreading their hyphal networks into the soil to acquire nutrients, such as phosphorous, which are then supplied to their hosts (Joner et al., 2000; Klironomos et al., 2000; Jeffries et al., 2003).

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Based on this explosion of new knowledge of rhizosphere interactions, the question becomes, how many molecules in the rhizosphere have important roles in plant productivity? And why are some molecules, from microbes and/or plants, harmful enough to destroy hectares of cultivars (Shieh et al., 1997; Weir et al., 2003; Oerke, 2006; Ejeta and Gressel, 2007; Joel et al., 2007)? With the advance of new technologies, such as proteomics and metabolomics, the ability to identify secreted molecules has revealed important clues about their possible functions (De-la-Peña and Loyola-Vargas, 2012; Badri et al., 2013; Martin et al., 2014; Neumann et al., 2014), but the ecological and environmental relevance of many of them remains unresolved. In this review, we will focus on how root exudates are key players involved in the selection of the microbial community during plant-microbe interaction and how this interaction affects the productivity of plants in the field.

BIOTIC INTERACTIONS IN THE RHIZOSPHERE ARE IMPORTANT FOR PLANT PRODUCTIVITY

The rhizosphere is an environment where plants interact with other plants, herbivores, and microorganisms (Lynch and Whipps, 1990; Barea et al., 2005; Bais et al., 2006). The rhizosphere not only represents the trade zone in which pathogens or neighbor roots interact with the plant but is also a preventive microbial buffer zone that protects against infection (Baetz and Martinoia, 2014). In general, the rhizosphere has three main zones: endorhizosphere, rhizoplane, and ectorhizosphere. The first zone, the endorhizosphere, includes the root cortical and endodermal tissue, while the rhizoplane encompasses the root epidermis and associated mucilage. The ectorhizosphere covers the soil near the root (Lynch and Whipps, 1990; Badri and Vivanco, 2009). The rhizosphere can contain up to 10^{11} microbial cells per gram of root (Egamberdieva et al., 2008) and more than 30,000 prokaryotic species that could influence plant productivity (Mendes et al., 2011, 2013). Although the total number of these microorganisms is likely underestimated due to culturing limitations, it is known that plants are able to shape their rhizosphere microbiome in order to recruit protective bacteria or fungi (Berendsen et al., 2012).

Plant development and growth have benefited from the diversity and complexity of the microbial society. There is not a single organism responsible for a beneficial effect in plants; rather, the multiple interactions between all the actors work together. The interspecies or interkingdom cross talk in the rhizosphere that is produced during plant-microbe or plant-plant interactions is essential for the function, health, stability, and sustainability of ecosystems, including the farming environment (Bais et al., 2004b; Shukla et al., 2008; Broz et al., 2010; Pellegrino and Bedini, 2014). Some of the most studied biotic relationships for plant productivity are those produced by plant growth-promoting rhizobacteria (PGPRs), AMF, and invasive plant species.

PGPR Important in Plant Productivity and Defense

Plant roots are able to recruit beneficial soil bacteria, called PGPRs, from a wide range of genera, including *Acinetobacter*, *Alcaligenes*, *Azospirillus*, *Bacillus*, *Pseudomonas*, *Rhizobium*, and others. These rhizobacteria are important due to their functions as producers of plant growth regulators, solubilizers of phosphorus, biofertilizers, and elicitors of tolerance to abiotic and biotic stresses (Yang et al., 2009; Bhattacharyya and Jha, 2012).

The major classification of the PGPRs is as biofertilizers, phytostimulators, and biopesticides (Bhattacharyya and Jha, 2012; Bhardwaj et al., 2014; Pérez-Montaño et al., 2014). The function of the biofertilizers is to promote plant growth by supplying nutrients to the host; examples of biofertilizers are *Allorhizobium* spp., *Trichoderma* spp. (e.g. *Trichoderma hamatum* and *Trichoderma asperellum*), *Pseudomonas fluorescens*, and *Rhizobium* spp. (Vessey, 2003; Badar and Qureshi, 2012; Bhattacharyya and Jha, 2012; Yadav et al., 2013). The phytostimulators, on the other hand, produce phytohormones such as indole acetic acid (IAA), GA_3, and cytokinins, which alter root architecture and promote plant development (Vessey, 2003; Spaepen et al., 2007; Apine and Jadhav, 2011; Duca et al., 2014). In this group are *Bacillus*, *Pseudomonas*, *Azosporillus*, *Enterobacter*, *Azotobacter*, *Pantoea*, *Streptomyces*, and *Rhizobium* spp. Finally, examples of biopesticides are *Pseudomonas* spp. (e.g. *P. fluorescens*), *Streptomyces* spp., and *Bacillus* spp. (e.g. *Bacillus subtilis*), which function to inhibit pathogen proliferation and help plant growth (Copping and Menn, 2000; Radja Commare et al., 2002; Bhattacharyya and Jha, 2012). Besides the biofertilizers, phytostimulators, and biopesticides, there are other PGPRs that induce tolerance in plants to abiotic stress. For instance, *Paenibacillus polymyxa*, *Achromobacter piechaudii*, and *Rhizobium tropici* confer tolerance to drought stress in Arabidopsis, tomato (*Solanum lycopersicum*), and common bean (*Phaseolus vulgaris*), respectively, possibly by abscisic acid accumulation and degradation of reactive oxygen species and 1-aminocyclopropane-1-carboxylate (Timmusk and Wagner, 1999; Mayak et al., 2004b; Figueiredo et al., 2008; Yang et al., 2009). *Achromobacter piechaudii* and *B. subtilis* are also involved in salinity tolerance in plants (Mayak et al., 2004a; Zhang et al., 2008; Yang et al., 2009). All these functions are important to improve crop productivity, and in a time of escalated climate change, the need to reduce mineral fertilizers and produce plants tolerant to abiotic stresses is becoming an international priority.

Much discussion has centered on the use of rhizobacteria as commercial biofertilizers. In a recent review, Shen et al. (2013) pointed out that in order to have the highest crop productivity, plants need an optimal nutrient input and resilience under stress. This allows plants to efficiently use soil nutrients through maximizing root/rhizosphere efficiency in nutrient mobilization and acquisition. Such mobilization is done at a high rate by rhizosphere bacteria (Koller et al., 2013; Parmar and Sindhu, 2013). Plant agriculture needs PGPRs to increase plant growth, facilitate nutrient availability, enhance seed emergence, and favor plant health (Suslow et al., 1979; Zehnder et al., 2001; Lugtenberg and Kamilova, 2009; Mia et al., 2010), and the way plants recruit these beneficial bacteria is through chemical root secretion. For instance, legumes release specific flavonoids to attract and initiate symbiotic relationships with rhizobia (Zhang et al., 2009). Other plants, such as maize (*Zea mays*), secrete a benzoxazinoid called 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one to attract the rhizobacterium *Pseudomonas putida* KT2440, which helps to repel other pathogenic microbes in the maize rhizosphere (Neal et al., 2012).

