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An extended root phenotype: the rhizosphere, its formation and impacts on plant fitness

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ABSTRACT

Plants forage soil for water and nutrients, whose distribution is patchy and often dynamic. To improve their foraging activities, plants have evolved mechanisms to modify the physicochemical properties and microbial communities of the rhizosphere, i.e. the soil compartment under the influence of the roots. This dynamic interplay in root-soil-microbiome interactions creates emerging properties that impact plant nutrition and health. As a consequence, the rhizosphere can be considered an extended root phenotype, a manifestation of the effects of plant genes on their environment inside and/or outside of the organism. Here, we review current understanding of how plants shape the rhizosphere and the benefits it confers to plant fitness. We discuss future research challenges and how applying their solutions in crops will enable us to harvest the benefits of the extended root phenotype.

Keywords: Root, soil, microbiome, biocontrol, plant nutrition, drought, salinity, rhizosphere, exudates.

INTRODUCTION

Plants, as sessile organisms, have evolved strategies to successfully address the challenges they face from a changing and unpredictable environment. In particular, plants need to mine the soil for resources such as water and nutrients, whose distribution is patchy and changes dynamically. Plants do so by modulating their root system architecture and root anatomy in response to environmental clues to explore different soil horizons and detect and exploit water and nutrient-rich patches (recently reviewed in Morris *et al.*, 2017 and Lynch, 2019). Besides these, plants have evolved mechanisms to modify soil physicochemical properties and microbial communities under the influence of roots (the rhizosphere) to improve their foraging activities (York *et al.*, 2016). Reciprocally, soil microbes that live on and/or in the plant root together with the changes in soil properties caused by the root, trigger important functional adjustments in the plant such as modification of root development and physiology. This dynamic interplay in the root-soil-microbiome interactions creates emerging properties that impact plant nutrition and health.

In this review, we will consider three habitats as integral parts of the rhizosphere continuum: the rhizospheric soil, the rhizoplane and the root endosphere (see York et al., 2016 for terms definition), as the apoplastic spaces in the root cortex (root endosphere) form a continuum of microbial colonization with the surrounding soil and the root surface (rhizoplane). Due to the properties of the rhizosphere that are largely influenced by the plant genotype, this could be regarded as an '*extended root phenotype'* as defined by Dawkins (1982) i.e. a manifestation of the effects of plant genes on their environment inside and/or outside the organism. This extended root phenotype has a profound impact on plant fitness and is likely to be under strong selection (Pérez-Jaramillo *et al.,* 2016, Schmidt *et al.,* 2016). Hence, a better understanding of the principles that govern the formation of the rhizosphere, critical in the interaction with the soil and the microbiota, could contribute to the development of more resilient crop varieties and the optimization of agricultural practices. However, while root architecture and anatomy traits are starting to become an integral target of crop breeding programmes (Wissuwa *et al.,* 2016, Lynch 2019), root-soil-microbiome interactions that configure rhizosphere traits are not yet considered. The delay in the use of these new root-soil-microbiome traits is due to two major factors: a) the majority of the root microbiome research has focused on characterising only one side of the interaction, the microbiota structure or the impact of edaphic factors on plant-microbe interaction, without paying attention to how plants shape these complex microbial communities, soil properties, their feedbacks on plant fitness, and ultimately, on agronomy; b) the methods that fully capture and measure the impact of roots on plant-soil-microbiome interactions are not well developed yet as it mobilizes knowledge from multiple disciplines (soil biogeochemistry, plant biology, microbial ecology). This bottleneck limits our ability to define corresponding plant root ideotypes.

Here, we review our current knowledge on how plants (focusing on annual plants) create an extended phenotype by changing rhizosphere traits through root-soil-microbiome interactions and the benefits it confers to plant fitness. While the rhizosphere is shaped by many others factors including the physicochemical properties of the soil and the environmental changes, in this review we only consider the influence of the plant on the rhizosphere formation and dynamic. We also highlight open questions and future challenges to be addressed (Box2) in order to reap the benefits of these extended root phenotypes.

CREATING AN EXTENDED ROOT PHENOTYPE: HOW PLANTS SHAPE A BELOW-GROUND NICHE

Root development changes the physical properties of the surrounding soil

Root growth in a new region of the soil contributes mechanically to the formation of a rhizosphere (Bengough *et al.,* 2011, Jin *et al.,* 2013, Kolb *et al.,* 2017). Growing roots displace soil particles in the vicinity of the root surface as the axial and radial growth pressures exerted at the root tip overcome the impedance of the surrounding soil. The recent advances in non-invasive techniques for soil and plant imaging opened new avenues for the study of soil-root interactions in natural soils at very fine (micron scale) resolution. For instance, X-ray computed tomography (XRCT) allowed *in vivo* dynamic visualisation and quantification of soil deformation around a growing root tip (Keyes *et al.,* 2016). It showed that soil particles displacement at the root tip occurs approximately perpendicular to the root surface. XRCT was also used recently to explore the interaction among root growth, soil structure, and soil porosity in different plant species (Helliwell *et al.,* 2017; Helliwell *et al.,* 2019). These studies revealed the formation of a gradient of soil porosity from the proximity of the root surface, with high presence of pores, to a dense soil area a few millimetres away from the root (Helliwell *et al.,* 2017; Helliwell *et al.,* 2019). The size of the soil densification zone varies according to plant species and soil structure, but is independent of root thickness.

Likewise, root hairs influence rhizosphere porosity depending on soil texture. In coarse textured soils with heterogeneous pore size distribution, root hairs favour large pores formation in the vicinity of the root surface. This is particularly evident in dry soils (Koebernick *et al.,* 2017). Surprisingly, root hair formation has no effect on finer textured soils with a more homogeneous pore structure (Koebernick *et al.,* 2019). Therefore, root hairs tend to influence soil inter-aggregates rather than intra-aggregates arrangement in the formation of soil pores in the vicinity of the roots.

These changes in soil density and porosity have a strong impact on plant water and nutrient accessibility and on soil microbial community composition. Indeed, Kravchenko *et al.,* 2019 using X-ray micro-tomography combined with micro-scale enzyme mapping have demonstrated that the soil pore formation driven by the plant is the main factor modulating carbon storage in soil. These pores define regions with high microbial activity related to carbon turnover and sequestration. Hence, root development modifies soil structure around the root and thus contributes to the formation of the rhizosphere (Figure 1).

