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Review article

Going underground: The importance of soil heterogeneity in shaping plant productivity and responses to saline soils

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ABSTRACT

Plants have to cope and respond to an ever-changing environment, including in soils. Their performance thus depends on their ability to perceive changes in the root zone and to adapt by altering resource allocation to growth, reproduction, or defense. With the majority of physiological and molecular research adopting a reductionist approach, which oversimplifies salinity as a single and uniform factor, conclusions drawn from these studies are likely to have underestimated the complex interactions that shape plant responses in field conditions. In this viewpoint, we argue that understanding root (and whole-plant) responses to soil heterogeneity, intended as the results of dynamic and multiple jointly acting abiotic stressors in saline environments, is central to salinity research. In particular, we introduce a conceptual agenda for studying roots under the dynamic and heterogeneous conditions found at the soil–root interface in saline soils, and its potential to provide new knowledge on how to deal with and adapt in a saltier world, with benefits for agriculture and natural resource management.

1. Spatial variability in saline soils: implications for plant adaptation and management

Soil heterogeneity is a fundamental characteristic of terrestrial ecosystems which critically influences plant performance, particularly in marginal environments (Baveye et al., 2015; Schouten and Houseman, 2019; Baer et al., 2020). This intrinsic heterogeneity is evident in saline soils, which exhibit pronounced spatial and temporal variability (as recently reviewed in Zhang et al., 2025; Valenzuela et al., 2022a) and both natural and human-driven factors constantly contribute to maintaining this heterogeneity in salt-affected environments. For example, naturally saline environments exhibit inherent spatial patchiness where salt concentrations can vary by several fold within the root zone of a single plant. This variability is not static; it shifts over time due to factors like soil parent material, specific physical and chemical characteristics (e.g., texture, sodicity), surface runoff, subsurface lateral water flow, saline groundwater intrusion, capillary rise of saline groundwater, and climatic conditions (e.g., rainfall leading to leaching, or droughts and heatwaves concentrating solutes). At the same time, in agricultural landscapes, agronomic practices, such as irrigation, profoundly influence soil salinity patterns, often creating more complex distributions. For example, micro-irrigation systems, common in arid regions, can lead to highly non-uniform patterns of water, salt, and nutrient deposition directly beneath the emitter (Fig. 1). Salts tend to accumulate at the wetting front or along the upper margin of the wetted volume due to capillarity and evaporation. Conversely, flood irrigation typically results in a more uniform horizontal salinity distribution but establishes a distinct vertical gradient, where salinity generally increases with depth (Isidoro and Grattan, 2011; Malash et al., 2008). While ecologists have long studied the effects of salinity heterogeneity on plant populations and community dynamics (e.g., Conti et al., 2017), physiological and molecular research has, in most cases, taken a reductionist approach, treating salinity as a uniform and static abiotic stressor. By oversimplifying salinity as a single and uniform factor, conclusions drawn

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from these likely underestimate the complex interactions that shape plant responses in field conditions.

The ability of plants to grow in heterogeneously saline environments is complex and multifaceted. In this context, adaptive traits for improved acquisition and use of available resources in heterogeneous environments may improve plant performance in saline soils. These include traits such as root exudation that modifies the rhizosphere, increases in root cortical aerenchyma, hydropatterning, and xerobranching (Busoms et al., 2023; Bao et al., 2014; Mehra et al., 2022; Mondal et al., 2025). Traits that enhance resource foraging in response to environmental patchiness may be just as important as classical salt tolerance mechanisms in maintaining plant function and productivity in inherently heterogeneous saline soils.

Several ecological studies provide compelling examples in support of the above hypothesis. For instance, in the hypersaline seashores around the Dead Sea, where salinity reaches two to three times that of seawater, the persistence of halophytic vegetation has been linked to the ability to use sporadic freshwater from rainfall or flood water rather than relying on hypersaline water near the root system (Yakir and Yechieli, 1995). A similar ability to "forage" for resources in more favorable patches is observed in the non-halophyte *Hydrocotyle bonariensis* (Evans and Whitney, 1992). This rhizomatous dune perennial was found to thrive in salt marshes with soil salinities ranging from 0.7 % to 1.5 %, thus exceeding the expected tolerance threshold for non-halophytes. The presence of this non-halophyte in saline soils was possible due to resource sharing amongst connected ramets, as *H. bonariensis* ramets growing in non-saline conditions supported those exposed to high salinity by sharing resources. Thus, understanding root (and whole-plant) responses to soil heterogeneity in saline environments, including fluctuations in and interactions with other abiotic factors such as nutrient and water availability, is central to advancing our knowledge of plant adaptive strategies to salinity. Traits that enhance resource foraging in response to environmental patchiness may be just as important as classical salt tolerance mechanisms in maintaining plant function and productivity in inherently heterogeneous saline soils.

It is however important to recognize that salt tolerance is defined differently based on the plant's intended use and value, with no single definition fitting all interest groups (Grieve et al., 2012). While ecologists often define salt tolerance in terms of plant survival, agricultural perspectives are more focused on minimizing the negative impacts on crop productivity (Grieve et al., 2012). Consequently, although spatial soil heterogeneity may promote species diversity and plant performance in ecological contexts, it poses significant challenges for agricultural management, resulting in inefficient application of inputs, including water and nutrients, complicating resource management at the field scale. This raises critical questions for improving soil management and for the development of crops with improved performance in salt-affected agricultural lands. Is it possible to harness the inherent responses of plants to soil heterogeneity and the combined effects of multiple stressors in saline environments to enhance crop performance? The complexity of this issue underpins a key, still unresolved, question in breeding for salt tolerance, first posed in the early 1980s: "Given its inherent heterogeneity, should selection for yield in saline soils focus on saline or non-saline areas?" (Richards, 1983).

