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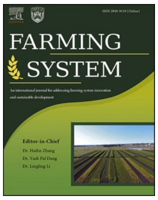

Roots and the rhizosphere: a perspective on the hidden engine of regenerative, antifragile, and digitally enabled agriculture

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ABSTRACT

For decades, agricultural optimization has focused primarily on aboveground yield and external inputs while neglecting the complexity and functional integrity of belowground processes. The rhizosphere, the dynamic zone surrounding roots, has long been investigated through isolated components but rarely in a holistic framework, despite its critical role in agroecosystem productivity, soil fertility, and sustainability. Moreover, the translation of this knowledge into routine farm-scale practice remains quite limited. This perspective argues for repositioning the rhizosphere at the center of agricultural innovation. In this review, roots and their microbial partners are not only fundamental for crop performance but also drivers of antifragility, enabling farming systems to withstand and even improve under environmental stresses, while sustaining productivity. Integrating advances in root biology, soil chemistry, microbial ecology, and agronomics, this review shows that rhizosphere processes drive key biogeochemical functions such as carbon sequestration, nutrient cycling, and stress adaptation. Critical gaps include limited integration of root-microbiome traits in crop breeding, lack of field-ready rhizosphere diagnostics, and variable performance of microbial inoculants across soils and climates. Addressing these challenges is essential to operationalize rhizosphere science at field scale and support reduced-input, climate-resilient farming systems. Looking forward, emerging technologies ranging from high-resolution imaging and spectroscopy to artificial intelligence offer unprecedented insight into belowground complexity and a unique opportunity to bridge the gap between experimental insights and real-world farming. Ultimately, the review calls for a paradigm shift embedding rhizosphere processes into crop breeding, farming system design, and management strategies. Recognizing the rhizosphere as a primary entry point for innovation is essential for translating science into practical levers for regenerative, antifragile, and sustainable agriculture.

1. Introduction

Modern agriculture is facing a pivotal moment, as the combined pressures of climate change and widespread soil degradation increasingly threaten global food security, demanding urgent solutions (Saleem et al., 2024). Meeting these challenges requires agricultural systems that are not only more sustainable but also inherently regenerative and resilient (Sher et al., 2024). However, when addressing crop productivity and agricultural resilience, attention has traditionally focused, and still largely focuses, on aboveground plant structures such as leaves, stems, fruits, seeds, and yield, while the equally crucial but less visible rhizosphere remains largely overlooked. Described as the narrow zone of soil directly influenced by root exudates and associated microbial activity (Philippot et al., 2013), the rhizosphere is not only an anchoring point but a dynamic hub where roots, microorganisms, soil organic fractions, and minerals interact, shaping processes crucial to

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agricultural productivity, environmental health, and climate resilience (George et al., 2024). In this context, a key mechanism is the release of a complex cocktail of exudates (Mimmo et al., 2014). These organic compounds are not simply metabolic byproducts; they centrally mediate the chemical and biological dialogue between roots and their environment, a role increasingly supported by chemical, molecular and ecological studies (Cesco et al., 2010; Eisenhauer et al., 2017). These dialogues stimulate the growth and activity of beneficial soil microorganisms, including nitrogen-fixing bacteria (NFB), phosphate-solubilizing bacteria (PSB), and arbuscular mycorrhizal fungi (AMF), that, in turn, enhance nutrient availability and soil fertility (Etesami et al., 2021; Pantigoso et al., 2023). Indeed, roots and their rhizosphere form an active belowground network, driving nutrient cycling, promoting biodiversity, and maintaining ecosystem stability.

Despite their agro-ecological importance, soil-root systems remain relatively neglected in field research, with studies often isolating soil, roots, or microbes, limiting agronomic application. This reductionism extends to perennial fruit crops, where rootstocks traits are sometimes targeted to improve overall crop performance (Warschefsky et al., 2016), while most innovation focuses on aboveground traits such as breeding for improved shoots, crop protection, and fertilizer refinement (Zhang et al., 2025). As a result, the potential of roots and the rhizosphere to address pressing agricultural challenges remains underutilized and underestimated (McGrail et al., 2020). In this context, the defining features of the current changing climate, including erratic weather patterns, increased temperatures, prolonged droughts, and recurrent flooding are progressively undermining root function, impairing water uptake, limiting nutrient availability, and disrupting the stability of critical rhizosphere interactions (George et al., 2024). In addition, the effects of unpredictable and intense atmospheric events call for timely and well-coordinated interventions immediately after disasters (*e.g.*, floods, landslides), especially in rural areas, to ensure the rapid recovery of agroforestry ecosystems (Cesco et al., 2024). Moreover, intensified agricultural practices like prolonged monoculture, deep soil tillage, and heavy reliance on agrochemicals further exacerbate soil degradation (Derpsch et al., 2024). Currently, over one-third of the world's soils show signs of degradation (Amelung et al., 2020; European Commission, 2023), manifested in reduced organic matter content, weakened stability, and declining biodiversity, severely compromising soils' ability to support robust root systems and healthy microbial communities. Projections indicate that, without effective mitigation actions, up to 90 % of global soils may experience some form of degradation by 2050 (Kraamwinkel et al., 2021).

In response, regenerative agriculture is emerging as a powerful model that not only sustains productivity but also restores ecological functions and strengthens socio-economic resilience. This paradigm is increasingly seen as essential to counter soil degradation, adapt farming practices to climate change, and safeguard productivity and competitiveness of agriculture (Sher et al., 2024). Central to this approach is the explicit recognition of roots and rhizosphere as essential drivers of soil regeneration and resilience (Asghar et al., 2025). Practices such as diverse crop rotations, cover cropping, reduced tillage, and management of beneficial soil microbes can significantly enhance root health, strengthen rhizosphere functions, and improve ecosystem services like carbon (C) sequestration, nutrients' cycling, and stress resilience (Khangura et al., 2023). This shift redefines system performance under stress to improve dynamic improvement, not just robustness, resistance and resilience. In this regard, it is interesting to note that the concept of *antifragility*, originally introduced by Taleb (2012), describes systems that not only resist shocks but actually improve through them. In Taleb's framework, *fragile* systems collapse under stress, *robust* systems resist change without improving, and *antifragile* systems evolve and strengthen through exposure to disturbances. In agroecosystems, the *antifragile* notion goes beyond the traditional ideas of *robustness* (resistance to change) and *resilience* (capacity to recover), emphasizing the potential of biological networks to adaptively evolve under stress. In the rhizosphere, *antifragility* can emerge when disturbances, such as drought, nutrient fluctuations, or pathogen pressure, select for microbial consortia and root traits that enhance future system performance. For instance, repeated exposure to drought can increase the abundance of drought-adapted bacterial taxa that support plant water relations and C use efficiency (Canarini et al., 2021). Likewise, variability in nutrient availability can foster dynamic plant-microbe signaling and symbiotic plasticity, improving phosphorus (P) mobilization and stress tolerance over time (Zobel et al., 2024). Thus, *antifragility* in the rhizosphere implies that the biological complexity of the system allows it not merely to recover, but to reorganize and strengthen its functional capacity through perturbations. For this reason, from this point onward, the term *antifragility* is preferred over resilience, unless used directly by cited sources, to capture the potential of systems to improve, particularly regarding belowground components.

Despite decades of agricultural research, the rhizosphere, in its full integrity and functional complexity, remains poorly known and understood, even though it has the potential to drive profound transformation in agriculture. This knowledge gap is increasingly problematic in the context of climate change and soil degradation (Fig. 1). Addressing this gap calls for a shift that places the rhizosphere at the core of agricultural design. In this light, exploiting the regenerative potential of roots and the rhizosphere requires building on existing knowledge while addressing persistent gaps. In fact, while insight into their roles in plant-soil interactions has advanced (White, 2019), the underlying mechanisms that connect root traits and rhizosphere processes to broader ecosystem functions remain insufficiently characterized. Critical questions remain on root systems responses to multiple stresses, exudate composition changes under such pressures, and microbial mediation in the field. These insights are rarely integrated into field management, limiting their application. Addressing this will require strategies to boost root adaptability, strategically modulate exudate composition, and harness microbial communities under field conditions.

On the basis of these premises, this manuscript adopts a rhizosphere-centric framework to identify challenges and emerging opportunities for rethinking agricultural systems from the ground up. A key contribution of this manuscript is to address the major translation gap between rhizosphere science and routine farm-scale practice by outlining operational biological and technological pathways for their potential implementation. Rather than providing an exhaustive review of all aspects of rhizosphere biology, it focuses on two complementary dimensions and the structure of the manuscript has therefore been designed to move from mechanisms to implementation, progressively linking rhizosphere processes to field-ready strategies and enabling conditions. First, it examines how root traits, exudation patterns and plant-microbe interactions govern rhizosphere-mediated C, N and water fluxes and can generate antifragile responses under multiple abiotic stresses, with implications for C sequestration and stabilization (*climate change mitigation*), nutrient use efficiency (supporting *crop adaptation*), and environmental stress antifragility (*enhancing capacity to thrive under variability*) (Section 2). Second, it considers how biological levers (*i.e.,* roots, microbes and their interactions) can be coupled with emerging technological levers (*i.e.,* imaging, sensing, modelling, genetic and microbial tools) to design rhizosphere-centric agroecosystems and operationalize these processes at field and farm scale (Sections 3-4). By enhancing soil function, resource-use efficiency and antifragility (Verma et al., 2025), rhizosphere-based approaches are proposed as a pathway for agricultural transformation and for aligning research, policy and practice around belowground processes as a central component of agroecosystem design. Finally, by situating these elements within a prospective framework, the manuscript aims to stimulate scientific discussion on the agroecological transitions required to translate rhizosphere science into mainstream practice.

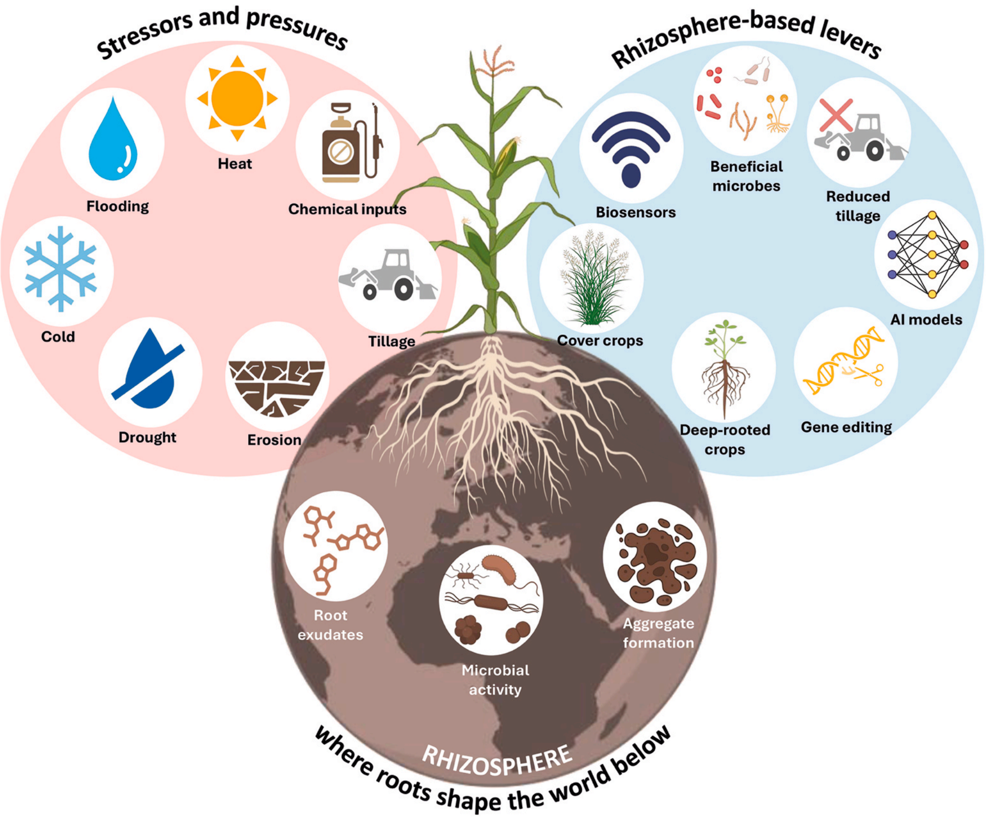

Fig. 1. Rhizosphere-mediated adaptation in regenerative systems. Environmental pressures increasingly challenge soil-plant systems (left circle). However, the way these pressures affect plants is shaped by what happens in the rhizosphere, the narrow zone around the roots where exudation, microbial interactions and soil aggregation work together to regulate nutrient flows, water movement and stress signalling (central circle). These living processes form the first line of adaptation. On the right circle, regenerative practices and emerging technologies help strengthen this rhizosphere interface. They support beneficial microbial networks, improve soil structure, encourage deeper rooting, and apply digital or molecular tools to fine-tune plant-soil feedback. When combined, these levers increase the system's ability not only to cope with stress but also to reorganize and improve its performance under repeated pressures, guiding agroecosystems toward resilience and even antifragility.

