

Review

Ensuring future food security and resource sustainability: insights into the rhizosphere

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SUMMARY

Feeding the world's growing population requires continuously increasing crop yields with less fertilizers and agrochemicals on limited land. Focusing on plant belowground traits, especially root-soil-microbe interactions, holds a great promise for overcoming this challenge. The belowground root-soil-microbe interactions are complex and involve a range of physical, chemical, and biological processes that influence nutrient-use efficiency, plant growth and health. Understanding, predicting, and manipulating these rhizosphere processes will enable us to harness the relevant interactions to improve plant productivity and nutrient-use efficiency. Here, we review the recent progress and challenges in root-soil-microbe interactions. We also highlight how root-soil-microbe interactions could be manipulated to ensure food security and resource sustainability in a changing global climate, with an emphasis on reducing our dependence on fertilizers and agrochemicals.

INTRODUCTION

Global population growth and resource depletion place an existential emphasis on improving food security and environmental health. Producing more food using less nutrients and water on less land in the future will require us to develop new and effective agricultural technologies. Since the synthesis of ammonia and the advent of modern chemical industry, fertilizers have made a great contribution to increasing grain production (Erismann et al., 2008). FAO statistics show that as early as 2012 the world's consumption of synthetic nitrogen (N) fertilizers reached 100 million tons per year, and total energy consumption in agriculture peaked at 8,728 trillion joules per year. Even though the application of synthetic fertilizers supports the continuous increase of grain yield worldwide, it also may cause serious environmental problems such as soil acidification, air pollution and water eutrophication (Guo et al., 2010; Savci, 2012). Attaining food security, resource efficiency, and environmental health has become a major challenge to the sustainable development of global agriculture and is also the key component of the future agricultural science and technology revolution.

Achieving the goal of "producing more food with fewer resources" requires harmonizing nutrient-use efficiency, crop productivity and environmental health (Chen et al., 2014; Shen et al., 2020). The rhizosphere, as the interface between roots and soil, is the gateway for nutrients and water to enter the plant from the soil (Curl and Truelove, 2012; Wang and Shen, 2019; Zhang et al., 2010). Roots absorb nutrients and water from the soil and exert influence on adjacent soil through rhizodeposition (Curl and Truelove, 2012). The roots of neighboring plants directly or indirectly affect the interaction processes between target plants and soil (Callaway and Li, 2019; Zhang et al., 2019a). Soil microorganisms also actively participate in root-soil interactions, with the soil-microbe and microbe-microbe interactions frequently regulated by roots (Berendsen et al., 2012; Hakim et al., 2021). The rhizosphere components (soil, roots, microorganisms, and their interactions) can all be manipulated or engineered to increase efficiency of nutrient resource use by plants (Ahkami et al., 2017; Dessaux et al., 2016; Hakim et al., 2021; Kumar and Dubey, 2020; Ryan et al., 2009; Zhang et al., 2010), but the extensive spatial and temporal variability makes achieving such manipulations uncertain. Root management (or rhizosphere engineering) can maximize the biological potential of roots by optimizing root-soil-microbe interactions and ultimately reduce our reliance on fertilizers and agrochemicals, but this is contingent on our understanding of the complex rhizosphere interactions (Hakim et al., 2021; Wang and Shen, 2019; Zhang et al., 2010). Addressing the global challenges of food insecurity exacerbated by climate change and population growth through better understanding and manipulation of

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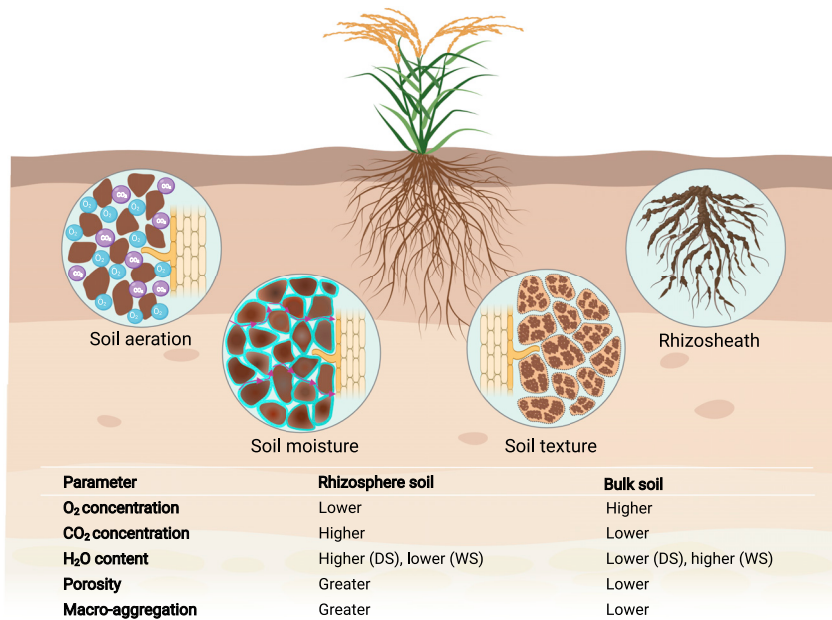


Figure 1. Root-dominated changes in the physical properties of rhizosphere soil

Root activity causes changes in the soil aeration, texture and moisture. The release of mucilage and exudates from the roots contributes to forming continuity of soil solution film around soil particles, and nutrients can move in that water film. Table lists the properties of rhizosphere soil (in comparison with bulk soil). DS, drying soil; WS, wet soil.

rhizosphere processes will be one of the most important scientific frontiers of the forthcoming decades (Wang et al., 2020b).

RHIZOSPHERE – THE MOST ACTIVE INTERFACE

The rhizosphere is the plant-soil interface with the most dynamic earth's biogeochemical processes, affecting all landscapes and many global-scale phenomena (Curl and Truelove, 2012; Huang et al., 2014; Wang et al., 2020b; York et al., 2016). Plants release about 10–40% of their total photosynthetically fixed carbon into the rhizosphere, where various forms of organic carbon (such as sloughed-off root cap and border cells, mucilage and exudates) have profound effects on the chemical, physical and biological processes (Curl and Truelove, 2012; Newman, 1985; York et al., 2016). Importantly, plant roots dominate these processes. For instance, the uptake of nutrients by plant roots generates a depletion gradient in the rhizosphere and changes the rhizosphere pH because of an imbalance in plant uptake of cations and anions, directly affecting nutrient availability (Kuzyakov and Razavi, 2019; Marschner, 2012). A variety of compounds secreted by plant roots, such as mucilage, enzymes, organic anions and amino acids, not only greatly modify the soil chemical properties, but also feed the microorganisms and influence the microbial community structure in the rhizosphere (Berendsen et al., 2012; Chai and Schachtman, 2022; Vives-Peris et al., 2020). In addition, many root exudates (e.g. coumarins, strigolactones and flavonoids) also participate in the rhizosphere signal transduction, affecting neighboring plants and/or rhizosphere microbial communities (Badri and Vivanco, 2009; Wang et al., 2021b). These changes in the rhizosphere relative to the bulk soil also modify root growth and nutrient absorption (Wang et al., 2020b).

