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EDITORIAL

Advances in the rhizosphere: stretching the interface of life

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"Stretching the interface of life" was the motto of the international Rhizosphere 4 Conference in Maastricht in June 2015. This motto reflects the key position that the rhizosphere has in each terrestrial ecosystem. Belowground interactions between plant roots, soil microbes and the abiotic soil environment drive important ecosystem processes such as productivity (Reinhart et al. 2010; Schnitzer et al. 2011), biogeochemical cycling (de Vries et al. 2013), and tolerance to biotic and abiotic stresses (Berendsen et al. 2012; Visioli et al. 2015). At the same time, this motto reflects the highly dynamic nature of the rhizosphere (Hinsinger et al. 2009; Philippot et al. 2013). The rhizosphere is a multifaceted, complex 'melting pot' of components and processes affecting plant growth and development, and thus ecosystem functioning. One main component of the rhizosphere is the root microbiome, which are all microorganisms inhabiting the root or rhizosphere (Lundberg et al. 2012; Mendes et al. 2013). Root exudates, i.e., a variety of small molecules excreted by plant roots are another important component in the rhizosphere (Bais et al. 2006; Hinsinger et al. 2009; Li et al. 2007; Suriyagoda et al. 2012). Plant roots are able to regulate these exudates and influence their root microbiome accordingly (Haichar et al. 2008). However, this is not a unidirectional path as the root microbiome also produces many metabolites and thus also able to affect the composition of the chemical cocktail in the rhizosphere.. These mutual interactions ultimately affect nutrient availability for all partners (Lambers et al. 2008), plant health (Berendsen et al. 2012) and root-root interactions (Semchenko et al. 2014), cascading into ecosystem functions such as productivity (Latz et al. 2012; Li et al. 2016) and soil formation (Lambers et al. 2009; Keiluweit et al. 2015; Lange et al. 2015). The challenge now is to reveal the functionality of these multifacetted interactions between plant roots, root exudates, microbial metabolites, the root microbiome and the soil..Management of this multicomponent complexity of the rhizosphere and its relationship to soil fertility will become crucial in order to maintain food production with reduced fertiliser and pesticide inputs (Bakker et al. 2012).

The rhizosphere, initially formulated by Hiltner as the 'soil influenced by roots' (Hiltner 1904; Hartmann et al. 2008) developed into a booming research field

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where scientists approach this specific zone around the plant root from different angles. The fourth international Rhizosphere Conference, following earlier successful meetings in this series (Hinsinger and Marschner 2006; Jones and Hinsinger 2008; Jones 2009; Tibbett et al. 2012), clearly reflected this multi-disciplinarity: 18 sessions covering molecular biology, agronomy, micro-biology, genomics, ecology, soil science, chemistry, etc., attracted more than 550 scientists from 46 countries to advance our understanding of the rhizosphere. This multi-disciplinarity is also reflected in this Special Issue of Plant and Soil, highlighting the state-of-the-art of rhizosphere research as presented at the Rhizosphere 4 Conference. The resulting set of papers comprises a wide range of topics that include root traits and the root microbiome, nutrient acquisition and nutrient cycling, water uptake, and rhizosphere signaling. This special issue not only covers experimental studies, but also provides an update of the state-of-art in modelling (Ahmed et al. 2016; Roose et al. 2016; Vetterlein and Doussan 2016), with as highlight the Marschner Review on imaging and modelling of rhizosphere processes (Roose et al. 2016). This Marschner Review summa-rizes cutting-edge knowledge of structural and chemical imaging of rhizosphere processes in the framework of multiscale mathematical image-based modelling. Roose et al. (2016) emphasize the need to integrate structural and chemical images through modelling explicitly root and microbe mediated processes occurring at the pore-scale, to fully understand the intimate functioning of the highly dynamic and heterogeneous micro-environments that make up the rhizosphere, at the heart of root-soil interactions.