2. The rhizosphere: hidden engine of agricultural transformation in antifragile agriculture

This section provides a synthesis of current scientific knowledge on rhizosphere functioning, focusing on root exudation, nutrient mobilization, and plant-microbe interactions. The objective is to integrate these processes into a coherent framework that explains how belowground mechanisms can support system robustness and adaptability. These insights provide the agronomic bases on which the following chapter will identify biological and technological levers, highlight persistent knowledge gaps, and outline strategies for designing antifragile agricultural systems.

2.1. Roots and microbes in dialogue: shaping the rhizosphere

One of the most powerful tools that plants use to shape the soil environment is the release of root exudates. These are a complex mixture of organic compounds (*e.g.*, sugars, amino acids, organic acids, flavonoids, phenolics, enzymes), and ions (*e.g.*, protons), supporting molecular signaling, nutrient solubilization, rhizosphere microbial assembly, and defense responses (Mimmo et al., 2014; Afridi et al., 2024). Root exudates first act at the biogeochemical level, directly modifying rhizosphere pH, redox status, and nutrient availability (Carvalhais et al., 2011). These chemical shifts drive microbial responses, influencing community composition, activity, and functional traits. Over time, the interplay between plant-driven chemistry and microbial dynamics underpins agroecosystem functions such as nutrient cycling efficiency, soil C storage, and stress-adaptive capacity. Among these biotic interactions, the symbiosis between plants and arbuscular mycorrhizal fungi (AMF) is one of the most pervasive and ecologically relevant. AMF colonize plant roots and develop extensive hyphal networks that extend the soil volume explored by the plant, improving P and micronutrients' uptake. In exchange, the host plant supplies the fungus with photosynthetically derived C, establishing a reciprocal relationship that enhances plant fitness and resilience under stress. Beyond nutrient exchange, AMF also influence soil aggregation, modulate hormonal signaling, and shape the assembly of other beneficial microbial communities in the rhizosphere (Genre et al., 2020).

A clear example is P, frequently present in soils in poorly available forms. To access these nutrient pools, species such as *Lupinus* spp. release organic acids like citrate, malate, and oxalate, which bind cations such as aluminum (Al), iron (Fe), and calcium (Ca), thereby mobilizing phosphate ions for root uptake (Tomasi et al., 2009; Zhou et al., 2020). Similarly, cereals like wheat improve P and Fe availability in calcareous soils by exuding organic acids (Zhao et al., 2014). The nutrient-mobilizing role of root exudates extends far beyond P. For instance, potassium (K) availability is enhanced through the secretion of organic acids that help solubilize mineral-bound K (Yang et al., 2019), while also stimulating K-solubilizing bacteria (KSB) such as *Bacillus* spp. and *Pseudomonas* spp. (Rallos et al., 2021). This plant-microbe integration is especially valuable under nutrient depletion or abiotic stress. A similar pattern occurs for nitrogen (N), whose dynamics are also strongly influenced by rhizosphere processes. Legumes such as *Glycine max* release flavonoids that activate nodulation genes in *Rhizobium*, initiating symbiotic N fixation (Biała-Leonhard et al., 2021; Haskett et al., 2025). In parallel, non-legume crops stimulate free-living N-fixing bacteria like *Azotobacter* and *Azospirillum* by altering rhizosphere chemistry (Smercina et al., 2019). Even sulfur (S) cycling can be influenced by root exudates, particularly through compounds that stimulate S-oxidizing bacteria (SOB) like *Thiobacillus* and *Acidithiobacillus* spp. (Santana et al., 2021). Shifts in exudate composition influence microbial activity and recruitment, with consequences for S availability (Ranadev et al., 2023). In the case of Fe, its availability is often limited due to its low solubility, particularly in calcareous or neutral/alkaline soils (Zuluaga et al., 2023). To overcome this, graminaceous plants release phytosiderophores (PSs), non-proteinogenic amino acids that bind Fe^{3+} and, thus, facilitate its solubilization and root uptake in the Fe-PSs complexed form *via* specific plasma membrane transporters like Yellow Stripe 1 (YS1) (Yamagata et al., 2022). Root exudates can also stimulate Fe-solubilizing microorganisms, enhancing Fe mobilization through microbial siderophores and rhizosphere acidification (Colombo et al., 2014). Furthermore, PGPRs such as *Azospirillum* can differentially trigger gene transcription to enhance root Fe acquisition mechanisms, thereby directly modulating both molecular and physiological responses of crops (Pii et al., 2016). Interestingly, some of the exudate-mediated processes involved in Fe mobilization are also relevant to S acquisition, as Fe and S homeostasis are closely linked at both metabolic and regulatory levels (Astolfi et al., 2020). Their coordinated uptake is essential for the synthesis of Fe-S clusters in proteins and for maintaining cellular redox balance (Astolfi et al., 2021). This capacity to adapt exudation in response to nutrient availability reflects a biogeochemical plasticity, through which plants, in coordination with microbial partners, actively shape rhizosphere conditions to mobilize nutrients and enhance their root acquisition. It should also be noted that also humified fractions of soil organic matter can *per se* influence nutrient availability and modulate root acquisition mechanisms, both providing Fe-complexes readily useable by plants and influencing root physiology; for a comprehensive review see (Zanin et al., 2019). The main nutrient-specific root exudation strategies and their microbial partners involved in rhizosphere nutrient mobilization are summarized in Table 1.

Table 1

Root exudation strategies and microbial partners contributing to nutrient mobilization in the rhizosphere. The table synthesizes major nutrients, plant exudation strategies (with model species), associated microbial partners, and their functional outcomes.

Nutrient	Root exudation strategy	Microbial partners	Functional outcome
Phosphorus	- organic acids (citrate, malate, oxalate) chelating Al/Fe/Ca (*Lupinus spp.*)	- *Bacillus*, *Pseudomonas* spp.	- mobilization of bound P, enhanced uptake
Potassium	- organic acids solubilizing mineral-bound K (*wheat*)	- K-solubilizing bacteria (KSB, *e.g.*, *Bacillus spp.*, *Pseudomonas spp.*, *Frateuria aurantia*)	- improved K availability under depletion
Nitrogen	- flavonoids activating nod genes (*Glycine max*) - chemical shifts stimulating free-living diazotrophs (*maize*, *wheat*)	- *Rhizobium*, *Azotobacter*,	- symbiotic and associative N fixation
Sulfur	- exudates stimulating S-oxidizing activity (*Brassica spp.*)	- *Thiobacillus*, *Acidithiobacillus*	- increased S availability *via* microbial oxidation
Iron	- phytosiderophores (PSs) binding Fe^{3+} (*Hordeum vulgare*, graminaceous spp.) - exudate-driven rhizosphere acidification (*maize*)	- Fe-solubilizing bacteria producing siderophores (*e.g.*, *Pseudomonas spp.*, *Bacillus spp.*, *Azotobacter spp.*) - PGPRs such as *Azospirillum* differentially triggering gene transcription to enhance root Fe acquisition	- solubilization and uptake of Fe - coupled regulation with S - modulation of plant molecular and physiological responses under Fe limitation

Low-molecular-weight organic compounds such as sugars, organic acids, and amino acids represent a major source of labile C in the rhizosphere, serving as key substrates for microbial metabolism (Ma et al., 2022). These inputs not only sustain microbial respiration but also contribute to the growth of microbial biomass, forming a dynamic rhizosphere trophic network (de Vries and Caruso, 2016). Notably, up to 20–40 % of assimilated C can be allocated to the roots and released as exudates (Rasmann and Hiltpold, 2022). For example, in the case of winter wheat, which can produce approximately 13 t/ha of dry biomass annually, equivalent to around 4 t/ha of organic C (Sukhoveeva, 2024), root exudates may contribute roughly a few tons of organic C per hectare in a single crop cycle. In this respect it is important to emphasize that a significant portion of microbial C is eventually transformed into microbial necromass (*i.e.*, the remains of dead microbial cells), which have been increasingly recognized as a dominant contributor to stable soil organic matter (SOM) formation (Wang et al., 2021). Furthermore, in fine-textured soils, clay particles promote organo-mineral associations, particularly with high-molecular-weight exudates such as mucilage and polysaccharides, which undergo physical stabilization against decomposition and contribute directly to long-term C storage (Mao et al., 2024).

While it may be tempting to view root exudation as a plant-driven process, rhizosphere microorganisms are also metabolically and functionally active players (Yang et al., 2024). They actively metabolize exudates and, in many cases, exert direct influence on plant physiology (Korenblum et al., 2020). For instance, specific strains of *Pseudomonas* and *Azospirillum*, produce auxins and cytokinins that modulate root system architecture, promoting lateral root proliferation and enhancing resource acquisition, particularly under drought or salinity stress (Omer et al., 2022). Other beneficial microorganisms including bacteria and fungi such as *Bacillus* spp. and *Trichoderma* spp., can induce systemic tolerance to abiotic stress by activating antioxidant defense pathways and stimulating osmolyte biosynthesis (Tiwari et al., 2017; Santoyo et al., 2024). Certain microbial strains produce antimicrobial compounds that selectively modulate rhizosphere colonization dynamics (Nicolle et al., 2024), while others regulate biofilm development and root surface colonization dynamics (Allard-Massicotte et al., 2016). Microbial communities can also adjust their metabolic outputs in response to the specific composition of root exudates, highlighting the co-adaptive and context-dependent dynamics of plant-microbe interactions (Seitz et al., 2022).

Nevertheless, it is crucial to recognize that not all microbial interactions are beneficial. Some pathogenic fungi and bacteria utilize root exudates as cues for host detection and colonization, intercepting and reprogramming the chemical signaling that would typically attract beneficial microbes (Asif et al., 2024). This duality reflects the complex evolutionary challenge that plants face in the rhizosphere, where they must simultaneously recruit beneficial partners while defending against pathogens, both processes being mediated through the same chemical signals (Lamichhane et al., 2024).

2.2. Genes, roots, and trade-offs in rhizosphere adaptation

2.2.1. Genetic and molecular regulation of root-rhizosphere interactions

Plants actively shape the structure and dynamics of the rhizosphere through the interplay of genetic programming and phenotypic plasticity (Liu et al., 2023). This influence ranges from molecular-level signaling (Bukhat et al., 2020) to morphological adjustments (Li et al., 2018;

Gifford et al., 2024), enabling plants to adjust root-rhizosphere interactions to changing environments.

In this adaptive framework, specific gene networks play a decisive role in regulating how plants acquire nutrients and establish interactions with microbial partners. For example, under conditions of P starvation, members of the PHR transcription factor family coordinate belowground adaptations, influencing root system architecture (Hu et al., 2025) and modulating the composition of root exudates (Yan et al., 2022) to enhance P uptake. In parallel, other regulatory families, such as MYB transcription factors, are central to root hair development and to the expression of genes involved in exudate biosynthesis, as shown in species such as *Arabidopsis thaliana* and rice (Dai et al., 2012; Li et al., 2019). These root hairs significantly increase root surface area, enhancing nutrient acquisition under limiting conditions. Beyond these roles, root hairs are also fundamental in shaping rhizosphere microbial communities. Their large surface area and continuous exudation of low-molecular-weight compounds create microhabitats that promote microbial colonization and activity at the root-soil interface. The density and length of root hairs can influence both the abundance and composition of associated microorganisms, favoring the establishment of beneficial taxa such as *Pseudomonas*, *Rhizobium*, and AMF that contribute to nutrient mobilization and stress tolerance (Quattrone et al., 2024; Wang et al., 2024). Therefore, genetic or hormonal regulation enhancing root hair proliferation can indirectly modulate microbial recruitment and overall rhizosphere functionality.

Plants also activate specific genetic pathways to support the recruitment of beneficial microbial partners. A key example is the biosynthesis of strigolactones, regulated by genes such as *D27*, *CCD7*, and *CCD8* (Ahmed et al., 2025). These compounds, upon release, act as signals, particularly in promoting symbiotic interactions with AMF, which are critical symbiotic partners for the acquisition of P and other nutrients in many crop species (Kodama et al., 2022). On the microbial side, plants recognize symbiotic signals (*i.e.*, lipo-chitooligosaccharides from *Rhizobium* and chitooligosaccharides from AMF), through LysM-domain receptor-like kinases such as NFR1, NFR5, CERK1, and LYK9 (Gough et al., 2018). This perception activates the common symbiosis (SYM) signaling pathway, which includes conserved components like DMI1, DMI2, and DMI3 responsible for initiating nuclear Ca oscillations (Granqvist et al., 2012). In rhizobia symbiosis, this leads to the activation of transcription factors such as Nodule Inception (NIN), initiating nodule development (Shen and Feng, 2024), whereas in AMF symbiosis, transcription factors like *CYCLOPS* and *RAM1* coordinate arbuscule formation (Pimprikar et al., 2016).

