

Opinion

Sustainable Cropping Requires Adaptation to a Heterogeneous Rhizosphere

Xin Wang,¹ William R. Whalley,² Anthony J. Miller,³ Philip J. White,^{4,5,6}
Fusuo Zhang,¹ and Jianbo Shen ^{1,*}

Root–soil interactions in the rhizosphere are central to resource acquisition and crop production in agricultural systems. However, apart from studies in idealized experimental systems, rhizosphere processes in real agricultural soils *in situ* are largely uncharacterized. This limits the contribution of rhizosphere science to agriculture and the ongoing Green Revolution. Here, we argue that understanding plant responses to soil heterogeneity is key to understanding rhizosphere processes. We highlight rhizosphere sensing and root-induced soil modification in the context of heterogeneous soil structure, resource distribution, and root–soil interactions. A deeper understanding of the integrated and dynamic root–soil interactions in the heterogeneously structured rhizosphere could increase crop production and resource use efficiency towards sustainable agriculture.

Challenges in Rhizosphere Research

The rhizosphere is the critical zone where roots access water and nutrients, and interact intimately with the physical, chemical, and biotic components of the soil. Rhizosphere processes, such as nutrient mobilization and movement, in addition to root proliferation and symbioses, have an important role in controlling efficient nutrient acquisition by crops [1,2]. Our understanding of the rhizosphere has advanced greatly over the century of research since Lorenz Hiltner first put forward the concept in 1904 [2,3]. Even though rhizosphere science has delivered several practices to agricultural production, such as rhizobial inoculants and fertilizer management strategies, it is still largely uncoupled with the ‘Green Revolution’ and agricultural sustainability [4]. As one of the most important characteristics of the rhizosphere, heterogeneity poses great challenges to rhizosphere research. By ignoring soil heterogeneity, we might have failed to describe realistic root–soil interactions and, thereby, limited the practical application of our knowledge of the rhizosphere to support agriculture [5]. Much theoretical work on resource acquisition by roots and root interactions with soil has been predicated on data obtained from simplified, uniform and often laboratory-based experimental systems (e.g., hydroponics, agar-media, or nonstructured sand), which do not accurately reflect the soil or its heterogeneity [6]. However, the heterogeneous distribution of soil particles and resources in the rhizosphere directs local responses of roots and rhizosphere processes. Although the root processes that underpin nutrient acquisition have been frequently reviewed, a better understanding of root–soil interactions with a focus on the heterogeneity of rhizosphere is now urgently needed.

In this opinion, we highlight the heterogeneity in structure and resource availability in the rhizosphere, the mechanisms by which plants sense these, and the consequent root-induced soil modifications, to explore more realistic root–soil interactions. Recent advances in both plant biology and soil physics and chemistry are summarized for a holistic understanding of rhizosphere processes. We argue that an appreciation of the contribution of soil heterogeneity in the structured rhizosphere can help to close the gap between rhizosphere

Highlights

Root–soil interactions, involving rhizosphere sensing, root architecture and function, as well as root-induced rhizosphere processes, are crucial for soil health, sustainable food security, and resource use efficiency.

Heterogeneity is an important feature of the rhizosphere and this poses a challenge to a thorough understanding of root–soil processes.

Uneven distribution of soil particles and resources shapes root activities and the consequent root-induced modification of the rhizosphere.

Understanding and integrating root biology with soil processes in the context of the heterogeneous physical structure and resource distribution in soil will help close the application gap between rhizosphere research and agricultural practice, thereby contributing to sustainable crop production.

¹Department of Plant Nutrition, College of Resources and Environmental Sciences, National Academy of Agriculture Green Development, China Agricultural University, Key Laboratory of Plant–Soil Interactions, Ministry of Education, Beijing 100193, PR China

²Rothamsted Research, West Common, Harpenden, AL5 2JQ, UK

³John Innes Centre, Norwich Research Park, Norwich, NR4 7UH, UK

⁴Ecological Science Group, The James Hutton Institute, Invergowrie, Dundee, DD2 5DA, UK

⁵National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan 430070, China

⁶Distinguished Scientist Fellowship Program, King Saud University, Riyadh 11451, Saudi Arabia

knowledge and its agricultural application and contribute to crop production in a more efficient and sustainable way.

