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Trends in **Plant Science**



Special issue: Root biology and soil health for a sustainable future

Review

Soil compaction sensing mechanisms and root responses

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Soil compaction is an agricultural challenge with profound influence on the physical, chemical, and biological properties of the soil. It causes drastic changes by increasing mechanical impedance, reducing water infiltration, gaseous exchange, and biological activities. Soil compaction hinders root growth, limiting nutrient and water foraging abilities of plants. Recent research reveals that plant roots sense soil compaction due to higher ethylene accumulation in and around root tips. Ethylene orchestrates auxin and abscisic acid as downstream signals to regulate root adaptive responses to soil compaction. In this review, we describe the changes inflicted by soil compaction ranging from cell to organ scale and explore the latest research regarding plant root compaction sensing and response.

The soil compaction problem

Modern agriculture has increasingly relied on the use of heavy machinery to meet the demands of a growing global population. Heavy machinery adoption will continue growing if enough food is to be produced for an expected world population of 10 billion by 2050. However, the use of heavy machines causes soil compaction, and the weight of agricultural machines has been increasing in the last 60 years [1], intensifying detrimental effects of soil compaction.

The compaction problem is complex because it impacts all soil compartments (i.e., physical, chemical, and biological). Compaction is caused not only by heavy machines but also by animals, cattle, and even humans [1,2]. Moreover, climate change is increasing the frequency and intensity of drought or flooding events, which can exacerbate the negative effects of soil degradation such as compaction. In plants, soil compaction greatly reduces root biomass, more than shoot biomass, as the mechanical impedance imposed by the soil restricts root growth, leading to lower water and nutrient uptake [3]. Ultimately, the detrimental effects of soil compaction drastically reduce the yield of staple crops (e.g., rice, wheat, soybean, and corn) [4]. The threat of soil compaction on food security, combined with climate change and the increasing world population [5,6], creates an intricate scenario that requires a holistic solution to these issues, particularly the development of compaction-resilient crops.

To develop such compaction-resilient crops, we need to understand the mechanisms underpinning soil compaction sensing and responses from molecular to plant scale. A pioneer work proposed a model by which roots sense compacted soils via the accumulation of the gaseous hormone ethylene [7]. Later, it was demonstrated that other hormones [auxins, abscisic acid (ABA)] are involved in the response of roots to compacted soil [8], which illustrates the complex ecophysiological responses by plants. Furthermore, it is imperative to identify the root anatomical traits that are favorable under soil compaction scenarios that allow roots to grow better and deeper to increase soil foraging. Ultimately, these questions can only be answered by interdisciplinary approaches because they involve soil science, molecular biology,

Highlights

Roots use ethylene to sense soil compaction due to restricted ethylene diffusion in soil micropores.

Ethylene uses abscisic acid and auxin as downstream signals to regulate root adaptive responses in compacted soil conditions.

Ethylene promotes lignification of outer cortical cells, providing mechanical stability for penetrating roots in compacted soil.

Mechanosensing eases root penetration by regulating root cap cell sloughing in compacted soil.

Ethylene also helps regulate the navigation strategies of root tips when encountering mechanical obstacles.

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mathematical modeling, and physiology. Fortunately, there is an increasing trend in research advocated to study soil compaction [9]. The present review aims to describe the latest research in these aspects and proposes the ideal root model for soil compaction-resilient crops.