Rhizodeposition: plants invest carbon to shape the rhizosphere physicochemical properties

Living roots release a wide range of organic compounds to the soil (i.e. rhizodeposits) that transform the physicochemical properties of the rhizosphere (Hinsinger *et al.,* 2009, Sasse *et al.,* 2018; Figure 1). Rhizodeposits include primary and secondary metabolism products, volatile organic carbon compounds, cells debris derived from the root cap (i.e. border cells) and metabolites originating from senescence of root epidermal cells as well as root turnover (Nguyen 2003, Jones *et al.,* 2009, Oburger and Jones*,* 2018). Therefore, rhizodeposition leads to a net carbon flux from the plant root into the soil estimated at 15% of the total plant belowground carbon allocation which may range between 17% and 40% of the total photosynthetically fixed carbon (Nguyen 2003, Badri and Vivanco 2009; Sasse *et al.,* 2018, Pausch and Kuzyakov, 2018). The quantity and composition of rhizodeposits vary considerably depending on the diversity of plant communities, plant species, genotypes, plant age and growing conditions (Hütch *et al.,* 2002, Nguyen 2003, Chaparro *et al.,* 2013, Oburger and Jones*,* 2018). Root tips are the first plant tissue sensing new soil environments and are major hotspots for exudation in diverse ways. Primary and secondary plant-derived metabolites either diffuse or are actively transported from root cells to soil. Low molecular weight compounds such as sugar, amino and organic acids flow out from root cells to the rhizosphere driven by concentration gradients. The absence of an apoplastic barrier (i.e. Casparian strip, suberin or schlerenchyma) in undifferentiated root tip tissues favours passive diffusion of hydrophilic compounds through the plasma membrane, as well as being mediated by specific transporters. Exudation of high molecular weight compounds such as polysaccharides, proteins, alkaloids and phenolics requires transmembrane primary active transporters (ATP-dependent transporters) such as ABC transporters or secondary active transporters (coupled with H+ pumps). Other complex molecules such as mucilage (polymerized sugars) are actively excreted from root cap cells, forming a gelatinous layer around the root tip which, together with root cap morphology, are major drivers defining root-soil mechanical interaction and consequently root tip penetration ability (Oleghe *et al.,* 2017; Keyes *et al.,* 2017). Root exudation mechanisms and the key transporters involved have recently been exhaustively reviewed (Canarini *et al.,* 2019; Sasse *et al.,* 2018).

Exudates and mucilaginous polymers released by plant roots (mucilage) and root associated microorganisms (mucigel) impact the mechanical stability and hydraulic processes in the rhizosphere. The intricate interplay between the physical properties of the secreted mucilage (high viscosity, low surface tension and capacity to adsorb water) and the porosity and texture of the granular media defines the spatial configuration and connectivity of the liquid phase in the rhizosphere (Carminati *et al.,* 2017, Kroener *et al.,* 2018, Benard *et al.,* 2019a). Water retention capacity and nutrient diffusion in the soil-root interface is defined by this complex interaction and it becomes particularly important in dry soils where the mucilage network reinforce the soil matric potential around the root, helping to keep the rhizosphere wet and preventing sudden drops in water flow particularly around the root tip (Carminati *et al.,* 2013 and 2016). Techniques such as neutron radiography have been used to monitor the changes in rhizosphere water content at the whole root system level (Carminati *et al.,* 2010). Furthermore, this technique in combination with experimental systems using chia seed mucilage combined with diverse soil mixtures aid to reproduce rhizosphere analogues where the dynamics of biophysical processes in response to changes in water content can be assessed at smaller scale. In this regard, recent work suggests that the increased water retention associated with mucilage secretion sustains higher soil enzymatic activity and the diffusion of the rhizospheric solutes in dry soils (Zarebanadkouki *et al.,* 2019). Importantly, the mucilage life-span extends significantly in response to low water availability ensuring a source of carbon that preserves the necessary microbial activity in the rhizosphere (Ahmed *et al.,* 2018, Benard *et al.,* 2019b).

The exudation of organic acid anions such as malate, citrate and oxalate, change the redox state and pH of the soil. This has strong repercussion for instance on the mobilisation of inorganic phosphorus (P) from P deprived soils. These organic acids may also act as chelates to improve aluminium toxicity tolerance in acid soils (Chen *et al.,* 2016). Fluctuation in the amount of rhizodeposition to the rhizosphere responds to changes in soil properties. For instance, amino acids exudation is influenced by the nitrogen concentration in the plant-soil interface and it is the signal for root N uptake (Kiba and Krapp, 2016, Canarini *et al.,* 2019). Similarly, rhizosphere acidification is tightly controlled by *A. thaliana* in response to phosphate limitation (increased acidification associated to miR156 gene, Lei *et al.*, 2016) or lead toxicity (reduced acidification linked to nitrate transporter NTR1.1, Zhu *et al.*, 2019).

Altogether, rhizodeposition has a profound effect on the physicochemical properties of the rhizosphere.

The rhizobiome: plant roots influence microbial communities

Roots influence soil microbial communities leading to a very specific rhizosphere microbiome characterized in general by a larger active microbial community, but exhibiting reduced diversity compared to bulk soil (Alegria Terrazas *et al.,* 2016, Lopes *et al.,* 2019). This microbial rhizosphere assembly is extremely dynamic and is mostly influenced by rhizodeposits that can act as major carbon sources for microbes, signalling molecules or antimicrobial agents (Figure 1). Indeed, different studies have shown the important role of some root exudates such as organic acids (Kandaswamy *et al.*, 2017), amino acids (Feng *et al.*, 2018) and sugars (Zhang *et al.*, 2015) as chemo-attractant for beneficial bacteria in different plant models favouring root colonisation (Chaparro *et al.*, 2013). In addition, some secondary metabolites such as coumarins, well known iron mobilising exudates, shape the rhizosphere microbiome in *Arabidopsis* (Stringlis *et al.,* 2019) through their antimicrobial effect on fungal pathogens (Stringlis *et al.*, 2018; Voges *et al.*, 2019). Similar functions have been inferred for other secondary metabolites like benzoxazinoids and canavanine from root exudates of crops like maize (Cotton *et al.*, 2019) and legumes (Cai *et al.,* 2009), respectively. Root system architectural traits such as root type (Kawasaki *et al.*, 2016) and root hairs (Robertson-Albertynm *et al.*, 2017) have also been found to significantly influence the composition of rhizosphere microbial communities in *Brachypodium* and barley, respectively.

Microbial colonisation along growing roots is shaped by differential exudation patterns, that change the distribution of microbial biomass along the root, and the kinematics of root tip growth through soil profiles (Lugtenberg and Kamilova, 2009; Compant *et al.,* 2010; Dupuy and Silk, 2016). Chemotaxis towards root secreted signalling molecules attracts microbes to the proximity of root surfaces whilst root elongation rate influences the dynamics of root surface adhesion and longitudinal transport along elongating roots. Generally, larger and varied number of active bacteria tends to accumulate around the root tip whereas fewer microbial taxa are associated with the root elongation zone (Watt *et al.*, 2006; Massalha *et al.*, 2017). Bacterial density decreases progressively from the elongation zone towards mature root zone. This is likely to reflect the rapid expansion in root epidermal cell size (up to thirty times in six hours as cells transit the elongation zone) which will, in effect, 'dilute' microbial cells resident on the root surface until they divide and create a continuous biofilm in the maturation zone. Dispersion of rhizosphere bacteria and chemotactic movements may also govern the shifts in rhizosphere communities favouring the occurrence of bacterial decomposers (DeAngelis *et al.*, 2009; Dupuy and Silk, 2016; Massalha *et al.*, 2017).