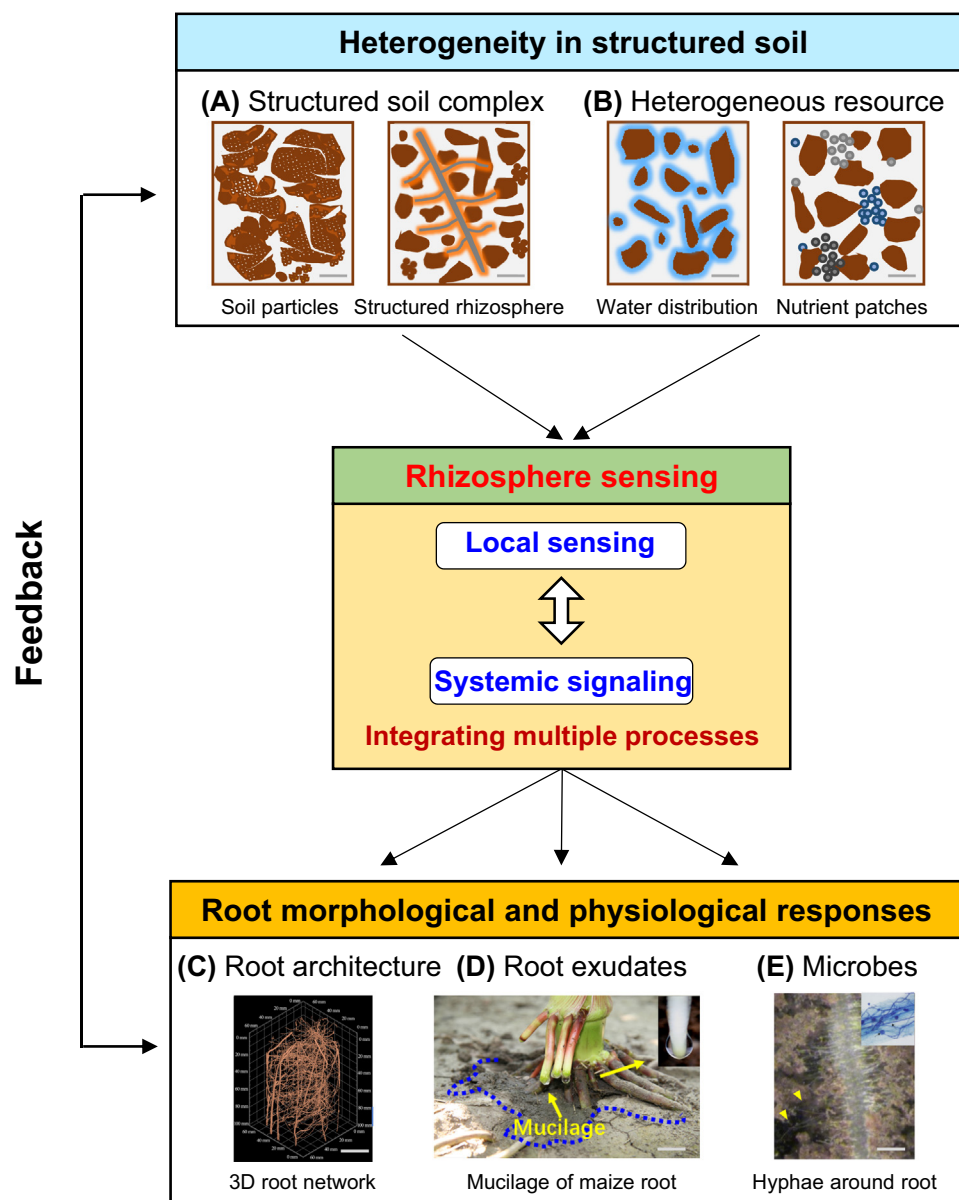
The Heterogeneously Structured Rhizosphere and Plant Root Elongation

The arrangement of soil components into soil structure varies greatly due to their tortuous nature. The heterogeneity of soil particles and pores makes it difficult to study root–soil interactions. Advances in imaging and modeling approaches take us one step forward in describing and understanding the heterogeneity of soil structure [7,8]. Tillage in agriculture can disturb the soil pore network in the cultivated surface layer [9]. Diffusion, the main pathway of nutrient movement towards the root, occurs in the liquid phase of networks of soil pores, and is governed by the water phase connectivity and arrangement of soil aggregates and pores. In the field, soil structure, an indicator of soil functions related to resource supply, such as storage and movement of water and nutrients [10], profoundly affects root growth and nutrient uptake.

Structured soil offers physical anchorage as well as mechanical resistance for root penetration. In agricultural systems, the mechanical resistance of soil to root growth can be modified greatly by compaction and irrigation. Generally, the soil tends to be mechanically weaker when irrigation is used to increase soil moisture [11], even though the size and velocity of waterdrops may induce localized surface soil compaction [12]. Agricultural soil management may lead to a soil profile with a loosened shallow layer and a denser compacted subsoil layer [13]. In this respect, the vertical variation of mechanical resistance to root elongation is often ignored: it increases with depth due to the hydrostatic effects that arise from the weight of soil. Deep roots may encounter stronger mechanical resistance caused by increased hydrostatic pressure (or overburden pressure), which increases with depth [13]. This implies that both the inherent and management-caused variation in rhizosphere structure and mechanical impedance in farmlands can influence both the distribution of roots and the pore networks in soil. Pore networks could be legacies from earthworm activity, and annual or perennial crops that establish deeper roots over time. The role of crop rotation in soil structure deserves more attention. Diverse crop rotations result in greater soil porosity, more aggregates [14], and lower penetration resistance compared with monocultures [15].

Roots can sense the surrounding heterogeneous structure and avoid obstacles, both at the microstructural (volumes less than mm³) and the macrostructural scales [10] (Figure 1). Roots prefer to locate and grow in existing pore networks to penetrate deeper into strong soil [16–18], because the axial pressure is smaller. When roots develop in pores, root extension growth is promoted [19]. The ability of roots to locate and utilize soil pores is determined by plant genotype [20]. The tendency of roots to spread at angles from the vertical, a trait that is also determined by plant genotype, may lead to differences in pore location by roots, although the evidence for this remains weak [16]. The ability of roots to detect soil physical structure is based on touch sensing [21]. When the root cap contacts hard objects, a bZIP transcription factor is induced by cytosolic calcium signaling cascades that interplay with root gravitropic signals [22] and polar auxin transport to facilitate root bending and obstacle avoidance [23]. Such studies shed light on the perception of obstacles by roots and root–soil physical interactions, revealing the plasticity of roots and how they deal with the challenging microenvironment of the rhizosphere with its constantly changing structure.