2.2.2. Root system plasticity and functional responses to environmental stress

Beyond genetic regulation, plant adaptation also relies on morphological strategies that confer flexibility to the root system. Plants exhibit marked root system plasticity, adjusting their architecture in response to heterogeneous and dynamic environmental conditions. This root plasticity, expressed through changes in depth, lateral branching, growth angle, and root hairs density, represents a fundamental mechanism of adaptation under stress (El Amrani, 2023; Du et al., 2025). For instance, drought-tolerant durum wheat, maize and rice genotypes often develop deeper root systems to access subsoil water (Uga et al., 2013; Klein et al., 2020), while some plant species increase lateral root proliferation in response to localized nutrient enrichment (Giehl et al., 2012; Shrestha et al., 2024). Under P deficiency, *A. thaliana* exhibits root hairs elongation, a response associated with upregulation of the RSL4 transcription factor, which increases root surface area and enhances P uptake efficiency (Fijn et al., 2025). Similarly, rice cultivars exposed to toxic Fe^{2+} conditions reduce root surface area to limit its uptake (Sonu et al., 2024), whereas in saline environments, rice often suppresses fine root growth while favoring the development of thicker, suberized roots as a strategy to reduce Na^{+} acquisition (Krishnamurthy et al., 2011). Over extended timescales, specific root traits also influence C flows into soil systems. For instance, deep-rooted species such as alfalfa contribute to the C cycle not only through the release of labile exudates but also by depositing structural compounds such as suberin and lignin into deeper soil layers *via* root necromass (Clément et al., 2022). These recalcitrant biopolymers tend to persist for decades, enhancing the formation of stable SOM fraction (Poirier et al., 2018). Moreover, root growth into deeper soil layers substantially modifies rhizosphere microbial communities by expanding the spatial distribution of root-derived carbon inputs and oxygen availability. In subsoil environments, where organic matter and microbial biomass are typically low, deep roots release exudates that stimulate microbial activity, enhance nutrient mineralization, and promote the establishment of distinct microbial taxa adapted to oligotrophic and low-oxygen conditions (Lattacher et al., 2025). These processes contribute to the vertical stratification of microbial functions and to long-term soil carbon stabilization, as root-driven carbon inputs in deeper horizons can persist and sustain microbial turnover over extended timescales (He et al., 2023).

2.2.3. Trade-offs, microbial mediation and implications for crop improvement

While root plasticity represents a crucial adaptive mechanism under stress, it also has inherent limitations, as it often entails significant metabolic costs. Developing deeper root systems can divert energy away from shoot growth, thereby constraining aboveground development and productivity, particularly in resource-limited environments (Lynch, 2013). Similarly, increased lateral root proliferation may increase metabolic demand and C use, especially under conditions where photo-assimilates are limited (Chandregowda et al., 2023). These functional trade-offs are highly context-dependent and highlight the importance of accounting for C and energy allocation patterns when selecting root traits in breeding programs.

The energetic burden associated with root plasticity can, however, be partly alleviated through microbial associations. In fact, beneficial microbes enhance nutrient availability and produce phytohormones that can reduce the need for extensive root architectural modification, effectively reducing the metabolic cost of plastic responses (Baudson et al., 2023). Mycorrhizal associations can help reduce the metabolic costs of the plant, functionally extending the nutrient-acquiring surface of the root system without requiring a proportional increase in root growth (Martin and Van Der Heijden, 2024).

Therefore, breeding for specific root ideotypes inevitably involves trade-offs that must be explicitly considered. Deeper and more vertically oriented root systems can enhance access to subsoil water and nutrients under drought or low-input conditions, but they may also divert assimilates away from leaf area development, reproductive structures and grain filling, potentially constraining yield in favorable, high-input environments. Likewise, highly branched shallow root systems can improve topsoil nutrient acquisition and early vigor, at the cost of increased maintenance of respiration and greater dependence on frequent water supply. Enhanced exudation and rhizodeposition can stimulate nutrient mobilization and beneficial microbiomes, but require a continuous allocation of carbon belowground, which may become limiting under combined stresses or in canopies with reduced photosynthetic capacity. From a breeding perspective, root traits cannot therefore be optimized in isolation. On the contrary, they need to be selected in combination with aboveground traits, considering whole-plant C budgets and the target stress scenarios. Rather than pursuing a single “universal” root ideotype, multi-trait, multi-environment breeding strategies are needed, prioritizing root architectures and exudation patterns that deliver net benefits across realistic climatic and management gradients while maintaining acceptable yield potential (Lynch, 2013, 2019).

Beyond targeted molecular and genetic interventions, it is also important to recognize that crop domestication itself has profoundly influenced plant-microbe interactions. The selection of agronomically desirable traits has often led to the loss or amplification of specific plant genes, resulting in directional shifts in the rhizosphere microbiota compared with wild relatives. These changes can alter root exudation patterns, microbial recruitment, and functional diversity, ultimately affecting nutrient acquisition and stress adaptation (Yue et al., 2023).

2.3. *Breeding, practices, and microbial tools*

Following the genetic and morphological determinants outlined above, the present discussion synthesizes current knowledge on three complementary approaches shaping rhizosphere processes: plant breeding, agronomic practices, and the application of microbial inoculants.

2.3.1. *Breeding for rhizosphere-oriented traits*

In recent years, targeted breeding for rhizosphere-associated traits has gained increasing attention as a promising approach to enhance crop performance in challenging environments. Breeding programs prioritize root system traits that enhance nutrient uptake, shape exudate chemistry, and support beneficial microbial interactions (Lynch, 2019; Sandrini et al., 2022). These characteristics contribute to improved adaptability, increased efficiency in resource use, and stronger soil health under field conditions. For example, maize lines with higher root cortical aerenchyma have been shown to reduce metabolic costs and improve P and N acquisition in low-input systems (Díaz et al., 2018), while carrot genotypes may differ in their ability to recruit bacterial taxa with distinct N-related functions through variations in exudate profiles (Saengwilai et al., 2014). The focus is increasingly moving beyond sterile laboratory conditions toward selecting plant genotypes that can form effective partnerships with native microbial communities and sustain yield potential under complex environmental stresses. Recent advances in high-throughput root phenotyping and imaging technologies now make it possible to characterize belowground traits with higher spatial and temporal resolution, enabling the identification and propagation of cultivars with enhanced rhizosphere functionality (Li et al., 2022). However, as highlighted by Pii et al. (2024), the full exploitation of these technologies in breeding programs still requires rigorous interpretation of the generated data, particularly when overlapping stress responses risk confounding phenotypic assessments.

2.3.2. *Agronomic practices shaping rhizosphere processes*

While breeding strategies provide a genetic basis for optimizing belowground traits, their effectiveness in the field is strongly influenced by agronomic practices that actively shape the rhizosphere environment. For example, crop rotations that include legumes such as chickpea or common bean enhance N availability through biological fixation mediated by symbiosis with nodulating rhizobia, reducing dependence on synthetic fertilizers while enriching the soil with organic matter and supporting microbial functional diversity (Wilker et al., 2019). Integrating deep-rooted species like sugar beet into intercropping systems can further enhance subsoil nutrient access and redistribute microbial activity vertically within the soil profile, improving rhizosphere functionality at greater depths (Czaban et al., 2023). Off-season cover crops such as oilseed radish (*Raphanus sativus*) or elbon rye (*Secale cereale*) can provide a valuable contribution by stimulating microbial biomass, enhancing enzymatic activity (*e.g.*, phosphatases, dehydrogenases), and accelerating nutrient mineralization and cycling processes (Tyler, 2020; Restovich et al., 2022). Additionally, conservative tillage practices, including no-till and reduced-till systems, support rhizosphere health by preserving soil structure and reducing erosion (Pearsons et al., 2023). In no-till maize systems, for instance, increased microbial biomass and SOM fraction have been observed, contributing to improved nutrient cycling and soil stability at the soil-plant interface (Wulanningtyas et al., 2021).

2.3.3. *Microbial inoculants: opportunities and limitations*

Alongside these practices, microbial inoculants are receiving increasing attention as bio-based tools to enhance nutrient uptake, stress tolerance, and overall crop performance. Inoculation with *Bradyrhizobium* in soybean (Ulzen et al., 2016), *Rhizobium* in common bean (Sousa et al., 2022), *Azospirillum* in maize (Takahashi et al., 2024), *Pseudomonas* and *Bacillus* strains in rice (Nguyen et al., 2017), AMF strains in grapevine (Berdeja et al., 2025), and several microbial strains in vegetables (Bona et al., 2017; Khalid et al., 2017) has shown promising results in improving nutrient acquisition and enhancing plant physiological performance under a range of environmental stresses. However, field performance of microbial inoculants shows variable efficacy. Large-scale trials consistently show that inoculant performance is highly context-dependent, influenced by existing soil microbial communities, climatic conditions, and local management practices (Kozjek et al., 2021; Kushwaha et al., 2024). In many cases, introduced strains fail to colonize or are rapidly outcompeted by native taxa (Čaušević et al., 2024; Koziol et al., 2025). In others, the desired functional effects, such as improved growth or physiological performance, are attenuated or not expressed (Wong et al., 2024). This variability has prompted a move toward customized microbial consortia, engineered or selected microbiomes designed for specific functional roles such as N fixation, P solubilization, or biocontrol, and adapted to local soil-root edaphic conditions (Emami et al., 2020; Cirillo et al., 2023). However, for microbial inoculants to be effective, they must not only survive in the soil but also successfully establish within the rhizosphere niche, where signaling, colonization, and nutrient exchange take place (Albright et al., 2022).

2.4. *Key insights*

The rhizosphere is a dynamic and complex biogeochemical interface where chemical signals, microbial responses, and plant traits are constantly reshaped by edaphic and climatic factors. The synthesis presented here integrates well-documented mechanisms, including nutrient mobilization *via* root exudates, genetic and morphological root adaptations, and the role of microbial partners, within a broader conceptual framework for developing antifragile agricultural systems. These processes are inherently interconnected, operating as continuous feedback loops that cannot be understood in isolation. From a systemic perspective, integrating plant genetics, root architecture, agronomic practices, and microbial tools with the chemical features of rhizosphere soil offers a coherent framework and, at the same time, an underexplored opportunity for agroecological innovation, although their full integration at field level remains limited. As follow, actionable levers, strategies, and research gaps to unlock this capacity are discussed.

3. Levers for action and gaps

Despite important advances in root biology and rhizosphere research, many belowground processes remain still poorly characterized. As agricultural systems increasingly face climate variability, soil degradation, and the need to sustain productivity with reduced inputs, roots and their associated rhizosphere are now recognized as central drivers for system adaptation and redesign (George et al., 2024). Far from being passive conduits for water and nutrient uptake, roots represent a regulatory interface for plant-soil interactions, actively sensing and shaping the surrounding environment *in real time*. Nevertheless, critical knowledge gaps are particularly evident, including i) how roots and their microbiomes respond to simultaneous abiotic stresses, ii) tracking and modelling rhizosphere processes *in real time* and at relevant spatiotemporal scales, iii) designing and managing systems for antifragility without incurring unintended trade-offs. At the same time, emerging technological platforms/tools, including non-destructive imaging, AI-driven modelling, precision sensors, and isotopic tracers, are beginning to uncover the functional dynamics of belowground interactions (Awais et al., 2023; Ahkami et al., 2024). This Section first examines the biological and technological levers that can help address the gaps (*opportunities*), and then identifies the barriers (biological, technological, and policy-related, including translational bottlenecks from experimental to field scale - *constraints*) that must be overcome to achieve broader adoption and measurable impact. This dual focus on *what can be done* and *what is still missing* is intended to guide research priorities and implementation strategies. To operationalize the mechanisms discussed above, this section outlines the biological and technological levers required to translate rhizosphere knowledge into everyday practice.

3.1. Biological levers: roots, microbes, and stress adaptation

As agriculture faces increasing climate challenges, biological determinants such as root traits, microbial partnerships, and their co-regulated responses to stress represent crucial tools for stress resilience and antifragility in agroecosystems. While earlier chapters highlighted the root system plasticity, here the focus is on the interplay between these adaptive traits and microbial alliances in mediating stress responses. Roots respond to drought, salinity, temperature, and nutrient scarcity not only by altering structure, but also by modifying exudation profiles and engaging microbial consortia that help buffer environmental impacts (Wu et al., 2024). These strategies highlight that roots operate as part of integrated plant-microbe networks, where collective responses support adaptation under challenging conditions. In this perspective, five major abiotic pressures (drought, salinity, extreme temperatures, nutrient deficiency, and pollution) are considered as key constraints to productivity. A synthesis of the main root traits and microbial contributions is provided in Table 2.

With respect to drought, it profoundly alters nutrient dynamics and plant homeostasis. Recent evidence for durum wheat reframes nutrient homeostasis as an actively regulated component of stress response linked to genetic diversity (Maghrebi et al., 2024; Quagliata et al., 2025). In cereals deeper rooting is associated with improved water and N uptake and beneficial changes in subsoil microbial communities (Odone et al., 2024; Lattacher et al., 2025). Rhizosphere-associated bacteria (*e.g.*, *Bacillus*, *Pseudomonas*, and *Paraburkholderia* spp.) further promote drought tolerance *via* phytohormones, exopolysaccharides, and volatile organic compounds (VOCs) (*e.g.*, *Pseudomonas chlororaphis*) that enhance root growth, soil water retention, and systemic stress signaling (Cho et al., 2008; Kudoyarova et al., 2019; Naseem et al., 2024). These traits and interactions represent validated functional mechanisms for developing cultivars with combined water- and nutrient-use efficiency and for designing microbiome-based interventions tailored to water-limited environments (Table 2). However, tools to monitor multi-stress root-microbe interactions in the field are still scarce.