Root-dominated changes in the rhizosphere soil structure

Roots dominate changes in the physical properties of the soil surrounding them (Figure 1). Some components of root exudates influence soil structure by binding soil particles, thus increasing the rhizosphere soil stability (Baumert et al., 2018; Galloway et al., 2020; Traoré et al., 2000). The interaction between root exudates and the soil drying and wetting cycle caused by plant transpiration influences soil particle aggregation (Bronick and Lal, 2005). The size, distribution, stability, adsorption capacity and hydrophilicity of soil microaggregates are significantly modified by root exudates (Baumert et al., 2018; Hinsinger et al., 2009). Polysaccharides secreted by plants can bind soil particles and help stabilize the rhizosphere soil

structure (Galloway et al., 2020). In contrast, organic acid anions adsorbed on soil particles increase the negative charge of clay minerals and exacerbate soil particle dispersion (Shanmuganathan and Oades, 1983). Plant species differ in how they influence the stability of aggregates, with barley root exudates tending to disperse soil and those of maize to bind it (Naveed et al., 2017). Maize root exudates contain large amounts of sugars that can bind to the soil particles, whereas barley root exudates are mainly organic acid anions that disperse soil particles (Naveed et al., 2017). These results highlight a clear potential for selecting genotypes with improved root traits (White et al., 2013). However, although some knowledge has been gained, a deep understanding of the physical properties and functions of the rhizosphere is still lagging behind [for instance, the debate whether rhizosphere soils can hold more water than bulk soils remains unresolved (Whalley et al., 2005)]. This is because (1) the rhizosphere is a very narrow and dynamic interface, (2) the rhizosphere characteristics vary in time and space, and (3) the rhizosphere processes depend on plant growth stage, and the biophysical and chemical factors driving rhizosphere functions are difficult to characterize (Hinsinger et al., 2009; Kuzyakov and Razavi, 2019; York et al., 2016).

Root growth exerts a high pressure on surrounding soil as the growing root tips push their way through (Bengough et al., 2011; Jin et al., 2013; Shen et al., 2021b). As a consequence, it is generally thought that the porosity is lower and the average pore size smaller in the rhizosphere compared with the bulk soil (Aravena et al., 2011). To help roots grow in structured soil, the root cap secretes mucilage, a high-molecular-weight viscous substance rich in polysaccharides (McNear, 2013). Mucilage also lubricates the soil to prevent desiccation, most notably by binding soil particles together to form aggregates that improve soil quality by increasing water infiltration and aeration (Galloway et al., 2020; Hinsinger et al., 2009; McNear Jr, 2013; Traoré et al., 2000). In addition, as roots grow, interactions among root exudates, microbial activity, and changes in soil water potential can significantly alter soil structure (Hinsinger et al., 2009; Shen et al., 2021b; Wang et al., 2020b), resulting in similar or higher porosity and larger pore sizes in the rhizosphere than bulk soil (Whalley et al., 2005). However, the mechanisms of root exudates affecting soil structure, and specifically mucilage-bound soil particles, remain to be elucidated further.

Some species in the grass (Poaceae) family form rhizosheath around their roots. The rhizosheath is a layer of tightly bound and highly aggregated soil influenced by roots, firmly attached to the root surface (Brown et al., 2017; Ndour et al., 2020). Its formation is thought to be driven by root hairs (Burak et al., 2021; Haling et al., 2010, 2014), root exudates (Albalasmeh and Ghezzehei, 2014) and the soil moisture status (Haling et al., 2014), and differs significantly among plant genotypes (Brown et al., 2017; Burak et al., 2021; Delhaize et al., 2015; George et al., 2014). The various functions of the root sheath have been demonstrated, including (1) improving drought resistance and protecting roots under drought conditions (Benard et al., 2016; Shane et al., 2010); (2) coping with abiotic stresses such as N, phosphorus (P) and zinc (Zn) deficiency (Brown et al., 2012; Haling et al., 2013), and stresses associated with soil strength (Albalasmeh and Ghezzehei, 2014; Haling et al., 2013, 2014) and soil acidity (Haling et al., 2010).

During the formation of rhizosheath, root hairs play an important role in increasing soil adhesion to roots (Burak et al., 2021; Haling et al., 2014). With the rapid development of non-invasive synchrotron radiation and computed tomography in recent years, root hair interactions with soil structure can now be investigated *in situ* with sufficient resolution. For example, Koebernick et al. (2017) found that root hairs profoundly altered the porosity and connectivity of the detectable pore space in the rhizosphere and increased the soil pore volume fraction at the root-soil interface. Numerical three-dimensional (3D) models of water and solute movement in a soil-root continuum can systematically enhance our understanding of the soil structural changes and the root absorptive functions, providing new tools for quantifying root-driven soil structural changes (Dunbabin et al., 2013; Rabbi et al., 2018). The challenge for the future is to apply these emerging technologies *in situ* to reveal the relevant root-soil interactions in intensively managed farmland.

Soil porosity and mechanical resistance profoundly affect the growth and development of roots in soil (Jin et al., 2017; Shen et al., 2021b). Soil contains biological and abiotic pores of various sizes, but how roots sense and find these pores remains unknown. Roots tend to grow in biologic pores left by root decay rather than vertical artificial pores (Passioura, 2002). Some studies have proposed potential mechanisms, suggesting that roots find and grow along pores in a random process, and the (near) horizontal growth of roots increases the probability of finding pores, but the exact mechanism still needs to be studied further (Kolb et al., 2017; Landl et al., 2017). We recently found that maize roots approached and grew along the

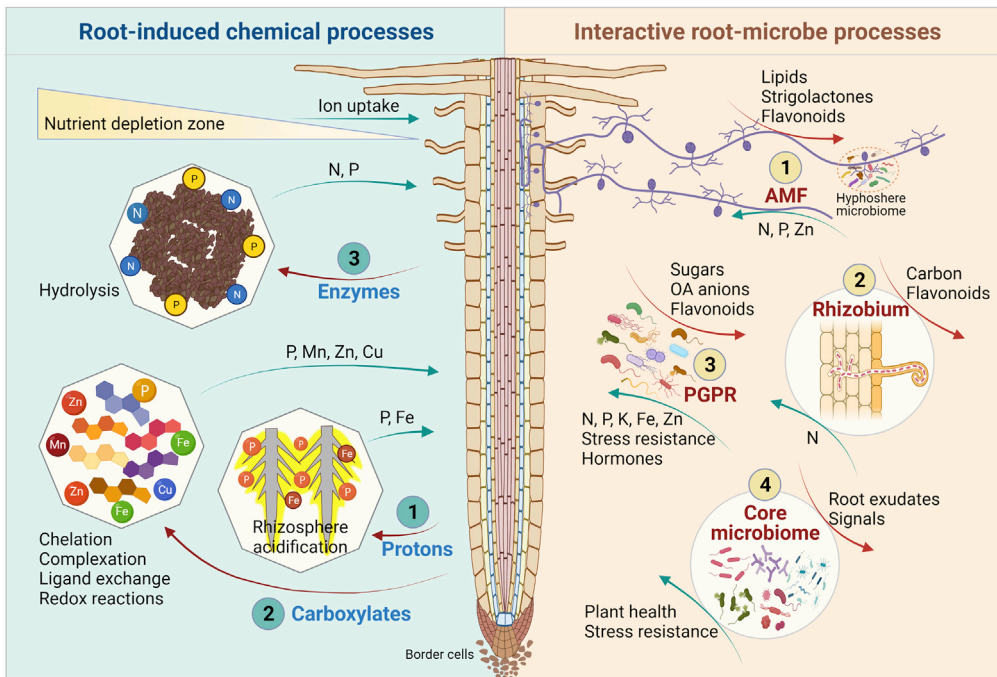


Figure 2. Rhizosphere biochemical (left) and microbial (right) processes influenced by roots

Rhizosphere chemical processes mainly include root absorption of nutrient ions leading to rhizosphere nutrient depletion (when nutrient uptake exceeds supply from soil); this process is aided by (1) root release of protons (acidifying the rhizosphere soil) and (2) organic acid (OA) anions (carboxylates) solubilizing sparingly soluble nutrient complexes and improving nutrient availability; and (3) root release of enzymes to hydrolyze organic compounds. Rhizosphere microbial processes include root interactions with (1) AMF, (2) N_2 -fixing bacteria, (3) PGPR, and (4) the structure and activity of the core soil microbiome.

faba bean roots in maize/faba bean intercropping systems (Zhang et al., 2019a), suggesting that the roots of one plant may create a suitable environment (biopores) for roots of another plant to grow in. The possible underlying mechanism is that the root exudates of faba bean mobilized insoluble soil P and improved the availability of P in the rhizosphere, thus creating the high-P patches for the growth of maize roots. In addition, a role for the biopores created by faba bean roots cannot be excluded. Elucidating the mechanism behind this phenomenon will help us better understand the foraging behavior of plant roots.