In the following sections, we introduce a conceptual framework for studying root functions, from the rhizosphere to root morphology, specifically under the dynamic and heterogeneous conditions found at the soil–root interface. Traditionally, soil heterogeneity, particularly regarding salinity, has primarily been addressed at larger field or landscape scales (Hopmans et al., 2021) and is increasingly targeted by precision agriculture strategies (Alkharabsheh et al., 2021; Minhas et al., 2020). However, heterogeneity at finer scales, especially within the plant root zone, and its impact on overall plant performance remains largely underexplored. By focusing on these micro-scale dynamics, we aim to establish a research agenda that promotes a deeper understanding of plant responses in salt-affected soils. Ultimately, our goal is to translate these insights from controlled studies into real-world farming systems.

2. What do we know about root responses to heterogeneous saline soil?

Plants employ various morphological adaptations at the root level to cope with the challenges posed by heterogeneous saline soils. One critical adaptive strategy observed under heterogeneous salinity is the plant's ability to preferentially take up water from, and exhibit compensatory root growth in, less-saline patches of the soil (Lei et al., 2019; Skaggs et al., 2006; Tzohar et al., 2021). While saline soils generally inhibit primary root growth (Munns and Termaat, 1986), strategic foraging is a key factor in optimizing resource acquisition and enhancing overall plant performance under such challenging conditions (Zou et al., 2022). Under saline conditions, root system growth is often inhibited to a lesser extent than shoot growth. This differential response typically leads to an increased root/shoot biomass ratio in many species, including important crops like sorghum, wheat, and rice. Such a shift indicates a preferential allocation of plant resources to the root system, a strategic adaptation to cope with the imposed stress (Munns and Termaat, 1986; Negrão et al., 2017).

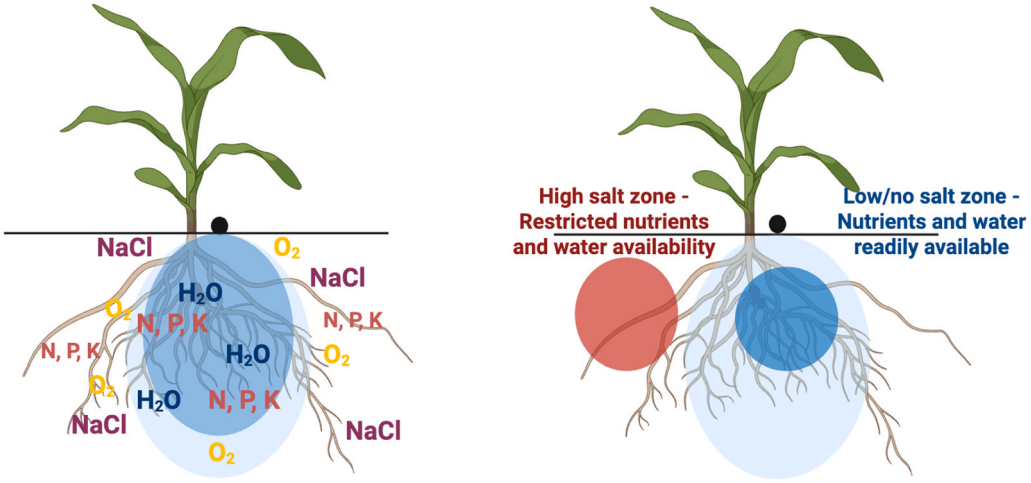

Fig. 1. Illustration of a drip irrigated single plant and how its roots are exposed to varied and heterogeneous conditions where parts of the root zone are exposed to conditions that are expected to promote stress reactions, while other parts are exposed to non-stressed conditions. Created with Biorender.

Moreover, plants can actively sense and respond to salt gradients by exhibiting negative halotropism, a directional growth response where roots grow away from areas of high salt concentration. This avoidance strategy is particularly evident in salt-sensitive species, such as tomato and sorghum (Galvan-Ampudia et al., 2013; Shelden and Munns, 2023). The underlying molecular mechanism involves the precise redistribution of the phytohormone auxin, which is regulated by specific auxin transporters (e.g., PIN2, AUX1) located in the root tip. Interestingly, overexpression of the Na^+ /H^+ antiporter SOS1 can diminish this halotropic response, suggesting a complex interplay between ion transport and hormonal signaling in modulating root directionality (Shelden and Munns, 2023).

Salinity has also been associated with significant alterations in lateral root branching patterns. For instance, in bread wheat, while primary root growth is inhibited, the elongation of lateral roots may be promoted. Similarly, in Arabidopsis, salt stress more severely reduces primary root length than lateral root elongation, and in some cases, lateral root emergence can even be promoted (Shelden and Munns, 2023). These changes suggest a strategic shift towards a root system that can explore a wider area for available water and nutrients (Shelden and Munns, 2023). Another crucial adaptation involves the development of deeper root systems. Plants can extend their roots deeper into the soil profile to access less saline water or more stable, deeper water sources, especially when upper soil layers are dry (Hodge, 2010). For example, maize genotypes characterized by fewer but longer lateral roots can achieve increased rooting depth, thereby improving their drought tolerance (Zhan et al., 2015). Likewise, wheat genotypes with a narrower seminal root angle tend to develop greater root depth, enabling them to obtain soil moisture from deeper layers (Shelden and Munns, 2023). Conversely, some desert plants have evolved to develop shallow lateral roots or specialized "rain roots" that emerge rapidly in response to transient soil moisture and are subsequently shed when the water evaporates (Ramachandran et al., 2025).