Under salinity, several plant species have evolved specialized root traits that mitigate ionic and osmotic stress. These include K^+ over Na^+ selectivity, enhanced suberization/lignification to restrict Na^+ influx, and root hairs proliferation to improve nutrient uptake (Assaha et al., 2017; Zou et al., 2022). In parallel, salt-tolerant rhizobacteria contribute *via* the synthesis of osmolytes (*e.g.*, proline, pinitol, glycine betaine, ectoine, soluble sugars and polyols), exopolysaccharides that improve soil aggregation and reduce Na^+ availability, and stimulation of antioxidant enzymes (Kumar et al., 2023; Xu et al., 2025). A synthesis is provided in Table 2, though field-level integration with other stresses remains poorly understood.

Extreme temperatures, both heat and cold, further threaten root function. Under heat stress, roots of heat-acclimated *Agrostis stolonifera* remodel membrane lipids toward saturated fatty acids (Larkindale and Huang, 2004). Rhizobacteria such as *Bacillus* and *Pseudomonas* mitigate heat stress *via* induction of heat shock proteins and stress-related enzymes (Ahmad et al., 2023). In *Arabidopsis thaliana*, sustained mild heat suppresses root hair initiation through downregulation of key transcription factors such as RHD6, RSL2, and RSL4, while RHD6 overexpression or ethylene treatment can restore root hair development, revealing an alternative adaptive mechanism (Du et al., 2025). Conversely, cold stress typically arrests root elongation and reduces membrane fluidity, limiting water and nutrient uptake (Su et al., 2025). Yet, auxin and cytokinin signaling regulate developmental and gravitropic responses, enhancing cold acclimation and rapid recovery, while cold exposure activates *DREB1/CBF* genes to promote cryoprotective proteins and soluble sugars (Tiwari et al., 2023). In addition, psychrotolerant rhizobacteria such as *Bacillus* and *Pseudomonas* spp. enhance tolerance by modulating ABA, producing antifreeze proteins, and sustaining root viability (Sun et al., 1995; Zubair et al., 2019). Table 2 summarizes these mechanisms, though SynCom and breeding integration under multi-stress conditions remains challenging.

Limited nutrient availability triggers compensatory strategies. For

Table 2

Root and microbial levers for abiotic stress adaptation in agroecosystems. The table summarizes major plant adaptations and microbial functions across five key stress contexts (drought, salinity, extreme temperatures, nutrient deficiency, and pollution). Root traits include structural, physiological, and exudation-based mechanisms, while microbial contributions cover symbioses, phytohormone and metabolite production, and pollutant degradation. The column *Application levers* highlights potential uses in breeding, agronomic practices, and microbiome engineering.

Stress type	Plant root traits/adaptations	Microbial contributions	Application levers
Drought	- Deeper rooting (*wheat, maize*) - Active regulation of nutrient homeostasis (*durum wheat*)	- *Bacillus, Pseudomonas, Paraburkholderia*: phytohormones & exopolysaccharides - *Pseudomonas chlororaphis*: VOCs priming plant defence & stress tolerance	- breeding for deeper roots & nutrient homeostasis - microbial inoculants improving drought tolerance
Salinity	- K^+/Na^+ selectivity (*rice, quinoa, Salicornia*) - Suberization & lignification (*rice*) - Root hair proliferation (*quinoa*)	- Osmolytes (proline, pinitol, glycine betaine, ectoine, sugars, polyols) - Exopolysaccharides - Induction of antioxidant enzymes	- breeding for ion exclusion - microbial consortia for osmotic protection - saline soil management
Extreme temperatures	- Heat: lipid remodeling (*Agrostis stolonifera*) - Heat: root hair regulation *via* RHD6, RSL2, RSL4 (*Arabidopsis*) - Cold: auxin/cytokinin signalling; DREB1/CBF activation; cryoprotective proteins & sugars (*Arabidopsis*)	- *Bacillus, Pseudomonas*: induction of heat shock proteins, modulation of stress enzymes (*wheat, rice*) - Psychrotolerant strains: antifreeze proteins, ABA modulation, sustaining root viability (*barley, maize*)	- breeding for heat/cold tolerance - microbial inoculants supporting thermal stress resilience
Nutrient deficiency	- N: *Soybean-Bradyrhizobium* symbiosis (*soybean*) - P: carboxylates, lateral root density (*wheat*) - Fe: PS secretion (*maize*) - AMF symbiosis (*maize, wheat, legumes*)	- *Azospirillum, Azotobacter, Pseudomonas*: N fixation, phytohormones (*maize, rice*) - *Azotobacter vinelandii, Bacillus subtilis*: siderophores (*maize, wheat*)	- breeding for exudation traits & symbioses - microbial inoculants - integrated nutrient management
Pollution	- Phytoextraction of heavy metals (*Brassica juncea, Helianthus annuus*) - Root architectural remodeling (*Brassica spp.*)	- Degradation of hydrocarbons & pesticides (*various crops, including maize and sunflower rhizospheres*) - Exudome shifts under agrochemicals stimulating xenobiotic-degrading microbes (*vineyard, horticultural crops*)	- breeding/selection for phytoremediators - microbial consortia for pollutant degradation - sustainable remediation practices

example, under N limitation, soybean establishes symbiotic associations with *Bradyrhizobium japonicum* mediated by flavonoids enabling N fixation (Szpunar-Krok et al., 2023). In addition plant growth-promoting rhizobacteria (PGPR, *Azospirillum*, *Azotobacter*, *Pseudomonas*) enhance N availability *via* N_2 fixation or phytohormone-mediated root growth (Zuluaga et al., 2024). In Fe-deficient conditions, maize upregulates phytosiderophore secretion to mobilize Fe, supported by microbes such as *Azotobacter vinelandii* and *Bacillus subtilis* that secrete siderophores (Ferreira et al., 2019). In response to P deficiency, wheat increases carboxylate exudation and lateral root density to solubilize otherwise inaccessible P (Shen et al., 2018). Plants also form AMF symbioses, enhancing nutrient acquisition under low P and micronutrient conditions (Cozzolino et al., 2013; Moreno Jiménez et al., 2024). These interactions reduce fertilizer reliance and improve nutrient-use efficiency, though performance under multi-nutrient limitations remains inconsistent (Table 2).

Soil pollution and phytoremediation present both opportunities and challenges. Certain plant species such as *Brassica juncea* (Bortoloti and Baron, 2022) and *Helianthus annuus* (Chauhan and Mathur, 2020) have demonstrated the ability to acquire and detoxify heavy metals through phytoextraction and sequestration mechanisms. Bochicchio et al. (2015) showed that plants may remodel their root architecture in the presence of metal pollutants avoiding polluted hotspots and seeking metal-free patches. Complementing these plant-based strategies, rhizosphere-associated microbes play a crucial role in the degradation of organic pollutants, including hydrocarbons and pesticides (Correa-García et al., 2018). Recent evidence indicates that agronomic practices, such as the foliar application of agrochemicals, can modulate the plant's metabolic response, reprogramming the exudome (*i.e.*, the overall profile of compounds released by roots) and selectively stimulating xenobiotic-degrading microbial communities (Cesco et al., 2021a). Such rhizosphere-based strategies show promise, though predictive models, regulations, and large-scale adoption remain unresolved (Table 2).

Overall, these diverse stress contexts illustrate how root traits and microbial partnerships can be mobilized as functional mechanisms for antifragility, while also highlighting key knowledge gaps (such as the need to better understand multi-stress interactions, to develop *real-time* field phenotyping tools, and to ensure consistent microbial inoculant performance) that define the frontier for research and application.

3.2. *Technological levers*

Emerging technologies capable of monitoring, modelling, and actively managing belowground processes under dynamic environmental conditions are critical to translate rhizosphere insights into scalable agricultural solutions. These analytical/technological levers, ranging from high-resolution imaging and *real-time in situ* sensing to advanced computational modelling, artificial intelligence (AI), and synthetic biology, are critical enablers to bridge biological insights with practical, climate-resilient management solutions. However, the concurrent occurrence of complex environmental (*i.e.*, copper [Cu] toxicity in soil) and edaphic (*i.e.*, nutrient deficiencies) conditions might hinder the capability of smart phenotyping approaches of correctly assign the detected symptoms to a physiopathy, making the role of trained professional essential (Pii et al., 2024).

3.2.1. *Analytical tools*

A first set of analytical tools involves non-invasive imaging and *in situ* sensing that reveals different dimensions of rhizosphere complexity. These technologies are becoming indispensable for visualizing root architecture and tracking resource dynamics directly *in situ*. Examples of applications of 2D and 3D imaging analytical techniques to rhizosphere studies are summarized in Fig. 2. Techniques such as X-ray computed tomography (CT) (Teramoto et al., 2020), magnetic resonance imaging (MRI) (Metzner et al., 2014) and neutron radiography (Tötzke et al., 2021) now enable three-dimensional reconstruction of root systems and resource fluxes within intact soil cores. CT has been used to assess wheat (*Triticum aestivum* L) root architecture under different P treatments (Flavel et al., 2017), root responses to soil texture in rice (Rogers et al., 2016) and to distinguish living roots from necromass in wetland environments (Chirol et al., 2021), while MRI and neutron radiography have enabled continuous *in situ* monitoring of water uptake dynamics in crops such as barley (Schneider et al., 2020 - Fig. 2a) and maize (Tötzke et al.,

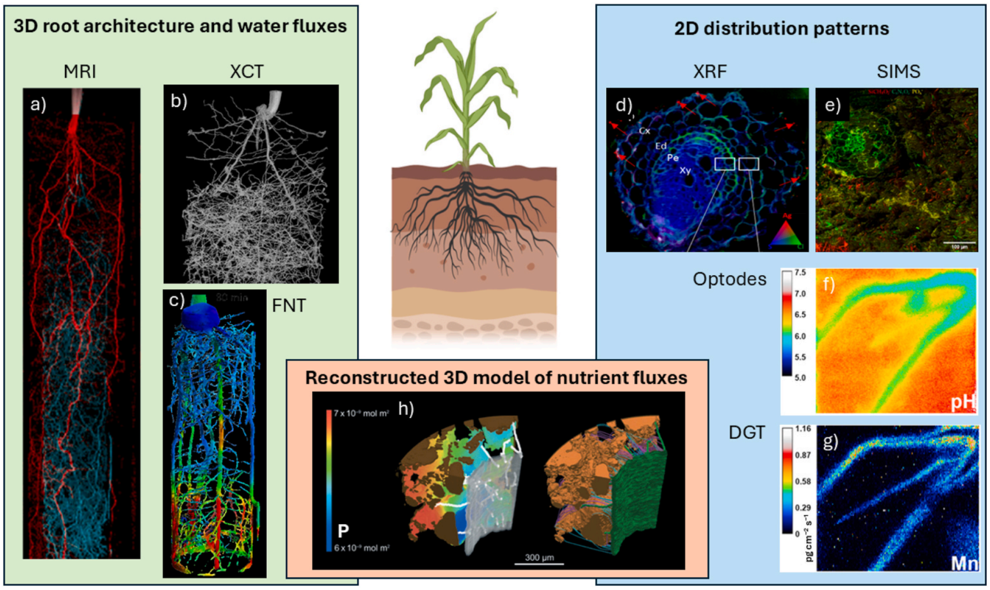

Fig. 2. Disentangling the heterogeneity and complexity of rhizosphere with 2D and 3D imaging analytical tools. Three-dimensional approaches (left panel) reconstruct whole-root structure and function at the plant scale, while two-dimensional chemical imaging techniques (right panel) resolve microscale chemical and pH gradients around roots. Together, these methods provide a multiscale view of root–soil interactions and enable integration into 3D nutrient flux models (center). Acronyms: MRI, Magnetic Resonance Imaging; XCT, X-ray Computed Tomography; FNT, Fast Neutron Tomography; XRF, X-ray Fluorescence; SIMS, Secondary Ion Mass Spectrometry; DGT, Diffusive Gradient in Thin films. Images adapted from: a) Schneider et al. (2020); b) Flavel et al. (2017); c; Tötzke et al. (2021); d; Pradas del Real et al. (2017); e) Bandara et al. (2021); f), g) Hoefer et al. (2017); h) Keyes et al. (2013).

2021 - Fig. 2c), respectively. Although offering lower spatial resolution, laser scanning and photogrammetry provide scalable and high-throughput alternatives that are increasingly applied in crop phenotyping efforts (Liang et al., 2024). Moreover, acquiring and elaborating 3D imaging data is usually time-consuming, especially for full rhizosphere visualization even using high performance computing suites. This can be accelerated by combining faster low-resolution acquisitions with deep learning and neural networks allowing the reconstruction of 3D images of sufficient quality for rhizosphere studies starting from noisy data (Teramoto et al., 2024).