Root exudates and nutrient availability

Plant roots exude a variety of compounds into the rhizosphere, including low-molecular-weight substances such as organic acid anions, amino acids, sugars, phenols and other secondary metabolites, as well as high-molecular-weight secretions such as mucilage and proteins (Badri and Vivanco, 2009; Vives-Peris et al., 2020). A wide variety of low-molecular-weight compounds account for the diversity of root exudates, whereas high-molecular-weight compounds have lower diversity but generally constitute a larger proportion of the mass of root exudates (Badri and Vivanco, 2009; McNear, 2013). Root exudates can directly or indirectly affect the availability of soil resources by altering soil chemical and biological processes (Chai and Schachtman, 2022; Vives-Peris et al., 2020; Wang and Lambers, 2019).

The change of rhizosphere pH is an important factor affecting the availability of soil nutrients (Figure 2). The main cause of pH change in rhizosphere is the imbalance of cation and anion absorption, and the factors affecting that balance include mainly N form supplied and symbiotic N_2 -fixation of legumes and some other plant species (Hinsinger et al., 2003). For every NH_4^+ absorbed, the plant releases a proton into the rhizosphere to maintain cell charge balance, resulting in a decrease in rhizosphere pH (Hinsinger et al., 2003; McNear, 2013). Conversely, for every NO_3^- absorbed, two H^+ are co-transported into the cell interior, accompanied by one H^+ extruded out by the H^+ -ATPase to maintain the proton gradient across the plasma membrane, resulting in an increase in the rhizosphere pH because of the net

consumption of one H^+ (Forde, 2000; Marschner, 2012). This provides a physiological basis for targeted regulation of rhizosphere pH based on fertilizer forms (physiologically alkaline fertilizers containing NO_3^- should be applied in acidic soils, and physiologically acidic fertilizers containing NH_4^+ should be used in alkaline soils) because the availability of most nutrient elements is good at near-neutral pH (Shen et al., 2013). Legume symbiosis with rhizobia directly reduces N_2 from the air to NH_4^+ , and in this process the roots release protons into the rhizosphere, resulting in a decrease in the rhizosphere pH (Fageria and Stone, 2006). The rhizosphere pH change caused by plant roots are of great significance to agricultural production, especially in diversified cropping systems. Intercropping legumes (e.g., faba bean, white lupin and chickpea) that have a strong rhizosphere acidification capacity and cereals (e.g., maize and wheat) has been proved to be an effective way to enhance crop productivity and nutrient-use efficiency (especially P, iron, zinc and other sparingly soluble nutrients) in calcareous soils (Bardgett and van der Putten, 2014; Cu et al., 2005; Li et al., 2021).

In addition to rhizosphere acidification, interactions between some components of the root exudates and nutrient-containing soil compounds (e.g., dissolution and chelation) are another way to improve nutrient availability (Wang and Lambers, 2019) (Figure 2). Phosphorus compounds with Ca ions (Ca^{2+}) as well as Fe and Al (hydroxy) oxides in soil are sparingly soluble, making that P unavailable to plants (Shen et al., 2011). Low-molecular-weight organic acid anions such as citrate, malate and oxalate in root exudates can form complexes with Fe^{3+} or Al^{3+} in ferric or aluminum phosphates, thus releasing plant-available P into the soil (Wang and Lambers, 2019). There are many adsorption sites for P (including inorganic and organic forms) on soil particles. Organic acid anions can also (1) occupy these sites and prevent P adsorption or (2) form complexes with cations on the surface of soil minerals (Raghothama and Karthikeyan, 2005). The released inorganic P can be taken up directly by roots, whereas the released organic P forms can be hydrolyzed by phosphatases or phytase (Wang and Lambers, 2019).

Recent studies suggested that plants exude carboxylates not only for P acquisition, but also for effective mobilization of micronutrients such as Fe, Cu, Zn and Mn; in particular, Mn can significantly accumulate in leaves even when plants grow in low-P soils with low exchangeable Mn (Lambers et al., 2015; Wen et al., 2021). Therefore, an alternative method (measuring leaf Mn) to indicate rhizosphere processes (e.g., carboxylate secretion) was proposed, which might be a good screening tool for an assessment of the belowground root traits associated with nutrient acquisition strategies among species growing in low-P habitats (Lambers et al., 2015, 2021). This approach, if proven in a wider range of species, would provide an easily measurable proxy for research and potentially crop breeding because accurate collection and quantification of root-released organic anions is not an easy task to achieve because of the complex interactions among root exudates, soil particles and soil microbial communities (Oburger and Jones, 2018).

Iron generally has low availability in aerated soils [plants need Fe concentration in soil solution of 10^{-6} to 10^{-5} M for optimal growth, but the concentration of soluble Fe in calcareous soils rarely exceeds 10^{-10} M (Frossard et al., 2000; Marschner, 2012)], but root exudates can mobilize Fe from non-soluble forms. Iron is present mainly in the form of Fe^{3+} in most aerated soils; this form is poorly soluble and insufficiently available to dicotyledons and nongraminaceous monocotyledonous plants (with strategy I), especially in calcareous soils with high bicarbonate concentrations (Robin et al., 2008). These strategy I plants promote Fe absorption mainly by releasing protons into the rhizosphere and by reducing Fe^{3+} to Fe^{2+} by the membrane-bound iron reductases in the rhizodermal plasma membranes (acidification-reduction strategy), usually with low efficiency (Kraemer et al., 2006). In addition, the release of phenolics (e.g., coumarin) and flavins combined with rhizosphere acidification facilitates Fe uptake (Tsai and Schmidt, 2017). In contrast, graminaceous species (with strategy II) release chelators (phytosiderophores) that have high affinity for Fe^{3+} , allowing complexed Fe^{3+} to diffuse to the root surface, where the entire phytosiderophore-Fe complex is absorbed (Chen et al., 2017; Kraemer et al., 2006). However, one exception is rice (as the only Strategy II plant) that is capable of absorbing Fe^{2+} without showing ferric iron reductase activity (Ishimaru et al., 2006), which may be related to the abundance of Fe^{2+} in the flooded soils (Ricachenevsky and Sperotto, 2014).