While deeper rooting and enhanced lateral branching are clearly beneficial for resource acquisition in heterogeneous saline soils, these adaptations are not without inherent trade-offs. Root growth, as a whole, requires a balanced allocation of resources between roots, shoots, and reproductive organs (Clark et al., 2023). Developing deep roots, for instance, requires a significant investment of carbon resources from the plant, potentially diverting energy from other growth processes. The principle that "roots grow as shallow as possible and as deep as necessary" (Pierret et al., 2016) implies an energy-efficient strategy. While deeper roots provide access to stable water sources, they might be less effective at capturing ephemeral surface rainfall or nutrients concentrated in topsoil. Conversely, extensive shallow lateral roots, while efficient for fertile topsoil, might be more vulnerable to the rapid and intense fluctuations in surface salinity (Schenk and Jackson, 2002). This means that optimizing the plasticity of root system architecture involves balancing competing demands, as the effectiveness of any root system architecture adaptation is not universal but depends on the specific environmental context, such as arid versus irrigated conditions, or transient versus persistent salinity.

Understanding how salt and nutrient heterogeneity affect root growth and anatomy is also critical. Interestingly, evidence from two split-root studies in which plants were exposed to both salt and nutrient heterogeneity suggests that nutrient availability (e.g., K^+) plays a more significant role in guiding root activity (water and nutrient uptake) than salinity (Lycoskoufis et al., 2005; Valenzuela et al., 2022b). In both studies, when nutrients were present only in the saline compartments, the plants maintained water uptake from these areas, leading to salt-induced growth inhibition similar to that observed in plants uniformly exposed to salinity. This result contrasts sharply with those from split-root studies examining only salt heterogeneity, where water and nutrient uptake predominantly occurred in the least saline compartment, resulting in compensatory growth and plant performance compared to uniform salinity (Bazihizina et al., 2012; Tzohar et al., 2021; Valenzuela et al., 2022a).

Potentially opposite stimuli are also likely to occur in the case of P deficiency and salinity. Phosphorus is a critical nutrient, yet its availability is often limited due to strong competition in soils, especially in saline environments, where the high concentrations of Na^+ and Cl^- in the soil solution, along with elevated soil pH in sodic soils, reduce chemical and biological P availability (Su et al., 2022; Xie et al., 2022). These two contrasting stresses, however, lead to opposite root adaptations: salt-stressed plants typically reduce root hair length and density to limit salt uptake (Julkowska et al., 2014; Shabala et al., 2003), whereas P-deficient plants require increased root hair density and elongation to access P from depleted soils (Rongsawat et al., 2021; Zhang et al., 2003). How do plants solve this dilemma? The combined effect of these stresses may result in intermediate phenotypes, or one stressor may dominate over the other. This interaction could lead to plant responses that are either beneficial or detrimental, and these outcomes are difficult to predict based on studies that examine each stressor in isolation (Morales et al., 2022; Renziehausen et al., 2024). In this context, soil microbiome adaptation under heterogeneous conditions could provide a potential solution to the plant's dilemma. In alfalfa seedlings exposed to heterogeneous salinities, the presence of arbuscular mycorrhizal fungi, especially in the saline root portions, alleviated local oxidative stress while improving ion regulatory mechanisms under heterogeneous salinity by reducing Na^+ accumulations in leaves by up to 25 % while improving K^+ and P concentrations by up to 14 and 52 % respectively (Xiong et al., 2025). This, in turn, enabled plants to maintain physiological functions and improve resistance to salt-induced damage.

To fully appreciate these trade-offs and the dynamic nature of root adaptation, it is essential to understand the underlying mechanisms governing plant root responses to varied conditions for water uptake, which can be broadly divided into short- (hours) and long- term processes (days, months, years) (Lobet et al., 2014; Munns, 2002; Munns et al., 2000). In the longer term, root growth is deviated into zones with better conditions for survival and uptake. Root density and number of young roots will be higher in the areas with a better balance of available water and nutrients, sufficient O_2, and minimal harmful material such as detrimental salts (Bazihizina et al., 2012; Munns, 2002). Short-term responses, enabling compensated uptake without changes in root distribution, are less understood. Possible drivers and explanations for short-term changes in uptake patterns are explainable based on the movement towards equilibrium of potential energy gradients, regulation of hydraulic conductivity within the roots as water moves from the root surface to the xylem via cell membranes, and root-facilitated hydraulic redistribution (Bazihizina et al., 2012; Bazihizina et al., 2017, Cai et al., 2018; Lei et al., 2019; Steudle, 2000; Thomas et al., 2020). Differential changes in hydraulic conductivity in different parts of the root zone of a single plant may improve plant-scale efficiency of water uptake by allowing more uptake from regions with higher water potential, where water is more available.

