CellPress REVIEWS

Opinion

Shaping an Optimal Soil by Root–Soil Interaction

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Crop production depends on the availability of water and mineral nutrients, and increased yields might be facilitated by a greater focus on roots–soil interactions. Soil properties affecting plant growth include drought, compaction, nutrient deficiency, mineral toxicity, salinity, and submergence. Plant roots respond to the soil environment both spatially and temporally by avoiding stressful soil environments and proliferating in more favorable environments. We observe that crops can be bred for specific root architectural and biochemical traits that facilitate soil exploration and resource acquisition, enabling greater crop yields. These root traits affect soil physical and chemical properties and might be utilized to improve the soil for subsequent crops. We argue that optimizing root–soil interactions is a prerequisite for future food security.

An Imperfect Soil

Roots grow in a complex soil environment. Natural soils exhibit considerable spatial and temporal variability in structure and resource availability, which generates a changing mosaic of soil patches differing in both size and composition (Figure 1, Key Figure) [1,2]. Plants must sense the physical and chemical characteristics of these heterogeneous patches, and their changes, to optimize the placement and activity of their root system [3,4]. Soil conditions such as drought, compaction, nutrient deficiency, mineral toxicity, high salinity, and submergence present significant challenges to root growth [5]. Soil drying inhibits root growth not only because it reduces water availability but also because it makes it more difficult for roots to penetrate [6]. Thicker, shorter, and less vigorous roots are observed when plants grow in hard soils [7–9]. Drought-resistant plants tend to develop a deeper root system, resulting in roots that can reach into still-moist deeper soil layers [10,11]. Lack of nutrients or mineral toxicities restrict plant growth on infertile or hostile soils [12,13]. Since both spatial and temporal variations in water and nutrient availability occur naturally, plants have adapted to deal with these limitations [14]. Adaptions that optimize root architecture for resource acquisition in nonideal soil environments can be exploited in agriculture. However, different root architectural ideotypes are required to optimize the acquisition of water and nutrients, such as nitrate, delivered to the root primarily by mass flow and nutrients that are delivered to the root mainly by diffusion, such as phosphate [12,13,15,16]. For nitrate acquisition, the root ideotype required is termed 'steep, cheap, and deep' and for phosphate acquisition it is termed 'topsoil foraging'. In this opinion article, we summarize root architectural and biochemical traits that facilitate soil exploration and resource acquisition, suggest that these traits can improve soil physical and chemical properties for future crops, and argue that optimizing root–soil interactions is a prerequisite for future food security.

Relationships between Root and Soil
Soil Properties Affect Root System Architecture

Soil structure and compaction are major factors influencing root growth in soil. Soil structure is heterogeneous, both spatially and temporally, due to effects of environment, soil management,

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Key Figure

Root–Soil Interactions in Cropping System Based on Temporal and Spatial Heterogeneous Soil Condition
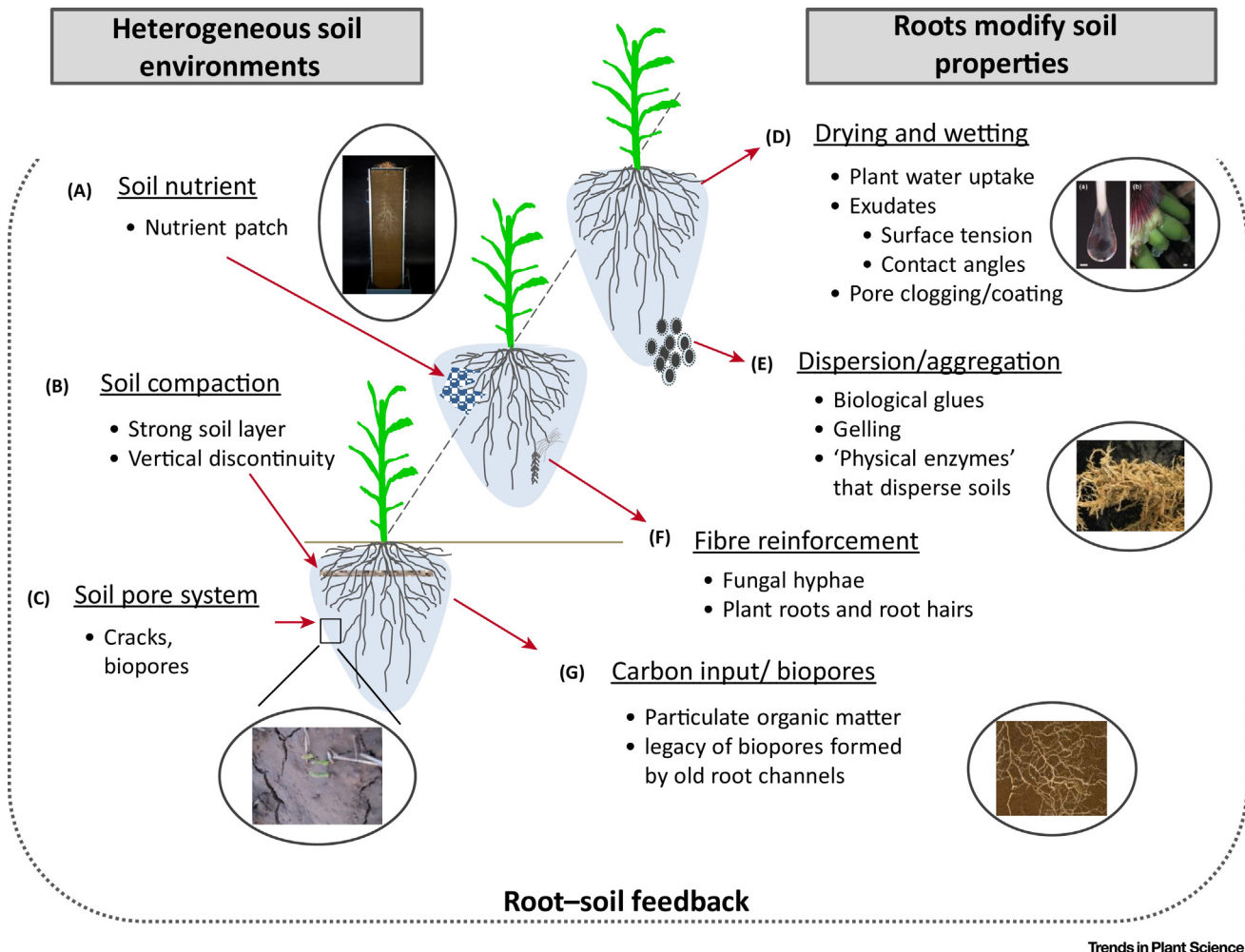