The way that PGPRs favor plant health is by calling for beneficial bacteria when a pathogen is attacking. For instance, the infection of Arabidopsis by *Pseudomonas syringae* pv *tomato* DC3000 is able to induce the expression of the L-malic acid (MA) transporter *ALUMINUM-ACTIVATED MALATE TRANSPORTER1*, increasing the secretion of MA by roots (Rudrappa et al., 2008; Lakshmanan et al., 2012). Once the MA is in the rhizosphere, it recruits the beneficial rhizobacterium *B. subtilis* FB17 in a dose-dependent manner and promotes the biofilm formation of *B. subtilis* FB17 on Arabidopsis roots (Rudrappa et al., 2008; Lakshmanan et al., 2013), producing a systemic resistance response against the pathogen. Besides MA, some bacteria secrete antimicrobial metabolites (e.g. cyclic lipopeptide surfactin and iturin A) that serve as a protective shield in roots against pathogenic fungi like *Rhizoctonia* spp. or pathogenic gram-negative bacteria such as *P. syringae* (Asaka and Shoda, 1996; Bais et al., 2004a). Although *P. syringae* is one of the most studied pathogenic bacteria, which has been accorded first place on a list of the top 10 plant pathogenic bacteria (Mansfield et al., 2012), this bacterium also has been useful in controlling crop diseases (Ligon et al., 2000). For instance, diverse species of the genus *Pseudomonas*, including *Pseudomonas cepacia*, *P. fluorescens*, *Pseudomonas aeruginosa*, and *Pseudomonas aureofaciens*, produce hydrogen cyanide, 2,4-diacetylphloroglucinol, pyrrolnitrin, phenazine, oomocyn A, and other compounds that in some way help protect the plant against diseases (Burkhead et al., 1994; Raaijmakers and Weller, 1998; Haas and Keel, 2003). The production of these compounds depends on different factors; for instance, oomycin A and 2,4-diacetylphloroglucinol are stimulated by Glc (Gutterson, 1990; Duffy and Défago, 1999), hydrogen cyanide is affected by light and temperature (Vickery et al., 1987), and an acid pH seems to enhance the production of pyrrolnitrin (Hwang et al., 2002). Therefore, it is tempting to speculate that changes in the soil environment due to climate changes (Davidson and Janssens, 2006; Frey et al., 2013) also could affect antibiotic production from beneficial bacteria, making plants more susceptible to pathogen attack and damaging plant productivity.

Other important compounds secreted by gram-negative bacteria, such as *P. aeruginosa*, *Erwinia chrysanthemi*, and many others, include *N*-acyl-homoserine lactones (AHLs), which are the principal signal components for quorum sensing (QS), the cell-to-cell communication system in bacteria (Dong and Zhang, 2005). Because the AHL signal is a key factor for virulence gene expression in pathogenic bacteria, this signal provides a way to manipulate the QS systems and interrupt communication between bacteria. There are several chemicals and enzymes that target different components of the bacterial QS system to disrupt QS signaling, a process known as quorum quenching (QQ; Hong et al., 2012). The first QQ enzyme, an AHL-lactonase, was isolated from *Bacillus* sp. 240B1 (Dong et al., 2000, 2001). These QQ molecules could be developed for agricultural applications through targeting the QS signals by inhibiting AHL biosynthesis or by degrading AHL as a strategy to avoid bacteria pathogenicity; both are likely to be ecologically benign. One of the most efficient quencher strains characterized is *Bacillus cereus* U92, which has been used as a biocontrol agent in the rhizospheres of tomato and potato (Zamani et al., 2013).

AMF

AMF belong to the ancient phylum Glomeromycota and have established biotic interactions with more than 80% of land plant families, including many agriculturally important crop species, such as maize, rice (*Oryza sativa*), wheat (*Triticum aestivum*), and soybean (*Glycine max*). As such, they contribute to plant nutrition and disease resistance (Gutjahr and Parniske, 2013). The colonization of roots by the AMF is carried out after an exchange of chemical signals among the fungi and the plant. The primary signal is produced and secreted by the roots of the host; it has been identified as various strigolactones (SLs; Akiyama and Hayashi, 2006), which induce germination and hyphal branching in AMF as well as stimulate fungal metabolism (Akiyama et al., 2005; Besserer et al., 2006; Zwanenburg and Pospíšil, 2013). The fungus responds to that signal, secreting tetrameters and pentamers of *N*-acetylglucosamine and lipochitin-oligosaccharides (Maillet et al., 2011; Czaja et al., 2012; Gutjahr and Parniske, 2013), which activate a signaling pathway in the roots of the host. Once the communication network has been established between the fungus and the plant, the main interface for symbiotic nutrient exchange begins (Bücking et al., 2012). The interaction between plants and AMF is bidirectional; AMF receive carbohydrates from the plant and compensate it with mineral nutrients, abiotic stress resistance (Bücking et al., 2012), and improved water supply (Parniske, 2008). This interaction is so important to the plant that it is able to transfer between 4% and 20% of its photosynthetically fixed carbon to the AMF (Wright et al., 1998).

The formation of AFM depends not only on host root exudates but also on soil phosphorus conditions (Nagahashi et al., 1996; Tamasloukht et al., 2003), normally through phosphorus fertilizer management (Grant et al., 2005). If the phosphorus concentration is too high (e.g. 10 mM), the growth of the fungal hyphae is inhibited and the AMF colonization is reduced (Nagahashi et al., 1996). Among other factors that could affect AFM colonization are the use of monoculture, tillage (Berruti et al., 2014), modern agricultural practices (Toth et al., 1990; Hetrick et al., 1992), and, still controversial, genetically modified crops (e.g. maize; Liu, 2010).