Additionally, plant life cycle imposes a temporal pattern in exudates secretion that sculpts the dynamics of root associated microbiota. For instance, recent studies have investigated the distinctive root microbiota associated with early and late stages of plant development in *Arabidopsis* (Chaparro *et al.,* 2013), rice (Edwards *et al.*, 2018) and oats (Zhalnina *et al.*, 2018). In oats, the increased abundance of sucrose at the seedling stage has been suggested to facilitate the establishment of symbiotic interactions with soil microorganisms, whereas shifts to aromatic compounds and amino acids during the vegetative phase may reflect enhanced plant defence responses. Cumulative secretion of amino acids in *Arabidopsis* has been suggested to be crucial for bacterial root colonisation (Chaparro *et al.*, 2013). These studies suggest the important coordination between plant developmental stage and changes in root associated microbiota to counterbalance plant immunity and nutrition needs.

Microbial communities in the rhizosphere can in return induce systemic adjustments in the root exudates (Korenblum *et al.,* 2020). Microbes colonising the root induce profound changes in the shoot and systemic root metabolomes, and transcriptomes (Korenblum *et al.,* 2020). Glycosylated azelaic acid was identified as putative microbiota-induced signalling compound that is later exuded as azelaic acid. Local microbial effects on root would therefore influence the exudation in other distant parts of the root system conditioning the rhizosphere (Korenblum *et al.,* 2020).

While many studies indicate a strong interdependence between plant genotype and rhizosphere microbiome composition (Jacoby *et al.*, 2017), very little is known about the plant genes underlying this process. In the study of Mwafulirwa *et al.*, (2016), closely related barley genotypes from a biparental cross between an elite and a wild accession were found to greatly differ in rhizosphere microbial activity as a consequence of genotypic variation in rhizodeposition. This study not only provided evidence of plant genetic control and heritability of the barley root microbiome, but also revealed the large potential of un-tapped exotic germplasm to contribute to enhanced plant-soil interactions. In addition, an interesting recent study using *Avena barbata* revealed that the fluctuations in chemical composition of root exudates during plant growth respond to the substrate metabolite preferences of rhizosphere associated microorganisms (Zhalnina *et al.*, 2018). The authors highlight the significant role of organic acids (and genes controlling their transport) in the establishment of the rhizosphere microbiome. Studies comparing current crops with landraces and its wild relatives highlight the risks that domestication and breeding programs have had on rhizosphere functions and diversity (Mwafulirwa *et al.*, 2016; Pérez-Jaramillo *et al.*, 2016). Domestication of crops and intensive agricultural practices have altered the plant carbon source and sink dynamics to favour aboveground allocation of photo-assimilates in the form of yield. This process has impacted the extended root phenotype by altering plant-soil feedbacks including plastic responses to heterogeneous and changing environments (Milla *et al.,* 2017; Carrillo *et al.*, 2019). For instance, recent studies on wild and domesticated beans (Pérez-Jaramillo *et al.*, 2017) and tomato (Carrillo *et al.*, 2019) reveal clear shifts in rhizosphere bacterial community composition and assembly between the two genepools. In barley, introducing genetic variation from wild accession into a modern cultivar promoted beneficial plant – soil interactions associated with soil carbon dynamics (Mwafulirwa *et al.*, 2016). These studies not only demonstrate the genetic basis underpinning root microbiome assembly but also the potential genetic loss in modern cultivars for beneficial associations in plant - root microbial communities for particular habitats.

BENEFITS OF THE EXTENDED ROOT PHENOTYPE

Plants invest carbon and energy in building a belowground niche, essentially because it comes with a large number of benefits for its overall fitness, and it facilitates plant's adaptation to a changing environment (Turner *et al.*, 2013). The description of the rhizosphere effect on plant fitness is not new, and it is intuitive to assume that the specific conditions that the rhizosphere provides (e.g. higher soil moisture or organic matter content and microbial activities or biomass) are beneficial for plant fitness. However, the mechanisms operating at finer scales in close proximity to the root and the strength of the relationships among the rhizosphere traits and plant fitness remains in large part unknown. This section describes the current relations that have been established between the extended root phenotype and plant health and productivity (Figure 2).

Physicochemical changes linked to the extended root phenotype impact plant fitness

As described in detail above, plants act as ecosystem engineers that modify the physical and chemical properties of the soil surrounding their roots. Major advances have been done in characterizing the effects of plants on soil redox potential, pH, aggregation, water or nutrient availability (Hinsinger *et al.*, 2009). However, explicit testing of the feedback effects of plant-induced changes in soil abiotic conditions on plant fitness are more limited.

Some studies report that rhizosheath (defined as a sheath of soil particles that adhere strongly to the root on excavation; George *et al.,* 2014; York *et al.,* 2016) is a key trait for plant fitness under water and nutrient-stressed conditions by improving phosphate and water uptake (George *et al.*, 2014; Liu *et al.*, 2019). Recently, Rabbi *et al.*, (2018) found that a drought-tolerant chickpea variety had a greater rhizosphere moisture storage linked to larger rhizosheaths resulting from greater mucilage exudation. Also, rhizosheath formation was related with increased water stress levels in foxtail millet and enhanced exploration of deeper soil horizons to access water (Liu *et al.*, 2019). Similarly, larger rhizosheath formation was found to correlate with greater shoot biomass in wheat and suggested to respond to an improved water uptake regardless of the nutrient stress imposed in the experiment (James *et al.,* 2016). Soil aggregation in the rhizosphere is highly variable between plant genotypes (Ndour *et al.*, 2017) and represents a rhizosphere emerging property crucial for plant water and nutrient uptake on which crop varieties could be selected.

Additionally, the modification of soil pH in the rhizosphere induced by root exudation and (micro)-organisms' respiration (1-2 pH units above or below the bulk soil) influences soil nutrient availability (Neumann and Römheld, 2012). Rhizosphere acidification potential differs between species and genotypes and thus represents a currently neglected trait to consider in the context of crop breeding or crop rotation and intercropping to improve nutrient acquisition or pollution resistance.