Linking root traits to function

Roots have long been 'the hidden half' of plants. Consequently, the true functionality of root charac-teristics (i.e., traits) for important processes such as nutrient or water uptake, plant performance, plant-plant interactions and ecosystem functioning re-mains to be unravelled. For example, ecologists have focused on the ability of roots to selectively forage for nutrients as a key trait determining plant performance and competitive ability (Fransen and de Kroon 2001; Hodge et al. 1999; Kembel and Cahill 2005), but these efforts have not yielded unequivo-cal evidence for selective root placement being a crucial trait. Instead, plant performance, and partic-ularly plant competitive ability, appear to be linked to a range of root traits, which probably also depend on the biotic and abiotic environment (Mommer et al. 2011a; Rajaniemi 2007; Schröder-Georgi et al 2015; Siebenkäs and Roscher 2016). Recently, the research on root traits has widened by focussing on a larger variety of traits, such as root length density, mean rooting depth, specific root length, and carbon to nitrogenratio. This broadened view allowed root traits to be placed in ecological frame-works, determining their role in plant performance and competitive interactions (Fort et al. 2013; Roumet et al. 2006; Schröder-Georgi et al 2015), ecosystem functioning (Bardgett et al. 2014; Cong et al. 2014) and the resource economics spectrum (Roumet et al. 2016; Weemstra et al. 2016). The study of (Ravenek et al. 2016) in this issue reflects this new direction, as it links root traits to pairwise interactions in eight grassland species, in homogeneous and heterogeneous nutrient conditions. In the short term, competitive success of a species was related to fast growth and a high root length density, irrespective of nutrient distribution. The work of Wang et al. (2016) also focusses on the role of root traits in competitive interactions, by exploring belowground interactions of graminoids and shrubs in the Siberian tundra. Differentiation in phenology (timing of root growth) and vertical distribution between the two functional groups are likely key determinants of the competi-tive outcome. Two other papers on root traits in this special issue investigate the relationship between root traits and phosphorus (P) acquisition. Haling et al. (2016) compare root growth and allocation to P efficiency of several legume species, using the grass *Dactylis glomerata* as a baseline. Species that had a lower external critical P requirement allocated fewer roots to fertilized patches than those with a higher critical P requirement. The first (e.g., *Ornithopus* spp.), however, gained their P share by having a higher P uptake per unit root mass than the latter. Such findings suggests that root allocation and selective placement in nutrient hotspots may be one way to compete for nutrients, but, alternatively, pro-ducing efficient roots at little biomass costs can be

similarly (or even more) functional (Kembel et al. 2008; Mommer et al. 2011b).

Nutrient acquisition and nutrient cycling

Plant roots are primarily designed to access below-ground resources, on top of providing anchorage, and thereby play a key role in nutrient acquisition and nutrient cycling (Hinsinger et al. 2009; Lambers et al. 2009; Bardgett et al. 2014). A great deal of research has been conducted and published in this domain in the past decades, and a section of the present special issue is dedicated to it. Root traits, such as root length and rooting depth, play a critical role in the uptake of rather mobile resources such as water and nutrients like nitrogen by plants. Higher nitrogen uptake is often linked to increased herbage yield of pastures, as well as to reduced nitrate leaching (Kristensen and Thorup-Kristensen 2004). Strategic (i.e., delayed) timing of nitrogen application after a harvest of *Lolium perenne* could thus affect root biomass and herbage yield. De Boer et al. (2016), however, did not find evidence that delayed nitrogen fertilization improves root biomass. Like *Lolium perenne*, *Trifolium repens* is also an important species in pastures. Czaban et al. (2016) demonstrates that this species can take up forms of organic nitrogen in hydroponics systems, which indicates that on top of inorganic nitrogen, this species might not only rely on its symbiosis with Rhizobium.

