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EDITORIAL

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Root phenotypes for the future

1 | ROOT PHENOTYPES FOR THE FUTURE: A RANGE OF PHENOTYPIC SCALES

Root phenotypes play profoundly important roles supporting plant growth and their adaptive responses to myriad environmental stresses. For example, architecture-scale traits such as root angle can have a major impact on foraging efficiency for immobile and mobile soil nutrients such as phosphate and nitrate, respectively (Schneider et al., 2022). Increasing evidence supports the importance of anatomical-scale traits, such as root hair length and xylem size, conferring abiotic stress tolerance in crops (Cai et al., 2022; Cornelis & Hazak 2022; Kohli et al., 2022), whilst major steps are being made to dissect molecular-scale adaptive mechanisms, such as ways roots detoxify metals and metalloids (Kirk et al., 2022; Podar & Maathuis, 2022). Knowledge of these root phenotypes and their underlying regulatory genes is vital for developing future crop varieties better adapted to the challenges presented by global climate change and the pressing need to support more sustainable agricultural practices. This represents a multi-scale and -disciplinary endeavour, spanning agronomy, molecular biology, phenomics, breeding, soil science, and ecology to study, discover and decipher the key environmental stresses, adaptive root phenotypes, and their underlying mechanisms (Figure 1). In this editorial, we give an overview of the content of the Special Issue of Plant, Cell & Environment on "Root Phenotypes for the Future." Based on the articles collated in this Special Issue we discuss emerging root traits and their regulatory mechanisms. The arising new insights underpin efforts to create crop varieties more resilient against future environmental stresses and better adapted to sustainable soil management practices.

2 | FROM ROOT PARTS TO ROOT ARCHITECTURE

Much of our understanding of the molecular pathways that underpin root development and root responses to the environment has been obtained in the model plant *Arabidopsis thaliana*. Arabidopsis roots have a relatively simple, hierarchical structure consisting of a main (primary) root from which lateral roots branch and subbranch, although some adventitious roots can also be formed during maturity. The multitude of architectures that can arise from this limited arsenal of parts under different environmental conditions is astounding. Hence deconstructing architectural changes into part-based processes is challenging and requires a fundamental understanding of how different parts of the root system develop and expand. The review by Dinneny and colleagues reminds us that the situation is further complicated in grasses, including major cereal crops such as rice and maize, because they feature an additional postembryonic nodal root system that emerges from basal regions of the shoot after germination (Goudinho Viana et al., 2022). Parts of this nodal system such as crown roots and brace roots often become the dominant determinants of the root architecture. The review offers an introduction into the developmental programmes that underpin the formation of different parts of cereal grass root systems, including crown roots and brace roots, followed by an overview of how they respond to environmental change.

3 | ROOT RESPONSE TO SOIL PHYSICAL CONSTRAINTS

The review article by Lynch and co-authors provides an insightful overview about how past, present, and future soil environments and management practices impact mechanical properties of soil and, as a result, root phenotypes of crops (Lynch et al., 2022). The authors initially describe how crop cultivation has altered the properties of native soils particularly in relation to disruption of soil structure and increased mechanical impedance. Such change in soil mechanical properties represents a major constraint for root elongation and branching, negatively impacting capture of soil resources and water availability (Keller et al., 2019; Tracy et al., 2011). The authors propose that crop root phenotypes have evolved to adapt to the increased impedance properties of cultivated soil during domestication. For example, a novel root anatomical phenotype associated with soil compaction resistance (termed multiseriate cortical sclerenchyma (MCS) characterized by small cells with thick cell walls in the outer cortex) has been observed in modern maize genotypes, but not landraces or wild ancestors (Schneider et al., 2018). However, the present shift towards Conservation Agriculture practices in high-input agroecosystems, returning cultivated soil impedance characteristics closer to native soils, could reverse the root phenotypes being selected (e.g., low MCS). In contrast, increasing soil degradation in low-input agroecosystems is likely to generate even more challenging impedance environments for root growth. The authors conclude by presenting promising root ideotypes as breeding targets for future soils, better adapted for the impedance properties in either high-input and/or low-input agroecosystems. For example, the gaseous signal ethylene has recently been reported to