Similarly, the role of genes controlling the expression of transport channels involved in the efflux of root exudates should be considered as significant targets for sustainable breeding programmes. In recent field evaluations, alleles conferring Al-tolerance were found concomitantly associated with a yield QTL displaying additive effect on grain yield in acid soils. The absence of yield penalties in non-stress conditions highlights the breeding value of the locus for improving sorghum grain yield on acid soils (Carvalho *et al.*, 2016). The rhizosphere is a unique biophysical and biogeochemical environment shaped by plant evolution to maximize plant fitness and more attention should be given to rhizosphere abiotic traits (e.g. acidification, aggregation, rhizosheath mass) to improve crop selection and production.

Role of the rhizosphere microbiome for plant nutrition and water uptake

Endosymbioses - Plants have evolved mechanisms to interact and support the growth of large numbers of beneficial microbial taxa that live in the proximity of the root or inside the root tissues. The nature of the beneficial root-microbial interactions ranges from symbiotic to commensalistic, and they are critical for plant nutrition. Two of these interactions have been thoroughly mechanistically explored: plant association with symbiotic mycorrhizal fungi (e.g. arbuscular mycorrhiza, ectomycorrhiza) and with nodule forming nitrogen-fixing bacteria (e.g. *Rhizobium*, *Frankia*).

Mycorrhizal fungi form symbiotic associations with almost all land plants, with current estimates of 50 000 fungal species forming associations with 250 000 plant species (van der Heijden *et al.*, 2015), with the most common association being established with arbuscular mycorrhizal fungi (AMF, phylum *Glomeromycota*, 74% of all land plants, Smith and Read 2008). AMF symbiosis plays a key role in plant P nutrition through a more efficient solubilization and uptake of orthophosphate (i.e. only form available to plants) by the extended fungal network that can contribute to up to 90% of plant P uptake (Ferrol *et al.*, 2019). This symbiotic interaction is especially relevant in ecosystems with low soil nutrient availability. Although, the abundance of AM fungi is often reduced in heavily managed agroecosystems due to fertilization and soil perturbation, most of the crops can form symbiotic associations with AM fungi (e.g. cereals, legumes, potato, tomato) with a significant impact on crop productivity. Experiments using a set of maize mutants able to establish a beneficial relationship with AM fungi but deprived of the mycorrhiza-specific orthophosphate transporter presented large decreases in aboveground biomass and reduced grains production when grown in agroecosystems with low phosphorus availability (Willmann *et al.*, 2013). AMF influences plant nitrogen nutrition at a lower extent than phosphorus, and it is highly context dependent (van der Heijden *et al.*, 2015). Plants associated with AMF present a higher water uptake and more effective scavenging for water in soil micropores. AMF network also promote a higher moisture retention and aggregation in soils (Augé, 2001; Augé, 2004), that sometimes are combined to a higher plant water-use efficiency (Birhane *et al.*, 2012). Indeed, AMF influence maize plant aquaporins activity resulting in higher water transport under water deficit that led to an improved photosynthetic capacity in the shoots

(Quiroga *et al.*, 2019). Overall, these combined nutritional and non-nutritional effects of AMF generate increases in plant yield and seed protein mass in greenhouse and field conditions that has justified the use of AMF inocula in agriculture for decades (Berruti *et al.*, 2016).

Legume plants (family *Fabaceae*) and the so-called actinorhizal plants (orders Fagales, Rosales, Curbitales) rely on their associations with nitrogen fixing microorganisms (e.g. *Rhizobium*, *Bradyrhizobium*, *Frankia*) for nitrogen nutrition. The association between plants and nitrogen fixers microbes are characterized by the formation of specialized root organs called nodules colonized by the nitrogen-fixing microbes where the atmospheric nitrogen is converted into a reduced nitrogen form and become available for the host plant (Masson-Boivin and Sachs, 2018). In this symbiosis, the plant provides the nitrogen fixers bacteroids with dicarboxylates (e.g. l-malate, succinate, fumarate), used as energy and carbon sources by the microorganism, and in return, bacteroids provide ammonium to the plant (Poole *et al.*, 2018). Across many plant hosts and *Rhizobium* symbionts a clear fitness alignment exists between the two members of the symbiotic relationship with a robust positive correlations between plant aboveground biomass and the number of nodules or nodules biomass (Friesen, 2012).

Additionally, as these symbiotic species always evolve in complex microbial communities with which they strongly interact, sometimes the establishment of a functional symbiosis may require the presence of other symbionts or microbial helpers present in the rhizosphere (Frey-Klett *et al.*, 2007). For instance, it has been reported in soybean that AMF inoculation improved both nodulation and nitrogen-fixation, especially because nodulation requires high phosphorus demand that can be addressed by an established symbiosis with AMF (Meena *et al.*, 2018). Also, nitrogen-fixing symbioses for legume trees from the *Piptadenia* genus in Brazil are efficient only in the presence of an AMF (Bournaud *et al.*, 2018). Hence, the plant can form multiple symbiosis with diverse microorganisms that can provide more than half of the plant nutrient demands and synergistically stimulate its fitness (van der Heijden *et al.*, 2016). Still, the AMF and nitrogen fixer symbiosis are extreme examples of strong associations between the plant and its rhizospheric microbes and they represent only a very small fraction of the rhizosphere microbiome abundance and diversity.

Beneficial activities of rhizosphere functional groups - Out of the myriad of microbes that live in the rhizosphere, only a small proportion can establish symbiotic interactions with the plant, mainly due to the tight control plant exert on the colonization of the endosphere. Non-symbiotic microorganisms can form less strict mutualistic or commensalistic relationships with the plant that still provide clear benefits for the plant nutrition. For instance, saprophytic microorganisms facilitate plant nutrient uptake by mineralizing soil organic matter and solubilizing non-bioavailable soil nutrients. The most studied nutritional functions performed by rhizosphere microbiomes are phosphate solubilization, organic phosphorus mineralization, and siderophore production (Vacheron *et al.*, 2013). Many bacteria (e.g. *Pseudomonas*, *Bacillus*) and fungi (e.g. *Penicillium*, *Aspergillus*) are able to solubilize soil mineral phosphate through excretion of organic acids (e.g. oxalic acids, citric acids) causing a local acidification or the chelation of the cations to which phosphate is bound (Richardson *et al.*, 2009). Additionally, a large diversity of microorganisms (e.g. Proteobacteria, AMF, ectomycorrhizal fungi), through extracellular phosphatase activities, can mineralize soil organic phosphorus and make it available for the plant (Spohn *et al.*, 2015; Menezes-Blackburn *et al.*, 2018). Rhizospheric microorganisms also contribute to plant iron uptake through the production of siderophores, small organic molecules, that chelate the ferric form of iron, normally not bioavailable, and make it absorbable by the plants (Saha *et al.*, 2013). Other microbial mechanisms modulate plant nutrition indirectly by the microbial production of phytohormones and other signals that stimulate lateral root branching and root hair growth, maximizing the soil exploratory capacity of the plant (Vacheron *et al.*, 2013).