Stress-induced signaling by roots to shoots may complicate the mechanisms of uptake from regions differing in their availability of water. Some studies suggest that heterogeneity with a plant's root-zone (e.g. partial root-zone drying) triggers root to shoot signaling with ABA or other hormones, which cause stomatal closure and reduction of transpiration and therefore uptake (Kang and Zhang, 2004). If this is the case, compensatory water uptake from low salt areas would be a function of and accompanied by less total water uptake, potentially without a cost to plant carbon sequestration (Sepaskhah and Ahmadi, 2012). Results from split-root experiments on tomatoes (Tzohar et al., 2021) suggest that as long as there is no hydraulic restriction for uptake in other areas of the root zone, temporal reduction in water availability due to salinity in some parts of the root zone will not affect plant-scale transpiration or plant activity. Tzohar et al. (2021) explain compensation by equilibration of water potential across the root system, with the system's hydraulics being the primary, if not sole, driver.

2.1. Soil microbiota: hidden partner in plant adaptation to heterogeneously saline soils

Soil salinity is known to significantly influence soil microbial community structure and function (Rath et al., 2019). This effect is partly driven by salinity-induced abiotic stress, which alters soil physical properties through plant root-mediated processes. Variations in root growth patterns and exudate composition can affect soil pore volume, connectivity, aggregation, and properties such as water surface tension and viscosity in the rhizosphere (Carminati, 2012; Carminati et al., 2013; Hallett et al., 2003; Read et al., 2003; Rötzer et al., 2023; Wang et al., 2020; Zarebanadkouki et al., 2016). For instance, controlled experiments with *Zea mays* have demonstrated that soil salinity dramatically reduces rhizosphere hydraulic conductivity by decreasing soil tortuosity and permeability (Wang et al., 2020). In this study, the saline treatment corresponded to a saturated-paste extract electrical conductivity of about 8 dS m^{-1} , and under those conditions the rhizospheric permeability declined by ~80 % compared with the control, while the combination of salinity and water deficit caused a reduction of ~90 %. Thus, while water deficit alone reduced soil permeability by approximately 60 %, salinity and the combination of salinity and water deficit caused reductions of 80 % and 90 %, respectively, compared to control conditions. Thus, moderate to high soil salinity (ECe ≈ 8 dS m^{-1}) can severely impair rhizosphere water transport, which likely mediates major shifts in microbial community structure and function under saline conditions.

Beyond its effects on soil physical characteristics, salinity also acts as a selective filter on microbial communities. In a study that incrementally increased soil salinity (from 0 to 22 mg g^{-1} NaCl), it was found that microbial communities adapted rapidly, with changes occurring already after the first days of salt exposure (Rath et al., 2019). The study assessed not only microbial community structure (16S rRNA sequencing) but also microbial community functions, including soil microbial respiration (CO_2 production), bacterial growth (leucine incorporation), and fungal growth (acetate incorporation into ergosterol) over a 40-day incubation. Although salinity initially suppressed all functions (respiration and growth), bacterial activity recovered within a week at moderate (in treatments up to 7 mg NaCl g^{-1}), eventually exceeding the no-salt control by more than 200 %, while fungal growth although initially slow at high salt eventually became dominant at the highest salinity (22 mg NaCl g^{-1}). This rapid adaptation involved a shift toward halotolerant microorganisms, indicating that microbial communities can reorganize both microbial communities' composition and functional activity to adjust in response to changing environmental conditions. At the same time, plants actively shape the rhizosphere environment through root-mediated processes that modify both soil chemical and physical properties. Such dynamic microhabitats influence microbial community composition (Chen et al., 2021; Furtado et al., 2019). For instance, studies on halophytes such as *Salicornia europaea* have shown that the composition of endophytic communities is strongly shaped by the surrounding soil micro-ecological environment, as endophytes are primarily recruited from the soil microbiome (Furtado et al., 2019; Szymańska et al., 2018). The benefits that these microbial communities can provide to plants include enhanced nutrient acquisition, increased stress tolerance, and improved disease resistance (Chen et al., 2023; Li et al., 2025).

Beneficial microbes such as plant growth promoting rhizobacteria and mycorrhizal fungi improve plant performance through multiple mechanisms (Chen et al., 2024; Etesami and Beattie, 2018). For instance, mycorrhizal fungi improve plant performance in saline soils by ameliorating soil structure and water retention and, as they increase the extension of the root system through their hyphal networks, by improving plant water and ion relations, in particular through higher P uptake and reduced Na^+ accumulation (Porcel et al., 2016). Likewise, salt-tolerant plant growth promoting bacteria utilize numerous mechanisms that affect salt-induced physiological, biochemical, and molecular responses. These range from enhancing plant tissue osmotic adjustment via altered ion homeostasis and osmolyte accumulation to improving oxidative stress response and growth maintenance through the synthesis of free radicals scavenging enzymes, phytohormones, and other metabolites (Mishra et al., 2021). Recent case studies showcase the potential of shaping microbial communities as a tool to sustainable increase production in salt-affected soils (Hanif et al., 2024). For example, the introduction of indigenous microalgae into saline soils has been shown to enhance soil health by forming algal crusts, increasing chlorophyll content, and improving soil structure (Zhang et al., 2024). In another example, the inoculation with bacteria containing the enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, to prevent the excessive increases in ethylene synthesis under various stress conditions, improved salt tolerance in several plant species (Orozco-Mosqueda et al., 2020). Ethylene interferes with auxin responses when overproduced; lowering ethylene removes that negative feedback, enabling IAA (including that produced by bacteria) to stimulate root and shoot growth even under stress. By reducing ethylene-mediated inhibition of root and shoot growth, plants inoculated with ACC deaminase producing bacteria often exhibit enhanced root elongation, more robust root systems, greater shoot and root biomass, improved physiological status (e.g., chlorophyll content), and better overall growth under saline conditions. This tolerance can manifest as increased growth despite similar tissue salt concentrations (physiological tolerance) or as growth dilution, in which enhanced biomass reduces the concentration of accumulated salts. Microbial associations thus represent an important strategy for plants to adapt to challenging environments.