Root Secretion of Invasive Species Increases Crop Losses

The plant-plant relationship is also an important biotic interaction that has significant repercussions on plant productivity. The allelopathy phenomenon, in which "one plant negatively affects another through chemicals exuded or secreted," may arise during the interaction between invasive and native species and may involve the microflora in the rhizosphere (Bains et al., 2009). Invasive plants, which are responsible for high negative economic effects (Vilà et al., 2009; McLaughlan et al., 2014), have different mechanisms to take possession of the land, frequently through altered pathways or adapted mechanisms that appear in the new environment. All plants secrete compounds; however, some invasive plants have evolved an adaptive mechanism(s) through which they secrete new compounds that adversely affect the native plant populations of their new habitat (enemy-release hypothesis). Allelochemicals can affect metabolite production, respiration, photosynthesis, and membrane transport and can inhibit root and shoot growth in susceptible plants (Einhellig, 1994; Weir et al., 2004).

Many allelochemicals have been identified as components of the root exudation of invasive species (Table I). One of the most studied has been catechin, a flavonoid present in the root exudates of the invasive spotted knapweeds *Centaurea maculosa* and *Centaurea stoebe*, which exhibits a strong inhibitory effect on a number of plant species (Bais et al., 2003; Weir et al., 2003; Tharayil and Triebwasser, 2010). It has been found that the concentration and effect of this compound increase in response to light intensity (Tharayil and Triebwasser, 2010). This resolves, in part, the question of why the concentration and the allelopathic effect of catechin change under different conditions (Perry et al., 2007). Perry et al. (2007) found that the concentration of catechin was higher during the months of May to August, when there are more hours of light. Although the molecular mechanism by which this is achieved is unknown, it has been proposed that light regulates flavonoid biosynthesis and, therefore, catechin accumulation (Tharayil and Triebwasser, 2010; Hong et al., 2014).

Other important allelopathic plants are black walnut (*Juglans nigra*), which produces juglone (5-hydroxy-1,4-naphthoquinone), and sorghum (*Sorghum bicolor*), which produces sorgoleone (2-hydroxy-5-methoxy-3-[(8′Z,11′Z)-8′,11′,14′-pentadecatriene]-*p*-benzaquinone), an oxidized form of a hydrophobic *p*-benzoquinone (Table I). Both compounds inhibit electron transport reactions of photosynthesis and respiration, killing both maize and soybean and other susceptible plants (Rietveld, 1983; Nimbal et al., 1996; Jose and Gillespie, 1998). Another important allelochemical is the phenolic gallic acid produced by the common reed (*Phragmites australis*), a large perennial grass found in the United States and Asia. It has been determined that there exist two populations of this plant, one invasive and one noninvasive (Saltonstall, 2002). The invasive one produces more polymeric gallotannin than the noninvasive one. This polymer is transformed to gallic acid by a tannase, an enzyme produced by various native plants and microbial community members of North America, a process that intensifies the aggressiveness of the common reed (Rudrappa et al., 2007; Bains et al., 2009). However, controversial evidence questioning the negative effect of gallic acid on nonnative genotypes of this plant has recently been released (Weidenhamer et al., 2013).

CHEMICAL PLAYERS IN PLANT PRODUCTIVITY

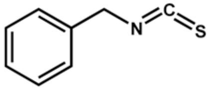
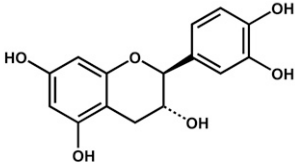
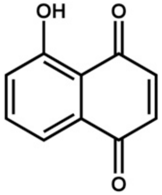
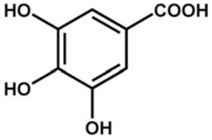
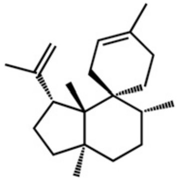
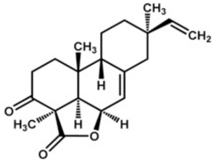
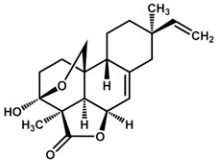
Although we do not pretend to discuss all chemicals secreted by the roots, we highlight below the role of those metabolites and proteins that have been found to be important players in plant productivity, either positively, such as auxins and glomalin, or negatively, such as SLs and polygalacturonase (PG; Fig. 1).

Auxins

Auxins are phytohormones generated by plants, some fungi, and PGPRs (Reineke et al., 2008; Simon and Petrášek, 2011; Duca et al., 2014). Some rhizobacteria are able to produce auxins, particularly IAA, in a range from 17 to 719 μmol L^{-1}, thus contributing to plant growth (Ivanova et al., 2001; Ali et al., 2010; Gumiere et al., 2014), although high concentrations of IAA can inhibit root growth and, therefore, plant productivity (Davies, 1995; Xie et al., 1996).

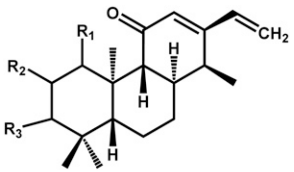
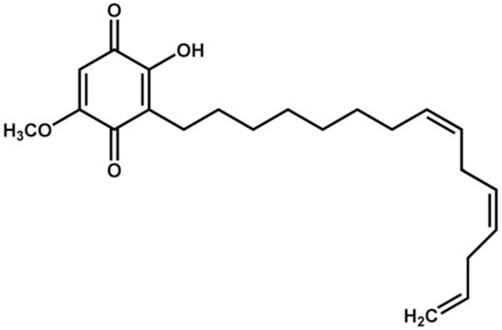
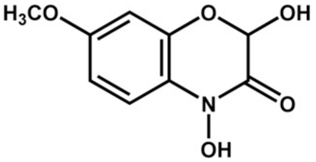
IAA in bacteria is synthesized from L-Trp (Duca et al., 2014), which can be obtained from compost, fertilizers, and root exudates (Jaeger et al., 1999; Kravchenko et al., 2004; Arkhipchenko et al., 2006). It has been reported that the presence of 5 mM Trp can cause a 5-fold increase in the IAA secretion in *Bacillus amyloliquefaciens* FZB42 (Idris et al., 2007) and up to a 100-fold increase in *Azospirillum brasilence* (Baca et al., 1994). Field and pot trials have revealed that by adding L-Trp to the soil, the growth and yield of several important crops can be improved, including rice, wheat, soybean, potato, and tomato (Zahir et al., 2000).