The research field of nutrient acquisition also benefits from current advances in molecular biology. Tanaka et al. (2016) took a mutagenesis approach of a rice cultivar to investigate heritability for micronutrient uptake, such as manganese and zinc, but also for the uptake of hazardous trace metals such as cadmium.

While much of the accumulated knowledge on plant nutrition and on the fate of nutrients in the rhizosphere has been obtained in hydroponics or microcosm experiments with a single crop or cultivar, there is a need to move towards more biodiversity-based agriculture for achieving sustainable intensification of agroecosystem, and thus to embrace the complexity of rhizosphere processes occurring in these systems, e.g. intercropping systems (Li et al. 2007, 2014). Positive plant-plant interactions, such as root-root facilitation, have been shown to play a significant role for P acquisition (Li et al. 2007; Brooker et al. 2015; Li et al. 2016; Zhang et al. 2016). Tang et al. (2016) further demonstrated the greater performance of such intercropping systems compared to single crop systems under field conditions along a P fertility gradient. They showed that the overyielding of the intercrops occurred at all levels of P fertility, discounting the stress gradient theory predicting more positive plant-plant interactions to occur under low P conditions. Their study showed, however, that, when considering the properties of the rhizosphere, P fertility had a major effect on rhizosphere microbial communities. A rhizosphere effect, namely the increase of microbial biomass C in the rhizosphere, occurred only at high P, as rhizosphere microbial communities were too much P-limited at the lower end of the fertility gradient. They also showed that intercropping had a significant effect on microbial properties of the rhizosphere only at the upper end of the fertility gradient. Soil fertility thus has a significant impact on the outcome of root-root and root-soil interactions, which needs to be further investigated in various types of ecosystems.

Soil fertility is linked to carbon sequestration via soil organic matter, and the most dynamic portion of soil organic matter, namely dissolved organic matter circulating in soils. Changes in nutrient availability and uptake may affect dissolved organic matter, for example via changes in decomposition rate. Robroek et al. (2016) studied the effect of the functional types of vascular plants on microbial enzymatic activity and the composition of dissolved organic matter. They concluded that global change affects the abundance of vascular plants in peat ecosystems, which in turn increases soil microbial activity and, hence, may affect C losses from such ecosystems.

Water relationships in the rhizosphere

Rhizosphere is more than interactions between roots and nutrients, since water is also an essential driver. This special issue focusses on two aspects of water relationships in the rhizosphere: the impact of the root age and function (Iversen 2010; 2014) on root water uptake and rhizosphere biophysics, and the need for functional structural modelling to integrate all these aspects in order to understand the fate of water in the root environment (Vetterlein and Doussan 2016). Currently, the theoretical developments and increase in computational power allow experimental quantification of properties such as hydraulic conductance variation, which is still
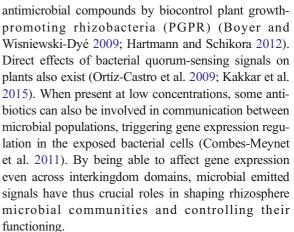
ahead of experimental evidence backing up the models. There is indeed surprising scarcity of data on root age distribution with depth, and on the fate of roots and root functioning, especially in annual crops. The functional properties possibly impacting water relationships in the rhizosphere that are affected by root age are however numerous: from axial hydraulic conductance, occurrence of apoplastic barriers, secondary growth or distribution of aquaporin expression to decay of root cortical cells and mucilage production (Vetterlein and Doussan 2016). Ahmed et al. (2016) start filling this gap by measuring the water repellency of root-exuded mucilage (i.e., plant specific polysaccharides) on maize plants under different soil conditions. This work, based on a combination of measurements and modelling, shows that, beyond a threshold concentration that decreased with increasing particle size and decreasing matric potential, root mucilage can turn the rhizosphere hydrophobic, ultimately resulting in a dramatic reduction of water flow at the root-soil interface. The work by Ahmed et al. (2016) is pledging for more work in this field of rhizosphere biophysics, given its major impact on the fate of water, and thus nutrients and other solutes in the root environment, at various scales from local up to the whole root system scale.