Soil compaction: a complex stress

Physical, chemical, and biological changes

Soil compaction increases soil hardness, reduces soil porosity, and creates mechanical impedance stress. Bulk density (BD; g cm⁻³) is a quick measurement that reflects how compacted a soil is, indicating how much mass of dry soil is present in a given volume; higher BD indicates higher compaction [10]. Increases in BD reduce the size of soil pores affecting mainly macropores as well as pore interconnectivity. With decreasing pore interconnection, proportion of gas-filled pores, and pore size, gas diffusivity is restricted [11] (Figure 1). As the soil becomes denser and harder, the mechanical impedance imposed by the soil increases and roots require more strength to grow into it. It has been suggested that mechanical impedance can be the main root growthlimiting factor in the soil if it reaches values of approximately 2 MPa (measured with a penetrometer) in plants such as maize or peanut [12]. Although BD is a useful indicator of soil compaction, soil properties such as soil type, texture, water content, or organic matter directly influence the soil deformation capacity [13]. This means that detrimental effects caused by compaction can be seen at different BD values across soils. As a specific example from a case study, volcanic ash soils present negative effects at lower BD values (0.85 g cm⁻³) compared with clay loam soils (1.39 g cm^{-3}) because they have different properties [14, 15]. Therefore, care must be taken when comparing different soil BDs; one must consider the soil properties to contextualize the BD value.



Figure 1. Soil compaction modulates root system architecture. Comparative figure showing root trait responses in noncompacted versus compacted soil conditions. Compacted soil environments reduce the ability of plant roots to explore soil resources due to inhibited root growth and reduced branching. However, roots tend to develop longer root hairs and thicker roots to maximize resource acquisition and provide mechanical support for root tip penetration in compacted soil. The modulation of root system architecture is primarily regulated by changes in soil structure, which affect gaseous and fluid diffusion due to reduced soil pore volume and a disrupted soil pore network in compacted soil conditions.



The increased soil hardness or BD can occur at both the topsoil and deeper soil layers [16]. Compacted topsoil can be broken with tillage methods, although excessive tillage can have detrimental effects on the soil health, such as soil erosion [17]. Remediation techniques aimed at subsoil compacted layers also exist, but research on the benefits of such methods is scarce, and not all remediation methods are effective for all soil types [18]. Although most attention is given to the topsoil layers because that is where compaction is most detrimental to root growth [19], increased penetration resistance imposed by the subsoil compaction cannot be ignored. Because the weight of farm machinery has the most impact on subsoil compaction and these machines have been made heavier and heavier every year for several decades, the risk of chronic subsoil compaction is increasing, with potential effects on soil function and productivity [1]. Thus, both soil layers must be considered for the design of compaction-resilient crops.

Increasing soil BD also has detrimental effects in the hydraulic dynamics of the soil: Depending on the type of soil, a 10%–20% increase in BD can reduce water infiltration capacity up to 82% and water storage capacity to 49% [13]. Harder topsoil also increases runoff events [20], which further degrades the soil by removing nutrients and organic matter [21]. Moreover, soil water retention is higher in compacted soils, reducing soil water availability [22] (Figure 1). Higher water retention and lower pore size and interconnection affect the gas exchange with the atmosphere [11]. Limited air exchange with the atmosphere restricts O₂ supply to the soil. If O₂ consumption is higher than supply, it can lead to hypoxic conditions [23]. Hypoxic or anoxic conditions changes the soil redox potential to a reduced state. Both the reduced soil state and the presence of anaerobic bacteria facilitate the shift of soil elements such as manganese and iron oxides to their reduced form [19,24,25], and these forms are known phytotoxins [26].

Compaction has negative effects on macrofauna organisms, too, such as earthworms. Although microflora and microfauna are not capable of directly modifying the soil structure, earthworms can change and improve soil structure due to their mass [27,28]. They contribute to nutrient and organic matter cycling, creating soil biopores and overall helping to sustain or enhance soil quality [29]. In a case study, a slight increase in BD from 1.46 to 1.57 resulted in a significant decline in both the number of adult earthworms and their biomass. Despite earthworms' biomass increase after 3 months of compaction, soil porosity, soil infiltration capacity, and earthworm burrow network took approximately 2 years to fully recover. Thus, compaction has negative effects not only on soil properties but also on soil organisms that directly contribute to improvement of the soil quality [30].