Table I. *Principal compounds found in root exudates with negative and positive effects on plant productivity*

Species	Compound	Structure	Function	Effect on Productivity	Reference
Alliaria petiolata	Benzyl isothiocyanate		Inhibits the growth of ectomycorrhizal fungi	Negative	Stinson et al. (2006); Wolfe et al. (2008)
Centaurea maculosa	(−)-Catechin		Reduces the growth of native plant species	Negative	Bais et al. (2003); Weir et al. (2003)
Juglans nigra	Juglone (5-hydroxy-1,4-napthoquinone)		Inhibits the growth of crops, mainly shoot elongation	Negative	Rietveld (1983); Jose and Gillespie (1998)
Phragmites australis	Gallic acid (3,4,5-trihydroxybenzoic acid)		Allelopathic agent	Negative	Saltonstall (2002)
Arabidopsis	Rhizathalene A		Defense against herbivores	Positive	Vaughan et al. (2013)
Rice	Momilactone A		Antimicrobial	Positive	Kato-Noguchi et al. (2008)
	Momilactone B		Allelopathic agent	Positive	Kato-Noguchi (2004)

(*Table continues on following page.*)

Table I. (*Continued from previous page.*)

Species	Compound	Structure	Function	Effect on Productivity	Reference
	Phytocassanes A to E[a]		Antimicrobial agent	Positive	Toyomasu et al. (2008)
Sorghum	Sorgoleone (2-hydroxy-5-methoxy-3-[(8′*Z*,11′*Z*)-8′,11′,14′-pentadecatriene]-*p*-benzaquinone)		Allelopathic agent	Positive	Uddin et al. (2014)
Maize	Benzoxazinoids (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one)		Antimicrobial agent	Positive	Neal et al. (2012)

[a] Phytocassane A, R1, R2, R3 = H, OH, O; phytocassane B, OH, OH, OH; phytocassane C, OH, H, OH; phytocassane D, H, O, OH; phytocassane E, OH, H, O.

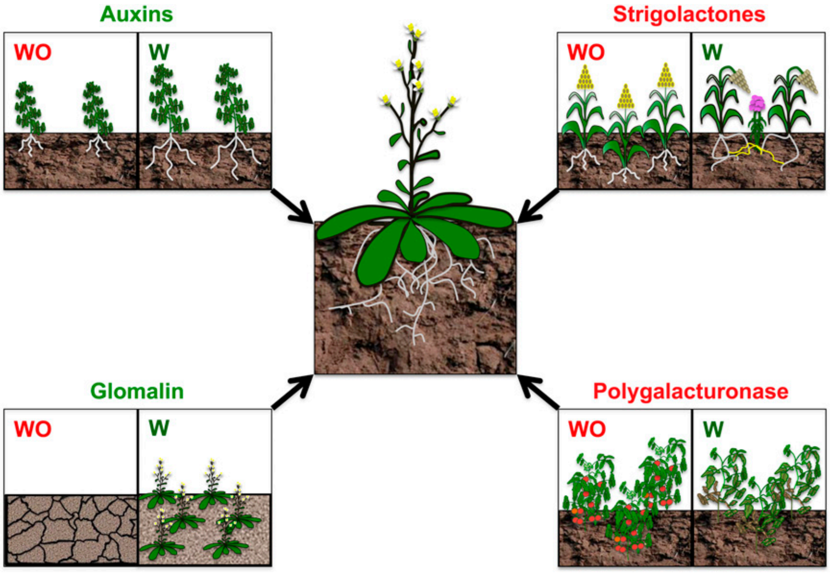


Figure 1. Effects of auxins, glomalin, SLs, and PGs on plant development and health. The presence (W) or absence (WO) of auxins, glomalin, SLs, and PGs can produce positive (green) or negative (red) effects on plants. The presence of a bacterium that secretes auxins helps the plants to stimulate roots, increasing nutrient acquisition from the soil. On the other hand, the absence of glomalin affects soil structure, facilitating soil erosion. Sorghum secretes SLs that induce the germination of the parasite plant *Striga lutea*, and PGs can disturb the plant cell wall in tomato, affecting plant productivity. [See online article for color version of this figure.]

Therefore, in managed crops, PGPR inoculation can still contribute to IAA production if L-Trp is applied alone to the plants (Zahir et al., 2005) or together with fertilizer (Zahir et al., 2007).

The benefits that auxins from bacteria have had in plant development and productivity have been documented. For instance, an increase in soil IAA is able to enlarge the tree stem diameter and intensify the growth height of 17-year-old *Pinus radiata* trees (Smaill et al., 2010). In yam (*Dioscorea rotundata*), it was found that IAA from *B. subtilis* increases the elongation of shoots 83.3% and the production of roots 63.5% (Swain et al., 2007), both of which favor nutrient uptake and distribution (Singh Gahoonia et al., 1997; Talboys et al., 2014). It is known that several rhizobacteria species increase root biomass by changing the auxin balance and, in consequence, the signaling process, by either producing and secreting the auxin themselves (Dobbelaere et al., 1999; Patten and Glick, 2002; Idris et al., 2007) or changing its homeostasis inside plant cells (Spaepen et al., 2007; Kurepin et al., 2014). The same positive effect of bacterial IAA has been observed in tomato (Pastor et al., 2014), sesame (*Sesamum indicum*; Kumar et al., 2009), maize (Fallik et al., 1989), wheat (Egamberdieva, 2009), and other crops.

SLs

SLs are sesquiterpene lactones, derived from carotenoids, found in the rhizosphere and secreted in very small amounts (pg $\text{plant}^{-1}\ \text{d}^{-1}$; Akiyama et al., 2005; Alder et al., 2012). These compounds are able to establish symbiotic and parasitic interactions (Soto et al., 2010; Zwanenburg and Pospíšil, 2013). Although SLs have been related to the stimulation of hyphal branching and nodule formation in alfalfa (*Medicago sativa*; Akiyama et al., 2005; Besserer et al., 2006; Soto et al., 2010), more attention has been paid to the negative effects that these molecules have on plant productivity (Bouwmeester et al., 2003).

Many important crops, such as sorghum, maize, cotton (*Gossypium hirsutum*), and cowpea (*Vigna unguiculata*), secrete SLs through their roots (Cook et al., 1966; Hauck et al., 1992; Müller et al., 1992; Siame et al., 1993). The SLs promote the germination of seeds of parasitic weeds, such as witchweed (*Striga lutea*), broomrapes (*Orobanche* and *Phelipanche* spp.), and *Alectra* spp. (Cook et al., 1966; Joel et al., 2007; Zwanenburg and Pospíšil, 2013). It has been reported that millions of hectares of crop fields and billions of dollars are lost annually due to *Striga* and *Alectra* spp. infestation in sub-Saharan Africa (Ejeta and Gressel, 2007; Joel et al., 2007) and to *Orobanche* spp. in the Mediterranean and western Asia (Parker, 2009). However, the mechanism by which the SLs induce seed germination is still controversial; it appears that the interaction of SLs with other molecules in the rhizosphere could contribute to their specificity and biological activities (Xie et al., 2010), although the catabolism of abscisic acid, allowing the germination of the parasitic seeds, also has been proposed (Lechat et al., 2012).