Plants can secrete some enzymes into the rhizosphere to mobilize organic nutrients (Figure 2). For instance, a widespread response of plants to P deficiency is the exudation of acid phosphatase (APase) that can effectively mobilize organic P in the soil (Vance et al., 2003). In most agricultural soils, organic P accounts for 30–80% of total P and must be converted to inorganic P before it can be absorbed by plants (Dalai,

1977). The exudation of APases into the rhizosphere could be detected a few minutes after placing the cluster roots of P-deficient plants (e.g. white lupin) on agar containing organic P (Vance et al., 2003). Similarly in chickpea, the increased activity of APases in the rhizosphere was associated with effective mobilization of soil organic P, promoting the interspecific facilitation in maize/chickpea intercropping (Li et al., 2004). Likewise, the APases activity in the alfalfa rhizosphere was twice as high as in the maize rhizosphere in maize/alfalfa intercropping (Wang et al., 2020a).

In summary, plants interact directly with various nutrient forms in the rhizosphere through root exudates, and the mechanisms can be summarized as: (i) rhizosphere acidification by proton exudation; (ii) chelation by organic acid anions, phenolics and phytosiderophores; and (iii) enzymatic hydrolysis of organic compounds (Figure 2). These processes often co-exist and may involve trade-offs between carbon costs for, and nutrient benefits to, plants (Wang and Lambers, 2019). Although there is a basic understanding of root exudates and recognition of their importance in soil nutrient mobilization, further characterization of the root exudate composition and concentration in the rhizosphere (including diurnal and long-term cycling and spatial gradients) in intensively managed cropland and their impact on nutrient availability is needed. There is currently a lack of suitable approaches for measuring root exudates in the rhizosphere *in situ*. Therefore, quantifying root exudates in natural plant-soil systems remains the focus of future research.

Interactions between roots and microorganisms

In the rhizosphere, root-microbe interactions play an important role in many vital ecosystem processes, especially in nutrient cycling (Figure 2). The plant-microbe interactions may have many beneficial effects on plants, such as increased nutrient availability (Hakim et al., 2021; Kumar and Verma, 2019; Pii et al., 2015), suppression of diseases (Kwak et al., 2018; Mendes et al., 2011) and generally improved resistance to biotic and abiotic stresses (Zamioudis and Pieterse, 2012; Zhang et al., 2017; Zolla et al., 2013). However, these benefits of microorganisms to plants do not come without cost. The rhizosphere is like a large “trading market” in which plants provide microorganisms with carbon sources (root exudates) as substrates or signals in exchange for various microbial services (Huang et al., 2014).

More than 80% of land plants are colonized by arbuscular mycorrhizal fungi (AMF), which assist plants in absorbing mineral nutrients (such as N, P and Zn) from the soil (Smith and Read, 2010). Arbuscular mycorrhizal fungal hyphae can extend up to 12 cm from the colonized root, greatly expanding the soil volume from which plants may obtain nutrients (Li et al., 1991). In return, the mycorrhizal fungi must get carbon from the plant. For instance, fungal partners of *Medicago truncatula* Gaertn increase nutrient transfer only to the roots that provide more carbohydrates (Kiers et al., 2011). Hodge (1996) reported that AM fungi in symbiosis with plants received 4–20% of the total photosynthetic carbon fixed by plants. Recent studies have demonstrated that plants transfer lipids to maintain the colonization of symbiotic mycorrhizas (Jiang et al., 2017). In addition, strigolactones secreted by roots have an essential signaling function during the early stage of AMF root colonization by promoting AMF hyphal proliferation (Besserer et al., 2006; Lanfranco et al., 2018; Ruiz-Lozano et al., 2016). Many flavonoids are also involved in plant interactions with AMF, but they are not essential for this symbiosis (Sugiyama and Yazaki, 2014).

In addition to the interaction between roots and AMF, mycorrhizal hyphae also interact with surrounding microorganisms in the hyphosphere, shaping the so-called second genome of AM fungi, which also contributes significantly to nutrient mobilization and turnover (Zhang et al., 2022). Fructose secreted by AMF hyphae stimulates the expression of phosphatase gene and the release rate of phosphatase in bacteria, thus promoting the mineralization of organic P and ultimately improving the utilization of organic P by AMF (Zhang et al., 2018). In addition, mycorrhizal mycelium provides a “highway” for flagellate bacteria to move towards organophosphorus patches, and the two work together to efficiently use organic P sources (Jansa and Hodge, 2021; Jiang et al., 2021a). Specific soil bacteria and protists also mediate the utilization of organic N by AMF. The gain of N by the AMF from the organic N source increased by at least 65% with the addition of *Paenibacillus* sp. and a protist *Polysphondylium pallidum* to the hyphosphere (Rozmoš et al., 2022). Plants integrate AMF and their extraradical hyphae and hyphosphere microbiome to exploit nutrient resources in soil efficiently, greatly expanding the foraging capacity of roots.

The symbiotic relationship between legumes and N₂-fixing bacteria is another important positive interaction between roots and microbes (Figure 2). It is estimated that 65% of the N used in agriculture

is fixed through biological N₂-fixing processes (Nihorimbere et al., 2011). A variety of bacteria collectively known as rhizobia can fix N₂ in symbiosis with legumes (Gyaneshwar et al., 2011; Sachs et al., 2018). However, legumes do not form symbiosis with all types of rhizobia, and their specificity varies from species to species. Flavones secreted by roots regulate the symbiosis between plants and rhizobia. For instance, legumes secrete flavones and flavonols to attract and initiate legume-rhizobia symbiosis under N deficiency conditions (Bosse et al., 2021; Zhang et al., 2009). Flavonoids attract rhizobia to the root surface by regulating the expression of *nod* genes that are responsible for the synthesis of Nod factors (lipochitooligosaccharides) and play an important role in nodule formation (Skorupska et al., 2017). Isoflavones and saponins are also important signal compounds for symbiosis between soybean and N₂-fixing bacteria (Sugiyama, 2019). Interestingly, evidence suggests that domestication reduces the capacity of legumes to associate with many rhizobial populations (Bourion et al., 2018; Perez-Jaramillo et al., 2016). Incorporating positive associations between crops and N₂-fixing bacteria and mycorrhiza into agricultural management and breeding in the future is one potential way to reduce the dependence on fertilizers (Preece and Peñuelas, 2020).

Root exudates act as mediators in plant-microbe interactions. Roots release phytochemicals into the rhizosphere as chemoattractants of beneficial microorganisms (Figure 2). For instance, canavanine (secreted by legumes) selectively recruits rhizobia resistant to this antimetabolite (Cai et al., 2009) and affects peptidoglycan structure, morphogenesis and fitness of Rhizobiales (Aliashkevich et al., 2021). The border cells and mucilage released by the root tips into the rhizosphere contain large amounts of arabinogalactan proteins that can attract beneficial microbes (bacteria and fungi) and repel root pathogens (Cannesan et al., 2012; Hromadová et al., 2021; Nguema-Ona et al., 2013). Plants also produce and release numerous secondary metabolites including benzoxazinoid, triterpenes, coumarin, flavonoids, and phytohormones to influence the proliferation or suppression of specific microorganisms surrounding the host roots (Pang et al., 2021). Benzoxazines secreted by maize roots can selectively recruit beneficial rhizosphere bacteria (e.g., attract *Chloroflexi*) and influence the assembly of maize microbiome, thus enhancing the adaptability of maize plants to their environment (Guo et al., 2016; Hu et al., 2018). A specialized triterpene biosynthetic network selectively regulates the *Arabidopsis* root microbiota (Huang et al., 2019). Increasing flavonoid concentrations in root exudates also enhances associations between AM fungi and *Triadica sebifera* (Tian et al., 2021). These advances highlight the importance of secondary metabolites in mediating plant-microbe interactions, but the functions of many secondary metabolites, especially their biological roles, remain unproven.