Soil compaction is linked to other abiotic stresses

Soil compaction sets off a cascade of several changes affecting soil quality, soil respiration, water and nutrient availability, and potential phytotoxins, to mention a few. Thus, soil compaction carries, to a certain extent, oxygen, nutrient, and water stresses. Nevertheless, these stresses could be further exacerbated by floods or drought, and it is expected that such combination would aggravate the stress level. For example, both soil waterlogging [23] and compaction reduce O₂ in the soil, thus imposing a more severe stress for plant growth. Indeed, wheat field trials showed that soil compaction combined waterlogging reduced grain yield by affecting the number of spikes and affected growth depending on the plant stage [31]. Combining compaction with salinity exacerbated the reduction in root length density and K⁺ uptake [32]. In addition, sodic subsoils subjected to compaction add additional challenges to the salinity stress due to reduced soil porosity and increased mechanical strength [33]. Soil compaction combined with drought further reduced the water potential of the soil, leaves, and roots [34]. Furthermore, a study analyzed various wheat hybrids with contrasting susceptibilities to drought and compaction, trying to assess responses to individual and combined effects of these two stresses. Albeit it is difficult



to separate the effects of compaction and drought, their results indicated that there was a strong interaction between the two stresses on growth and various physiological traits, depending on the hybrid genotypes [35]. In peanut, combining N deficiency with soil compaction led to a significant decline in shoot biomass and impacted the capacity of nodule formation in the roots while intensifying the decline in the accumulation of metabolites related to the tricarboxylic acid cycle already caused by N deficiency [36].

Compaction sensing and responses from molecular to plant scale

Sensing soil compaction

Regulatory mechanisms of root in sensing and responding to soil compaction. Soil compaction has a significant physiological impact on the entire plant system, leading to reduced stomatal conductivity, photosynthesis, carbon assimilation, leaf area, and shoot biomass in various crop species [6]. However, as the primary interface between the plant and soil, the root and root system architecture (RSA) are extremely sensitive to the soil compaction (Figure 1). The alteration of RSA facing soil compaction includes severe growth reduction, suppression of branching, root hair elongation, crown root number enhancement, and thickening of roots [4,22,37,38].

Soil compaction increases the impedance of root growth, leading to decreased total root length and increased root diameter [4,22]. In rice, soil compaction reduces primary root growth by 30% by limiting the elongation of epidermal cells [8]. Moreover, in the elongation and differentiation zone, compaction induces the cortical cell layers' radial expansion and thicker root dimeters [39]. However, the biological significance of increased root diameter under soil compaction remains controversial. Earlier studies suggested that the thicker roots have a greater capability to explore hard soil, because radial expansion provides higher mechanical support and reduces the risk of root buckling while root penetrates the compacted soil [40–42]. However, recent evidence revealed that thinner root may be more advantageous for plants in dealing with the compacted soil, and stronger mechanical support from enhanced root anatomical features is also crucial for better performance in compacted fields [7,8,43,44].

Although compacted soil is attributed to higher mechanical impedance, which inhibits root growth, the role of mechanosensing in compaction stress remains unclear. When root tips initially encounter a hard soil aggregate (compacted soil), mechanosensing pathways may regulate the direction of root growth and prompt swift responses to avoid the hard soil. Notably, root growth through a compacted soil layer is distinct compared with root tips just touching a mechanical obstacle, because the former involves significant structural changes in soil physical properties, limiting gas exchanges, water movement, despite inflicting physical stress. Therefore, it appears that mechanosensing may prime root tips by alerting them to mechanical barriers. However, during sustained growth through compacted soil, restricted diffusion-based signaling paradigms seem to play a key role that guides the root tip growth by assessing the accumulation of gases such as ethylene.

 Ca^{2+} -mediated mechanosensing. To decipher how plants respond to soil compaction, the first step is to elucidate the underlying sensing mechanisms. According to conventional understanding, roots struggle to penetrate compacted soils because the axial growth force exerted by the root tips is less than the mechanical resistance presented by the compacted soil. Thus, roots are thought to sense the soil compaction by detecting mechanical stress. Following this idea, mechanical sensing–associated genes in *Arabidopsis* have been identified with a hard agarbased genetic screening (Figure 2). The first identified mechanical sensing–related regulator is Mid1-complementing activity 1 (MCA1) [45–47]. MCA1 is a plasma membrane–localized Ca²⁺ channel that mediates the mechanical stress–induced Ca²⁺ influx, resulting in cytoplasmic Ca²⁺