There have been scientific advances in understanding the biochemistry and production of SLs in order to avoid crop losses. One example is the use of carotenoid inhibitors (Jamil et al., 2010). Although carotenoid inhibitors such as fluridone, amitrole, clomazone, and norflurazon reduce SL production (Jamil et al., 2010), it is not known how these inhibitors could directly or indirectly affect other processes in the plant, such as abscisic acid biosynthesis (Gamble and Mullet, 1986), and, in consequence, plant productivity.

The secretion and activity of SLs are influenced by several factors, such as temperature, light regime, and even soil moisture (Weerasuriya et al., 1993; Xie et al., 2010; Toh et al., 2012). Therefore, it is tempting to speculate that if we are experiencing severe global climate change, the secretion of these molecules could be affected by means that we do not yet know.

Glomalin

Soil structure impacts the flux of water, gases, and nutrients and is thus an important consideration for agriculture, particularly under current farming practices, which demand more fertilizers, water, and pesticides (Angers and Caron, 1998; Tilman et al., 2002). Soil health is very important not only for crop productivity but also for microbial livelihood. One of the microorganisms responsible for soil physical structure is the AMF, which have positive effects on plant development. These fungi produce an iron-containing glycoprotein named glomalin (Wright et al., 1996; Purin and Rillig, 2007), insoluble in water and resistant to heat degradation (Singh et al., 2013), which moves into the soil and works as a glue among soil particles, contributing to a decrease in soil erosion (Haddad and Sarkar, 2003). It has been found that the glomalin content in the soil is higher in the summer season and in places with high moisture content (Emran et al., 2012; Gispert et al., 2013). This finding could explain why the concentration of this protein is lower in the desert (1 mg g^{-1}; Bai et al., 2009) than in tropical forest (100 mg g^{-1}; Rillig et al., 2001).

Glomalin has been used as an indicator of the effects of land-use change (Rillig et al., 2003) and is considered to contribute to carbon (Rillig et al., 2001) and nitrogen (Nichols and Wright, 2006) storage, which can help reduce the release of nitrous oxide, probably by influencing nitrification and denitrification, into the atmosphere and, therefore, greenhouse gases (Janzen, 2004; Nichols and Wright, 2006; Singh et al., 2013). Studies on sandy loam soils treated for 21 years with continuous fertilization have shown that fertilization affected the community composition of AMF and glomalin-related soil protein content (Dai et al., 2013). Also, it has been suggested that prolonged cultivation can reduce glomalin content in the soil, facilitating the disturbance of the soil and causing a decline in crop production (Preger et al., 2007). Soil glomalin is related to net primary productivity (Treseder and Turner, 2007), and a possible link between coffee (*Coffea arabica*) productivity and glomalin levels in the soil has been proposed (Banks et al., 2011). Therefore, glomalin, like auxins, also can be considered a positive player in plant productivity.

PGs

PGs are cell wall-degrading enzymes that cleave glycosidic bonds linking D-galacturonic acid residues, which are the main components of pectin. These enzymes are important pathogenicity factors produced by fungi (e.g. *Fusarium* spp., *Botrytis cinerea*, *Colletotrichum lindemuthianum*, and *Aspergillus* spp.; Lafitte et al., 1984; Di Pietro and Roncero, 1996; ten Have et al., 1998; Lang and Dörnenburg, 2000) and bacteria (e.g. *P. syringae*, *Pseudomonas solanacearum*, *Erwinia carotovora*, and *Ralstonia solanacearum*; Salmond, 1994; Vasse et al., 1995; Lorenzo et al., 1997; Huang and Allen, 2000).

PGs are one of the factors responsible for causing severe diseases in many plants (Collmer and Keen, 1986; Magro et al., 1994; Shieh et al., 1997; Aysan et al., 2003). For instance, *Aspergillus flavus*, a saprophytic fungus responsible for important losses in maize, peanut (*Arachis hypogaea*), and cotton (Lillehoj et al., 1974; Shieh et al., 1997; Asis et al., 2005), produces a PG, P2c, which causes intercarpellary membrane damage due to the loss of pectin integrity, thus helping the spread and invasion of the fungus (Shieh et al., 1997). Furthermore, studies in bacteria have shown that PGs from *R. solanacearum* and *P. solanacearum* are necessary to colonize the tomato root cortex, infect vascular parenchyma, and invade xylem elements, causing the devastating disease bacterial wilt (Wallis and Truter, 1978; Vasse et al., 1995; Huang and Allen, 2000). It has been found that PGs can be secreted by *P. syringae* (De-la-Peña et al., 2008) and *P. solanacearum* (Schell et al., 1988). Therefore, it could be that PGs secreted into the rhizosphere can reach and degrade the pectin of root cell walls, allowing the bacteria to enter and move throughout the vascular parenchyma.

Although bacteria and fungi have developed a mechanism to use PGs against plants, plants are able to defend themselves using polygalacturonase-inhibiting proteins (PGIPs), which favor the accumulation of oligogalacturonides (elicitors of the defense response) and limit pathogen infection (De Lorenzo et al., 2001; De Lorenzo and Ferrari, 2002; D'Ovidio et al., 2004). Studies in bean and tomato have shown that PGIP protects the plant cell walls from *C. lindemuthianum*, *B. cinerea*, and *Fusarium oxysporum* f. sp. *lycopersici* (Jones et al., 1972; Lafitte et al., 1984; Powell et al., 2000). These proteins also have been found in the secretome of Arabidopsis roots when the plant is infected with *P. syringae* (Magro et al., 1994; De-la-Peña et al., 2008), which indicates that PGIPs participate in defense response signaling in the rhizosphere during bacterial attack. Therefore, PGIPs could be exploited as a strategy for protecting crops against PG-producing pathogens.

OMIC APPROACHES TO STUDY RHIZOSPHERE DYNAMICS AND CHEMICAL PLAYERS

Most of the information about the rhizosphere and the principal compounds, genes, functions, and mechanisms has been achieved using omic approaches, such as genomics, transcriptomics, proteomics, metabolomics, and, very recently, epigenomics (Fig. 2). However, there are still many secrets to be uncovered.