Root exudates are important factors affecting the rhizosphere microbial community. Plants attract specific microbes, thereby altering the composition and diversity of microbial communities in the rhizosphere in plant-specific ways (Berendsen et al., 2012; Broeckling et al., 2008; Leoni et al., 2020). For instance, vanillic acid secreted by cucumber roots alters the rhizosphere soil microbial community (Zhou and Wu, 2013). Phenolic compounds also play important roles in shaping the rhizosphere microbial communities (Fang et al., 2013; Zhou et al., 2018). The abundance of various bacterial genera (described as plant growth-promoting rhizobacteria, PGPR) in the rhizosphere of wheat is highly correlated with the concentration of organic acid anions, and the secretion of organic acid anions varies significantly with plant growth stages (Chen et al., 2019). In addition, more recently developed germplasm recruited fewer microbial taxa involved in the supply side of the N cycling and larger microbial populations that contribute to N losses (Favela et al., 2021), suggesting a loss of some beneficial rhizosphere traits in genotypes bred more recently (Preece and Peñuelas, 2020). Therefore, comprehensive consideration of plant-microbe interactions mediated by root exudates presents an important opportunity in agricultural management and breeding.

Rhizosphere microbes also affect plant root exudation. Rhizosphere microbes can induce changes in plant metabolites, leading to alterations in the biosynthesis of known plant metabolites or to induction of yet unknown metabolites (Etalo et al., 2018). The colonization by AMF increased the secretion of phenols and gibberellins, but decreased the secretion of sugars (Jones et al., 2004). The abundance and characteristics of root-associated fungi also affect the root exudation rate (Meier et al., 2013). Different microbial communities can induce specific systemic changes in root exudates. Local colonization by bacteria of the genus *Bacillus* triggers exudation of acylsugar secondary metabolites with glycosylated azelaic acid being a potential microbiome-induced signaling molecule (Korenblum et al., 2020). Although the understanding of the interactions between microorganisms and root exudation is deepening gradually, the number of plant and microbial species investigated to date barely represents the tip of the iceberg.

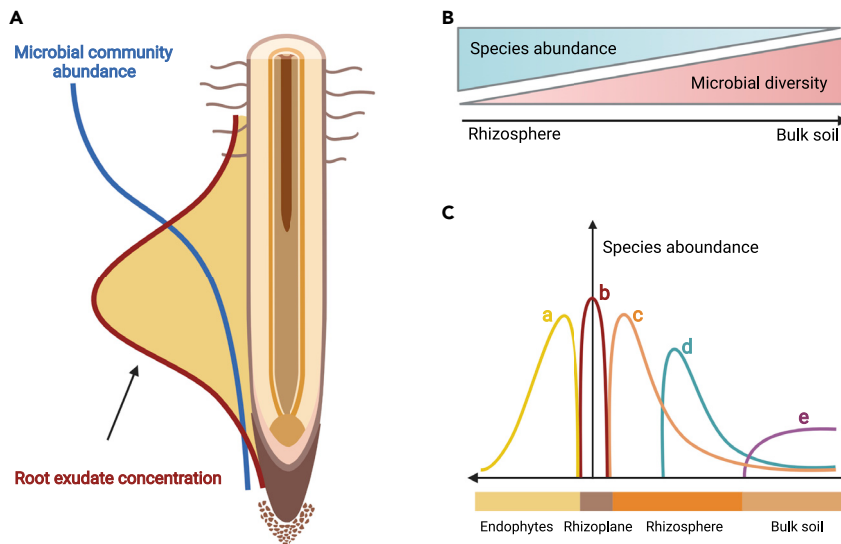


Figure 3. Spatial distribution patterns of root exudates and microorganisms in the rhizosphere

(A) the number of rhizosphere microorganisms increases from the root tip to the maturation zone (blue line); in contrast, the concentration of root exudates (especially mucilage) is maximal close to the root tip (red line). Adapted from Marschner (2012), copyright (2012), with permission from Elsevier.

(B) the diversity of rhizosphere microbial community is far lower than that of bulk soil, but the abundance of specific microbial taxa is higher in the rhizosphere than bulk soil.

(C) endophytic space, rhizoplane and rhizosphere are populated by different microbial taxa: (a) endophytes; (b) rhizoplane microbiota; (c) microorganisms that feed on root exudates or the metabolites of rhizoplane microbiota; (d) microorganisms that use secondary metabolites of rhizosphere microbiota; (e) microorganisms that cannot live in the rhizosphere. The curves represent the relative abundance of microorganisms. Adapted from Bazin et al. (1990), copyright (1990), with permission from John Wiley & Son.

Some seminal questions remain unanswered, particularly how the rhizosphere microbiome regulates root metabolism and exudation as well as how plants coordinate the complex network of belowground interactions.

Spatial distribution of root exudates and microorganisms in the rhizosphere

Because of the variation in the composition and quantity of root exudates, rhizosphere microorganisms are likely to show variation in the spatial distribution in the rhizosphere (including distribution along the root axis and away from the root surface, Figure 3). The root tips are the most active zone of releasing exudates into the rhizosphere, so the concentration of root exudates around the root tips is the highest (Figure 3A). In contrast, the abundance of rhizosphere microorganisms increases from the root tip to the maturation zone (; Marschner, 2012; Nguyen and Guckert, 2001) (Figure 3A). The spatial separation of the peak exudate concentration and the peak microorganism abundance along the root axis ensures that root exudates are not degraded quickly, remaining at relatively high concentration for a period of time to influence the properties of the surrounding soil. This distribution pattern should be correct for the total root exudates and the rhizosphere microbial community, but may differ for a specific exudate or specific microbial taxa.

The diversity of microbial community is lower, and the abundance of specific microbial taxa is higher, in the rhizosphere than bulk soil because of the recruitment of specific microorganisms by root exudates (Kuzakov and Razavi, 2019; Marschner, 2012) (Figure 3B). Detection of microbial community diversity on the millimeter scale in the root elongation zone of wheat and faba bean showed that the root-associated (rhizoplane and rhizosphere) microbiomes had significantly reduced bacterial diversity compared to the bulk soil (Attia et al., 2021), providing direct evidence for this distribution pattern. From root cortex to the bulk soil, the abundance of endophytes in the root cortex decreases significantly between the epidermis and the stele (Figure 3C-a). Microorganisms that are competitive or beneficial to plants can be abundant at the rhizoplane (Figure 3C-b) and near the root surface but become scarce with radial distance from the root surface (Figure 3C-c). Other microorganisms that are less competitive, or can