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Figure 2. How plant roots sense and respond to soil compaction. High bulk density of soil causes increased mechanical impedance for root penetration due to enhanced soil strength. This high bulk density reduces macroporosity, leading to restricted diffusion of the gaseous hormone ethylene. Trapped ethylene in soil micropores induces elevated ethylene signaling, which reduces root tip elongation, promotes longer root hairs, and causes swelling of root tips. Ethylene uses abscisic acid (ABA) and auxin (Aux) as downstream signals to regulate root thickening and elongation responses, respectively. Ethylene signaling enhances auxin biosynthesis through YUC8 at root tips, which is then redistributed to elongation and differentiation zones by the AUX1 transporter. Mechanical stress, such as that caused by high-density agar, also promotes Ca²⁺ waves through mechanosensitive ion channels such as Mid1-complementing activity 1 (MCA1) and PZO1. Feronia (FER; a mechanosensitive receptor–like kinase) regulates Ca²⁺ fluxes and coordinates the sloughing of lateral root cap cells during root tip penetration in high-density agar systems. Abbreviation: MCS, multiseriate cortical sclerenchyma.

oscillation. In *mca1*-null mutant, the primary root cannot penetrate hard agar, revealing the crucial role of Ca²⁺ signaling in mechanotransduction [45]. In animals, Piezo1 and 2 are essential components of mechanically activated cation channels [48]. Piezo2 has been determined as the major transducer of mechanical forces for touch sensation in mice [49]. *Arabidopsis* encodes an ortholog of Piezo1 and 2 named PZO1 [50]. The expression level of *PZO1* in roots can be significantly induced by the hard agar mimicked mechanical stress. Loss function of *PZO1* reduces the cytosolic Ca²⁺ response and partially dismisses the capability of root penetration into the harder agar plate, supporting the Ca²⁺-dependent mechanosensing [50]. The mechanical stimulation inducing transient cytosolic Ca²⁺ is regulated by the receptor-like kinase FERONIA (FER) [51]. In *fer* mutants, the Ca²⁺ oscillation was impaired after mechanical bending or local touch stimulation, leading to reduced expression of several downstream touch inducible genes.



Furthermore, the *fer* mutants were defective in response to various mechanical stresses, such as reduced penetration to the hard agar and abnormal tracking response encountering an impenetrable barrier [52,53]. Although these results support the hypothesis that Ca²⁺ signaling is essential for mechanical sensing, it remains unknown whether the hard agar approach properly mimics the mechanical stress as well as physical and biological stresses arising from soil compaction.

Sensing soil compaction with the phytohormone ethylene. In addition to mechanical stimulation, soil compaction increases soil BD and decreases porosity, particularly reducing macropores (Figure 1), which disrupts the conduction between soil macropores and limits gas exchange [22,53]. A recent finding discovered that roots use ethylene, a gaseous phytohormone, to sense the soil compaction [7]. The compacted soil builds a physical barrier that restricts ethylene diffusion, leading to the accumulation of root-released ethylene in the rhizosphere (Figure 2). This high concentration of ethylene in the rhizosphere can activate the endogenous ethylene signaling pathway in the root tip. Likewise, exogenous ethylene treatments can inhibit primary root growth and induce root radial expansion, precisely mimicking the typical root phenotype observed under soil compaction. Moreover, the rice ethylene insensitive mutants, *osein2* and *oseil1*, are unable to respond to ethylene and penetrate the compacted soil. This study identified restricted ethylene diffusion rather than mechanical forces as the primary signal to sense soil compaction and established the ethylene signaling pathway as the core mechanism to regulate root response to soil compaction [7].