When interest in root secretion first began, the available technologies were based on analytical separation and biological detection (Knudson and Smith,

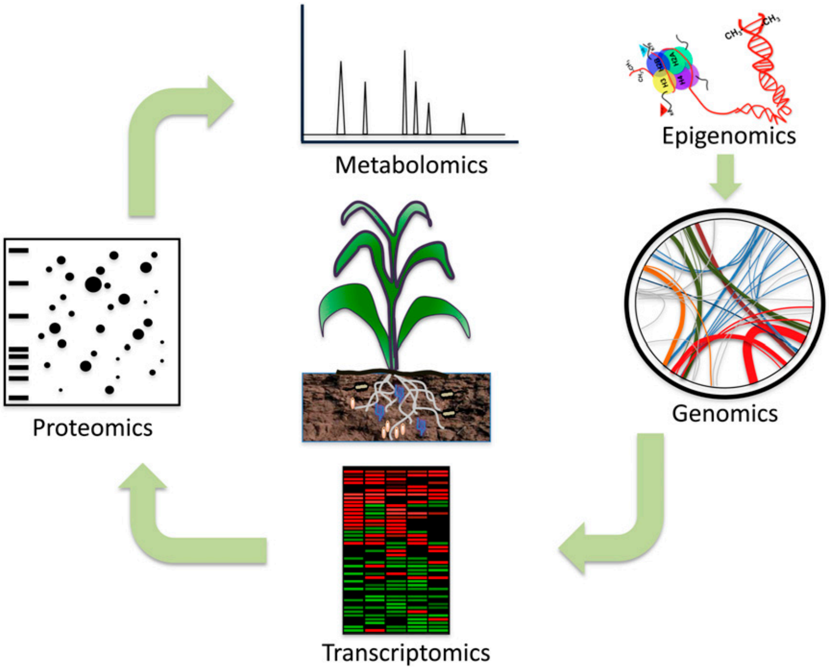


Figure 2. Omic approaches to the study of rhizosphere dynamics in order to improve plant productivity. Many organisms visit plants; however, some can be used to increase crop productivity, and others just kill the plant. In the case of the rhizosphere, the interactions between bacteria (white and cream), fungi (blue), and roots have been studied extensively from different omic approaches, such as genomics, transcriptomics, proteomics, and metabolomics. Epigenomics, the newest omics in the rhizosphere, is starting to be a focus of attention (De-la-Peña and Loyola-Vargas, 2012), which could have a great impact on what we already know about plant productivity and environmental stress. [See online article for color version of this figure.]

1919; Flores et al., 1999; Akiyama et al., 2005). One of the pioneering biochemical studies on root secretion ran from 1919 to 1920 and was headed by Dr. Lewis Knudson from Cornell University (Knudson and Smith, 1919; Knudson, 1920). In his articles, he explains step by step how and why root secretion was analyzed. Now the technology is much more specialized, sensitive, and complex (Diggle et al., 2007), and the resulting information is more precise, accurate, and quantitative. In the past, it was enough to use the PCR technique (Mullis and Faloona, 1987; Mullis et al., 1986) to investigate gene expression. Now the use of quantitative reverse transcriptase-coupled PCR is almost mandatory in order to have better and more robust information about a specific gene. This technique, introduced for the first time in 1992 (Higuchi et al., 1992), allows the quantification of RNA transcription levels by monitoring the amplification of a target sequence in real time using fluorescence detection. Now, a new layer of complexity has developed, with information given on chromatin remodeling in order to have more information about regulation in gene transcription. Therefore, advances in technology seem to favor the development of knowledge to improve our understanding of plant development, plant-pathogen interaction, root/microbe secretion, and rhizosphere dynamics (Dennis et al., 2010).

Epigenomics

Epigenomics is one of the newest omics and will likely increase our understanding of the dynamics of the rhizosphere and their function in improving plant productivity. Epigenetics has provided a new layer of complexity to the understanding of gene regulation for agricultural applications (Boyko and Kovalchuk, 2013; Us-Camas et al., 2014). Epigenetics are typically studied by three different mechanisms: DNA methylation, histone modification, and small (sRNA; 50–250 nucleotides) or micro (19–25 nucleotides) noncoding RNAs.

DNA methylation can be analyzed by different methods depending on the type of information needed (Fraga and Esteller, 2002). The most frequently used techniques to analyze DNA methylation are HPLC (Kuo et al., 1980; De-la-Peña et al., 2012b; Chen et al., 2013), methylation-sensitive amplification polymorphism (Sha et al., 2005; Park et al., 2009; Hubbard et al., 2014), and bisulfite sequencing (Frommer et al., 1992; Cokus et al., 2008; Li and Tollefsbol, 2011). In the case of histone modifications (e.g. methylation, acetylation, phosphorylation, etc.), the use of antibodies is necessary to observe global histone modifications or loci-specific modifications. Western blots are normally used to study global histone modifications (Nic-Can and De-la-Peña, 2012; Nallamilli et al., 2014). In the latter case, chromatin immunoprecipitation is useful (He et al., 2003; Saleh et al., 2008; Liu et al., 2014). For sRNA analysis, northern blots or microarrays can be used (Altuvia, 2007), and the microRNAs can be analyzed by quantitative reverse transcriptase-coupled PCR (Monavar Feshani et al., 2012; Verma et al., 2014) or northern blot (Válóczi et al., 2004; Xie et al., 2005).

Plant epigenetics can be modified in response to environmental conditions (Lira-Medeiros et al., 2010; Boyko and Kovalchuk, 2013; Bräutigam et al., 2013), and the progeny can inherit regulatory mechanisms to cope with such stresses. For instance, while in recent decades increasing temperatures have caused major losses in food crops (Peng et al., 2004), it has been found that plants exposed to heat stress can inherit epigenetic changes that result in offspring better adapted to extreme heat, a finding that could improve plant productivity (Lang-Mladek et al., 2010; Pecinka et al., 2010; Tittel-Elmer et al., 2010; Mirouze and Paszkowski, 2011).