It is, however, critical not to overlook the highly heterogeneous dynamic nature of the rhizosphere, which results in distinct microbial assemblages across spatial and temporal scales. Indeed, soil heterogeneity plays a fundamental role in shaping microbial diversity and ecosystem functionality at the rhizosphere scale. As for soil salinity, this heterogeneity is shaped by: (*i*) inherent rhizosphere physical (pore volume, connectivity, and aggregation) and biogenic (surface coatings, mineral associated carbon) structures, that both affect water, O_2, and ion distribution and availability (Jiao et al., 2021; Kuzyakov and Blagodatskaya, 2015; Li et al., 2024; Zhang et al., 2023); (*ii*) management-induced variation in soil texture that inevitably alters rhizosphere structure (e.g. mechanical impedance in farmlands can influence both root distribution and the pore networks in soil), influencing plant root growth patterns and microarthropod biodiversity and activity (Correa et al., 2019; Giuliani et al., 2024; Wendel et al., 2022); (*iii*) and spatially and temporally variable root processes (from root growth to the release of exudates, e.g. mucilage or extracellular polysaccharides) that can alter soil aggregation, pore connectivity, and rhizosphere hydraulic conductivity (Carminati, 2012, Carminati et al., 2013; Hallett et al., 2003; Read et al., 2003; Zarebanadkouki et al., 2016).

This inherent rhizosphere heterogeneity creates a wide range of diverse microhabitats that support distinct microbial assemblages (Compant et al., 2010; Delgado-Baquerizo et al., 2020; Fierer, 2017; Oburger and Schmidt, 2016; Kuzyakov and Blagodatskaya, 2015; Li et al., 2023; Pérez-Jaramillo et al., 2018; Wang et al., 2020; Zhang et al., 2023). Such spatially variable microbial activity can help plants thrive in saline environments (Gao et al., 2021; Pérez-Jaramillo et al., 2018), with halotolerant and halophilic microbes dominating in the high-salinity patches, and less saline microsites supporting a broader range of microbial species (Oren, 2019). This spatial structuring enhances ecosystem stability and resilience by ensuring microbial functional redundancy, where multiple microbial species perform similar ecological roles, such as decomposition and nitrogen fixation, thus reducing the risk of ecosystem collapse despite environmental fluctuations (Jiao et al., 2021; Li et al., 2021; Philippot et al., 2021).

Root architectural traits decisively play a role in structuring rhizosphere microbial communities, particularly under saline conditions. The rhizosphere microbiome composition is closely aligned with key root

functional traits such as root diameter, branching intensity, root hair density, and whole-root system architecture, which collectively define resource acquisition patterns and microhabitat formation (Galindo-Castañeda et al., 2024; Lin et al., 2024; Naylor et al., 2018). In saline soils, the influence of root architecture is amplified because salinity generates steep microscale gradients in water potential, ion concentrations, and oxygen availability within the rhizosphere (Hinsinger et al., 2009). Fine, highly branched root systems with dense root hairs increase rhizosphere surface area and create heterogeneous microsites with contrasting salinity and moisture conditions, thereby supporting more diverse and functionally redundant microbial assemblages (Naylor et al., 2018). Root architectural traits further regulate the spatial distribution of rhizodeposition and mucilage release, with downstream effects on soil aggregation, pore connectivity, and rhizosphere hydraulic properties under saline stress (Carminati and Vetterlein, 2013). Trait-based frameworks link acquisitive roots to microbial communities optimized for rapid nutrient cycling, phytohormone production, and stress mitigation, while conservative roots associate with microbial assemblages adapted to persistence, resource efficiency, and osmotic stress tolerance (Bardgett et al., 2014). Overall, root architecture emerges as a primary driver of rhizosphere spatial heterogeneity and microbial network organization in saline soils, with direct implications for nutrient acquisition, ion homeostasis, and plant water relations.

To fully realize the potential of altering and managing the root zone microbiome, however, a deeper understanding of microbial network dynamics in spatially heterogeneous saline environments is needed. In particular, multiscale insights into root–soil–rhizosphere interactions, from the nano- and microscopic levels of the root–soil interface to the whole root organ and the plant scale, are critical. Certainly, the evidence in the literature supports the view that by shaping the rhizosphere microbial assemblage it is possible to boost soil foraging abilities of the plant in a heterogeneous soil, enhancing crop productivity and long-term sustainability in salt-affected regions (Pérez-Jaramillo et al., 2018). These findings underscore the importance of considering both taxonomic and functional microbial diversity in heterogeneous saline soils and emphasize their importance in enhancing soil fertility and ecosystem resilience.

2.2. *Conceptual framework for studying roots in specific environments*

Over the last decades, considerable progress has been made in understanding plant responses to salt stress. Nevertheless, breeding of salt-tolerant crop varieties remains a difficult task, with only limited progress in delivering salt-tolerant crops (Hu and Schmidhalter, 2023, Melino and Tester, 2023; Morton et al., 2019).