Plant responses to soil compaction

Modulating soil compaction response through an ethylene-ABA-auxin hormonal network

The next question is how the ethylene signaling pathway controls the root response to soil compaction (Figure 2). Several phytohormones, including auxin and ABA, have been reported as downstream targets of ethylene signaling [54,55]. A pioneer study identified the coordination between auxin and ABA as crucial downstream regulatory targets of ethylene during rice root response to soil compaction [8]. In compacted soil, many ABA biosynthesis genes, such as MHZ4 [54], MHZ5 [55], and ABA2 [56], are induced, leading to high ABA concentration in the root. Exogenous ABA treatment can induce the root radial expansion in wild-type plants and ethylene insensitive mutants, osein2 and oseil1, indicating that ABA functions downstream of ethylene signal to regulate the root thickening under soil compaction. Consistently, the ABA biosynthesis mutants, osmhz4, osmhz5, osaba1, and osaba2, showed less primary root growth inhibition and radial expansion, confirming that ABA serves as an essential regulator in response to soil compaction. Soil compaction causes auxin accumulation in rice root epidermal cells. This epidermal accumulation of auxin is mediated by YUC8-involved auxin biosynthesis [57] and AUX1-mediated auxin transport [58]. The knockout mutants of YUC8 and AUX1 showed better root penetration under soil compaction. The genetic and physiological evidence indicates that auxin accumulation during soil compaction inhibits primary root growth but did not affect root radial expansion. This study revealed that ABA and auxin are downstream regulatory components of the ethylene signaling pathway in dealing with soil compaction, but they have unique roles in modulating radial expansion and root growth inhibition.

A recently defined root trait called 'multiseriate cortical sclerenchyma' (MCS), a set of highly lignified outer cortical cells, enhances the mechanical support for root penetration of compacted soil by increasing tensile strength and root tip resilience [59]. MCS exhibits heritable natural variations among different varieties of maize, wheat, and barley. Interestingly, exogenous ethylene treatment can promote the MCS development in non-MCS maize genotypes by modulating its initiation. With higher lignin deposition in the cell wall, maize genotypes with MCS showed



significantly better root penetration and greater shoot biomass than non-MCS genotypes in compacted soil under the field condition, without affecting normal plant growth in noncompacted soil. Genome-wide association mapping study (GWAS) identified an MEI2-like RNA binding protein highly associated with the MCS phenotype variation. This striking discovery highlights that the lignified MCS is a vital downstream output of ethylene, enabling roots to adapt to compacted soil [59].

In addition to its core role in sensing and responding to soil compaction, ethylene also participates in root circumnutation. Root circumnutation, the helical movement of the root tip, was first observed by Charles and Francis Darwin during their classical study of plant tropisms [60]. This circumnutation was proposed to facilitate the root penetration in the heterogeneous soil by enabling the root tip to navigate past obstacles, such as rocks and compacted soil compartments. Recently, a regulatory network coordinating ethylene, auxin, and cytokinin was identified as a central mechanism in establishing root circumnutation [61]. Loss of function in *OsHK1/MHZ1*, which encodes the rice histidine kinase 1 and acts as a positive regulator of ethylene response [62], results in the complete loss of the organized circumnutational pattern during primary root growth and simultaneously increasing the primary root length. Genetic and physiological evidence demonstrated that OsHK1/MHZ1 promotes the root circumnutation via downstream cytokinin and auxin response. Interestingly, through a series of experiments simulating root growth encountering obstacles in heterogeneous soil, researchers discovered that circumnutational growth of roots helps them bypass hard obstacles in the soil during early growth stages. This adaptation enables the roots to penetrate deeper into the soil, facilitating better seedling establishment.