High mechanical impedance leads to root morphological and physiological modifications, such as a reduction in root system size, slower root elongation rate, deformed root tips, and mucilage exudation into the rhizosphere [24,25]. The root cap mediates the sensing of mechanical impedance [26], and gibberellin [27] and ethylene [28] signaling pathways are involved in plant



Trends in Plant Science

Figure 1. The Central Role of Rhizosphere Sensing in Root–Soil Interactions Matching Inducible Root Traits with the Heterogeneous Soil Structure and Resource Distribution. (A) Structured soil complex. Soil particles are in dark brown and the soil pore spaces in white. Scale bar in left panel: 200 μ m; in right panel: 5 mm. (B) Heterogeneous resource. Soil particles are in dark brown, soil water in light blue, and nutrients are blue and gray dots. Scale bars: 1 mm. (C) 3D root architecture of a maize seedling [80]. Scale bar: 3 cm. (D) Maize root exudates in the field [81]. Scale bar: 2 cm. (E) Hyphae of root-associated fungi in the maize rhizosphere. Scale bar: 1 mm.

responses to mechanical impedance. Recent studies showed that root hairs and the physical shape of root tip govern root penetration [29,30]. The anchoring force of the root hair to the rhizosphere soil aids root penetration [29], whereas sharper root tips with a small root tip radius: length ratio can result in lower axial forces, enabling plant roots to elongate in strong soil [31]. However, the synergistic effects between root tip geometry and root hairs in penetrating strong

soil remain largely unknown. Further studies are needed to investigate how root architecture contributes to penetration in strong soil to identify traits that can be used in crop breeding. Moreover, exploring how the root cap perceives the mechanical impedance and generates hormone signals after the physical interactions is critical for further understanding of root–soil physical interactions.

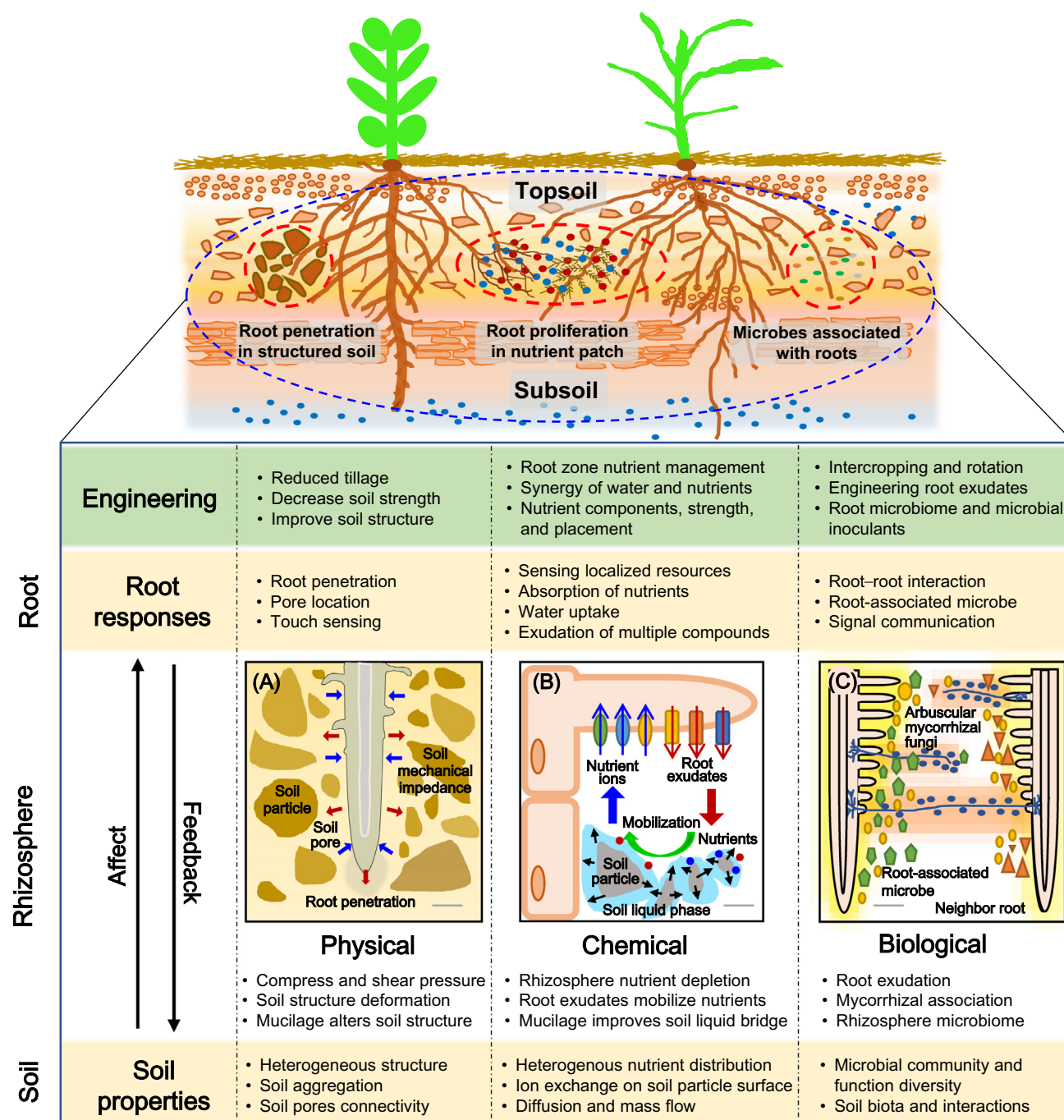
Heterogeneous Resources and Root Foraging