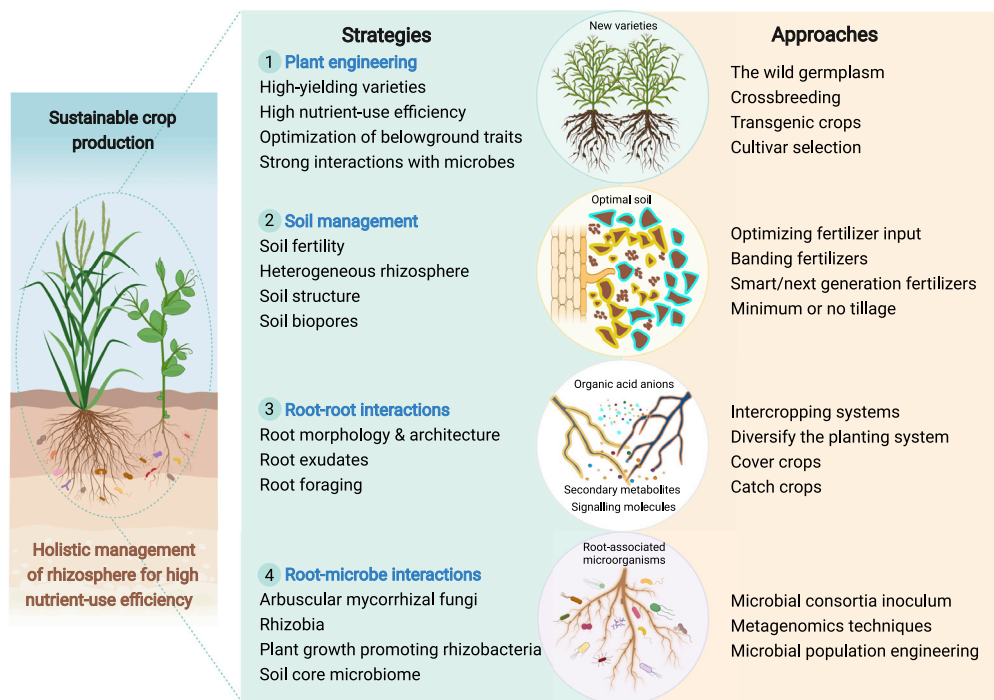


Figure 4. Holistic rhizosphere management strategies and approaches

Strategies and approaches for rhizosphere management were proposed through the four levels of plant, soil, root-root interactions, and root-microbe interactions. The ultimate goal is to maximize plant biological potential and achieve efficient nutrient utilization, resource sustainability and food security by holistically integrating aboveground and belowground plant environments.

only use the decomposition products of microorganisms situated near the root surface, are found farther away from the root surface (Figures 3C-d, e) (Bazin et al., 1990; Kuzyakov and Razavi, 2019). This distribution pattern is still tentative, and more evidence is needed to characterize it.

HOW TO MANAGE THE RHIZOSPHERE?

The rhizosphere surrounding roots (as the main organ for absorbing nutrients and water) is the hub for controlling nutrient flow and information exchange in the plant-soil system. Mycorrhizal fungi and other microorganisms greatly expand the volume of soil explored and contribute to the root function of acquiring soil nutrients. Microbial community gradients, macroorganisms, mucigel, the extent of soil structural modification and spatio-temporal gradients of nutrients, water, root exudates, volatiles and gases constitute a complex and dynamic 'holistic rhizosphere' (York et al., 2016). Recently, the opinion article has suggested that plant-root-rhizosphere-hyphosphere-soil and the associated microorganisms represent a continuous living community called 'rhizobiont' (Shen et al., 2021a). Therefore, the rhizosphere must be manipulated from a systematic perspective (including plants, soils and microbes and their interactions, Figure 4). Developing the rhizosphere management measures that maximize plant biological potential to minimize fertilizer and agrochemical use based on a better understanding of multitude of rhizosphere interactions offers a potential for future food security.

Build comfortable home for root growth–root-zone nutrient management

Many reports have discussed rhizosphere engineering (Ahkami et al., 2017; Dessaux et al., 2016; Hakim et al., 2021; Ryan et al., 2009), but an important point seems to have been overlooked: other rhizosphere engineering methods can only be implemented under the premise of good management of root-zone nutrients; otherwise, it is difficult to achieve benefits. Here, we emphasize that root-zone nutrient management is the most critical link for maximizing root/rhizosphere efficiency because root-zone nutrient concentrations are linked to almost all rhizosphere processes (Figure 4).

Nutrient concentration in the root zone profoundly affects plant root morphology and rhizosphere processes. It is widely recognized that insufficient nutrient supply can affect the growth and development of both roots and shoots. However, excessive N application significantly inhibited maize root development in intensively managed farmland (Shen et al., 2013). Similarly, the total root length and the proportion of fine roots (considered to be the most efficient in nutrient absorption) were significantly reduced in soil with excess P supply (Wen et al., 2017). For white lupin and some species from Proteaceae family, excessive P supply severely limits cluster root formation (Tang et al., 2013; Zhao et al., 2021). Fertilizers are often overused in intensive cropping systems characterized by high inputs and high outputs. However, excessive fertilizer application cannot improve the grain yield beyond a certain point; instead, it squanders resources and causes environmental problems (Ahmed et al., 2017; Chen et al., 2014; Guo et al., 2010), and may even stimulate pathogenic microbes (Toniutti et al., 2017). More and more studies show that optimizing fertilizer input can represent a win-win situation of resource preservation and yield improvement because the biological potential of roots is utilized effectively under such conditions (Chen et al., 2014; Ding et al., 2020; Jiao et al., 2016; Mai et al., 2018). For instance, maize maintained high root efficiency and optimal root morphology in terms of root surface area, root growth vitality and mycorrhizal colonization in the soil with optimized P supply (5–10 mg Olsen P kg⁻¹ soil), resulting in high grain yield (Deng et al., 2014). However, a large number of field experiments are still needed to validate the optimality of root-zone nutrient management practices in different soil conditions and climatic regions.

Another important strategy in root-zone nutrient management is to change the method of applying nutrients – to create nutrient-rich zones of appropriate quality and intensity as well as duration for optimal root exploration (Shen et al., 2013; Wang et al., 2020b; Zhang et al., 2010; Zhang et al., 2016). In farmland ecosystems, various management practices (including fertilization, tillage, irrigation, crop rotation, and straw return) often result in heterogeneous nutrient distribution. In particular, banding fertilizers at specific distance from seed at sowing (starter fertilizers) is widely used in intensive crop production. This is based on plants being able to preferentially allocate their roots to nutrient-rich areas. For example, banding of NH₄⁺-N and P profoundly altered maize root morphology (inducing root proliferation in the nutrient-rich zone) and increased the release of protons and acid phosphatase from roots to the rhizosphere, simultaneously achieving high grain yield and a 30% decrease in the amount of P fertilizer needed (Jing et al., 2010, 2022; Ma et al., 2015). It is urgent to elucidate how banding fertilizers influences soil microbial communities, especially in the nutrient-rich zone where soil properties are significantly different from those in the adjacent areas. The optimized banding of fertilizers in intensive agriculture should take into account soil, fertilizer properties, crop species and varieties because there is evidence of significant differences in the response of different crops to localized application of nutrients (Li et al., 2014a). This is related to the plasticity of root traits; hence, the benefits of rhizosphere management can be maximized in crops with strong root-trait plasticity. In addition, fertilizer banding may be more beneficial in low-input agriculture where resources are scarce (e.g., some African countries) because evidence suggests that banding application of high P rates, even though stimulating maize root proliferation, does not increase shoot biomass compared with low P rates (Wang et al., 2021a).

Choose good neighbors for crops – fully explore interactions between species

Plants have evolved diverse resource acquisition strategies, suggesting there should be combinations of species with complementary traits and strategies that would boost agricultural production. In both natural and agricultural ecosystems, increased biodiversity enhances ecosystem functions, particularly regarding nutrient uptake and productivity (Bardgett and van der Putten, 2014; Barry et al., 2019; Liao et al., 2020; Li et al., 2014b). The mechanisms underpinning the positive relationships between productivity and species diversity are based on complementarity and facilitation (Barry et al., 2019; Hector et al., 1999). Complementary resource use and spatial and temporal niche differentiation lead to increased resource availability, reduced interspecific competition, and possibly increased access to limited resources (Tilman et al., 2001). Belowground traits complementation is crucial for improving nutrient-use efficiency via differences in rooting depths, targeted exploration of localized nutrient patches and/or mobilization of specific insoluble nutrient forms (chemical niches differentiation) to optimize nutrient acquisition (Li et al., 2014b; Yu et al., 2021b).