Figure 1. (A) Nutrients are distributed in soil both spatially and temporally. On encountering a nutrient-rich soil patch, the roots of many plant species increase their rate of growth and branching [3]. (B) In addition to soil nutrient status, soil compaction and structure greatly affect root growth. Structural discontinuity often occurs between aggregated seedbeds and compacted soil below or between a tilled layer and an untilled subsoil [8,22]. (C) Soil pore system is also heterogeneous and its heterogeneity is induced by soil management as well as nutrient and water movement [26]. Plant roots are capable of modifying soil structure to accommodate their growth. (D and E) The heterogeneity of water extraction by roots gives rise to tensile stresses, which lead to the production of small soil aggregates [42]. The release of mucilage and water from the root surface can make the soil water content of the root zone greater than bulk soil, and the mucilage secreted by the cells of the root cap can also bind the soil (Reproduced, with permission, from [43]). (F) Root–microbe interactions have been shown to play an important role in the aggregate stability [44]. Root hairs also aid in soil penetration by anchoring the root surface to pore walls [31]. (G) Plant roots can also have a longer-term influence on soil structure through their contribution to soil organic matter and soil pores formation [41,45].

and plant growth (Figure 1). Soil compaction is a phenomenon that involves significant interrelationships between most recognized physical and biological properties of soils [17,18]. Soil pore space, mechanical resistance, and nutrient availability are all modified by soil compaction. Roots growing in soils typically experience a mixture of loose and compact soil

[19,20]. Layered soil compaction (a vertical discontinuity in soil density) often limits root growth and resources use efficiency. The spatial variation in mechanical resistance affects the degree of clustering of the roots [21]. Usually, the dense layers are localized in the lower layers of the soil profile, due to the effects of tillage, and are manifested by layers of strong soil [8,22]. Under these conditions, root systems encountering hard compact zones of soil have the opportunity to proliferate in zones of looser soil. Even in compact soils, areas of lower mechanical impedance are found due to shrinkage cracks and channels formed by earthworms or the legacy features of root growth of earlier crops or vegetation [23,24].

In natural soil, cracks, biopores, structural voids, and the network of interaggregate pores comprise the soil pore system [25]. Roots can exploit cracks, voids, and large pores, or enlarge smaller pores by displacing soil particles. Gao *et al.* [21] suggested that in mineral soils deep roots can only be found when they are able to exploit existing pore networks because soil strength increases with depth irrespective of any compacted layers. The heterogeneous location of pores is principally induced by soil management and the movement of water and nutrients [26]. To help understand the complexity of soil structure, fractal analysis of microtomographic images has been used extensively [27]. Kravchenko *et al.* [28] found that the distribution of voxels belonging to large pores was most heterogeneous in the soil beneath native successional vegetation, followed by soil from no-till and conventional tillage systems, respectively. Bodner *et al.* [29] studied the effect of wetting–drying cycles on soil pore-size distribution, and showed that wetting and drying enhanced macroporosity while decreasing pore heterogeneity. Peng *et al.* [30] conducted a detailed laboratory study by varying the intensity and number of cycles of wetting and drying on soil pores. The results suggested that pore heterogeneity increased with the number of cycles.