Due to the complexity of soil structure and multiple soil processes, spatial and temporal variation in soil resources occurs ubiquitously [32]. In agricultural systems, heterogeneous nutrient distributions are caused by various management practices, including fertilizer applications, irrigation, crop rotations, straw incorporation, and tillage. Banding of fertilizers is widely used as the starter fertilizer in intensive crop production [33,34]. Unevenly distributed soil habitats with contrasting properties generate a range of different soil microbial communities [35]. Species richness, which is determined by spatiotemporal heterogeneity and structural complexity of natural habitats, is closely related to ecological resilience [36,37], implying the important role of resource heterogeneity in maintaining natural and agroecosystem biodiversity and function.

The expression of root morphological and physiological traits depends on both plant nutrient status and the sensing of local nutrients (Figure 1) to enable better access to the heterogeneously distributed resources in the soil [38]. One important consequence of soil structure is its effect on water movement, which affects the availability, diffusion, and mass flow of nutrients directly. In addition, the arrangement of soil aggregates and pores determines water drainage and, thereby, soil aeration, which impacts oxygen availability for biotic processes, microorganism movement, as well as nutrient availability through soil redox potential [10]. Plant roots generally show hydrotropism, aiding water foraging [39]. High water content locally upregulates the synthesis and transport of auxin and promotes lateral root development in humid soil [40]. Plant roots are preferentially allocated to nutrient-rich areas. When locally available to plant roots, ammonium triggers lateral root branching [41], nitrate and iron stimulate lateral root elongation [42,43], and phosphate improves lateral root formation and elongation [44]. These results suggest that root system architectural responses to local nutrient supply are regulated by nutrient-specific rhizosphere-sensing processes. When nitrate is heterogeneously located in the soil, a nitrate transporter and sensor in the plasma membrane, which transports both nitrate and auxin, directs lateral root proliferation in patches with a high nitrate supply [45]. For phosphate, there is evidence that sensing occurs at the root apex [46]. The sensing of local rhizosphere nutrient availability can mediate systemic alterations in the physiology of the whole plant by long-distance signaling [47]. When nitrate is heterogeneously located in the soil, peptides generated from the parts of the root system that lack nitrogen are translocated to the shoot and act as a root-derived nitrogen starvation signal [48]. Cytokinins produced in roots with a high nitrate supply serve as a root-derived signal of local nitrate availability and, thus, coordinate with the peptide signal [49]. Similarly, signaling peptides are translocated from the shoot to the root in the phloem, upregulating the nitrate transport capacity of roots with a locally high nitrate supply specifically [50]. These observations indicate that roots can sense local variation in nutrient availability and integrate these local signals into the systemic signaling system [51]. Thus, it is now important to integrate the local sensing of nutrient supply, and the local responses of the root system, into models describing the acclimatory responses of plants to nutrient availability.

Coupling of Multiple Factors in Rhizosphere Sensing

We have emphasized the local effects of heterogeneous structure and resource availability in the rhizosphere on root system architecture, activities, and resource capture. In the field, multiple heterogeneities may coexist and vary temporally [52] (Figure 2). Neighboring plants can also create soil heterogeneity and shape root development and resource acquisition by root–root



Trends in Plant Science

Figure 2. Conceptual Model of Root–Soil Physical (A), Chemical (B), and Biological (C) Interactions in the Rhizosphere in the Soil Profile and Rhizosphere Engineering for Sustainable Crop Production. (A) Roots penetrate the structured soil and put pressure (red arrows) on the surrounding soil. Soil particles, which provide mechanical impedance (blue arrows) to roots, are in brown. Scale bar: 1 mm. (B) Roots take up nutrient ions from the soil through transporters (green, blue, and yellow circles) in the plasma membrane of root hairs, and secrete root exudates into the rhizosphere (yellow, orange, and blue rectangles). Soil particles are in gray, the liquid phase around soil particles is in blue, and nutrient ions are red and blue dots. The green arrow indicates that root exudates help to mobilize nutrient ions from the soil. Scale bar: 50 μ m. (C) Roots interact with neighboring roots and rhizosphere microbes (yellow circles, orange triangles, and green polygons). Arbuscular mycorrhizal fungi associated with roots are indicated as blue lines and other microbes in the mycorrhizosphere are represented as blue dots. Scale bar: 1 mm.

interactions in shared rhizospheres [53–55]. The next challenge is to understand the integration of the multiple sensing processes occurring in the rhizosphere. A possible opportunity is to explore the multiprocess interactions in the plant signaling system. From a biological viewpoint, the ability of plants to cope with various environmental factors depends on the crosstalk of local and systemic signaling pathways [47]. Recent advances in our understanding of the integrated nitrogen and phosphorus signaling networks [56] have introduced us to the potential coupling of multiple signaling processes in plants. Nitrate perception enhances the interaction between nitrate and phosphate sensing and activates both phosphate- and nitrate-responsive genes [56]. Phytohormones are crucial in regulating root growth and functioning, and might provide the connections whereby multiple processes interact with each other. For example, auxin is intimately involved in modifying root branching in response to multiple rhizosphere environmental factors [57], including responses to the heterogeneous distribution of iron [43] and nitrate [58]. Auxin may serve to integrate local and systemic signals to determine lateral root formation [59]. Since auxin is involved in modulating numerous physiological processes and can crosstalk with other hormone pathways, this offers an opportunity for plants to respond uniquely and appropriately to combined stresses by integrating multiple signaling systems [59]. In the future, exploring the integration of multiple rhizosphere sensing processes could be an important research area.