In bacteria, epigenetics are also important. For instance, sRNAs have been involved in carbon metabolism and transport, amino acid metabolism, metal sensing, QS, biofilm formation, microbial virulence, and infection (Michaux et al., 2014). It has been found that two sRNAs, RsmY and RsmZ, are regulated by the global activator GacA, which is required for the production of exoenzymes, virulent factors, and secondary metabolites in *P. aeruginosa* (Reimmann et al., 1997; Kay et al., 2006). These sRNAs sequester the *rsmA* (for regulator of secondary metabolism) gene, inhibiting secondary metabolism and biofilm formation and activating motility and type III secretion (Sonnleitner and Haas, 2011). In fact, it has been found that when the sRNA *rsmZ* is overexpressed, biofilm development, which is associated with pathogenicity in *P. aeruginosa*, is reduced (Petrova and Sauer, 2010).

Although the epigenetics of rhizosphere interactions have not been studied, De-la-Peña and Loyola-Vargas (2012) have suggested that the secretion of certain chemicals into the rhizosphere could be due to epigenetic changes during plant-pathogen interaction. There are data that strongly suggest that changes in protein secretion could be due to epigenetic changes. For instance, De-la-Peña et al. (2008, 2010), working with Arabidopsis defense-impaired mutants *nonexpressor of PATHOGENESIS-RELATED GENES1* (*npr1-1*; a mutant that does not express *NPR1*), constitutive expressor of PATHOGENESIS-RELATED GENES5 (cpr5-2; a mutant that accumulates large amounts of salicylic acid), and *salicylate hydrolase* (*NahG*; a mutant that is unable to accumulate salicylic acid), found that these mutants had a different protein root secretion pattern. Moreover, it was found that the defense-responsive genes in Arabidopsis, like *CPR5* and *NPR1*, could be mediated by epigenetic factors (De-la-Peña et al., 2012c), suggesting that protein root secretion also could be modified due to epigenetic changes.

However, much work remains to be done in this area in order to apply this knowledge to improving plant productivity, as the examples are all complex and highly case specific. Some very new techniques, such as bisulfite sequencing or chromatin immunoprecipitation, hold promise as means to understand the intricate gene regulation during the cross talk of plants with their neighbors.

Genomics

In parallel to the biochemical and classical molecular approaches, genomic contributions, especially metagenomics in relation to rhizosphere interactions, have been enormous (Kakirde et al., 2010; Mendes et al., 2011). Many microbes have been identified using the metagenomic approach, but few have been characterized (Mendes et al., 2011). The microbial biodiversity in the soil seems to have specific biological functions in plants. For instance, recent genomic research on five different *Sinorhizobium* spp. (*Sinorhizobium meliloti*, *Sinorhizobium medicae*, *Sinorhizobium freddi*, *Sinorhizobium terangae*, and *Sinorhizobium saheli*) has found that each bacterium has adopted a slightly different strategy to interact with diverse *Medicago* spp. host plants and soil environments. This work also shows that the genes involved in the biosynthesis of the Nod factor (lipochitooligosaccharides secreted by rhizobia that are important in the interplay of recognition between roots and microbes) and polysaccharides, denitrification, and secretion systems vary within and between species (Sugawara et al., 2013).

The identification of genes not only in one genus but also across the plant kingdom to improve crop traits is a common goal that scientists need to pursue. Moreover, the techniques of insertion mutagenesis and positional cloning have helped to illuminate the nodulation process (Webb et al., 2000; Stougaard, 2001), which also can give some clues about the species-specific relationship between rhizobacteria and legumes. Takahara et al. (2013), using deleted regions in hypernodulating mutants (*tml-1*, *tml-2*, and *tml-3*), map-based cloning, and next-generation sequencing analysis in *Lotus japonicus*, characterized and identified a root factor named *TOO MUCH LOVE* (*TML*) that acts during the autoregulation of nodulation in this legume. Although these mutants have not been used to study root secretion, it would be interesting to investigate whether the proteins and molecules secreted are affected by these mutations. Probably, the mutations impair or enhance the secretion of an important chemical player, maximizing its potential in plant productivity.

Transcriptomics

The use of transcriptomics has become an important tool to identify genes involved in plant-microbe interactions (Ramachandran et al., 2011; Schenk et al., 2012; Lakshmanan et al., 2013). For instance, transcriptomics has been used to compare *R. leguminosarum* adaptation in the rhizosphere of a host legume (pea [*Pisum sativum*]), a nonhost legume (alfalfa), and a nonlegume (sugar beet [*Beta vulgaris*]; Ramachandran et al., 2011). Although a common core of bacterial genes was identified, 66% were of unknown function and several were plant specific. In the rhizosphere of pea, *R. leguminosarum* expressed genes related to bacterial metabolism and Nod factor synthesis, while in the presence of the alfalfa rhizosphere, the genes involved in lignin breakdown and metabolite transporters were up-regulated (Ramachandran et al., 2011). Studies on the gram-positive rhizobacterium *B. amyloliquefaciens* in response to root exudates from maize revealed that 8.2% of the bacterial transcriptome was altered in the presence of these exudates (Fan et al., 2012). The majority of the altered genes were up-regulated, and most of them are involved in nutrient utilization, bacterial chemotaxis and motility, and antimicrobial peptides. However, there were some genes found with unknown functions, opening new questions about the role of root exudates in rhizobacteria behavior.

Transcriptomics is a powerful tool that produces a massive amount of data, which need to be focused in order to find candidate genes useful for plant productivity. Mitra et al. (2004) focused the results of the transcriptome data on one candidate, Ca^{2+}-calmodulin-dependent protein kinase. They show that transcript-based cloning is a valid approach for cloning genes and that this method does not require the construction of a genetic map. This approach also could be used to study plant productivity and rhizosphere dynamics, as was done in some recent reports (Fan et al., 2012; Alavi et al., 2013; Carvalhais et al., 2013). Other important genes discovered with transcriptomics are the nodule Cys-rich antimicrobial peptides (NCR) genes. It has been found that NCRs control the terminal differentiation of intracellular *S. meliloti* bacteroids by manipulating the bacterial cell cycle (Van de Velde et al., 2010; Penterman et al., 2014). Penterman et al. (2014) provided strong evidence about the molecular mechanism by which NCR peptides control the *S. meliloti* cell cycle during symbiosis. Working with NCR247, the authors found that these peptides specifically block cell division without affecting DNA replication. Thus, NCR perturbs the expression of genes involved in motility, cell division, and cell cycle regulation.