As previously mentioned, several key issues complicate the application of plant salt tolerance in agriculture. First, plant salt tolerance and response mechanisms are incredibly diverse, varying significantly among species and controlled by multiple genes. Numerous different genes have been identified for mitigating osmotic stress, ion toxicity, oxidative stress, and other aspects of salt tolerance (Liang et al., 2018). Second, a disconnect often exists between a plant's protective mechanisms against salinity and its overall salt tolerance (survival). Mechanisms that help a plant survive in saline conditions often conflict with agricultural productivity goals. For example, if a plant achieves salt tolerance by reducing salt uptake through its roots, this mechanism is likely to also inadvertently decrease the uptake of essential water and nutrients. The consequence is often limited growth and reduced yield. Therefore, genes promoting this type of salt tolerance offer no agricultural value for crop improvement (Munns and Gilliham, 2015; Munns et al., 2020).

We argue that to truly understand what it takes for plants to thrive in saline environments, or to minimize the negative impact of salinity on crop productivity, it is critical to consider spatial and temporal soil variability and the corresponding root-level responses. In saline soils, roots constantly face a changing environment. Their performance and survival therefore, depend on their ability to quickly sense these environmental shifts and mount an adaptive response that alters resource allocation for growth, reproduction, and defense. While reductionist experiments of soil heterogeneity, such as split-root studies, have substantially expanded our understanding of how plants respond to salinity heterogeneity (and are the subject of several reviews, e.g., Bazihizina et al., 2012, Valenzuela et al., 2022a and Zhang et al., 2025), a significant gap remains in translating these findings to crop improvement. Specifically, most laboratory studies maintain constant low-salt areas, whereas in field conditions, these favorable patches are likely to be small, short-lived, and rapidly depleted. This discrepancy highlights critical questions regarding the development of salt-tolerant crops: future work must integrate root-growth models with explicit resource-consumption dynamics and quantify the water- and nutrient-carrying capacity of transient soil patches to better predict crop performance in the field.

Given that rhizosphere boundaries are dynamic in size and shape and that diverse soil parameters change in varied and partly divergent ways over time and space (Wang et al., 2020), how fast do these changes in salinity, water, and nutrient concentrations occur, what is their relevance for the roots, and how do they affect overall plant response and salt tolerance? What are the temporal and spatial limits of the favorable soil patches that roots can exploit and the costs incurred by plants when foraging these areas? Indeed, in the experimental work using split-root studies low-salt areas are generally maintained constant, whereas in the field they are likely to be small, short-lived, and rapidly depleted. Future work should quantify the water- and nutrient-carrying capacity of these patches and integrate root-growth models with explicit resource-consumption dynamics. It will also be essential to assess the plant C costs associated with modifying root architecture to continually explore and exploit favorable soil patches and compare them with those required for an enhanced tissue tolerance, needed when taking up resources from high salt areas.

What is the ideal root ideotype for inherently heterogeneous saline soils, considering associated variations in salt, water, and nutrient distribution? Are there any specific root traits (morphology, anatomy and function) that might facilitate resource foraging (water and nutrients) while reducing root metabolic costs associated with salt tolerance? Aside from typical salt tolerance mechanisms (e.g. increased tissue tolerance or salt exclusion), the inherent spatial and temporal variability of salinity stress, particularly in environments where such patterns can be anticipated (e.g. in a managed agricultural system) offer an opportunity to strategically target root and rhizosphere traits to enhance crop performance in saline soils. For example, in environments where salt concentration is higher in the topsoil (often due to irrigation practices), plants with deep root systems can be advantageous (Fig. 2). These roots enhance foraging for water and nutrients in deeper, less saline zones while minimizing growth in the saline topsoil. Specific root traits contributing to this could include a few axial roots with steep growth angles and fewer, but longer lateral roots. Additionally, the temporal regulation of root growth to coincide with periods of lower salt concentration (e.g., after rainfall or irrigation) can be highly beneficial. During these windows, roots can grow more actively, capitalize on the temporary salinity reduction, and enhance overall plant health. A diverse microbial community that promotes nutrient cycling and salt detoxification, coupled with increased production of root exudates that modify soil structure, can further alleviate salt stress in these conditions. Conversely, when salinity primarily resides in deeper soil layers (as seen with brackish groundwater or seepage), plants with shallow root systems may be more advantageous (Fig. 2). This would involve shallow growth angles, many axial roots, and numerous short lateral roots to optimize foraging in the less saline topsoil and avoid deeper, highly saline zones. In such cases, robust apoplastic barriers (including exodermis and endodermis) in deeper roots can prevent salt uptake from critical zones, while enhanced aquaporin expression in shallow roots