Root-Induced Feedback on Rhizosphere Structure and Resource Heterogeneity

Root activities, including root growth, exudation, and symbioses [60], also modify rhizosphere properties by root-induced feedback processes [16,61,62]. Therefore, root–soil interactions are bi-directional and dynamic processes [63]. Roots can increase the porosity of the rhizosphere soil [64], possibly due to soil drying and the associated shrinkage of soil. Mucilage exuded from roots and rhizosphere bacteria is considered to be critical in the formation of liquid bridges at the root–soil interface [65,66], influencing mechanical stability and hydraulic properties in the rhizosphere [65] and the formation of the rhizosheath [67]. Indeed, the 3D architecture of rhizosheaths, and the influence of root hairs and root exudates on this, illustrate the profound effect that roots have on engineering the rhizosphere and its properties [61]. The porosity and connectivity of soil pores in the rhizosphere have been shown to be shaped by root hair development [68]. Thus, the rhizosphere structure is related to inherent soil properties, but is highly modified by root activities.

Root-induced processes modify resource availability in the rhizosphere. Uptake of nutrients by plant roots induces depletion gradients in the rhizosphere [69]. Plant roots exude a range of compounds, such as mucilage, enzymes, organic anions, and protons, which greatly modify soil chemical properties. These organic substances feed the microbiome and increase the microbial community in the rhizosphere [70]. It is clear that rhizosphere microorganisms are highly enriched and incorporate root-derived photosynthetically fixed carbon [71]. In addition, many root exudates are involved in rhizosphere signaling and shaping root-associated microbial communities [72–74]. Agricultural activities, such as fertilizer application and irrigation, drive changes in root-associated microbiomes by affecting the release of organic exudates from roots [75,76]. Regulated by rhizosphere sensing and signaling, root activities modify the physical, chemical, and biological properties of the surrounding soil. This offers opportunities to ameliorate rhizosphere properties by selecting plant genotypes with beneficial root traits [62]. For example, deep roots can penetrate the subsoil layer and access deep soil water and nutrients, which helps to improve the physical structure and resource supply in subsoil [13,17,77]. By manipulating root traits, we could achieve positive root–soil feedback to improve soil health and crop production.

Engineering the Rhizosphere to Achieve Sustainable Crop Production

How to manage soil heterogeneity in agricultural systems remains an open question: the traditional aim of agricultural management is to maximize homogeneity to provide an optimized

environment for crop establishment and growth. However, we know that roots forage effectively for resources distributed heterogeneously in the soil and this trait might be advantageous for crop production in nutrient-limited environments [78,79]. Plants have evolved efficient foraging responses to facilitate resource acquisition and these foraging strategies are still evident in modern crop varieties (even though some symbioses, such as nitrogen-fixing and mycorrhizal systems, could be inhibited with increasing nutrient input), offering possibilities to maximize the potential of the root system plasticity to acquire nutrients rather than relying solely on high fertilizer input. Indeed, traditional intensive farming practices with high-intensity tillage and high fertilizer input may be reducing soil heterogeneity and the biological potential of crops. Recent more sustainable practices of minimal or no tillage might result in greater soil heterogeneity. Current crop varieties that were bred for intense production in more homogeneous soils may not be optimized for nutrient capture in a more sustainable heterogeneous soil. The challenge is to understand how to induce suitable spatial variability to maximize root-foraging capacity to enable sustainable crop production. Local heterogeneities in the rhizosphere can alter root activities significantly and the consequent soil modification produces a feedback on root responses. To construct a better rhizosphere that maximizes the potential of root–soil interactions for resource acquisition, the rhizosphere can be manipulated from two directions: (i) from the soil, to create an ideally heterogeneous environment and resource distribution to stimulate the biological potential of roots; and (ii) from the plant, to manipulate the sensing and response to heterogeneous nutrient supply to effect root traits that benefit soil function. Thus, an integrated understanding of root–soil interactions with a consideration of soil physical heterogeneity and resource distribution can help us to develop new approaches for rhizosphere manipulation to realize more sustainable crop production.

Concluding Remarks and Future Perspectives

The application of current rhizosphere research to agricultural production has encountered bottlenecks, but there are opportunities to break through. Future rhizosphere research should seek to understand root–soil interactions in an integrated manner with consideration of soil heterogeneity and root responses to this. Studies of the rhizosphere focusing on a single process, and without considering the complexity of soil heterogeneity, can limit our ability to understand root–soil interactions. For the plant scientist, one challenge is to understand how the sensing and responses to the heterogeneous availability of multiple resources in the rhizosphere is integrated. Identifying the key molecular components involved in integrating these processes would be an important future research objective. Moreover, the root–soil interactions are bi-directional and dynamic processes. Thus, more non-invasive, real-time, and *in situ* investigations of local rhizosphere processes are urgently required. Interdisciplinary approaches are also needed to integrate plant biology and soil science to describe local root–soil interactions in the rhizosphere. Exploring root–soil interactions in the structured rhizosphere with an appreciation of heterogeneity could inform future strategies to engineer rhizosphere physical, chemical, and biotic properties to improve nutrient use efficiency, preserve soil functions, and enhance crop productivity in a sustainable manner (see Outstanding Questions).