In intercropping systems, P-mobilizing plants increase P availability from water-insoluble inorganic P (oxide and hydroxide complexes or other unavailable forms) or organic P by releasing carboxylates, protons and enzymes (Li et al., 2014b), thus increasing P availability to the non-mobilizing species. In

addition, intercropped plants may acquire Fe with increased efficiency. For plants with strategy I, chlorosis of young leaves because of Fe deficiency is common in agricultural production (Robin et al., 2008). However, such chlorosis can be alleviated by intercropping with strategy II plants. For instance, in maize/peanut intercropping, Fe^{3+} is mobilized by phytosiderophores released by maize roots and, because of the closeness of the maize and peanut roots, Fe^{3+} is reduced to Fe^{2+} at the peanut root surface, thus improving Fe nutrition of peanut (Xue et al., 2016; Zuo et al., 2000). Such cases demonstrate that optimal combination of crop species in agricultural production (in contrast to monocultures) can effectively improve nutrient efficiency through complementation of belowground traits, providing a great potential for improving resource-use efficiency and crop productivity.

Mounting evidence suggests increasing the diversity of cropping systems can result in not only similar or higher crop productivity and economic returns (Li et al., 2020, 2021; Smith et al., 2008) compared to the monocultures, but also improve soil fertility (Cong et al., 2015; Li et al., 2021), resist pests and diseases (Murrell, 2017; Zhu et al., 2000), and reduce the input requirements for fertilizers and agrochemicals (Li et al., 2020, 2021). In addition, ecosystem services from diversified cropping systems can also contribute to increasing the resilience of these systems to weather variability related to climate change (Roesch-McNally et al., 2018). However, even though many of the benefits of diversified cropping systems are recognized, there are many challenges to expanding them on a larger scale, in particular regarding the optimal combination of crops for different climatic regions and the agricultural systems dependent on large machinery. Another challenge is persuading farmers that it is economically beneficial to intercrop, as dual-crop management is intensive and complex, so the economic benefits need to be clear.

Cooperate with belowground partners – marshalling soil microorganisms

Plant growth, health and productivity depend not only on soil nutrient status, but also on plant-microbe interactions. Alternative strategies for reducing the fertilizer and agrochemical use are effective utilization of mutualistic plant-microbe interactions. Among the rhizosphere microorganisms, PGPR can stimulate plant growth, enhance nutrient availability to plants, inhibit the growth of pathogenic bacteria, and improve soil structure, thus playing a key role in the sustainable crop production (Kumar and Verma, 2019; Pii et al., 2015). PGPR can be divided into two categories: intracellular PGPR, such as various rhizobia that live in root cells and form special organs (nodules), and extracellular PGPR, such as *Arthrobacter*, *Bacillus*, *Azotobacter*, *Micrococcus* and *Pseudomonas* that live in the rhizosphere soil (Hakim et al., 2021). The positive effects of PGPR on plant growth occur directly through N_2 fixation, mobilizing soil nutrients (e.g., P, Fe and Zn), and phytohormone production as well as indirectly via producing antibiotics, siderophores, ACC-deaminase, and lytic enzymes to enhance plant resistance against abiotic and biotic stresses (Ahkami et al., 2017; Dessaux et al., 2016; Hakim et al., 2021).

Plants selectively recruit specific rhizosphere microbial populations to provide essential functions for plant growth and health. A deeper understanding of plant-microbe interactions can enable targeted manipulation of plants and/or microorganisms to establish and maintain beneficial plant-microbe associations. The proportion of bacteria related to N cycling in the rhizosphere was greater in *Oryza indica* (N-efficient) than *Oryza japonica* varieties, which was regulated by the host nitrate-transporter gene *NRT1.1B* (Zhang et al., 2019b). In maize, the flavonoids secreted by roots predominantly promoted the enrichment of Oxalobacteraceae (order Burkholderiales) in the rhizosphere, which in turn was associated with improved lateral root development and increased maize growth and N uptake (Yu et al., 2021a). In symbiotic N_2 fixation, NLP (a plant-specific transcription factor) activates the expression of leghemoglobin gene in root nodules by directly binding to the double Nitrate Response Element (dNRE), regulating the depleted oxygen micro-environment necessary for N_2 fixation (Jiang et al., 2021b). The P-starvation response (PHR) transcription factors are at the core of the mycorrhizal symbiotic transcription regulatory network. The PHRs positively regulate arbuscular mycorrhizal symbiosis by binding to the P1BS *cis*-acting elements to activate the expression of genes related to mycorrhizal symbiosis (Shi et al., 2021). Such insights make it possible to manipulate plant-microbe interactions to conserve N and P fertilizers.

Traditional intensive farming practices with tillage and high fertilizer and agrochemical inputs may profoundly inhibit activity and function of soil microorganisms. More sustainable practices of minimal or no tillage and diverse cropping systems (e.g., intercropping, cover crops, fallow, etc.) may benefit microbial communities (Figure 4). The challenge is to understand how plant-microbe interactions can be manipulated to maximize resource-use efficiency for sustainable crop production. To build improved

rhizosphere microbiome and maximize the potential of plant-microbe interactions for nutrient acquisition, at least the following three aspects can (should) be manipulated (Dessaux et al., 2016; Hakim et al., 2021; Ryan et al., 2009): (i) create optimal soil environment to regulate microbial community structure; (ii) breed host plant genotypes suitable for symbiosis with target microorganisms; (iii) maximize microbial functions and potential benefits to plant growth and health (Figure 4). However, these are huge tasks of natural system engineering, whereby all components interact, and poor suitability of just one component may result in adverse outcomes, with the system failing to fulfill its intended purpose. Therefore, a holistic understanding of plant-microbe interactions with a consideration of soil conditions and the properties of host plants and soil microorganisms is essential in developing new approaches for rhizosphere engineering to achieve more sustainable crop production.

CHALLENGES AND WAYS FORWARD

In recent years, rhizosphere research has made great progress in methodology, such as *in situ* chemical/isotope imaging, high-throughput sequencing, omics techniques, and CT scanning (see details in Oburger and Schmidt, 2016), which have greatly improved our understanding of rhizosphere processes. However, the rhizosphere is a complex and highly dynamic environment hidden belowground, and the multi-component processes occur on the sub-millimeter scale, which presents a hefty obstacle to comprehending rhizosphere fully (York et al., 2016). In addition, plant physiologists and soil physicists, chemists and microbiologists with different interests and concerns have studied the rhizosphere independently, often attempting to understand only a single rhizosphere process without giving due consideration to the multitude of root-soil-microbe interactions. Interdisciplinary knowledge must be integrated to systematically elucidate the rhizosphere and continue to develop advanced techniques for identifying, tracking, quantifying and visualizing rhizodeposits and the resulting biogeochemical and physical changes. Many of the present methods are not directly applicable to the field conditions, which substantially limits our ability to reveal the interactive processes in the field. Only with a better understanding can we manipulate the rhizosphere to optimize abiotic and biotic interactions occurring there.