Communication in the rhizosphere

Signaling in the rhizosphere can be divided into four categories: among plants, among microbes, from plants to microbes, and from microbes to plants (van Dam and Bouwmeester 2016; Venturi and Keel 2016). The Rhizosphere 4 conference points out the huge diversity of signal molecules involved and summarized here briefly. In this special issue, we more particularly focus on the modulation of plant metabolism by microbes, with a specific highlight on the impact of bacterial inoculation on plant volatiles (including ethylene) and as a consequence plant stress alleviation.

One main mechanism of communication between bacteria at both intraspecies and interspecies levels is known as quorum-sensing. It allows bacterial populations to synchronize their behaviour to cell density, through the exchange of a huge range of signal molecules (Boyer and Wisniewski-Dyé 2009; Venturi and Keel 2016). Quorum-sensing is involved in the regulation of several bacterial processes, such as biofilm formation, virulence in pathogenic bacteria, production of

antimicrobial compounds by biocontrol plant growth-promoting rhizobacteria (PGPR) (Boyer and Wisniewski-Dyé 2009; Hartmann and Schikora 2012). Direct effects of bacterial quorum-sensing signals on plants also exist (Ortíz-Castro et al. 2009; Kakkar et al. 2015). When present at low concentrations, some antibiotics can also be involved in communication between microbial populations, triggering gene expression regulation in the exposed bacterial cells (Combes-Meynet et al. 2011). By being able to affect gene expression even across interkingdom domains, microbial emitted signals have thus crucial roles in shaping rhizosphere microbial communities and controlling their functioning.

Interactions between microbes are regulated by root exudates, having a high diversity of primary and secondary metabolites (sugars, organic acids, amino-acids, phenolic or terpenoid compounds) (van Dam and Bouwmeester 2016). With the progress in metabolomics methods coupled to multivariate analyses (van Dam and Bouwmeester 2016) and metabolic networks identification, major advances were recently made regarding the characterization of plant root exudate composition and their differences among plant genotypes, environmental conditions or even experimental conditions at harvest (as discussed in a Rhizosphere 4 round table meeting). Exudate molecules can affect the rhizosphere bacterial populations by acting as nutrient or signal molecules. Through their nutritive effects, exudates will affect the structure of soil microbial communities, favoring cell division of bacteria able to catabolize them. Though microbe-plant chemical dialogues are well-known in the case of symbiotic interactions between legumes and nitrogen-fixing rhizobia (Limpens et al. 2015; Li et al. 2016) or in plant mycorrhiza (Parniske 2008), these are less well characterized in plant-PGPR interactions.

Plant-microbe communication involves also a wide range of signaling molecules produced by the microbe partner, some being involved in the direct control of plant growth and development; these include phytohormones like auxin, cytokinin, and gibberellin (Vacheron et al 2013). Other bacterial molecules can trigger induced systemic resistance and improve plant defence against pathogens (Venturi and Keel 2016). Two studies from this special issue focused on the place of ethylene signaling during plant-PGPR cooperation. Ethylene is a plant volatile hormone, which is produced in greater amounts when plants face adverse conditions, and may