Acknowledgments

This study was supported by the National Natural Science Foundation of China (31772402 and 31330070) and the National Key Research and Development Program of China (2016YFE0101100 and 2017YFD0200200). F.S.Z. and J.B.S. are supported by the project of Beijing's advanced disciplines and the key project of the Chinese Academy of Engineering. W.R.W. is supported by the Biotechnology and Biological Sciences Research Council (BBSRC) Designing Future Wheat Cross-Institute Strategic Programme (grant number BB/P016855/1). A.J.M. was funded by the UK BBSRC Institute Strategic Program Grants 'Molecules from Nature' (BB/P012523/1) and 'Plant Health' (BB/P012574/1) and the John Innes Foundation. P.J.W. was supported by the Rural and Environment Science and Analytical Services Division of the Scottish Government (RESAS) of the Scottish Government. Collaboration between X.W., W.R.W., A.J.M., and J.B.S. was facilitated by a BBSRC exchange project BB/P025595/1 'China: A Virtual Centre for Monitoring the Rhizosphere'.

Outstanding Questions

Given that it is important to investigate root–soil interactions when considering resource acquisition, how can we characterize and quantify root–soil interactions in a heterogeneously structured rhizosphere?

There is an urgent need to apply non-invasive technologies to monitor root–soil interactions in the field. New technologies, such as magnetic resonance imaging and computed tomography, have been applied in controlled environments, but how can these be applied under the field conditions?

How does the relationship between soil structure and resource distribution in the rhizosphere affect plant performance?

How do plants sense, integrate, and respond to the heterogeneity of multiple resources in the rhizosphere?

Can we monitor *in situ* local rhizosphere processes to understand the feedback between plant and soil processes?

How can we manage rhizosphere heterogeneity in agriculture to maximize the potential of plant plasticity and increase crop production?