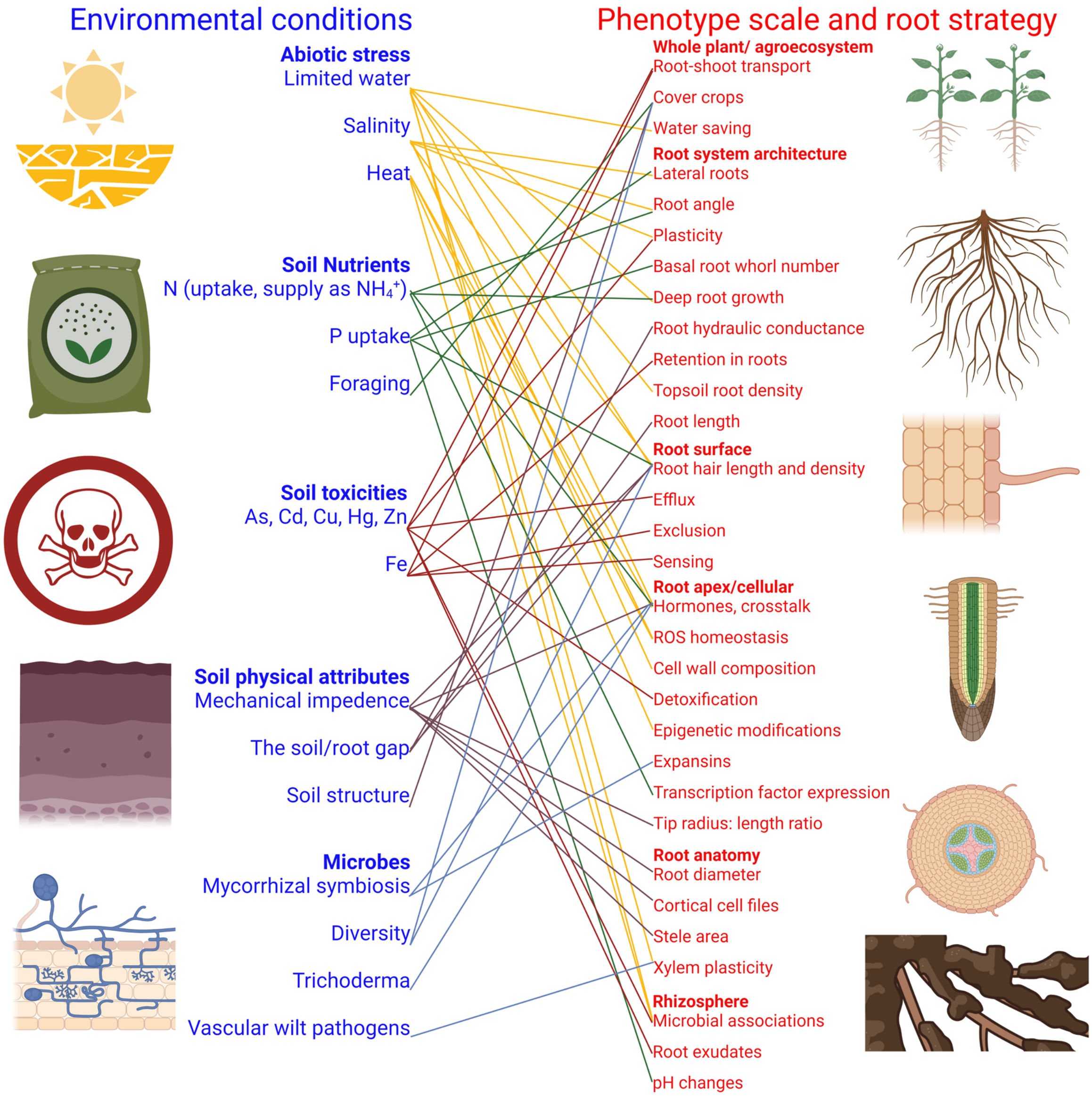

FIGURE 1 Overview of root strategies for improved plant response to the environmental conditions. The environmental stimuli and the phenotypes listed, and the proposed connections between them, are extracted from the research collated in this Special Issue, illustrating the necessity of mutliscale approaches to address key environmental constraints to plant growth. The chart highlights hormone crosstalk and root hairs as promising targets for adjusting root phenotypes to a wide range of environmental conditions. Created with BioRender.com

accumulate around root tips when growing in compacted soil which triggers radial expansion and growth inhibition, whereas ethylene response mutants remain narrow and are able to continue to grow (Pandey et al., 2021). In this issue, Vanhees et al. (2022) report that reduced root ethylene-responsive growth and narrow roots are excellent phenotypic predictors for reduced sensitivity to soil compaction conditions. These results are in contrast to the previously proposed ideotype of thicker roots for penetrating compacted soil. This example illustrates how new knowledge about the signals and mechanisms regulating root responses to impedance can help select novel stress-resilient crops for future soils.

4 | NUTRIENT AND WATER ACQUISITION STRATEGIES IN HIGH- AND LOW-INPUT SYSTEMS

High-input agroecosystems often involve the application of high levels of fertilizers. Root traits can help improve the efficient capture of nutrients like nitrate which is highly mobile in soils. In this issue, combining models for root architecture and for crop performance, Ajmera et al. (2022) identified synergistic effect of several root phenes in rice that were linked to better performance under low nitrogen supply. Wacker et al. (2022) report how deeper rooting winter wheat varieties exhibit reduced nitrate (N) leaching losses and increase N uptake. The authors employed an elegant semi-field root-phenotyping facility (termed RadiMax) to grow winter wheat genotypes and measure >80 root traits at key stages. At anthesis, roots were exposed to ^{15}N via subsurface drip irrigation, then mature ears were analysed for ^{15}N content. Strikingly, rooting depth was the only root trait that predicted ^{15}N uptake. In another research paper in this Special Issue, Schneider et al. (2022) report that even when applying N at the soil surface, deeper rooting traits improve N capture. The authors initially measured nodal root angles of approximately 480 field-grown maize diversity lines. They then used genome-wide association mapping to identify several associated single nucleotide polymorphisms (SNPs) within the root expressed CBL-interacting serine/threonine-protein kinase 15 (*ZmCIPK15*) gene (LOC100285495). A maize Mu insertion line disrupting *ZmCIPK15* exhibited a steeper root angle and improved N uptake compared to the parental background, confirming the importance of deeper rooting on efficient capture of nitrate. Computer simulations predicted that a steeper nodal root angle provided the maize root system with more time to take up this mobile nutrient as it passed through the soil profile. Both papers demonstrate how selecting deeper rooting varieties, either using phenomic approaches or by employing gene editing or marker-assisted selection for targets such as *ZmCIPK15*, will greatly facilitate ongoing efforts to develop new crop varieties with optimal root architecture for improved performance under high-input agroecosystem conditions.