Roots Modify Soil Properties

Although soil structure can influence the distribution of roots in the soil, plant roots are capable of modifying soil structure to accommodate their growth. Plant roots affect soil structure through a variety of mechanisms including direct penetration, anchorage, water extraction, and the exudation of compounds into the rhizosphere (Figure 1) [31,32]. Roots can deform the soil when growing in existing pores or through the soil matrix and create high compressive stresses [24,33]. The process of pore formation by roots is believed to be particularly important in undisturbed or no-till soils, as tillage tends to disrupt the continuity of the pore system. Root diameter is closely related to root stiffness, which is important for penetrating hard soils [34]. Chimungu *et al.* [35] found that root anatomical phenes ('phene' is to 'phenotype' as 'gene' is to 'genotype', [36,37]), such as root diameter or the size of cells of particular cell types, are important predictors for the ability of roots to penetrate strong soils. For example, roots with smaller cells in the outer cortical region are less susceptible to buckling and collapse during penetration of hard layers [35]. Radial pressure exerted by growing roots will compress the soil in their vicinity [38] and decrease the porosity in the surrounding soil [39]. Root hairs aid soil penetration by anchoring the root surface to pore walls [31]. Bodner *et al.* [25] found that in root systems differing in morphology-induced distinctive pore dynamics, greater root biomass increased the area and length of macropores (cracks) and coarse root systems could increase macroporosity by 30%.

Root architecture and growth also modify soil–water relationships. Water uptake by roots usually results in an increase in soil strength [6,11]. The heterogeneity of water extraction by roots gives rise to tensile stresses, which lead to the production of small soil aggregates. Compression resulting from water extraction by roots leads to aggregates that are denser and of greater tensile strength than those in unplanted soils [40]. Bardgett *et al.* [41] mentioned that the water uptake by roots promoted a reorganization of clay and that this microenvironment was very rich in root mucilage. The release of mucilage and water from the root surface can

make the soil water content of the root zone greater than the bulk soil (Figure 1, [42,43]). Angers and Caron [44] provided evidence that intact mucilage released by maize root tips significantly increased soil aggregate stability and found that this increase was independent of any microbial activity since it occurred immediately after the incorporation of the exudates in the soil.

In addition to the immediate and short-term effects of roots on the soil structure, which have already been described, plant roots can also have a longer-term influence on soil structure through their contribution to soil organic matter [41,45]. The compounds secreted by roots principally include amino acids, organic acids, sugars, phenolics, and various other secondary metabolites [46]. The mucilage secreted by the cells of the root cap can bind the soil into a rhizosheath, which is 'a peculiar sheath composed of agglutinated particles of sand' [47,48]. The size of the rhizosheath has been correlated with resource acquisition and tolerance to abiotic stresses in some plant species [48]. Some compounds identified in root exudates have been shown to play an important role in root–microbe interactions [49]. For example, flavonoids can activate genes responsible for the nodulation process [50] and other root exudates are responsible for vesicular–arbuscular mycorrhiza colonization [51]. By modifying the soil physical environment and thereby access to water and nutrients, root-induced changes in soil structure can affect crop production potential [14]. The effects of root-induced changes in soil structure on water and nutrient acquisition and their eventual feedback on plant growth and crop production are important aspects of future food security.

The Root System Ideotypes for Soil Resource Capture

The principal roles of the root system are to provide anchorage and to capture soil water and nutrients [52,53]. Plants require rigid elements in their anchorage systems to prevent them from lodging, and resistance to lodging can be improved by increasing the bending strength and angle of spread of adventitious roots [53,54]. The acquisition of each nutrient requires a partly overlapping, but ultimately unique set of root traits [12,13]. The roots of many plant species increase their rate of branching when they enter a patch of soil rich in nitrogen or phosphorus [55]. Studies with *Arabidopsis* have found that auxin-mediated nitrate signaling by NRT1.1 participates in the adaptive response of root architecture to the spatial heterogeneity of nitrate availability [56]. Li *et al.* [57] found that the localized release of phosphate from soil organic matter affected the distribution of cluster roots of white lupin in the soil profile. Similar observations have been made on other crops [12]. Phosphorus uptake and plant biomass of maize are associated with morphological plasticity and greatest in plants accessing the largest nutrient-rich patches [58]. Recently, root phenes reducing the metabolic costs of soil exploration and nitrogen acquisition have been described by Lynch *et al.* [16,59,60] and embodied in a root ideotype termed 'cheap, steep, and deep'. The 'topsoil foraging' ideotype for phosphorus acquisition has also been explored systematically in various crops, including maize, common bean, and soybean, allowing genotypes to be developed for low-phosphorus soils in several geographical regions [36,61]. A better understanding of root–soil interactions will offer the potential to identify further root system traits to improve crop nutrient acquisition in specific soil environments.