Proteomics

Proteomics has been frequently used to find proteins secreted into the rhizosphere and involved in plant-microbe interaction (De-la-Peña et al., 2008; De-la-Peña and Vivanco, 2010; Yang et al., 2012; Wang et al., 2013), and it has been considered an important biotechnological tool for crop improvement (Eldakak et al., 2013). The proteomic field has taken advantage of new technologies, and many of them are applicable for studying plant-microbe interaction, such as matrix-assisted laser-desorption ionization-time-of-flight-mass spectrometry (Watt et al., 2005; Noir et al., 2009), liquid chromatography-mass spectrometry (Larrainzar et al., 2007; Koch et al., 2010), isobaric tags for relative and absolute quantification-mass spectrometry (Taylor et al., 2008; Kaffarnik et al., 2009; Li et al., 2014) and multidimensional protein identification technology-tandem mass spectrometry (Wen et al., 2007; Kaschani et al., 2009). *Medicago truncatula* has been the model legume from a proteomic point of view (Sumner et al., 2007; Colditz and Braun, 2010; Lee et al., 2013), and it has opened an avenue to studying the proteomics of major crops such as wheat, maize, soybean, and rice (Song et al., 2007; Eldakak et al., 2013).

Proteomics also has been useful in the study of bacterial and fungal secretomes. In the case of the bacterial secretome, *B. subtilis* has been widely used (Hirose et al., 2000; Tjalsma et al., 2000, 2004; Antelmann et al., 2006). It was found that this bacterium secretes around 300 different proteins into the soil. Fungi also secrete many proteins that have been related to virulence factors (Song et al., 2009), adhesion to the plant surface (Newey et al., 2007), host tissue penetration and invasion (van Esse et al., 2008; Panstruga and Dodds, 2009; Dong et al., 2011), and symbiotic formation (Plett et al., 2011). Like transcriptomics, proteomics has a big problem with unknown proteins. In fungi, 208,883 putative secretory proteins have been identified (Choi et al., 2010), but only a small fraction of them have been studied, and so far, nobody knows the biological/ecological role of most of them. On the other hand, there are many reports describing the use of plant mutants, pathogenic bacteria, and symbiotic microbes that highlight the vast diversity of proteins or even the function of a group of proteins during plant-microbe interaction (De-la-Peña et al., 2008; Afroz et al., 2013; Alberton et al., 2013; Dam et al., 2014). These and other proteomic reports can be used to study proteins important to plant productivity. Also, in vitro and controlled systems could be used with other omic analyses to help assign function and/or identification through reducing environmental noise.

Metabolomics

Metabolomics of the rhizosphere is another big omic topic highly studied. The principal technologies used to detect metabolites are NMR spectroscopy, HPLC, liquid chromatography-mass spectrometry, gas chromatography-mass spectrometry, and capillary electrophoresis-time-of-flight-mass spectrometry. Important compounds such as SLs have been identified using liquid chromatography-tandem mass spectrometry (Xie et al., 2007; López-Ráez et al., 2008), and hundreds of metabolites have been found to highlight the importance that chemical cross talk between roots and microbes has in the initial recognition and species-dependent response.

Vauclare et al. (2013), using NMR spectroscopy, analyzed the metabolite profiles of *Bradyrhizobium japonicum* cells and the bacteroids from soybean nodules. Fan et al. (2001) used this same spectroscopy technology to examine the importance of root exudates from barley (*Hordeum vulgare*) and wheat in the acquisition of cadmium. Furthermore, Tawaraya et al. (2013) identified by capillary electrophoresis-time-of-flight-mass spectrometry 65 metabolites from root exudates of rice under phosphorous deficiency, and more than 30% of these showed a higher concentration at low phosphorous levels. This novel technique also can be used to determine the metabolites secreted during plant-microbe interaction. Like proteins (De-la-Peña et al., 2010), metabolites secreted from roots change depending on the developmental stage of the plant and have different effects on root microbes (Chaparro et al., 2013; Ziegler et al., 2013). Among the major bioactive metabolites found in the rhizosphere are flavonoids, phenolic compounds, exopolysaccharides, antibiotics, and QS signals. Badri et al. (2013), working with phytochemicals characterized by gas chromatography-mass spectrometry from root exudates, found that some phenolic-related compounds are able to modulate soil microbes. Moreover, the authors propose that the use of natural compounds to establish a positive interaction between plants and soil microbes could improve crop yield and sustainability. Therefore, understanding how microbes are selected in the rhizosphere and how plants affect microbial activity will provide new opportunities to increase crop production (Berendsen et al., 2012). Moreover, this will lead to a better understanding of the ecological relevance of the interaction among all the components of agricultural ecosystems as well as support the development of sustainable management technologies.

CONCLUSION

Although much of what we know about exudates has been done in Arabidopsis, it is necessary expand the research to important crop and nonmodel plants in order to understand more about the dynamics of the rhizosphere. It is known that different types of plants (Haichar et al., 2008) or even different ages of a plant (Chaparro et al., 2013; İnceoğlu et al., 2013) can harbor totally different microbial communities. A recent work argues that Arabidopsis is a limited model for investigating the impact of stress on rhizosphere community composition and function (Blee et al., 2013). Furthermore, expanding rhizosphere investigations to other species will speed the discovery of new molecules or compounds in the rhizosphere, which may enable the expansion of some plants' abilities in symbiosis, defense, and development to other crops to improve plant fitness, increase tolerance of biotic and abiotic stress, and enhance plant productivity.

It is also important to study the microbiome of different cultivars, under different environmental conditions and in the presence of different neighbors, to analyze the compounds secreted in specific circumstances. Such work will uncover the numerous soil microorganisms, functions, and genes that remain unknown and demonstrate their usefulness for diverse applications. It will also provide the information necessary to engineer plants better adapted to extreme and changing environments, leading to improved agriculture. These improvements might include a better capacity of plants to resist invasive species, efficiently acquire nutrients, detoxify contaminated soils, and attract beneficial PGPRs, improving plant productivity.

Plants as well as microbes have the ability to change in response to other organisms at different omic levels. For instance, mycorrhizal fungi can change not only the transcriptome of a plant by inducing the regulation of many genes (Liu et al., 2003) but also modify the plant metabolome in order to establish a symbiotic contact with roots (Duhamel et al., 2013; Zhao et al., 2013). On the other hand, proteomics and epigenomics studied in Arabidopsis have shown that if the plant is in contact with a pathogen, the secretion of proteins (De-la-Peña et al., 2008) as well as different histone modifications in the plant (De-la-Peña et al., 2012c) are altered. Therefore, all these approaches could be used to improve plant productivity under stressful conditions and enhance the diversity of beneficial microbes in the rhizosphere.

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