Different analytical and imaging techniques are often combined for investigating and unraveling the heterogeneity and complexity of rhizosphere processes and reactions with increasing resolution, from millimeter to nanometer scale (Keyes et al., 2022). In fact, there is not a single analytical technique capable of capturing the full intricacy of rhizosphere processes, but each technique is specialized in elucidating a limited portion of the overall complexity. However, combining different imaging techniques is not trivial since each of them has its own constraints in terms of sample throughput, sample size, phase contrast, image resolution, and type of information gained. In addition, employing such multimodal and multiscale approaches brings about the issue of image and data correlation. Images and data obtained by different techniques, each operating at different fields of view or scales, pose considerable challenges for alignment. This is particularly evident when attempting to integrate spectroscopic maps (*e.g.*, infrared spectroscopy-IR, Raman spectroscopy, x-ray fluorescence spectroscopy-XRF, secondary ion mass spectrometry-SIMS, scanning and transmission electron microscopy coupled to energy dispersive spectroscopy-SEM/TEM-EDS, etc.), which are often 2D, with structural datasets that typically arise from 3D explorations (*e.g.*, CT, MRI, etc.). To simplify correlation issues, nano-positioning reference devices (nano-GPS, that act as fiducial markers to align images from different instruments) have been developed to allow data correlation using different instruments for the same 2D sample (Acher et al., 2021). Obtaining full 3D data is often challenging and limited to analytical techniques that can *look inside* matter like X-rays, NMR or proton/neutron-based techniques (Fig. 2a, b, c). Gaining 2D information is often easier and less demanding in terms of data management. Obtaining 2D pictures of complex 3D rhizosphere processes is either achieved through sectioning (Lippold et al., 2025) and analyzing sections with a suitable succession of analytical methods (*e.g.*, XRF - Fig. 2d, SIMS - Fig. 2e) to avoid artifacts, or using planar devices capable of collecting target chemicals (either molecules or ions) in the rhizosphere region that can be afterwards analyzed for their chemical composition [*e.g.*, diffusive gradients in thin film DGT systems (*i.e.*, thin-film devices that accumulate ions from the rhizosphere) Fig. 2g] (Hoefer et al., 2017; Doolette et al., 2022).

Complementing advanced imaging platforms, miniaturized soil sensors now provide high-resolution, *real-time* monitoring of rhizosphere dynamics (Ahkami et al., 2024). These tools measure key physicochemical parameters, including pH, nutrients' concentrations, redox potential, and temperature, offering fine-scale insights into root exudation patterns and microbial activity (Xie et al., 2024). Applications include ion-selective electrodes (ISEs) and ion-sensitive field-effect transistors (ISFETs), which enable *in situ* monitoring of ions like nitrate, K^+, and phosphates (Chen et al., 2020), and planar optodes (*i.e.*, optical sensor foils for pH and O_2) for visualizing pH values and oxygen gradients in the rhizosphere (Hoefer et al., 2017 - Fig. 2f; Koop-Jakobsen et al., 2018).

Stable isotope labelling, especially with ^{13}C and ^{15}N, is increasingly used to trace elemental fluxes from root exudates into microbial biomass and SOM fraction. For instance, it was shown that by using $^{13}CO_2$ labelling and ^{15}N natural abundance, the rhizosphere priming effects (*i. e.*, root-induced changes in the rate at which soil organic matter is decomposed after fresh C inputs) enhanced microbial necromass turnover, *i.e.*, the recycling of dead microbial biomass, increasing plant N uptake. The effect was especially evident in subsoil, where root-derived C inputs strongly stimulated decomposition of organic N sources (Pausch et al., 2024). Complementing these approaches, high-resolution mass spectrometry combined with *in situ* microsensors has been shown as a powerful, non-destructive approach to monitor *real-time* changes in root exudation and associated biogeochemical fluxes (Garcia Arredondo et al., 2024). However, the vastness and complexity of the data generated by these systems require the use of computational tools to transform them into actionable information, thereby supporting interpretation and modelling. For example, Keyes et al. (2013) developed a model of P uptake by wheat root hairs based directly on the geometry of hairs and associated soil pores as revealed by X-rays CT imaging (Fig. 2h).

These imaging and sensing platforms directly address gaps described in 3.1 by enabling *real-time* observation of root-microbe responses to drought, salinity, temperature, and nutrient stresses under realistic soil conditions. However, their wider adoption is limited by high costs, data processing complexity, and the lack of standardized protocols for field deployment, particularly in low-resource agricultural systems.

3.2.2. *AI implementation*

Building on these observational capabilities, AI and predictive analytics are becoming essential. AI, machine learning (ML) and deep learning (DL) have become essential tools for interpreting the complex datasets generated by modern rhizosphere research (Weihs et al., 2024). Such tools can reconstruct root system architecture from imaging data, simulate nutrient dynamics, and predict plant-microbe-soil interactions across spatial and temporal scales (Pace et al., 2025). For example, convolutional neural networks have been applied to segment root structures from X-ray CT datasets with high accuracy (Teramoto et al., 2024), while ML models have also been used to identify root traits that best predict and correlate with vegetative biomass in spinach under varying N conditions (Awika et al., 2021). AI is also being explored as a tool to optimize N and C fixation pathways in plants by guiding enzyme design and refining metabolic networks, with the goal of enhancing resource-use efficiency and stress resilience (Zhao et al., 2025). Building on these capabilities, generative AI is now opening new frontiers in rhizosphere science. While conventional AI focuses on pattern recognition and prediction based on historical or observed data, generative AI can generate synthetic datasets, models, or design hypotheses from learned patterns (Shahriar et al., 2025). In the context of soil-plant-microbe systems, this includes simulating hypothetical stress-response scenarios, designing candidate genes or microbial consortia, and constructing synthetic biological circuits tailored to specific environmental conditions. A particularly promising application of these AI innovations lies in the development of digital twins, continuously updated, interactive virtual replicas of real agroecosystems. Digital twin models integrate data streams from imaging, sensing, and omics platforms to simulate the behavior of crops, soils, and microbial communities under dynamic environmental conditions (Cesco et al., 2023; R. Zhang et al., 2025). Generative AI significantly enhances these systems by simulating numerous *what-if* scenarios that may not be observable through historical data alone, enabling researchers and decision-makers to explore potential responses to emerging stresses, management strategies, or climate variability (Shahriar et al., 2025). For example, prototype digital twin models have been used to simulate *real-time* root system architecture responses to soil moisture dynamics (Parewai and Köppen, 2025) and predict crop N management (Weckesser et al., 2022). These models offer a powerful platform for developing decision support systems (DSS) that can guide site-specific, *real-time* agronomic decisions (Cesco et al., 2023). Building on these advances, *spot farming*, a form of hyper-localized, precision agriculture, has emerged as a promising application of AI and digital twin technologies (Schroeder et al., 2022). By integrating digital twin outputs with root system architecture and soil microbiome data, *spot farming* might enable precise management of rhizosphere zones within a field (*e.g.*, targeted nutrient delivery, microbial inoculation, or irrigation based on *real-time* biological and environmental conditions), translating complex, high-resolution insights into regenerative interventions. Despite these advances, many AI-driven tools remain largely confined to research settings, with limited integration into practical crop management, mainly due to technological complexity, high costs, and limited scalability (Varriale et al., 2025). Bridging this gap will require adapting these tools for field-scale use, emphasizing affordability, usability, and responsiveness. As digital twins evolve and generative AI becomes more accessible, their combined potential may be key to transforming scientific insights into actionable strategies that enhance the efficiency, antifragility, and sustainability of agricultural systems (Ray, 2024). By integrating AI and predictive modelling with biological levers, it becomes possible to anticipate plant-microbe system behavior under climate-driven stress combinations. Although, most AI-driven tools remain confined to research contexts due to technological complexity, high computational demands, and limited operationally deployable interfaces, it is important to note that the current reliability of AI-based systems remains limited by data quality, model transparency, and contextual transferability (Gardezi et al., 2024). Before these tools can be deployed at scale, robust validation frameworks and safeguards are needed to ensure their accuracy, reproducibility, and ethical use in agricultural decision-making. The main challenge is to adapt these systems for practical use at the farm scale, ensuring that their predictive capacity translates into timely and site-specific interventions.

3.2.3. *Integrating new tools into crop management*

While these tools enhance our ability to observe and predict rhizosphere processes, the next step is to actively manipulate root traits and soil interactions to drive functional outcomes and to embed these analytical platforms directly into decision-support systems for on-farm application. These analytical approaches provide the mechanistic detail needed to interpret plant-microbe responses to climate-driven stresses such as nutrient depletion or pollutant accumulation, complementing imaging and AI-based predictive tools. Field applications already illustrate how these technological levers can be embedded into agroecosystem management. Image-based high-throughput field phenotyping platforms have been used in maize and wheat breeding trials to extract root architectural traits from field-grown plants and excavated root crowns, enabling selection for deeper and steeper root systems associated with improved water capture under stress (Bucksch et al., 2014). Non-invasive geophysical approaches such as spectral electrical impedance tomography have recently been piloted in sugar beet and maize trials to derive electrical root indices that correlate with root biomass and spatial distribution without excavation, providing repeated *in situ* measurements of root system development over the season (Michels et al., 2025). In parallel, AI-driven decision-support systems integrating soil and climate sensors, remote sensing products and machine-learning models are being tested in commercial and pilot farms to optimize irrigation scheduling and N fertilization, reducing water use and input losses while maintaining yields (Abioye et al., 2022; Gobbo et al., 2022). These examples show that high-resolution imaging, geophysical methods and AI-based modelling are already moving from proof-of-concept studies toward operational tools, offering a practical basis for incorporating rhizosphere-relevant information into agroecosystem management. However, their use in daily operational agriculture is limited by high instrumentation costs, the need for specialized expertise, and the difficulty of scaling laboratory precision to the field. Overcoming these barriers will require portable, automated, and cost-effective analytical platforms that can feed directly into decision-support systems for on-farm application.

3.2.4. *Genetic and microbial tools*

Finally, genetic and microbial tools provide direct intervention capabilities. Breeding and biotechnological tools such as marker-assisted selection, genomic selection, and gene editing tools like CRISPR-Cas9 are being actively deployed to enhance nutrient uptake and stress resilience (Kumar et al., 2024). Genes influencing root system architecture, exudation profiles, and symbiotic signaling are increasingly targeted for precise edits aimed at improving nutrient use efficiency and abiotic stress tolerance (Ragland et al., 2024). For instance, a rare *OsNPF6.1* allele (HapB) found in wild rice and activated by *OsNAC42*, improved NO_3^- uptake and yield, while its CRISPR/Cas9 knockout reduced yield, confirming its role in N use efficiency (Tang et al., 2019). In another case, rice lines harboring CRISPR/Cas9-induced mutations exhibited enhanced primary root elongation and an intensified response to drought stress (Ogata et al., 2020). Similarly, manipulating root growth angle through natural and edited variants of *qSOR1*, a homolog of *DRO1*, has been shown to enhance rice yield in saline paddies by promoting soil-surface rooting, allowing plants to avoid salt-affected zones and reducing stress exposure (Kitomi et al., 2020). In *Arabidopsis*, *PERK13* was found to regulate P starvation-induced root hairs elongation, with both knockout and overexpression lines enhancing root hairs growth under low P, suggesting its dual role in modulating root hairs development in response to nutrient stress (Xue et al., 2021). Perhaps most promising is the engineering of root-microbe interactions. Rather than modifying only the plant, researchers are increasingly exploring ways to engineer the rhizosphere itself, particularly through the use of synthetic microbial communities (SynComs, artificially assembled consortia of strains with defined functions). These carefully assembled consortia of beneficial microbes are designed to perform specific functions, such as N fixation, P solubilization, or stress mitigation, under defined environmental conditions (Zuluaga et al., 2024). For instance, SynCom comprising *Variovorax*, *Novosphingobium*, *Hydrogenophaga*, and *Acidovorax* strains has been shown to enhance P uptake in rice under field conditions (Ma et al., 2024). Similarly, targeted SynComs have been developed to improve the soil environment by suppressing soil-borne fungal pathogens and promoting the recruitment of antagonistic bacteria and beneficial microbes (Qiao et al., 2024). Unlike traditional inoculants, SynComs can be rationally designed for compatibility with specific host plant genotypes and local soil microbiomes, guided by high-resolution sequencing (*i.e.*, metagenomic, metatranscriptomic) and trait-based functional screening approaches (Delgado-Baquerizo et al., 2025). Advances in predictive modelling and multi-omics integration are enabling more precise SynCom design, offering a scalable platform for microbiome-based interventions that build antifragility into crop systems. Nevertheless, while considerable progress has been made in understanding and engineering plant-microbiome interactions, translating SynCom-based strategies into field applications remains a major challenge (Delgado-Baquerizo et al., 2025). Environmental variability, the complexity of native microbiomes, and the current limitations in monitoring microbial dynamics under real-world conditions continue to constrain large-scale deployment (Sessitsch et al., 2019). Although promising technologies, such as portable sequencing platforms, biosensors, and AI-based predictive models, are beginning to address these barriers (Yuan et al., 2023), their integration into agroecosystem management frameworks is still in its early stages. Continued innovation in scalable monitoring and management tools will be critical to fully harness the potential of microbiome engineering to foster not just resilience but true antifragility and local adaptation in crop systems. These genetic and microbial tools represent the most direct technological route for implementing biological levers (Section 3.1), enabling targeted improvement of root traits and their associated microbial partnerships for stress resilience. However, their potential remains underexploited in real-world agriculture due to environmental variability, unpredictable interactions with native microbiomes, and regulatory hurdles. Progress will depend on integrating SynCom design with environmental modelling, developing field-ready microbial monitoring systems, and creating policy frameworks that facilitate safe and rapid deployment.