The microorganisms harbouring these beneficial functions are known as Plant Growth Promoting (PGP) microbes and some culturable species are used as biofertilizers (e.g. *Pseudomonas fluorescens*, *Azospirillum brasilense*). Microorganisms harbouring the same PGP functions (e.g. phosphate solubilization, siderophore production) can be categorized as functional groups that can be studied together and not as single strains using sequencing and qPCR on functional genes or high-throughput cultivable approaches (Vacheron *et al.*, 2013). These PGP functional groups can be seen as biotic traits of the extended root phenotype that when better characterized (e.g. size, composition, structure, activity of the group) could help us understand the importance of these functions under variable environmental conditions (e.g. low nutrient availability, soil or climatic disturbance, plant life stage). These approaches have been well developed to characterize the nitrogen-fixer functional group in the rhizosphere using the *nifH* gene (Tan *et al.*, 2003; Coelho *et al.*, 2009; Bouffaud *et al.*, 2016) but it needs to be developed for other important microbial functions performed by rhizospheric microorganisms.

Currently, this field of research is transitioning from studying a single PGP strain inoculated alone on the plant, in axenic conditions or on the field, to testing the effects of an assemblage of

PGP strains (Vorholt *et al.,* 2017, Finkel *et al.*, 2017). The goal is to determine if complex inocula with diverse or redundant functions provide more efficient plant growth promotion and improve our understanding of the collective effects of the hundreds of PGP microorganisms that live and interact naturally in the rhizosphere. Some studies that inoculated a consortium of PGP strains reported higher increases in crop biomass and yield as compared with a single strain inoculum, suggesting additive or synergistic effects associated to microbial interactions and niche complementarity (Nain *et al.*, 2010; Lally *et al.*, 2017). However, in other studies strain consortia performed similarly or worse than single strains (Lampis *et al.*, 2015) or even caused bacterial community collapse and a loss of plant protection (Becker *et al.*, 2012). These findings highlight the necessity to develop a better understanding of microbe-microbe interactions in complex communities to design efficient microbial-based solutions for agriculture.

Microbiome level - Overall at the rhizosphere microbiome level, rhizodeposition stimulates the growth of hundreds of heterotrophic microbial species. These microbes do not necessarily harbour PGP traits but contribute in making the rhizosphere a nutrient hotspot for the plant through the degradation of soil organic matter (e.g. litter degradation). The definition and interpretation of the overall impact these microbes have on plant nutrient acquisition and use is challenging. It requires the development of synthetic plant microbiomes, that through the assemblage of multiple microbial strains simulate realistic rhizosphere microbial communities. Reductionist approaches based on synthetic plant microbiomes offer incredible opportunities to establish causality between microbiome characteristics (e.g. structure, composition, functions) and plant phenotypes under variable biotic and abiotic conditions (Vorholt *et al.*, 2017). Synthetic ecology approaches have already been successfully used on the model plant *A. thaliana* where the reproducibility and flexibility of these systems have been demonstrated under *in vitro* plant growth conditions (Bodenhausen *et al.*, 2014; Finkel *et al.*, 2019).

Pioneering work on rice synthetic microbiomes reveals bacterial consortia enriched in the *indica* genotypes contribute to higher nitrogen use efficiency than in *japonica* genotypes and also resulting in higher growth rates (Zhang *et al.*, 2019). In *A. thaliana*, the colonization of a synthetic bacterial community under *in vitro* conditions led to a 20-to-40-fold increase in orthophosphate concentration in shoots of phosphate starved plants after 3 days of supplementation with phosphate (Castrillo *et al.*, 2017). Subsequent work showed that bacterial synthetic communities modulate plant phenotypes, like orthophosphate content, root elongation and shoot surface area in a predictable way (Herrera-Paredes *et al.*, 2018).

Beneficial effects of plant microbiota are highly context dependent where, abiotic conditions or plant genotypes, may cause them to become neutral or negative for plant fitness. Using a 185-member bacterial synthetic community representative of the *A. thaliana* rhizosphere, Finkel *et al.* (2019) observed contrasted effects of the synthetic community on rosette size and orthophosphate accumulation in shoots, depending on orthophosphate concentration in the medium and the presence of specific taxonomic groups (e.g. *Burkholderia*). When the plant was phosphate-stressed, *Burkholderia* strains exacerbated plant phosphate starvation (Finkel *et al.*, 2019). These findings demonstrate that many rhizospheric microorganisms can either have beneficial or detrimental effects on plant fitness depending on the dynamic of multiple biotic and abiotic parameters that remain to be uncovered (Haney *et al.*, 2015; Hacquard *et al.*, 2017).

Role of the rhizosphere microbiome for abiotic and biotic stress tolerance

Plants face multiple abiotic and biotic stressors during their lifetime and they use a large repertoire of mechanisms to mitigate the effects on their fitness. Emerging evidence suggests that rhizospheric microbiota can enhance plant tolerance to drought, salt stress, pollutants, pathogen outbreak, herbivory or competition with other plants. In this section, we will detail how root-associated microbes and their functions provide a diverse arsenal to help the plant survive under stressful conditions and act as an extended immunity.

Tolerance to abiotic stressors (drought, salinity, pollution...)

A large number of studies on stress tolerance mediated by the rhizosphere microbiome focused on drought stress that is one of the most destructive abiotic stressors for plants in both natural and agricultural ecosystems. PGP microbes are known to play a role in drought stress alleviation for various crops through the production of exopolysaccharides, different phytohormones, 1-aminocyclopropane- 1-carboxylate (ACC) deaminase or volatile compounds (reviewed in Naylor and Coleman-Derr, 2018). At the microbiome level, it was found that an increase in endospheric Actinobacteria and especially of the *Streptomycetaceae* family was associated to higher drought tolerance across 30 phylogenetically diverse host plant species in a common garden experiment (Fitzpatrick *et al.*, 2018).

Hence, the presence of specific PGP microbes or families can lead to higher drought tolerance but these beneficial effects are dependent on different historical factors, like previous exposure to drought or the host plant. Lau and Lennon (2012) demonstrated that adaptive plant responses to drought were mainly driven by the responses of soil microbiomes and highlighted that microbial communities pre-adapted to drought maintained a higher fitness for *Brassica rapa* in a mesocosm experiment. This is consistent with the finding that soil microbiomes from more constant environments are more sensitive to change and have a poorer functional acclimatisation compared to microbiomes from more fluctuating environments (Hawkes and Keitt, 2015). Additionally, Zolla *et al.* (2013) demonstrated that microbiomes historically exposed to the host plant (i.e. sympatric communities) provided higher drought tolerance than microbiomes previously exposed to other plant species. The presence of these sympatric microbiomes reduced the expression of drought response marker genes in the host plant and plant biomass was significantly increased compared to non-sympatric microbiomes conditions. These results highlight that plants benefit from their associated microbiomes to resist drought stress, especially when the microbial communities have been pre-exposed to this stressor and the host plant in previous seasons. These findings encourage more research to determine the adaptive potential of plants and their microbiomes to rapid changing climates but also in agriculture in the context of transition to new cropping systems or rotations.