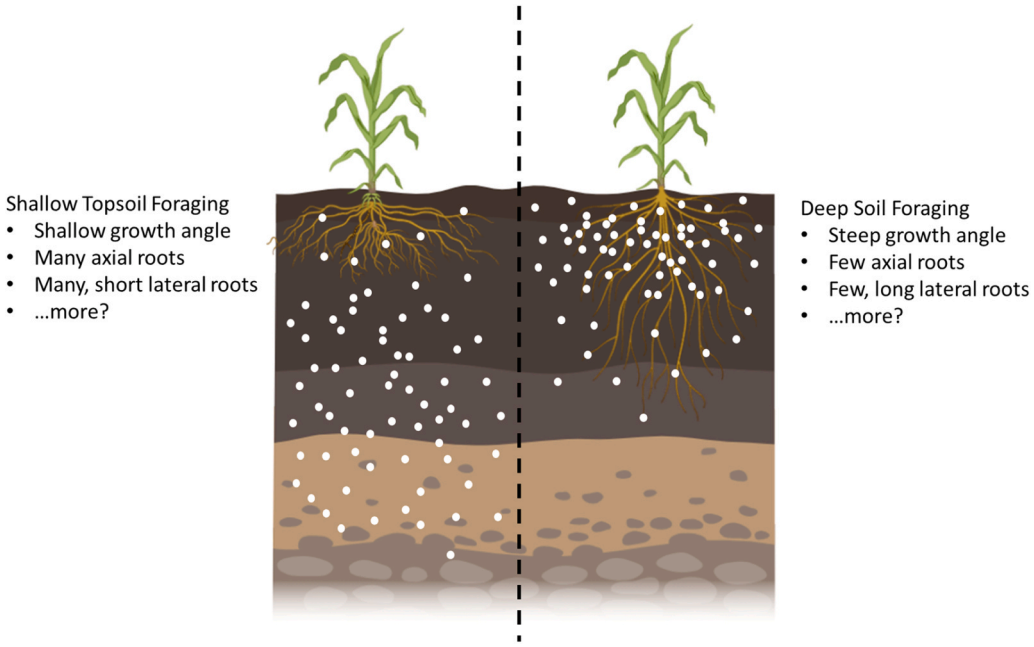

Fig. 2. Illustration of possible but conflicting ideal root ideotypes for inherently heterogeneous saline soils suggesting the need for root plasticity. On the left, shallow foraging roots in cases where deeper soil is saline, potentially due to saline groundwater. On the right, deep foraging roots in cases of shallow salinity, potentially due to irrigation or evaporation.

maximizes water uptake from less saline upper soil layers. A stable and resilient microbial community in the upper soil layers, alongside the exudation of organic acids to alter soil pH and reduce salt solubility, could also be crucial adaptations.

Ultimately, a proposed salt-tolerant root ideotype emphasizes root plasticity: the ability of roots to actively grow away from highly saline soil zones (negative halotropism) while still efficiently acquiring water and nutrients from less saline patches. This requires a delicate balance between salt avoidance and essential resource acquisition. It is crucial to consider that salinity, and its spatial and temporal variability, exerts strong selective pressures that reshape both plant economics and rhizosphere microbiome assembly (e.g., Busoms et al., 2023; Tripathi et al., 2025). Studies are therefore needed to elucidate how root traits modulate plant–rhizosphere/soil feedbacks in heterogeneous saline soils and their cascading impacts on root and plant economics, and ultimately yields, across the salt-tolerance continuum as trade-offs are likely to occur between salt tolerance, construction costs, and resource-foraging capacity. These trade-offs may differ quite substantially between species that rely primarily on salt exclusion and those that depend on increased tissue tolerance or salt secretion. This new knowledge will ultimately enable farmers and researchers to make informed decisions about the appropriate traits to select for a given crop depending on field characteristics and production goals.

2.3. *Issues and recommendations for future research*

Researchers sometimes acknowledge the oversimplification of laboratory conditions by adding Ca^{2+} to better represent and balance ionic strength. However, field salinity is far more complex, often involving diverse ionic combinations. Some salts, beneficial at low concentrations, become toxic and osmotically problematic at higher concentrations or with prolonged exposure. While modeling could bridge the gap between experimental results and field conditions, current models largely address heterogeneous root zone conditions using mathematical "fudge factors" rather than mechanistic understanding. This raises a crucial question: could a more complex field scenario alter root responses, from sensing to whole-plant effects? For instance, recent studies highlight the importance of light quality (e.g., presence vs absence ultraviolet B radiations) and intensity in root nutrient uptake (Zhao et al., 2025) and in shaping water and ion relations in salt-affected plants, ultimately influencing salt-induced responses and plant performance (Guardigli et al., 2025). Furthermore, research on multiple stressors has now demonstrated that responses to multiple stressors often cannot be reliably predicted from the individual effects of each stressor alone (Zandalinas et al., 2021). Clearly, a key challenge is to consider roots and their activity in terms of combinations of all these variables to account for interactions in uptake mechanisms regarding water, nutrients, salts, and O_2, also considering other environmental factors that act at the shoot level influencing root activity (e.g. light). Currently, answering these questions is challenging due to a lack of basic information on the trade-offs and energy costs of specific plant mechanisms in complex salt-affected soils, especially when considering the broad spectrum of plant tolerance strategies.

A significant gap exists between controlled laboratory experiments and real-world field conditions. Current understanding of plant response and uptake processes is primarily based on experiments where conditions are spatially and temporally uniform. In reality, however, these conditions constantly change. This discrepancy affects not only naturally saline landscapes but also agricultural systems, including both dryland and irrigated soils. Commercial irrigation, for instance, inherently introduces temporal dynamics; traditional surface methods, aiming for longer intervals between events, lead to severe wetting and drying cycles, while modern drip and micro-irrigation create highly heterogeneous two- or three-dimensional spatial patterns within the root zone.

There is limited understanding of root uptake processes and mechanisms in such heterogeneous environments. What happens when parts of a plant's root system are exposed to stress-inducing conditions while other parts face optimal conditions? Time scales also play a critical role. Long-term (days or more) static or repeating patterns of wetting and drying are expected to trigger root growth and activity that reflect the relative ease of uptake (water, nutrients, oxygen) and avoidance of stress (dryness, salinity, hypoxia). In contrast, short-term (days or less) dynamics in heterogeneous root zones are more likely addressed by compensatory mechanisms, where uptake from superior regions makes up for reductions from inferior ones, which may or may not involve root-to-shoot signaling (as detailed in several reviews addressing this topic,

Bazihizina et al., 2012; Valenzuela et al., 2022a; Zhang et al., 2025).