3.2.5. A combined approach

Taken together, these technological levers (from imaging and sensing platforms to AI-driven predictive models, advanced analytical techniques, and genetic/microbial engineering) can substantially broaden the scope of what can be measured, modelled, and manipulated in the rhizosphere. In combination, they provide the operational capacity to translate the biological insights described in Section 3.1 into targeted breeding strategies, precision management practices, and microbiome engineering solutions tailored to climate-resilient, low-input agriculture. However, their transformative potential remains only partially realized, constrained by persistent challenges in cost, scalability, interoperability, and regulatory acceptance. These constraints, along with those identified for biological levers, converge in the broader set of barriers (biological, technological, and policy/translational) that must be overcome before belowground innovations can achieve widespread impact in real-world agricultural systems. Translational levers are therefore needed to close this gap and enable adoption at farm scale.

3.3. From lab to field: bridging gaps with translational levers

3.3.1. Participatory and technological enablers

Effective farm scale change requires translating biological and technological levers (Section 3.2) into field-ready strategies. This requires not only technological innovation, but also the intentional design of policies, incentive structures, extension networks, and knowledge transfer systems that enable agronomists/farmers to actively manage the rhizosphere as a dynamic component of agroecosystems and an integral part of crop management. Taken together, the biological and technological levers discussed above illustrate the central challenge addressed in this manuscript: the translation of rhizosphere knowledge into routine farm-scale practice. While rhizosphere processes are well documented scientifically, their integration into everyday management requires concrete operational pathways, enabling technologies, and supportive policy frameworks. The following section highlights how these components converge into a rhizosphere-centric, antifragile design for real-world agroecosystem management. In this perspective, multi-site, long-term field experiments together with networks of *on-farm* trials are crucial to test rhizosphere-oriented practices under realistic climatic and management variability, generating evidence that is directly relevant to everyday farming decisions.

A first persistent gap is the limited co-design between researchers and end-users. Too often, tools and technologies are developed without sufficient input from farmers, agronomists, or land managers. Participatory innovation approaches, such as collaborative field trials, decision-support tools, living labs (*i.e.*, on-farm experimental platforms co-designed with farmers and advisers), agricultural innovation hubs/villages, and adaptive management frameworks (Taskin et al., 2025), are essential to ensure that rhizosphere-oriented strategies are not only scientifically robust but also scalable, site-specific, and adapted to local agroecological conditions (Maughan and Anderson, 2023). In such arrangements, farmers contribute to defining experimental questions, management options and evaluation criteria, thereby increasing the likelihood that successful practices are rapidly adopted and disseminated through farmer networks and peer-to-peer learning.

Another critical enabler is the technology accessibility (also called *technology democratization*). Innovations such as mobile phenotyping platforms, low-cost spectrometers, and *real-time* soil health diagnostics must be scaled and adapted for adoption, particularly in smallholder and resource-limited agricultural systems (Adams and Jumpah, 2021). Strategic investments in open-access hardware, open-source software, and capacity-building initiatives are essential to ensure that advances in rhizosphere science translate into broad-based benefits, rather than remaining concentrated within well-funded research institutions and large-scale operations (Hackfort, 2024). However, their effective deployment depends on reliable digital infrastructure, and in many rural areas insufficient broadband connectivity remains a major barrier to the integration of precision technologies and data-driven applications (Duanmu et al., 2025). When basic connectivity is available, integrating sensor data (*e.g.*, soil moisture, temperature, electrical conductivity, nutrient proxies) and remote-sensing products into simple dashboards and advisory tools can provide farmers with near real-time indications on rhizosphere-relevant conditions, supporting adaptive decisions on irrigation, fertilization, cover crop termination, or traffic management.

3.3.2. Biological integration and field-level decision making

From the perspective of biological integration, breeding programs should integrate root and microbiome-associated traits, along with key soil characteristics, from the earliest stages of selection, supported by advances in high-throughput root phenotyping, marker-assisted selection, and microbiome-informed selection indices (Sinha et al., 2023; Cernava, 2024). Similarly, nutrient management strategies must move beyond conventional product-based recommendations (*e.g.*, fixed fertilizer doses) toward rhizosphere-centered approaches that explicitly account for soil chemical properties, soil ecological processes, soil-microbe-plant interactions, and site-specific dynamics (Zuluaga et al., 2024). At field scale, this implies translating complex process-based understanding into a limited set of operational indicators and decision rules (*e.g.*, combining soil tests, crop status and simple structural assessments), which can be used by advisers and farmers to align fertilization, organic amendments and crop choice with rhizosphere functioning.

Policy interventions have a critical role in shaping the future of sustainable agriculture. Current agricultural incentives often prioritize short-term yield maximization, reinforcing input-intensive systems while undervaluing belowground ecosystem processes. Aligning economic incentives with rhizosphere health may involve payment schemes for ecosystem services, C credits linked to belowground C sequestration, or certifications based on rhizosphere biodiversity, supporting practices such as cover cropping, reduced tillage, the application of organic amendments, and/or microbial inoculation (Piñeiro et al., 2020; van Asseldonk et al., 2023; Imran and Ortas, 2025). Such instruments can help to offset transition costs, reduce perceived risk, and reward farmers for investing in soil and rhizosphere management whose benefits emerge over longer time horizons than a single season. Specifically with respect to microbial inoculants, it should be noted that their field performance is often highly variable across soil types, climates, and crop systems. For example, field trials of arbuscular mycorrhizal fungal (AMF) inoculants found that many commercial products failed to establish under non-sterile field conditions, highlighting the challenge of translating greenhouse efficacy to real agroecosystems (Thomsen et al., 2021). Similarly, legume inoculation studies with rhizobia have shown that effectiveness depends strongly on soil background rhizobia populations, native microbial competition, and edaphic context (Mendoza-Suárez et al., 2021). The mechanisms driving inoculant success or failure include (i) competition with indigenous microbiota for colonization niches; (ii) limited survival or establishment of the inoculant under adverse abiotic conditions; (iii) host genotype-microbe compatibility; and (iv) agronomic management practices such as fertilizer levels and tillage regime (O'Callaghan et al., 2022). Therefore, the most consistent outcomes are observed when inoculants are developed with local soil-microbe context in mind and integrated into management systems that support microbial persistence and function rather than assuming one-size-fits-all solutions.

3.3.3. Policy, education, and institutional scaling

Education and extension services must evolve alongside technological and scientific advances. Farmers and agronomists require not only access to tools but also the knowledge and skills necessary to monitor, interpret, and manage rhizosphere processes effectively. In this context, training and capacity building are essential to ensure the proper interpretation, implementation, and dissemination of these innovations (Cesco et al., 2021b). Experiences such as FAO's Farmer Field Schools show how experiential learning, combined with locally adapted knowledge systems, can successfully embed soil and rhizosphere health practices into everyday management (van den Berg et al., 2020). Embedding rhizosphere concepts into advisory curricula, vocational education and continuous professional development can further support the mainstreaming of belowground-focused practices.

Scaling rhizosphere-based innovations will require coordinated institutional efforts. The inherent complexity of soil-microbe-root interactions demands cross-disciplinary integration, involving collaboration among soil scientists, soil ecologists, plant scientists, agronomists, data scientists, agricultural engineers, and policy makers (Afridi et al., 2024). Emerging research hubs, living laboratories, agricultural innovation villages, and innovation accelerators operating at the interface of science and practice offer promising platforms for developing and testing rhizosphere-centric solutions (Yousefi and Ewert, 2023). Without these translational levers, even the most advanced rhizosphere science risks remaining confined to research trials rather than shaping the future of agriculture. Developing antifragile and climate-resilient agroecosystems will require not only technical solutions, but also systemic coordination among researchers, farmers, practitioners, policymakers, and local communities. In this process, agricultural professionals, whether farm owners or technical advisors, play a pivotal intermediary role, translating complex knowledge into site-specific action. As highlighted by the FAO (2012), engaging decentralized expertise is essential to ensure that lab-to-field knowledge transfer reinforces long-term agroecosystem resilience. Overall, field trials, real-time monitoring, farmer engagement and enabling policy and economic frameworks represent complementary pillars for scaling rhizosphere science into everyday farming practice.

4. A call for a rhizosphere-centric paradigm

Building on the biological and technological levers outlined in Sections 3.1 and 3.2, and on the translational frameworks discussed in Section 3.3, the next step is reframing the rhizosphere as a central design principle of agroecosystems. This section integrates the translational elements described earlier into a coherent operational model for rhizosphere-centric agroecosystem design. Fostering antifragility requires coordinating systemic change beyond incremental adjustments, correcting the historical bias toward aboveground traits. In fact, a growing consensus in agricultural science now recognizes that research and management practices have historically focused disproportionately on aboveground traits. For decades, efforts have focused on optimizing canopy structure, chlorophyll content, harvest index, *i.e.* every conceivable trait that is easily observed and measured, ultimately aimed at improving crop performance. Meanwhile, the rhizosphere, encompassing the soil-microorganism-plant system in its full complexity and functional integrity, has often received limited and inappropriate attention in agronomic research. Yet, in an era marked by climate instability, soil degradation, and growing constraints on agrifood systems, a shift in focus is urgently needed. Embracing a rhizosphere-centric paradigm requires a fundamental reframing of how agroecosystems are conceptualized. Thus, placing roots and their microbial partners alongside the other key players in system design unlocks new possibilities for enhancing soil structure, optimizing resource flows, and fostering agroecosystems that are productive, ecologically adaptive, and increasingly antifragile in the face of disturbance.

4.1. Redesigning agriculture from below

Regenerative agriculture often uses reduced tillage, organic amendments, and nutrient cycling to improve soil health. However, as mentioned above (Section 2), the rhizosphere, where roots and microbes actively shape soil structure, chemistry, and biological activity, is the primary driver of soil regeneration (George et al., 2024). To recognize the rhizosphere as a structural and functional determinant of soil systems, agriculture needs to move beyond treating breeding, management, and microbial inputs as isolated actions and instead view them as interconnected components of an agroecological whole. The effectiveness of any practice should be evaluated by its support of essential rhizosphere functions such as nutrient cycling, microbial recruitment, water retention, and C stabilization, particularly under variable and stress-prone conditions. In this view, optimal rhizosphere functionality underpins healthier soils and, thereby, crop resilience. Importantly, the rhizosphere regenerative power lies in its capacity to restructure soil physical and biochemical properties from within. Root growth and microbial activity drive soil aggregation, enhance porosity, and regulate water dynamics. Through a constant exchange of exudates and microbial metabolites, plants and their microbiomes co-construct a biologically active and structurally dynamic soil matrix (Ma et al., 2022). Strategic use of leguminous cover crops like crimson clover or deep-rooted species such as white lupin stimulates microbial diversity and accelerates nutrient turnover (Bak et al., 2022). Crops like soybean and wheat, through sustained C input and rhizodeposition, play a central role in building long-term SOM fraction, particularly in deeper layers where C stabilization has the greatest impact (Lattacher et al., 2025). Even the physical penetration of roots into compacted or degraded sub-soils contributes to regeneration, forming biopores that facilitate gas exchange, moisture infiltration, and vertical redistribution of organic matter (Lucas et al., 2023). These are not linear improvements but dynamic feedback loops, enabling soils to adapt and improve over time in response to disturbance. However, realizing the regenerative potential of the rhizosphere means also rethinking plant genetics and agronomic practices (including chemical features of rhizosphere soil and crop physiological characteristics) as co-evolving elements of an integrated system. Breeding efforts should focus on root and microbiome-associated traits in terms of their functional role within specific soil and microbial contexts. For instance, a root trait such as depth or branching density may be beneficial in one system but counterproductive in another depending on organic matter inputs, tillage practices, or microbial composition (Lattacher et al., 2025). Likewise, management practices must be reconstructed as components of a coordinated system, where crop rotations, cover cropping, conservation tillage, and organic amendments function as integrated interventions that shape the temporal and spatial dynamics of the rhizosphere. For example, rotating crops with contrasting exudation profiles can promote microbial diversity and functional resilience, while synchronizing organic amendments with periods of peak root activity can amplify beneficial plant-microbe feedback (Town et al., 2023). Similarly, reducing tillage in zones of elevated microbial activity helps preserve critical belowground networks and structural integrity (Domnariu et al., 2025). Ultimately, these management decisions should be informed by the biological rhythms and dynamic processes of the rhizosphere, rather than by rigid agronomic calendars.