inhibit the growth of plant roots. Ethylene is synthesized from 1-aminocyclopropane-1-carboxylate (ACC) by ACC oxidase. Bacteria that harbor ACC deaminase hydrolyze ACC, leading to a decrease of plant ethylene content and thus to enhanced root growth (Glick et al. 2007). In addition, by lowering the level of ethylene, AcdS$^+$ bacteria (AcdS being the gene encoding for ACC deaminase synthesis) can protect the plant against certain damage. Matsuoka et al. (2016) show that ACC deaminase-producing endophytes, isolated from fruits and vegetables (including carrots), are able to modify stress-induced volatile metabolic profiles of carrots, and thereby can modify the flavour of carrots. Volatiles were decreased in the carrot leaves in response to bacterial inoculation and increased in the roots. In particular, green leaf volatiles that derived from linoleic and linolenic acids were reduced in plants inoculated with AcdS$^+$ strains. This study suggests that AcdS$^+$ bacteria can fine tune the plant defense pathway as well as affects the quality of agricultural products. As the expression of the ACC deaminase synthesis-encoding *acdS* gene is activated in presence of ACC, the contribution of this bacterial enzymatic activity to stimulation of plant growth depends on the levels of exuded ACC in the rhizosphere. Vacheron et al. (2016) provide evidence that maize genotypes differ in their ability to enhance the expression of the *acdS* gene of an inoculated PGPR. When the ethylene pathway is strongly activated by stress conditions, the maize genotype that strongest induced *acdS* was the one benefiting from the PGPR inoculation.

Root microbiome

The description of the root microbiota has received a boost by the development of high-throughput sequencing techniques (Mendes et al. 2013; Pieterse et al. 2016). Initially, the field focussed on *Arabidopsis* in controlled conditions (Badri et al. 2009; Bulgarelli et al. 2012; Lundberg et al. 2012; Sugiyama et al. 2013) but nowadays the rhizobiome of crop species are also determined, under filed conditions (Bulgarelli et al. 2015; Peiffer et al. 2013). It will now be the challenge to move beyond the 'collection of stamps', i.e. to move from the description of root microbiomes towards the understanding of the functionality for plant performance. Such knowledge is relevant in order to understand belowground plant competitive interactions (Mommer et al. 2016) as

well as plant responses under abiotic or biotic stress, in soils with different limiting nutrients (Thomson et al. 2015), or in response to a changing climate. Gschwendtner et al. (2016) described the effect of nitrogen fertilisation on the diversity of bacterial communities. Fertilised soil reduced the incorporation of labelled carbon (^{13}C) into microbial biomass, specifically in the Proteobacteria and Actinobacteria, suggesting altered composition of rhizodeposits as a function of nitrogen availability (Gschwendtner et al. 2016). Knowledge of the root microbiota will be important for optimization of plant-microbe interactions, which is of interest to breeders and farmers (Bakker et al. 2012; Philippot et al. 2013). An example of this is the selection of the optimal PGPR strain of *Bacillus subtilis*, a beneficial growth promoting rhizobacterium involved in salt tolerance in the halophyte grass *Puccinellia tenuiflora*. This study provides physiological and molecular evidence that application of selected bacteria to salt tolerant monocots can ameliorate deleterious effects of high soil saline toxicity (Niu et al. 2016). Stroheker et al. (2016) determined the development of the community structure of dark septate endophytes of the *Phialocephala fortinii-Acephala applanata* species, being root colonisers in forests. An earlier study had showed that this community was very stable, but an assessment after 10 years showed significant turnover within this species complex.

Outlook

The Rhizosphere 5 Conference will be held in Saskatoon, Canada, in 2019. The field of the rhizosphere will have further developed by then, with high-throughput sequencing techniques and meta-omics approaches becoming cheaper and more advanced; bioinformatics pipelines developed and made accessible to non-bioinformaticians. Moreover, imaging techniques improve rapidly, and complex functional-structural modelling as well. We expect future studies to make major leaps forward in revealing the functionality of the complex interactions between plant roots, root exudates, microbial metabolites, and root microbiomewithin the context of 'true' soil environments, i.e., in field conditions. The focus of the research will shift to understanding the rhizosphere 'melting pot' in the real world: managing the rhizosphere will be crucial to advance agricultural practices and move towards a more

biodiversity-based agriculture. The increasing demand for food with reduced inputs of fertilisers and pesticides is pressing. Similarly, the sustainability of natural eco-systems is of great importance, where rhizosphere management will be crucial in mitigating climate change and maintaining ecosystem functioning.

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