To ensure sustainable agriculture and boost plant productivity in saline soils, future research must adopt a multidimensional perspective on how soil heterogeneity shapes root responses to salt stress. Comprehensive studies at both the molecular and physiological levels are needed to understand adaptation mechanisms across the entire continuum of plant salt tolerance from salt-sensitive glycophytes to extreme obligate halophytes. The outcomes will likely vary depending on the strategies implemented (e.g., root exclusion versus vacuolar sequestration in leaf vacuoles) and their associated costs. Furthermore, RNA sequencing (RNA-seq), proteomic, and metabolomic approaches should complement the study of morphological and anatomical adaptations in root systems across the salt tolerance continuum using advanced imaging techniques, and complemented by three-dimensional modeling of soil heterogeneity effects on root development.

From a management perspective, an important question emerges: can agronomic practices that regulate soil water and salt dynamics be used to engineer spatially heterogeneous salinity patterns in agricultural fields? Precision fertigation (as modeled by Valenzuela et al., 2022a, 2022b) and targeted soil amendments offer promising avenues. By supplying water (or improving water retention) and nutrients to localized zones that stimulate root proliferation, such strategies may create localized low-salinity zones with optimized water and nutrient dynamics, while limiting root exploration of more saline regions, thus transforming salt heterogeneity from an important constraint into a deliberate management tool for improving crop performance. This however requires the evaluation of the long-term effects of soil management practices (which alter salt and water dynamics in the soil and rhizosphere, e.g., using soil amendments like gypsum or sulfur, and biochar) and symbiotic microorganisms (rhizobacteria, mycorrhizal fungi). Addressing these questions will require a substantial expansion of experimental approaches, moving from pot studies to controlled field trials and long-term monitoring in salt-affected landscapes. This progression will have to span multiple spatial and temporal scales, from fine-resolution root phenotyping and soil characterization using rhizotrons and minirhizotron systems, to larger-scale, continuous monitoring enabled by in-field IoT sensor networks (e.g., Dong et al., 2024). Emerging technologies such as low-field magnetic resonance imaging, microtensiometers, electromagnetic induction, and time-domain reflectometry will be essential for capturing dynamic interactions between roots, water, and salinity *in situ* (Bagnall et al., 2022; Teramoto and Uga, 2025; Autovino et al., 2025). These studies should not only measure the effects of these applications on the physicochemical properties of saline soils (pH, electrical conductivity, cation exchange capacity) but also their contributions to root development, plant growth, nutrient uptake, and water use efficiency across different scales. Critically, cost-effectiveness analyses are crucial from both economic and ecological feasibility perspectives, along with a consideration of environmental sustainability parameters (carbon footprint, water consumption, impacts on biodiversity). For instance, the applicability of organic matter addition or microorganism inoculations in large-scale agricultural systems needs optimization through rigorous testing under laboratory, greenhouse, and field conditions. Such interdisciplinary research promises innovative, data-driven solutions for reclaiming saline soils and enhancing plant activities. Finally, international collaborative initiatives like COST Actions should be encouraged to evaluate the applicability of these findings across diverse climate and soil types globally.

The dynamic and spatially variable nature of soil salinity, whether natural or irrigation-induced, demands dynamic and localized management strategies instead of uniform, blanket approaches. Traditional agricultural management, which often assumes or applies uniform conditions across fields, leads to inefficient resource use and either over- or under-application of inputs. This uniform approach is simply inadequate for addressing the complexities of real-world field conditions (Pierpaoli et al., 2013). Fortunately, the availability of precision agriculture tools such as unmanned aerial vehicles, proximal soil sensors, electrical conductivity maps, and satellite imagery enables near real-time mapping of this heterogeneity. This technological capability allows for the development and implementation of highly site-specific management plans, including tailored irrigation schedules, precise nutrient application, and optimized crop selection. Understanding soil heterogeneity thus transcends an academic concept to become a direct practical imperative for optimizing resource utilization and effectively mitigating stress in saline agricultural environments.

3. Conclusions

Plant roots and their associated rhizosphere represent a dynamic and complex frontier, profoundly influenced by the inherent heterogeneity of soil environments, particularly under saline conditions. This viewpoint has highlighted that plant survival and thriving in saline soils are not merely a function of inherent salt tolerance but critically depend on the roots' remarkable plasticity to navigate and exploit spatial and temporal variability in soil properties.

Future research must prioritize the development of more realistic experimental protocols that can mimic the spatial and temporal variability in soil properties encountered in field conditions. There is also a need for a deeper understanding of the energetic trade-offs associated with various root architectural adaptations, ensuring that breeding for specific traits does not inadvertently compromise overall plant fitness. Furthermore, comprehensive studies on the long-term dynamics of plant-microbe interactions in heterogeneous saline soils are crucial for harnessing the full potential of microbiome-based solutions. By addressing these gaps, the scientific community can pave the way for developing climate-resilient crops and implementing precision agricultural strategies that ensure sustainable food production in an increasingly salinized world.

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Giulia Atzori: Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Nadia Bazihizina:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Nuray Cicek:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Eleftheria Dalmaris:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Bliss Furtado:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Hannah Schneider:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Alon Ben-Gal:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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