In addition, to unlock the full regenerative capacity of the rhizosphere, microbial management should evolve from reliance on generic microbial inoculants toward the design of systems that foster the integration and persistence of microbial communities aligned with plant and soil function (Delgado-Baquerizo et al., 2025). This might involve transitions to low-input systems, targeted organic inputs, or pH and moisture adjustments to create favorable conditions for microbial symbiosis (Pandey and Saharan, 2025). In this context, microbial success is not defined by initial colonization, but by durable establishment and sustained contributions to rhizosphere functions. Importantly, maximum benefits arise only when genotype, management, and microbial ecology are aligned as components of a self-reinforcing system. For example, a drought-tolerant genotype may underperform when paired with incompatible microbiomes or when soil amendments interfere with the establishment of beneficial root-microbe associations (Guo et al., 2023). Likewise, a microbial consortium optimized for P solubilization may fail to deliver expected benefits when root exudation is mismatched or when tillage practices disrupt microbial habitat (de

Zutter et al., 2022). Such alignment enables the rhizosphere to act as a self-reinforcing system. Within this paradigm, agriculture should shift from isolated variables control toward the management of dynamic biological interactions. Such interactions, designed to reorganize under stress, can generate agroecosystems that increase their functional capacity when exposed to environmental pressures. Redesigning agriculture from below means leveraging the rhizosphere as a living interface capable of driving adaptive and regenerative agroecosystems from within. This concept is visually captured in a Unified Modeling Language (UML)-based systems diagram (Fig. 3) that illustrates a systemic crop model grounded in the integration of environmental pressures, plant species characteristics, cultivation techniques, and processing technologies. Because Fig. 3 adopts a UML-based systems notation, its purpose is to represent structural relationships, information flows, and decision pathways at a high level of abstraction. This modelling approach is intentionally more complex than conventional figures, as it aims to convey system architecture and functional integration rather than simple visualization. To illustrate these dynamics, Fig. 3 synthesizes the key processes through which roots, microbes, and agronomic practices interact to strengthen the antifragility of agroecosystems. At the core is the crop system, which results from the dynamic interaction of three key dimensions: crop pressing and stressing, crop attitude, and crop management. A critical feature is the role of rhizosphere management (highlighted in red), which plays a central part in influencing the antifragility of the agroecosystem. This intervention enhances its adaptive capacity, moving it beyond mere resilience toward proactive optimization under pressure. From a practical agronomic perspective, Fig. 3 underlines that rhizosphere management is not an isolated input but a structural lever that integrates plant traits, environmental constraints, and cultivation practices into a self-reinforcing system. When these dimensions are aligned, the rhizosphere acts as a technical driver of antifragility, enabling agroecosystems to reorganize under stress and convert biological interactions into measurable gains in soil structure, nutrient cycling, and long-term system performance.

4.2. Rhizosphere-mediated C, N, and water fluxes

4.2.1. Rhizosphere control of carbon fluxes and stabilization

Beyond being a structural architect, the rhizosphere is a key biogeochemical driver. Carbon, N, and water are fundamental fluxes, regulated at the rhizosphere interface. As previously discussed, optimizing these flows is a core design challenge for regenerative, climate-resilient agroecosystems. While C sequestration is widely recognized as a climate-mitigation strategy, assessments still focus mainly on aboveground biomass and residues. However, data from Sukhoveeva (2024) show that root necromass contributes around 10 % of the total biomass in a single growing cycle in six major crops, including cereals and legumes. This represents a substantial input of organic carbon (0.08–0.38 t ha^{-1}) largely missing from C budgeting models. These values are clearly underestimated, since fine roots and root hairs are

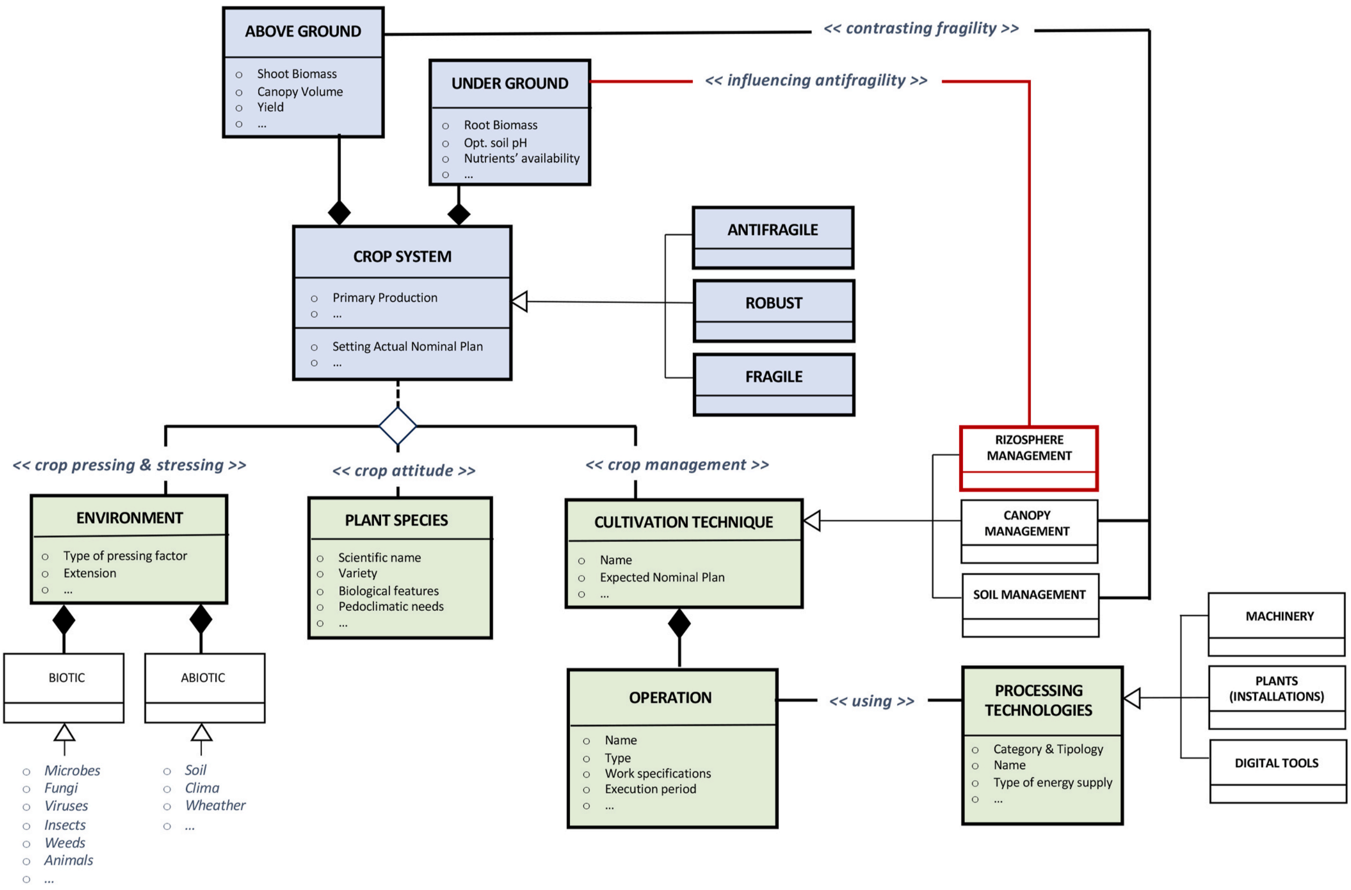

Fig. 3. UML-based conceptual framework of the rhizosphere as a biological lever for antifragile agriculture. The diagram represents the dynamic interaction between roots, microbes, and management practices, highlighting key processes (nutrient mobilization, C cycling, stress resilience) that drive soil regeneration through integrated, adaptive agricultural design. Diagram notation guide: green background: entity (*e.g.*, environment, plant species, operation); blue background: relationship or process (*e.g.*, Crop System); white background: specialization or categorization (*e.g.*, biotic/abiotic stressors); black diamond (◆): composition, indicates that one component is made up of others; white diamond (⋄): ternary relationship, represents a three-way connection (*e.g.*, among environment, plant, and technique); triangle (△): inheritance, used for generalization/specialization; red arrow: highlights causal, amplifying, or system-enhancing effect (*e.g.*, rhizosphere management → antifragility). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

often lost and exudation inputs are rarely included. Nonetheless, although root biomass represents a limited fraction, it still provides a direct and consistent pathway of organic matter into soil, with important implications for long-term C stabilization. In line with this, Kuzyakov and Domanski (2000) reported that cereals and grasses may channel even larger amounts of C belowground, reaching approximately 1.5–2.2 t ha^{-1} per season. However, such estimates remain context-dependent (Sukhoveeva, 2024). Root-to-shoot ratios are highly variable and depend on plant genotype, developmental stage, and environmental factors such as drought stress, nutrient availability, or atmospheric CO_2 (Seidel et al., 2024). More importantly, such values remain largely experimental and cannot yet be translated into standardized agronomic indices. This highlights a critical gap: while rhizosphere studies provide important insights into belowground C fluxes, we still lack operational tools and metrics to integrate them into practice. Nonetheless, it emphasizes the substantial role of root-derived inputs, both through exudation and necromass, in shaping soil C dynamics, still underestimated in C budgeting models. Moreover, the rhizosphere plays a central role in C stabilization through intricate soil-microbe-root-interactions. Carbon cycling begins at the root-microbe interface, where root-derived inputs (*i.e.*, exudates, sloughed cells, and root turnover) fuel microbial metabolism and play a central role in the formation of stable SOM fraction, particularly in the form of microbial necromass (Wang et al., 2021; Sokol et al., 2024). In this respect, it should be noted that the qualitative and quantitative composition of exudates strongly influences these pathways. Labile compounds such as sugars and amino acids are rapidly metabolized, supporting microbial growth and the production of cell-wall components and extracellular polymeric substances, which subsequently become stabilized as mineral-associated organic matter or are occluded within aggregates. In parallel, exudates rich in organic acids and chelators promote mineral weathering and the release of polyvalent cations, thereby enhancing organo-mineral associations and aggregate stabilization. Over repeated plant-microbe cycles, this *exudate-microbial* pathway not only contributes to long-term C storage but also improves aggregate stability, porosity, and water-holding capacity, reducing erosion risk and enhancing soil health. In this sense, exudation patterns act as a biochemical lever through which plants, in concert with microbial partners, regulate the balance between short-term C turnover and the build-up of persistent C pools that underpin multiple ecosystem services, from C storage and nutrient retention to regulation of infiltration and runoff. These belowground inputs not only support microbial biomass but also facilitate aggregate formation and mineral associations, especially in deeper soil horizons, as observed in crops such as wheat (Hirte et al., 2018). Importantly, the same plant-microbe processes, when strategically aligned with breeding and management choices, can reinforce antifragility by generating feedback loops that stabilize structure and fertility even under stress conditions (Equihua et al., 2020; Lucas et al., 2023). Although these processes are highly context-dependent (*e.g.,* plant genotype, soil properties, and environmental conditions), their combined effect underscores the rhizosphere's role as a key driver of both soil fertility and long-term C stabilization. From a management perspective, optimizing C flow through the rhizosphere involves selecting root traits that enhance exudation, maintaining continuous root cover to sustain microbial activity, and aligning organic input strategies with plant growth stages to support microbial turnover and promote C stabilization. In this sense, the challenge for agronomy is to move from experimental measurements of belowground C dynamics toward the development of decision-support tools and management indicators that can guide farmers in adopting rhizosphere-based strategies for soil C enhancement.

4.2.2. *Rhizosphere-mediated nitrogen cycling and climate mitigation*

Nitrogen remains one of the most limiting and environmentally problematic nutrients in agricultural systems, with substantial losses occurring through leaching, volatilization, and gaseous emissions (Fudjoe et al., 2023). However, when strategically managed, the rhizosphere provides key leverage points for improving N use efficiency and reducing environmental impacts. Symbiotic interactions between legumes and N-fixing microbes such as *Rhizobium* and *Azospirillum* can substantially reduce reliance on synthetic inputs while mitigating nitrous oxide (N_2O) emissions, a potent greenhouse gas (Schulman et al., 2025). This is not merely a biological advantage, but a climate-mitigation mechanism rooted in rhizosphere ecology. Beyond biological fixation, N cycling is closely tied to rhizosphere C dynamics. In C-rich environments, common in regenerative or low-input systems, microbial guilds such as denitrifiers can perform complete denitrification, converting nitrate (NO_3^-) to inert dinitrogen gas (N_2), thereby reducing N_2O emissions and enhancing N retention (Saggar et al., 2013; Fudjoe et al., 2023). Such integrated C-N linkages illustrate how managing the rhizosphere as a coupled biogeochemical system can deliver both productivity and environmental benefits. Agronomically, better C stabilization and N efficiency mean higher yields, less fertilizer use, and greater stability under variable climates. At the same time, reduced N losses and lower N_2O emissions contribute directly to climate-change mitigation and improved water quality, emphasizing that rhizosphere-mediated N dynamics are central not only to crop nutrition but also to environmental protection.

4.2.3. *Rhizosphere regulation of water dynamics and integrated antifragility*

The regulatory influence of the rhizosphere extends beyond nutrient dynamics into the domain of water cycling, shaping the hydrological conditions that underpin both plant performance and broader ecosystem functions (Vetterlein et al., 2020). Root-microbe interactions actively modulate soil porosity, infiltration rates, and moisture retention, thereby enhancing drought resilience and buffering against excess rainfall (Vetterlein et al., 2020). In both dryland and wetland systems, specific root traits play a key role in controlling rhizosphere hydrology. In dryland environments, deep taproots enhance access to subsoil water and facilitate vertical water redistribution (Bleby et al., 2010). Conversely, in wetland crops such as rice, aerenchyma formation allows oxygen diffusion into anoxic soils, promoting methane (CH_4) oxidation by methanotrophic bacteria and reducing CH_4 emissions (Ge et al., 2024). In such systems, the rhizosphere functions as a biologically mediated buffer regulating redox dynamics and greenhouse gas (GHG) fluxes, modulating GHG fluxes not through synthetic inhibitors but *via* biologically mediated oxygen diffusion and microbial oxidation pathways (Haviland and Noyce, 2024). In this respect, the role of roots in facilitating gas exchange, particularly oxygen, should not be neglected. Root-derived biopores efficiently connect atmosphere and soil, often more than animal-derived ones (such as those formed in the *drilosphere*) (Uteau et al., 2022).