References

- Shen, J. *et al.* (2013) Maximizing root/rhizosphere efficiency to improve crop productivity and nutrient use efficiency in intensive agriculture of China. *J. Exp. Bot.* 64, 1181–1192
- Lynch, J.P. (2019) Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture. *New Phytol.* 223, 548–564
- Tracy, S.R. *et al.* (2020) Crop improvement from phenotyping roots: highlights reveal expanding opportunities. *Trends Plant Sci.* 25, 105–118
- Hartmann, A. (2015) From the foundations of rhizosphere research in the 19th century to the present high-tech bioanalytical based research approaches. In *Rhizosphere 4 conference*. 21–25 June, 2015, Maastricht, the Netherlands, pp. 1, <https://www.rhizo4.org/>
- Watt, M. (2019) Rhizosphere dynamics and interventions to increase crop productivity. In *Rhizosphere 5 conference*. 7–11 July, 2019, Saskatoon, Saskatchewan, Canada, pp. 93, <https://www.rhizo5.org/>
- Chapman, N. *et al.* (2012) Roots, water, and nutrient acquisition: let's get physical. *Trends Plant Sci.* 17, 701–710
- Daly, K.R. *et al.* (2018) Determination of macro-scale soil properties from pore scale structures: image-based modelling of poroelastic structures. *Proc. R. Soc. A* 474, 20170745
- Pierret, A. *et al.* (2002) 3D reconstruction and quantification of macropores using X-ray computed tomography and image analysis. *Geoderma* 106, 247–271
- Soracco, C.G. *et al.* (2019) Hydraulic conductivity and pore connectivity. Effects of conventional and no-till systems determined using a simple laboratory device. *Geoderma* 337, 1236–1244
- Rabot, E. *et al.* (2018) Soil structure as an indicator of soil functions: a review. *Geoderma* 314, 122–137
- Whalley, W.R. *et al.* (2006) Does soil strength play a role in wheat yield losses caused by soil drying? *Plant Soil* 280, 279–290
- Vaezi, A.R. *et al.* (2017) Contribution of raindrop impact to the change of soil physical properties and water erosion under semi-arid rainfalls. *Sci. Total Environ.* 583, 382–392
- Gao, W. *et al.* (2016) Deep roots and soil structure. *Plant Cell Environ.* 39, 1662–1668
- Munkholm, L.J. *et al.* (2016) Relationship between soil aggregate strength, shape and porosity for soils under different long-term management. *Geoderma* 268, 52–59
- Burgos Hernández, T.D. *et al.* (2019) Assessment of long-term tillage practices on physical properties of two Ohio soils. *Soil Tillage Res.* 186, 270–279
- Atkinson, J.A. *et al.* (2020) Soil strength influences wheat root interactions with soil macropores. *Plant Cell Environ.* 43, 235–245
- White, R.G. and Kirkegaard, J.A. (2010) The distribution and abundance of wheat roots in a dense, structured subsoil - implications for water uptake. *Plant Cell Environ.* 33, 133–148
- Stirzaker, R.J. *et al.* (1996) Soil structure and plant growth: impact of bulk density and biopores. *Plant Soil* 185, 151–162
- Bengough, A.G. (2012) Root elongation is restricted by axial but not by radial pressures: so what happens in field soil? *Plant Soil* 360, 15–18
- McKenzie, B.M. *et al.* (2009) Deep rooting and drought screening of cereal crops: a novel field-based method and its application. *Field Crops Res.* 112, 165–171
- Kolb, E. *et al.* (2017) Physical root-soil interactions. *Phys. Biol.* 14, 065004
- Tsugama, D. *et al.* (2018) Calcium signalling regulates the functions of the bZIP protein VIP1 in touch responses in *Arabidopsis thaliana*. *Ann. Bot.* 122, 1219–1229
- Lee, H.J. *et al.* (2020) PIN-mediated polar auxin transport facilitates root-obstacle avoidance. *New Phytol.* 225, 1285–1296
- Correa, J. *et al.* (2019) Soil compaction and the architectural plasticity of root systems. *J. Exp. Bot.* 70, 6019–6034
- Potocka, I. and Szymanowska-Pulka, J. (2018) Morphological responses of plant roots to mechanical stress. *Ann. Bot.* 122, 711–723
- Dreyer, J. and Edelmann, H.G. (2018) Root cap-mediated evaluation of soil resistance towards graviresponding roots of maize (*Zea mays* L.) and the relevance of ethylene. *Ann. Bot.* 122, 791–800
- Coelho Filho, M.A. *et al.* (2013) The involvement of gibberellin signalling in the effect of soil resistance to root penetration on leaf elongation and tiller number in wheat. *Plant Soil* 371, 81–94
- Okamoto, T. *et al.* (2018) Omeprazole enhances mechanical stress-induced root growth reduction in *Arabidopsis thaliana*. *Plant Cell Physiol.* 59, 1581–1591
- Bengough, A.G. *et al.* (2016) Root hairs aid soil penetration by anchoring the root surface to pore walls. *J. Exp. Bot.* 67, 1071–1078
- Haling, R.E. *et al.* (2014) Root hair length and rhizosheath mass depend on soil porosity, strength and water content in barley genotypes. *Planta* 239, 643–651
- Colombi, T. *et al.* (2017) Root tip shape governs root elongation rate under increased soil strength. *Plant Physiol.* 174, 2289–2301
- Farley, R.A. and Fitter, A.H. (1999) Temporal and spatial variation in soil resources in a deciduous woodland. *J. Ecol.* 87, 688–696
- Jing, J. *et al.* (2010) Localized application of phosphorus and ammonium improves growth of maize seedlings by stimulating root proliferation and rhizosphere acidification. *Field Crops Res.* 119, 355–364
- Li, H. *et al.* (2016) Root over-production in heterogeneous nutrient environment has no negative effects on *Zea mays* shoot growth in the field. *Plant Soil* 409, 405–417
- Fierer, N. (2017) Embracing the unknown: disentangling the complexities of the soil microbiome. *Nat. Rev. Microbiol.* 15, 579–590
- Lindenmayer, D. (2019) Small patches make critical contributions to biodiversity conservation. *Proc. Natl. Acad. Sci. U. S. A.* 116, 717–719
- Wintle, B.A. *et al.* (2019) Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proc. Natl. Acad. Sci. U. S. A.* 116, 909–914
- Giehl, R.F. and von Wiren, N. (2014) Root nutrient foraging. *Plant Physiol.* 166, 509–517
- Dietrich, D. (2018) Hydrotropism: how roots search for water. *J. Exp. Bot.* 69, 2759–2771
- Bao, Y. *et al.* (2014) Plant roots use a patterning mechanism to position lateral root branches toward available water. *Proc. Natl. Acad. Sci. U. S. A.* 111, 9319–9324
- Lima, J.E. *et al.* (2010) Ammonium triggers lateral root branching in *Arabidopsis* in an AMMONIUM TRANSPORTER1;3-dependent manner. *Plant Cell* 22, 3621–3633
- Krouk, G. *et al.* (2010) Nitrate-regulated auxin transport by NRT1.1 defines a mechanism for nutrient sensing in plants. *Dev. Cell* 18, 927–937
- Giehl, R.F. *et al.* (2012) Localized iron supply triggers lateral root elongation in *Arabidopsis* by altering the AUX1-mediated auxin distribution. *Plant Cell* 24, 33–49
- Wang, X. *et al.* (2020) Heterogeneous phosphate supply influences maize lateral root proliferation by regulating auxin redistribution. *Ann. Bot.* 125, 119–130
- Mounier, E. *et al.* (2014) Auxin-mediated nitrate signalling by NRT1.1 participates in the adaptive response of *Arabidopsis* root architecture to the spatial heterogeneity of nitrate availability. *Plant Cell Environ.* 37, 162–174
- Abel, S. (2017) Phosphate scouting by root tips. *Curr. Opin. Plant Biol.* 39, 168–177
- Ruffel, S. (2018) Nutrient-related long-distance signals: common players and possible crosstalk. *Plant Cell Physiol.* 59, 1723–1732
- Tabata, R. *et al.* (2014) Perception of root-derived peptides by shoot LRR-RLKs mediates systemic N-demand signaling. *Science* 346, 343–346
- Poitout, A. *et al.* (2018) Responses to systemic nitrogen signaling in *Arabidopsis* roots involve trans-Zeatin in shoots. *Plant Cell* 30, 1243–1257
- Ohkubo, Y. *et al.* (2017) Shoot-to-root mobile polypeptides involved in systemic regulation of nitrogen acquisition. *Nat. Plants* 3, 17029
- Bouain, N. *et al.* (2019) Getting to the root of plant mineral nutrition: combinatorial nutrient stresses reveal emergent properties. *Trends Plant Sci.* 24, 542–552