Another abiotic stress that plants face frequently is soil salinity, especially in arid or coastal areas, that leads to large decreases in plant growth and yield. Some halotolerant PGP microbes, like *Halomonas* strains have been shown to promote plant growth under salt stress (Mapelli *et al.*, 2013) and this higher salt tolerance was often linked to the bacterial production of ACC deaminase or volatile organic compounds (VOC) that helps the plant determine its sodium homeostasis (Yang *et al.*, 2009; Siddikee, 2010). Additionally, anthropogenic activities are causing a large release of organic and metallic pollutants in the atmosphere and in soils that can cause oxidative stress in plants and decrease their fitness. Many rhizospheric microorganisms are able to accumulate or detoxify heavy metals and are playing a crucial role for the management of heavy metal stress in plants (Mishra *et al.*, 2017). In particular, mycorrhizal fungi through their hyphal networks and the secretion of organic acids (e.g. oxalic acid, citric acid, gluconic acid, acetic acid) can solubilize, chelates and absorb heavy metals in soil and reduce their bioavailability for plants (Gube, 2016).

In conclusion, rhizosphere microorganisms are able to enhance plant tolerance to a wide array of abiotic stressors and to illustrate this phenomenon the umbrella concept of Induced Systemic Tolerance (IST) was proposed to describe all physical and chemical changes induced in plants by microorganisms that result in higher abiotic stress tolerance (Yang *et al.*, 2009).

Rhizosphere microbiomes provide an extended immunity against biotic stressors

The commensal and mutualistic microorganisms of the rhizosphere also provide an extended immunity to the plant when exposed to biotic stressors, like pathogens, parasites or herbivores. In particular, many studies are available on the role of plant microbiota in mediating disease resistance (Vannier *et al.*, 2019). For instance, it was demonstrated that the resistance of a tomato variety to the soil borne pathogen *Ralstonia solanacearum* was driven by a native bacterial strain affiliated to the genus *Flavobacterium* (Kwak *et al.*, 2018). Interestingly, for the same pathogen it was also demonstrated that the pathogen success was influenced by the microbial network structure, particularly when communities presented a higher stability and niche overlap with the pathogen (Wei *et al.*, 2015). These two examples highlight that microbiota-mediated disease resistance operate at multiple levels in the microbiome, from single strains to emerging properties at the community level. This can be explained by the fact that microbiomes provide an extended immunity to their hosts through multiple mechanisms. Microorganisms can stimulate the plant innate immunity through a mechanism called induced systemic resistance (ISR) or priming, which is dependent of jasmonic acid and ethylene signalling (Pieterse *et al.*, 2014). Recent studies show that plants modify their exudation pattern when exposed to pathogens as a "call for help" that enable the recruitment of beneficial ISR-inducing bacteria (Berendsen *et al.*, 2018; Yuan *et al.*, 2018). Second, the plant microbiota can decrease pathogen success through direct microbial competition that complement plant innate immunity (Vannier *et al.*, 2019). Native microorganisms can decrease pathogen invasion and fitness through resource and space competition, the production of antimicrobial compounds or hyperparasitism. Several studies show that the entire microbial community or the presence of a microbial consortium can act collectively as a barrier to pathogen invasion or emergence that are at the origin of disease-suppressive soils (Yin *et al.*, 2013; Santhanam *et al.*, 2015; Hacquard *et al.*, 2017). Hence, some studies encourage to apply well established ecological theory to plant microbiome research on the relationships between biodiversity and ecosystem functioning that suggest that resistance to pathogen invasion increases with species diversity (i.e. diversity-resistance relationship, Hu *et al.*, 2016; Mallon *et al.*, 2015; Mallon *et al.*, 2018). For instance, Hu *et al.*, (2016) showed in simplified conditions that pathogen density and disease incidence decreased with increasing *Pseudomonas* diversity due to an intensification of resource competition and interference with the pathogen. Additionally, pioneer work considering multi-kingdom microbial consortia shows that *A. thaliana* survival in agar-based growth medium depends on the presence of a community of bacteria with redundant biocontrol traits to protect against fungi and oomycetes that are not kept at bay by the plant immune system alone (Durán *et al.*, 2018). Thus, plant microbiota plays a crucial role for plant fitness during pathogen invasion and emergence through competitive exclusion that constitutes the first barrier for pathogens to circumvent and then through a modulation of plant immunity.

Similar findings on the role of plant-associated microorganisms for the suppression of aboveground insect pests through direct (e.g. pathogenicity against herbivores) and indirect mechanisms (e.g. microbial ISR against insects, modification of the leaf metabolome) are currently emerging (Pineda *et al.*, 2017). For instance, the root-endophytic fungus *Trichoderma atroviride* can induce resistance in maize against the herbivore insect *Spodoptera frugiperda* through an activation of plant defence responses and the production of volatile terpenes that reduces foliar consumption (Contreras-Cornejo *et al.*, 2018). At the microbiome level, a study that performed inoculations of contrasted soil microbiomes on the roots of *A. thaliana* showed that most microbiomes induced inhibition of *Trichoplusia ni* larvae herbivory compared to non-inoculated plants, that was likely associated with changes in the leaf metabolome (Badri *et al.*, 2013). Altogether, these findings show that plants can survive to diverse biotic stressors with the help of their associated microbiomes harbouring a large repertoire of protective mechanisms that offers promising research perspectives to improve plant protection.

Rhizosphere microbiomes influence plant phenology

The association of plants with microorganisms starts as soon as seed formation and germination. The composition of the seed microbiome can impact seed viability and this has been particularly well studied in the context of negative impacts of seed pathogens on germination and emergence. In contrast, limited work has been conducted to investigate the beneficial role of seed microbiota on germination rates and seedling growth, despite potential important implications for agricultural production (Truyens *et al.*, 2015; Shade *et al.*, 2017; Lamichhane *et al.*, 2018). For instance, quinoa seeds harbour consistently *Bacillus* endophytes that have high catalase activities and superoxide contents that help the host during cell expansion and induce a priming of the immune system. This association with *Bacillus* strains helps to explain in part the incredible capacities of quinoa seeds to germinate in minutes under hostile conditions, to regenerate when broken or even resuscitate (Pitzschke, 2016). Yet, despite these promising findings, to date no experimental evidence using seed microbiome manipulations (e.g. synthetic communities) has been performed to assess the influence of seed microbiota on seed germination rates or seedling emergence (Lamichhane *et al.*, 2018). Hence, exciting research perspectives exist to determine the influence of seed microbiota on plant phenology during these critical stages of the plant's life cycle that can have profound impacts on plant health and productivity.