When rhizosphere processes are strategically coordinated, they not only regulate water dynamics but also transform environmental stressors into catalysts for improved performance, as discussed in Section 3.1 for drought-microbiome interactions (Axenie et al., 2024). Achieving antifragility in agriculture requires an integrated approach to belowground architecture and biology. For instance, strategically timing cover crop termination can help retain soil moisture and sustain rhizosphere activity when crops are most vulnerable (Van Eerd et al., 2023). These management practices tailored to specific root traits reflect the broader principle that, in regenerative systems, effective water management is intrinsically linked to rhizosphere ecology. Biogeochemical fluxes depend not on single interventions but on aligning biological processes to enable cooperative, self-reinforcing function. Just as aboveground canopies are designed for light interception and airflow, belowground systems must optimize flows of resources and energy. In a rhizosphere-centric paradigm, managing C, N, and water means directing biological processes through intentional system design. This tuning of subterranean flows unlocks the potential for climate-adaptive, ecologically informed agriculture. At broader spatial and temporal scales, these coordinated rhizosphere-mediated fluxes underpin ecosystem services that are directly relevant to global sustainability goals, including long-term soil C storage for climate-change mitigation, improved nutrient-use efficiency and reduced nutrient losses for water and air quality, and the maintenance of biologically active, structurally stable soils that support biodiversity and reduce land degradation. In this sense, rhizosphere-mediated fluxes act as a central coordination hub where plant physiology, plant genetics, microbial ecology, soil chemistry, and agronomic management converge, translating into agroecosystems that do not merely resist disturbance but improve through it. By embedding these flows in systemic frameworks linking research, policy, and farmer-led innovation, C, N, and water cycles can be steered toward productivity and antifragility, completing the transition to integrated, rhizosphere-driven design. This precise tuning, aligned with genetic, microbial, and management levers, unlocks the full potential for climate-adaptive, ecologically intelligent agriculture.

5. Concluding remarks: priorities for the operational transition

After decades focusing on aboveground traits, the rhizosphere is now recognized as a critical frontier driving soil formation, nutrient cycling, stress adaptation, and long-term C stabilization. Rather than a passive zone, the rhizosphere is a dynamic biological interface, whose structure and function evolve in response to environmental variability, often enhancing system performance under stress, an expression of the antifragile potential in which disturbances can stimulate reorganization and improved functional capacity. Advances in molecular ecology, imaging, and phenotyping reveal how roots influence microbial recruitment, how exudates respond to environmental stress, and how microbial necromass contributes disproportionately to stable SOM fraction, highlighting rhizosphere central role in achieving key agricultural goals. Despite this progress, translating rhizosphere knowledge into field practice remains a challenge. In fact, breeding programs still prioritize aboveground traits, diagnostic tools for rhizosphere health remain largely confined to research, and farm management and policy frameworks often favor extractive models over antifragile ones. In a context like this, meeting the challenge ahead means adopting a true rhizosphere-centric paradigm, redesigning agriculture from the root up. This involves integrating rhizosphere traits into crop breeding, tailoring cover crop rotations to influence microbial assembly and C flows, and managing soil as a living, feedback-driven system. These approaches pave the way for future agroecosystems that not only recover from disturbances but also grow stronger. Moreover, the convergence of new analytical, digital, and biotechnological tools now provides the opportunity to transform rhizosphere science into operational strategies for agriculture. To translate this vision into practice, Fig. 4 presents a systems-oriented crop model that embeds rhizosphere-level processes within broader cultivation strategies. Specifically, it offers a UML-based operational scheme illustrating the flow of information, from imaging, *in situ* sensors, and omics data, through predictive models and digital twins, to precision management decisions. Because this diagram uses UML systems notation, its purpose is to represent the underlying information architecture

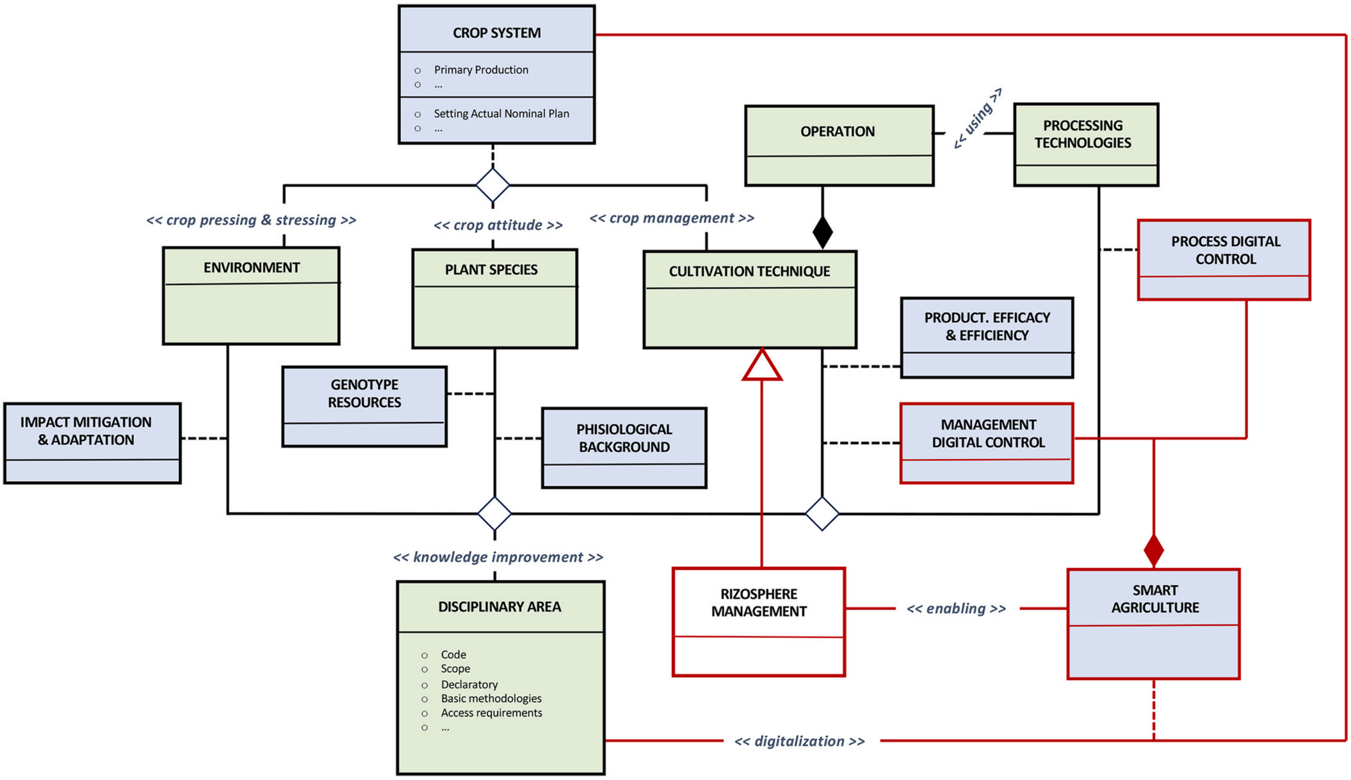

Fig. 4. UML-based operational scheme for implementing a rhizosphere-centric paradigm supported by digital technologies for an AI-driven antifragile agriculture. This framework integrates data from imaging, *in situ* sensors, and omics into predictive models and digital twins, translating outputs into precision management decisions such as nutrient delivery and irrigation. System performance is assessed using agronomic indicators including carbon sequestration, resource-use efficiency, and yield stability.The diagram uses UML notation: green for entities, blue for systems and processes, white for knowledge domains, and diamonds/arrows for compositional and causal relationships. Diagram notation guide: green background: entity (*e.g.*, environment, plant species, cultivation technique); blue background: relationship or digital process (*e.g.*, crop system, digital control); white background: specialization or knowledge category (*e.g.*, TRL knowledge, crop attitude); black diamond (◆): composition, indicates that one component is made up of others; white diamond (⋄): ternary relationship, represents a three-way connection (*e.g.*, plant-environment-technique); red arrow or line: causal or digitalizing effect (*e.g.*, knowledge → Smart Agriculture); dashed red arrow: digitalization pathway linking scientific knowledge to operational control. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and decision pathways required to operationalize rhizosphere knowledge, emphasizing system logic rather than visual simplification. This representation complements the conceptual framework of Fig. 3 by translating principles into actionable, digitally supported interventions, showing how rhizosphere-level processes can be embedded into *real-time* management through data integration, predictive modelling, and decision-support tools. Rather than treating rhizosphere management as a marginal input, the diagram positions it as a foundational component of cultivation techniques, strategically connected to digital control pathways that support system-level feedback and adaptive optimization. This framework illustrates how digital and biological intelligence converge to form smart, antifragile agroecosystems, capable of adapting, optimizing, and improving under pressure. Importantly, the integration of sensor networks with AI is not merely descriptive but establishes the basis for a predictive and adaptive agronomy, where management decisions can be continuously optimized *in real time* according to soil-microbe-plant dynamics. At the core of this convergence lies an integrated biological intelligence (a form of *collective intelligence*) emerging from the interaction between soil, microbes, and roots. By integrating sensors and AI, it becomes possible to read and interpret biological signals *in real time*, transforming the rhizosphere into an augmented decision-support system. This data-driven rhizosphere intelligence supports more precise and regenerative crop management, fostering antifragile responses that not only withstand stress but improve system performance through it. This approach embraces the intrinsic ecological complexity of agroecosystems, where uncertainty is not eliminated but adaptively managed. Moving beyond rigid planning, antifragile systems use adaptive structures, *real-time* feedback, and multiple perspectives to thrive under change. This transition is already visible in practice: farmers are testing root-led rotations and mycorrhizal strategies, researchers are developing digital twins to model root-soil interactions, and policymakers are beginning to embrace soil health indicators that reflect microbial and ecological functions. However, to better bridge the gaps discussed in this work, several concrete near-term priorities can be outlined for different actors like researchers, policymakers, or farmers/professionals/advisors. For the first, key steps can include i) co-designing long-term, multi-site field experiments that explicitly link root traits, exudation patterns and rhizosphere microbiomes with soil C, N and water fluxes under contrasting stress and management scenarios, ii) developing a set of operational rhizosphere indicators (such as rooting depth and distribution, aggregate stability and simple biological activity metrics) that can be measured with affordable tools, and iii) translating process-based understanding into models and decision rules that can be embedded in breeding pipelines and advisory tools. For policymakers, priorities include a) incorporating rhizosphere-relevant metrics into soil health frameworks, C farming schemes and agri-environmental payments, b) supporting living labs, advisory services and farmer networks that experiment with rhizosphere-centric practices (*e.g.*, diversified rotations, cover crops, reduced tillage, context-specific microbial tools), and c) deploying risk-sharing and investment instruments that lower the economic barriers to adoption, including support for digital infrastructure in rural areas. Finally, for farmers and professionals/advisers, immediate entry points lie in progressively redesigning crop rotations to include deep-rooted species and legumes, maintaining year-round root presence through cover crops, minimizing disruptive tillage where feasible, testing microbial inoculants and rhizosphere-oriented practices in small on-farm strips, and using simple field indicators, such as rooting depth, soil structure, residue decomposition and visible mycorrhizal colonization, to track belowground responses over time.

In conclusion, the future of antifragile, digitally integrated agriculture depends on making rhizosphere science operational in the field. The rhizosphere should therefore be framed not only as a hidden engine of plant productivity, but as a key entry point for agricultural innovation, capable of reshaping agricultural practices from the ground up. Advancing from insight to impact will require keeping the rhizosphere firmly at the center of agronomy and agricultural innovation, ensuring that this biological frontier becomes the foundation for real antifragile and climate-adaptive agriculture.

CRediT authorship contribution statement

Stefano Cesco: Writing – review & editing, Writing – original draft, Conceptualization. **Monica Yorlady Alzate Zuluaga:** Writing – review & editing, Writing – original draft, Conceptualization. **Luciano Cavani:** Writing – review & editing. **Luigimaria Borruso:** Writing – review & editing. **Vito Armando Laudicina:** Writing – review & editing. **Fabrizio Mazzetto:** Writing – review & editing. **Tanja Mimmo:** Writing – review & editing. **Youry Pii:** Writing – review & editing, Writing – original draft. **Roberto Terzano:** Writing – review & editing. **Stefania Astolfi:** Writing – review & editing, Writing – original draft, Supervision.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work the authors used ChatGPT 5.0 in order to improve readability and language. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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- Spoke 4 Multifunctional and resilient agriculture and forestry systems for the mitigation of climate change risks (SC, YP, LB, FM, TM).
- Spoke 3 Enabling technologies and sustainable strategies for the smart management of agricultural systems and their environmental impact (RT).

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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