Rhizosphere management provides a potential opportunity to achieve simultaneously high resource-use efficiency, high crop yields and effective environmental protection. It is necessary to realize that synthetic fertilizers are used not only to provide mineral nutrients to crops, but more importantly as regulators of root growth and rhizosphere processes (Shen et al., 2013; Wang and Shen, 2019). Matching fertilizer types, amounts and application methods to the plant needs is key to maximizing the biological potential of roots. A practical problem, however, is that in many cases the fertilizer market is dominated by the chemical industry that responds slowly and poorly to the real needs of agriculture. Moreover, traditional fertilizer products are often not developed according to the crop requirements and have low use efficiency. Therefore, agricultural scientists and chemistry researchers must cooperate to develop fertilizers better suited to crops. Research and development of smart fertilizers is also necessary. We are already seeing a number of new fertilizer products, such as nano-phosphate fertilizers, that can significantly improve the efficiency of phosphate fertilization (Ma et al., 2021; Solihin et al., 2021), but nano-products still need to be of acceptable quality and cost-effective. More importantly, application of fertilizers must be done based on fertilizing roots and rhizosphere rather than the whole soil. In theory, once all the fertilizer is situated in the rhizosphere, it will be taken by plants without entering the environment, but the technology to approach that goal is not currently available. Therefore, the precision fertilization technology needs to be developed to optimize resource use.

High soil fertility created by over-use of synthetic fertilizers and the breeding of modern, nutrient-inefficient crop varieties have disrupted the specific rhizosphere microbiota with which the wild progenitors of crops have evolved, resulting not only in a loss of crop genetic diversity, but also in the reduced diversity of crop-related soil microbiome and the crop capacity to interact with beneficial microorganisms (Favela et al., 2021; Preece and Peñuelas, 2020). Evidence suggests that modern crop varieties have a compromised capacity to maintain relationships with AMF and PGPR (Bourion et al., 2018; Favela et al., 2021; Perez-Jaramillo et al., 2016). Therefore, the desirable traits of wild crop relatives must be incorporated into modern breeding programs (Preece and Peñuelas, 2020). Genetically modified (GM) crops generally have excellent aboveground performance, such as improving plant pest resistance through specific genetic modification. However, proteins secreted by roots of GM crops after harvest may persist in the soil for months even seasons and have widespread effects on the soil microbiota (Liu et al., 2020). For instance, compared with non-transgenic cotton, repeated planting of transgenic cotton had significant negative effects on

soil microbial community and rhizosphere enzyme activity (Koch et al., 2015). Conversely, other study suggests that soil bacterial communities are more affected by soil texture than by GM crops (Fließbach et al., 2012). More crop types and long-term experiments are needed to continue investigating the interaction of GM crops with soil biota.

PGPR inoculants have some potential for sustainable agriculture as they are one of the recognized alternatives to synthetic fertilizers, pesticides, phytohormones, and other additives (Hakim et al., 2021). However, these bioinoculants generally do not show the expected results under field conditions, possibly because of a lack of consistent establishment and proliferation of these microbes in natural agricultural soils in competition with native microflora. Microorganisms that have the capacity to solubilize compounds containing P, K, and Zn play critical roles in soil biogeochemical cycling and plant growth promotion. So far, studies on PGPR inoculation or biofertilizers have focused on the description of the taxonomic composition of the rhizosphere microbiome, mostly aggregated at the above-the-species levels. However, a deeper understanding of the functions of the rhizosphere microbiome is pivotal to improving plant adaptation to specific environments, the future research should focus on engineering the rhizosphere microbial community rather than adding a single microbial strain.

Metagenomics and synthetic biology tools make it possible to reveal the composition and function of rhizosphere microbial communities. The next-generation sequencing technology (NGS) greatly reduces the cost and increases the depth of sequencing, and has been widely used in the study of rhizosphere microbial community structure, core microbial community and root-microbe interactions, which provided abundant information on the structure, diversity, spatial distribution and a response to changes in soil properties (White et al., 2016b, 2017b). The rhizosphere microbiome of model plant *Arabidopsis thaliana* (Bulgarelli et al., 2012) and food crops maize (Peiffer et al., 2013), soybean (Mendes et al., 2014), rice (Edwards et al., 2015) and wheat (Chen et al., 2019) was characterized based on the NGS. Metagenomics reconstructs complete to nearly complete genomes from unknown and uncultured phyla by using *de novo* assembly, making it possible to directly deduce the metabolic potential of rhizosphere microbial communities (White et al., 2016a). However, metagenomics cannot be used to infer whether any metabolic genes were expressed at the time of sampling; answering this information requires metatranscriptomics. Combining metatranscriptomics with temporal and/or spatial measurements can answer questions about when functions are transcriptionally present and active in relevant time and space (White et al., 2017b). At present, the greatest challenge in using NGS for the rhizosphere science is data analysis and data storage (see details in Thomas et al., 2012; Oulas et al., 2015; White et al., 2017a).

Metaproteomics enables large-scale evaluation of production and/or modification of proteins in microbial communities (Wilmes et al., 2015) and has been used to characterize the rhizosphere environment associated with litter decomposition (Schneider et al., 2012) and methanotrophs in the rhizosphere of rice (Bao et al., 2014). Plants release root exudates including primary metabolites and secondary metabolites into the rhizosphere for chemical communication with surrounding soil microbes. Metabolomics (targeted and untargeted) provides the technical capacity for the analysis and identification of these metabolites (van Dam and Bouwmeester, 2016). Many studies based on metabolomics have demonstrated that root metabolites mediate the communication between plants and beneficial microorganisms as well as defend against pathogen attack (Hölscher et al., 2014; Watson et al., 2015; Ding et al., 2021). The comprehensive characterization of a complex rhizosphere metabolome remains a significant challenge. It is very difficult to extract biological molecules such as DNA, RNA, proteins and metabolites from the rhizosphere soil because of the large amounts of interfering substances such as humic acids from soil matrix, as well as plant polyphenols and other macromolecules (White et al., 2017b). How to effectively separate the metabolites of interest from interfering compounds is critical for high-resolution omics results and also the difficulty to be resolved in the future research.

CONCLUDING REMARKS AND PERSPECTIVES

The major challenge in feeding the world's growing population is to continuously increase crop yields with less fertilizers and agrochemicals on limited land. A systematic understanding and manipulation of the root-soil-microbe interactive processes to maximize the biological potential for improving crop yields and resource-use efficiency is a credible solution to meet this challenge. However, such understanding is reliant on considering the multi-directional and dynamic complexity of root-soil-microbe interactions. Future studies should comprehensively consider plant, soil, microorganisms, and their interactions to

seek optimal ways of rhizosphere manipulation. In particular, non-invasive, real-time and *in situ* visualization and characterization of rhizosphere processes are needed urgently to identify key components involved in amalgamating the multi-directional and dynamic interactions in the rhizosphere. Interdisciplinary approaches are needed to integrate plant biology, genetics, soil science, microbial ecology, and breeding to select highly efficient varieties with excellent belowground traits based on a systematic understanding of the rhizosphere, supported by optimal nutrient management strategies and cultivation techniques, to achieve the global goal of food security and resource sustainability.

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AUTHOR CONTRIBUTIONS

L.W. and J.S. conceived and proposed the topic of the manuscript. L.W., K.Z., K.J., Y.L., L.Z., and L. C. investigated the literature and prepared the outline. L.W. wrote the manuscript. Z.R., J.S., and F.Z. revised the review critically for complete and comprehensive intellectual content. All authors approved the final version of the manuscript.

DECLARATION OF INTERESTS

The authors declare they have no conflicts of interest.

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