Optimal Root–Soil Interactions: A Strategy

An intriguing observation by Stirzaker *et al.* [62] was that roots are more effective at exploiting old root channels than artificial pores. However, the relationships between soil structural geometry and root architecture are poorly understood. The current paradigm is summarized in Table 1, showing some critical soil physical and chemical parameters. The range of soil bulk density, soil pore size, soil water content, and soil strength is important for root growth in different soil types. These constitutive properties of the soil fabric tell us little about the pore networks that enable roots to elongate to depths where, for example, soil strength is high. Recently, Landl *et al.* [63] described a mathematical model for root proliferation that considered

Table 1. The Optimal Ranges for Root Growth of Some Critical Soil Physical and Chemical Parameters

Soil conditions	Requirements		Refs
	Minimal	Maximum	
Soil bulk density restricting root growth (g/cm^3)	–	1.4 clay	[71]
	–	1.8 sand	
Pore size in diameter for rooting (allow root to drain out and air to enter)	0.05–0.5-mm roots	–	[72]
	0.0005–0.05-mm lateral roots, root hairs	–	
Penetration strength (water content dependent)	0.01 kPa	2–2.5 MPa	[20,73]
Air pore space in soil (for root growth)	10%	60%	[73]
Water content in soil	12%	40%	[72]
Oxygen in soil atmosphere (for root survival)	4%	21%	[72]
Temperature limits to root growth	4 °C	34 °C	[72]
pH of soil (wet test)	3.5	8.2	[72]
Total nitrogen	0.5 g/kg	2.0 g/kg	[74]
Olsen-P	10 mg/kg	35 mg/kg	[75,76]
K	40 mg/kg	160 mg/kg	[75,77]

the effects of macropores. A key challenge will be to integrate such models for root elongation with models of soil structure that take into account the complexities of soil structure. This might provide hypothesis-driven approaches for testing the effects of contrasting soil management practices on root–soil interactions. If we can modify soil conditions based on these, and related criteria, then an optimal soil for improved crop yields might be possible.

There are two complementary strategies to increase crop production: agronomic innovation [64,65] and crop breeding [15,37]. The heterogeneity of natural soils poses a considerable challenge to the agronomic approach. Some agronomic approaches such as zero tillage and straw return can benefit plant growth by encouraging the development of stable structure, for example, with a network of resilient channels formed by roots over time [66]. However, other agronomic practices damage the soil structure, particularly intensive cultivation. As well as being expensive (labor and machinery) and time consuming, intensive cultivation tends to form a soil less heterogeneous, which is physically unstable, can be compacted, and not environmentally friendly [35]. Moreover, the objectives of cultivation are often poorly defined.

Crop breeding would exploit the main strategies plants adopt to acquire heterogeneously distributed soil resources through modification of their root system architecture and activity [12,13], which appears to provide an evolutionary advantage [67,68]. Preferential root growth occurs in less-compacted soil with large macropores, lower mechanical resistance, or a high nutrient availability [69]. It would be useful to understand how to match the soil structural pore space and root system architecture to provide the optimal environment for water and nutrient acquisition for crops. If innovative agronomy can be combined with appropriate root system architectures in a synergistic fashion, we might anticipate an increase in crop production in the future.

Concluding Remarks and Future Perspectives

Sustaining a human population of 10 billion in a changing climate is the primary challenge of the 21st century [70]. Although root–soil interactions have a large effect on plant growth and crop production, the effects of roots on soil structure, and how to exploit these, remain to be determined. Shaping an optimal soil, utilizing the plasticity of root system architecture, and the diversity of physical and biochemical interactions between roots and soils might provide us with a novel opportunity to improve soils for agricultural production, increase crop yields, and provide food security in a sustainable manner (see Outstanding Questions).

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Outstanding Questions

How to detail the conception of an optimal soil and how to propose the studies through laboratory, field, and model methods to draw a picture of 'an ideal soil'?

What are the key soil structural factors that can be modified by root architectural or anatomical traits, and how to promote the root traits-based soil management to achieve an optimal soil under different soil texture?

How to develop novel visualization methods to enable researchers to monitor the root and soil interaction in real time and in situ?

How to develop a root growth model to simulate and predict the root adaption response to different soil conditions and root–soil interactions?

How to increase the potential of making root as a major breeding target in future based on the root traits that are screened in optimal root–soil interactions?

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