The impact of rhizospheric microbes on plant flowering has been more extensively studied on various plant species and environmental conditions (e.g. soil types, drought, plant competition). Using natural soil microbial communities or manipulated communities inoculated into different sterile soils, several studies demonstrated that soil microbiota can alter flowering time of *A. thaliana* or *Boechera stricta* by 1 to 5 days (Lau and Lennon, 2012; Wagner *et al.*, 2014; Lu *et al.*, 2018; Fitzpatrick *et al.*, 2019). In addition, Panke-Buisse *et al.*, (2015) provided an elegant demonstration using a multi-generation experiment with *A. thaliana* that specific soil microbiomes can induce earlier or later flowering times. The inoculation of these microbiomes to the soil of different *A. thaliana* genotypes or *Brassica rapa* led to similar changes in flowering time, indicating that microbiome effects on plant fitness can be reproducible across plant hosts. These results demonstrate that microbiomes at different stages of the plant life play a role in the phenotypic plasticity of their host and thus contribute to their rapid adaptation to new colonized environments or local disturbed conditions.

Conclusion/perspectives/future directions

Plant roots are constantly interacting with the soil they grow in and the complex biodiversity it harbours. Plants have therefore evolved mechanisms to shape this environment to increase their foraging capacity and control bioagressors. This extended root phenotype provides the plants with new functions or redundant functions (additive effects), and can have priming effects.

Much more research is needed to characterize the genetic control of the extended root phenotype such as soil acidification or soil aggregation that represent emerging properties resulting from the complex abiotic and biotic transformations operating in the rhizosphere impacting plant fitness under different environmental conditions. This requires researchers to bridge soil sciences, plant sciences and microbial ecology to fully understand the rhizosphere, a complex and dynamic environment. For instance, the majority of the rhizosphere microbiome, and its contribution to the extended root phenotype of the host, is not well defined. Important components of the rhizosphere biodiversity (e.g. protists, viruses) are also currently largely overlooked while they could have large contributions to microbiome structure and function (Henkes *et al.,* 2018; Kuppardt *et al.,* 2018; Pratama and van Elsas, 2018; Gao *et al.,* 2019; Roossinck, 2019).

Importantly, the microbiome is strongly influenced by the plant genome and may be considered as an extension to form a second genome or collectively to form a pan-genome (Turner 2013). We need to better characterize the extra functions provided by the rhizosphere and under which conditions they are expressed to improve plant fitness. Currently, very few studies have uncovered the links between rhizosphere traits and plant fitness, yield, stress tolerance or disease resistance and this constitutes a major knowledge gap in our understanding of plant biology and ecology. Future research should address these gaps and aim at quantifying the cumulative effects of this extended root phenotype on plant fitness to determine the most crucial functions to select for. Altogether, the consideration of the rhizosphere as an extended root phenotype could lead to a completely new paradigm in sustainable agriculture.

Box 1: Summary

- **The rhizosphere is a unique biophysical and biogeochemical environment shaped by plant roots in their interdependent and dynamic interaction with soil microbial communities.**
- **Plants genotype influence root biomechanical interactions with the soil and rhizodeposition and thus, the rhizosphere physico-chemical properties mediating root growth and access to soil resources.**
- **Beneficial root-microbial interactions range from symbiotic to commensalistic and are critical not only for plant nutrition and water acquisition but also confer plant with an extended immunity**
- **Rhizosphere microbiota play a role in the phenotypic plasticity of their host and contribute to their adaptation to new environments or locally disturbed conditions**
- **The genetics controlling extended root phenotype remain as a huge untapped genetic resource that needs to be explored in the transition to more sustainable production systems**

Box 2: Open Questions

- **What is the best strategy to quantify and rank the relative contribution of each rhizosphere trait to a specific plant phenotype?**
- **What are the key evolutionary trade-offs faced by plants during rhizosphere niche construction that ultimately drives the variability observed between genotypes?**
- **How do rhizosphere viruses and protists influence the structure and function of the rhizosphere microbiome and plant fitness?**
- **Can plant breeding based on rhizosphere traits (soil aggregation, acidification, exudation profiles, microbiome structure) improve crop productivity and resistance to biotic and abiotic stressors?**
- **What are the most efficient solutions to manipulate the rhizosphere microbiome to improve plant productivity and health?**

DATA STATEMENT

All relevant data can be found within the manuscript and its supporting materials.

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AUTHORS CONTRIBUTIONS

CdFC, MS, LM, MJB, GC and LL designed the original review outline. CdFC and MS made the figures. All authors contributed to the text and corrected the different versions of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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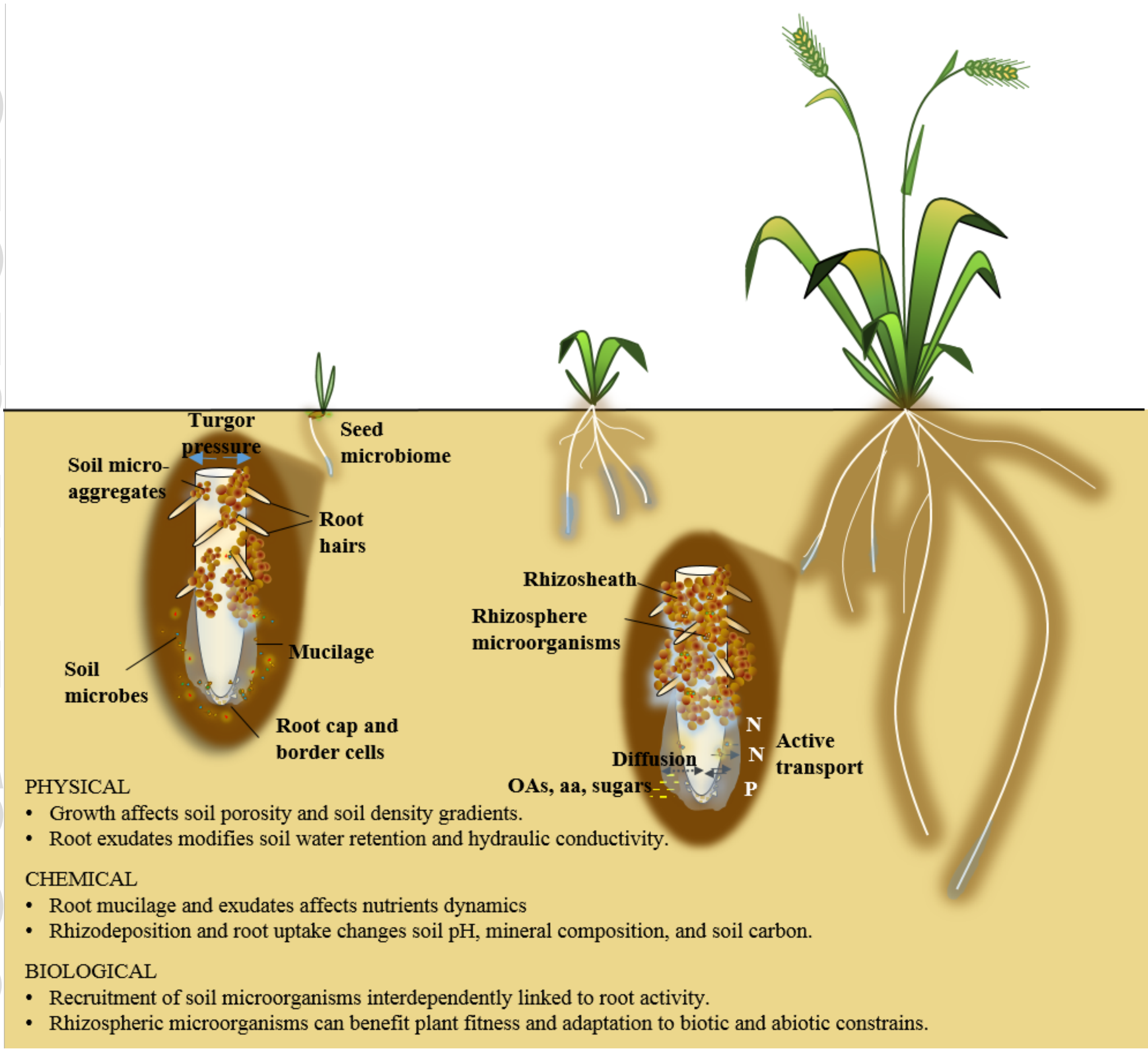
FIGURE LEGENDS