Design principle of crop roots resistant to compacted soil

Roots, the prime site of nutrient and water absorption, constitute a vital nexus for plant growth and development. Soil compaction has profound ramifications on root architecture, including growth inhibition, radial expansion of root cells, and diminished branching. Ethylene-insensitive lines penetrate the compacted soil conditions in rice, Arabidopsis, and maize [7,44]. However, ethylene-insensitive mutants have several pleiotropic defects, such as compromised responses to biotic challenges, stunted plant growth, and poor yields. Therefore, designing tissue-specific (root tip) ethylene-insensitive plants can provide compaction resistance without compromising ethylene signaling in the entire plant. More realistically, identifying less ethylene-sensitive plants from natural germplasm can open the window to test them in hard soil conditions. Thus, allele mining for ethylene insensitivity in large germplasm collections can bypass the negative impact of ethylene insensitivity on overall plant growth and development. The compaction-resistant crops can improve the subsoil structure. For example, perennial crops improve soil structure because they tend to have deeper and more extensive root systems than annual crops, allowing them to penetrate deeper into compacted subsoil layers [63]. As a result, these compactionresistant crops can create channels and increase soil macropores in compacted subsoil layers. Additional traits can be understood from naturally compaction resilient plants: Cyperaceae plants (e.g., Carex filispica, a grass found in alpine regions of China such as the Himalayas) produce dauciform roots after trampling events. The formation of these roots is positively correlated with higher aboveground biomass and recovery speed, even benefiting other plants that do not produce such roots [64].

Recently, the vital role of highly lignified tissue in the outer cortical parts of the root provided mechanical strength to root tissues, thereby facilitating the penetration of roots into the compacted soil [59]. Thick and strong cell walls can provide mechanical strength to root tips to cope with the compaction stress. Indeed, very small forces are required to slow root growth (<0.2 mN), and root regions between the elongation and maturation zones present mechanical weaknesses that can





lead to root bending [65]. Therefore, discovering the key genes and loci regulating cell wall thickness and stiffness in different crop species will be useful to develop compaction-resistant crops. Root cap cells are the first layer of cells that bear the brunt of compacted soil. Their conical shape stands as an ingenious stratagem, reducing axial pressure and forging a path of lesser resistance through the compacted soil environment [66]. Similarly, shedding of lateral root cap cells, in tandem with the secretion of mucilage, acts as a lubricant, mitigating the friction between the soil and the root cells [12,67]. Several 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase-producing bacteria (*Pseudomonas, Bacillus, Burkholderia, Azotobacter*, etc.) can degrade ACC. Using these strains could help reduce ethylene levels by breaking down ACC, thereby mitigating the negative effects of soil compaction on root growth and foraging. This approach has already proved successful in managing various abiotic stresses, including drought, heat, and salinity [68]. Therefore, these microbes can tweak diffusion-based ethylene signaling and suppress compaction-sensing mechanisms.

Finally, root aerenchyma formation is known to enhance internal tissue O_2 status while reducing the energy demands of the roots [69,70], which could be beneficial under the compaction-induced hypoxia. Therefore, reengineering crops equipped with thin roots possessing rigid cell walls, more MCS, conical and sharp root cap shape capable of shedding more root cap cells, formation of aerenchyma, and high elongation may provide the design principle to create compaction-resistant crops.

Concluding remarks and future perspectives

Roots grow in complex and highly heterogeneous soil environments, influenced by dynamic changes in soil structure, microbial communities, and the distribution of critical resources such as water and nutrients. The complexity of soil environments increases further under edaphic stresses such as soil compaction, which alone can alter nearly all physical, chemical, and biological properties of the soil. Unlike other stresses, such as droughts or floods, soil compaction driven by farming machinery does not require environmental events such as prolonged high temperatures or heavy rainfall. As long as heavy farming machines are used, soil compaction will remain a pertinent issue. In addition, in light of the compounded complexity due to compaction stress, frequent changes in weather patterns, and erratic rainfall, deciphering root tip navigation strategies in real plant soil conditions becomes even more daunting. To truly understand how root tips navigate in compacted soil (see Box 1), we must adopt biological approaches and transcend current state-of-the-art methodologies in real soil conditions (see Box 2 and Outstanding questions). This seminal knowledge is most necessary to develop the perfect root effective in