52. Oldroyd, G.E.D. and Leyser, O. (2020) A plant's diet, surviving in a variable nutrient environment. *Science* 368, eaba0196
53. Li, L. *et al.* (2014) Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. *New Phytol.* 203, 63–69
54. Zhang, D. *et al.* (2016) Increased soil phosphorus availability induced by faba bean root exudation stimulates root growth and phosphorus uptake in neighbouring maize. *New Phytol.* 209, 823–831
55. Zhang, D. *et al.* (2020) Neighbouring plants modify maize root foraging for phosphorus: coupling nutrients and neighbours for improved nutrient-use efficiency. *New Phytol.* 226, 244–253
56. Hu, B. *et al.* (2019) Nitrate-NRT1.1B-SPX4 cascade integrates nitrogen and phosphorus signalling networks in plants. *Nat. Plants* 5, 401–413
57. Kazan, K. (2013) Auxin and the integration of environmental signals into plant root development. *Ann. Bot.* 112, 1655–1665
58. Yu, P. *et al.* (2016) Root type-specific reprogramming of maize pericycle transcriptomes by local high nitrate results in disparate lateral root branching patterns. *Plant Physiol.* 170, 1783–1798
59. McCleery, W.T. *et al.* (2017) Root branching plasticity: collective decision-making results from local and global signalling. *Curr. Opin. Cell Biol.* 44, 51–58
60. Wen, Z. *et al.* (2019) Tradeoffs among root morphology, exudation and mycorrhizal symbioses for phosphorus-acquisition strategies of 16 crop species. *New Phytol.* 223, 882–895
61. Rabbi, S.M.F. *et al.* (2018) Plant roots redesign the rhizosphere to alter the three-dimensional physical architecture and water dynamics. *New Phytol.* 219, 542–550
62. Jin, K. *et al.* (2017) Shaping an optimal soil by root-soil interaction. *Trends Plant Sci.* 22, 823–829
63. Mariotte, P. *et al.* (2018) Plant-soil feedback: bridging natural and agricultural sciences. *Trends Ecol. Evol.* 33, 129–142
64. Helliwell, J.R. *et al.* (2019) The role of plant species and soil condition in the structural development of the rhizosphere. *Plant Cell Environ.* 43, 1974–1986
65. Carminati, A. *et al.* (2016) Biophysical rhizosphere processes affecting root water uptake. *Ann. Bot.* 118, 561–571
66. Carminati, A. *et al.* (2017) Liquid bridges at the root-soil interface. *Plant Soil* 417, 1–15
67. George, T.S. *et al.* (2014) Understanding the genetic control and physiological traits associated with rhizosphere production by barley (*Hordeum vulgare*). *New Phytol.* 203, 195–205
68. Koebemick, N. *et al.* (2017) High-resolution synchrotron imaging shows that root hairs influence rhizosphere soil structure formation. *New Phytol.* 216, 124–135
69. Kreuzeder, A. *et al.* (2018) *In situ* observation of localized, sub-mm scale changes of phosphorus biogeochemistry in the rhizosphere. *Plant Soil* 424, 573–589
70. Sasse, J. *et al.* (2018) Feed your friends: do plant exudates shape the root microbiome? *Trends Plant Sci.* 23, 25–41
71. Vidal, A. *et al.* (2018) Linking 3D soil structure and plant-microbe-soil carbon transfer in the rhizosphere. *Front. Environ. Sci.* 6, 9
72. Venturi, V. and Keel, C. (2016) Signaling in the rhizosphere. *Trends Plant Sci.* 21, 187–198
73. Korenblum, E. *et al.* (2020) Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling. *Proc. Natl. Acad. Sci. U. S. A.* 117, 3874–3883
74. Zhalnina, K. *et al.* (2018) Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nat. Microbiol.* 3, 470–480
75. Chen, S. *et al.* (2019) Root-associated microbiomes of wheat under the combined effect of plant development and nitrogen fertilization. *Microbiome* 7, 136
76. Dai, Z. *et al.* (2020) Long-term nutrient inputs shift soil microbial functional profiles of phosphorus cycling in diverse agroecosystems. *ISME J.* 14, 757–770
77. Thorup-Kristensen, K. *et al.* (2020) Digging deeper for agricultural resources, the value of deep rooting. *Trends Plant Sci.* 25, 406–417
78. Ma, Q. *et al.* (2013) Localized application of $\text{NH}_4\text{-N}$ plus P at the seedling and later growth stages enhances nutrient uptake and maize yield by inducing lateral root proliferation. *Plant Soil* 372, 65–80
79. White, P.J. *et al.* (2013) Matching roots to their environment. *Ann. Bot.* 112, 207–222
80. Gao, W. *et al.* (2019) A shape-based method for automatic and rapid segmentation of roots in soil from X-ray computed tomography images: Rootline. *Plant Soil* 441, 643–655
81. Zhang, F.S. *et al.* (2010) Rhizosphere processes and management for improving nutrient use efficiency and crop productivity: implications for China. *Adv. Agron.* 107, 1–32