Figure 1. Rhizosphere establishment and increased complexity throughout plant life cycle. Key physical, chemical and biological processes and traits conforming the extended phenotype

Figure 2. Main benefits provided by the extended root phenotype to the host plant. Changes induced by the plant in the rhizosphere cause major modifications of soil abiotic conditions and microbial communities. The reshaping of the soil environment surrounding the roots have positive feedbacks on nutrient and water acquisition by the plant, on the plant resistance to abiotic and biotic stressors, and also it modifies plant phenology. * Nodulation is observed only in a limited number of plant species (Fabaceae, Fagales, Rosales, Curbitales).



PHYSICAL
- Growth affects soil porosity and soil density gradients.
- Root exudates modifies soil water retention and hydraulic conductivity.

CHEMICAL
- Root mucilage and exudates affects nutrients dynamics
- Rhizodeposition and root uptake changes soil pH, mineral composition, and soil carbon.

BIOLOGICAL
- Recruitment of soil microorganisms interdependently linked to root activity.
- Rhizospheric microorganisms can benefit plant fitness and adaptation to biotic and abiotic constrains.

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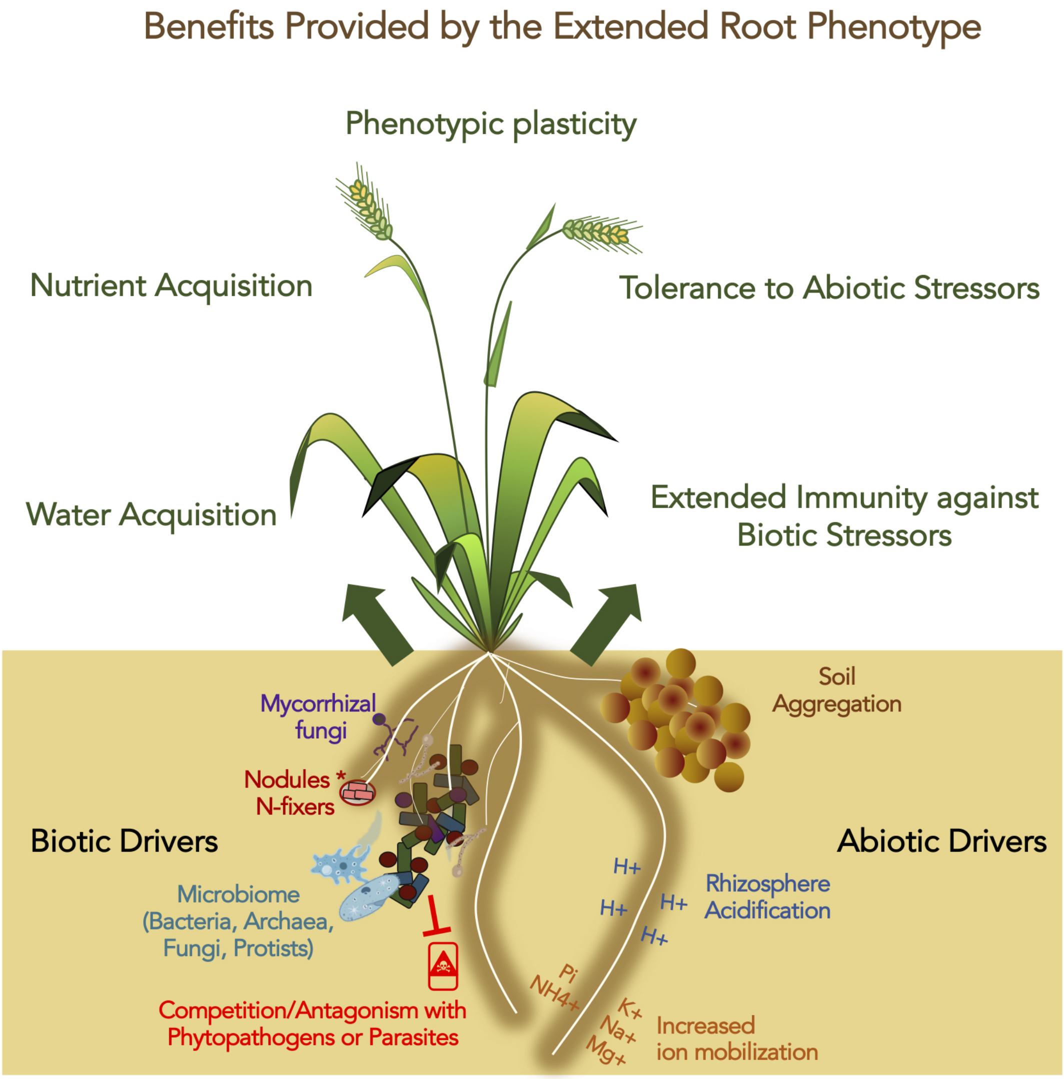

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