Box 1. Gaseous signals trigger plant acclimations depending on the soil stress

Heterogeneous soils become progressively harder with depth due to the decrease in tillage, organic matter, and biological activity, coupled with increased compaction from overburden pressure and the accumulation of fine soil particles. These factors contribute to a gradient from soft, friable topsoil to denser, harder subsoil layers. This heterogeneity makes a world of difference to penetrating roots. In real-world soil conditions, ethylene is used by plants to inhibit root growth in compacted layers, favoring root growth toward nearby noncompacted soil. Moreover, compacted soil affects the gaseous exchange of key gases such as oxygen, which is needed for root growth [23], particularly when moisture levels are higher in the compacted soil layer. Interestingly, Plantago major ssp. from trampled (compacted) soils showed better performance when grown under flooding conditions [71], suggesting that trampling-induced compaction primed (through hypoxia) the Plantago major ssp. to better adapt to flooding conditions. Similarly, aerenchyma formation is induced under flooded conditions to transport oxygen from the shoot to the roots [23]. However, when combined with soil compaction, hypoxiainduced aerenchyma formation was blocked, likely due to restricted diffusion of oxygen in the compacted soil micropores [72]. Notably, water deficit also induces aerenchyma formation in roots to support root growth [73]. However, although water deficit increases mechanical impedance by raising soil strength, it does not restrict the diffusion of gases such as in soil compaction stress. This is why roots can grow deeper during water stress, despite experiencing relatively higher mechanical impedance. Therefore, the diffusion of gases will affect root responses, depending on the prevailing complex stress conditions.

Outstanding questions

What is the molecular mechanism by which soil compaction is sensed under combined stress conditions such as drought and compaction or flooding and compaction?

How can we image the movement of water from soil pores to root cells in compacted soil conditions to decipher the microscale heterogeneity of water distribution?

What are the most effective methods for generating single-cell transcriptomic, spatial transcriptomic, spatial metabolomics, and proteomics data sets in crop roots growing under different soil compaction regimes?

How does the microbiota influence the ethylene-based compaction sensing mechanism in various soil conditions?

How can we develop methods to image and quantify rhizosphere exudates, and how do these exudates affect root tip navigation in compacted soil conditions?

What other gaseous and chemical signals are involved in sensing heterogeneous soil environments under compacted soil conditions, and how can we decode them?



Box 2. Bridging the gap: from petri dishes to real soil

Plants are sessile organisms with roots anchoring in the soil. Thus, it is difficult to study the response of roots to various environmental stresses through direct observation. In soil compaction research, the increased soil density makes it even more challenging to observe root morphology by digging up the soil without damaging the roots. To overcome these challenges, experimental systems using high-concentration agar medium [37,74] or wax layers [75,76] systems to mimic soil compaction have often been used to evaluate plant root responses to hard substrates.

Some studies determined a linear relationship between agar concentration penetration resistance, demonstrating the increase in stiffness in the media as agar concentration is increased from 0.5% to 1.1% (maximum penetration resistance of ~0.1 MPa), after which linearity was lost [77]. Earlier studies found a linear relationship between agar concentration and penetrometer resistance up to 3% (~0.3 MPa) [78]. Nevertheless, real soil conditions show different penetration resistances: 0.4 MPa and 1.25 MPa for noncompacted and compacted conditions, respectively [79], markedly higher values than agar media. Recent advances in artificial transparent soils (Nafion), 2D rhizotron systems, and 3D printed soil columns offer promising solutions for overcoming some challenges in compaction research. These tools allow precise observation of root behavior in controlled environments, providing insights into plant responses to compaction. However, soil compaction is influenced by soil texture, organic content, and moisture levels. This dynamic integration of variables underscores the complexity of compaction stress, making it essential to consider these factors when studying and addressing soil compaction.

The discovery of the gaseous hormone ethylene as a sensor of soil compaction in rice root demonstrates that agar medium–based systems may miss essential information present in real soil environments. However, X-ray computed to-mography (X-ray CT) is a feasible approach to fill the gaps between artificial systems and real soil. X-ray CT is a noninvasive 4D imaging technique allowing collection of *in situ* temporal information on root architecture, such as root depth, thickness, angle, and number of lateral roots [80–82] while acquiring information on soil structure [7]. Still, X-ray CT does have some limitations, such as equipment cost, trade-off between soil column size and resolution, or slow data processing.

navigating the soil complexities of soil compaction and potential additional interactions with other stresses.

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Declaration of interests

The authors declare no conflicts of interest.

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