Low-input agroecosystems rely on the efficient use of nutrients existing within field soils and/or limited environmental resources such as rainwater. In this issue, Ndoye et al. (2022) review how root traits play a key role in the efficiency of resource capture under low-input agroecosystems in Africa, where small-holder farmers have limited access to fertilizers irrigation, and mechanization. The authors highlight three case studies that illustrate how crop improvement, through selecting for specific root traits, can improve food security and crop resilience under these challenging conditions. In the first case, targeted selection of root traits for an important legume crop in SE Africa, common bean (*Phaseolus vulgaris*), has helped small-holder farmers to double their yields on soils containing low phosphorus (P). As P is known to preferentially accumulate in the top soil, Lynch and co-workers selected bean varieties with increased numbers of basal root whorls that accumulate close to the surface in combination with longer root hairs. This elegant combinatorial strategy was observed to deliver "phene synergism," where much higher levels of P were taken up compared to bean lines featuring just one of these root traits. The second case study describes improvements to sorghum and pearl millet which, although they are adapted to arid and semi-arid environments found in sub-Saharan Africa, deliver low yields and are sensitive to intermittent droughts that are increasingly common in this region. The authors describe ongoing efforts to select improved root ideotypes for water-saving strategies. These breeding targets include multiscale root phenotypes ranging from deeper rooting for improved water capture, smaller root metaxylem area for water conservation, and increased root exudation for improved rhizosheath formation and retention of root-rhizosphere hydration. The final case study discusses how in West African rice agroecosystems breeding for denser root systems in the topsoil and interactions with arbuscular mycorrhizal (AM) fungi promises to optimize water-saving alternate wetting and drying practices.

5 | WATER UPTAKE: MORE THAN JUST DEEP ROOT GROWTH

Greater variation in rainfall patterns due to climate change requires future crops to feature traits that improve water stress resilience across a range of soil types. In this issue, Liao et al. (2022) document how deeper root growth by rice under drought stress may be a response to fluctuating soil moisture conditions and identified nodal root diameter class as a key trait linking early season root growth with later season root growth and grain yield based on path analysis and GWAS co-locations. Cai et al. (2022) identified the soil/root gap as a key constraint to water uptake, in contrast to most previous work which focuses on traits to access more water (i.e., drought avoidance). The author proposes a hydraulic framework to explain the interplay between soil and root hydraulic properties on water uptake, introducing the concept of critical soil water potential (ψ^{c}_{soil}) which corresponds to the point at which plants downregulate transpiration. Their conclusions are based on a comprehensive data set of transpiration, leaf, and soil water potential measurements for 11 different crops and 10 contrasting soil types. As anticipated, ψ^{c}_{soil} was found to vary depending on soil textures and root hydraulic phenotypes such as longer roots to sustain transpiration in drying soils. However, a beneficial effect of root length during soil drying has not been seen consistently. More research is required to identify the key root phenotype(s) and signals which impact $\psi^{c}_{soil,}$ since root hydraulic phenotypes that trigger earlier stomatal closure would help save water, whereas those that maintain transpiration during soil drying would (potentially) help maintain growth. In this issue Zhang et al. (2022) report that signals from the plant hormones abscisic acid (ABA) and auxin play important roles to help maintain tomato root growth during soil drying. The authors applied a multi-phasic water stress treatment, first involving moderate water stress (3 weeks), then severe drying (2 weeks), followed by re-watering (3 days), to both wildtype and *notabilis* (*not*) ABA biosynthesis mutant plants. This clever application of realistic phases of increasing water stress revealed novel, dynamic changes in root systems architecture and gene expression. The study also revealed the critical role ABA plays regulating these adaptive phenotypic and transcriptional responses to maintain wildtype tomato root growth (vs. *not*) during soil drying. Intriguingly, auxin treatment was able to partially reverse the *not* mutant defects, suggesting that auxin acts downstream of ABA during root water stress responses. Greater knowledge about the targets of ABA and auxin regulation during root water stress adaptive responses is clearly needed to engineer climate-resilient crops.

6 | ROOT CELL TYPE-SPECIFIC PHENOTYPES

Whilst key root architectural traits have been identified as important for stress adaptation, the phenotypes of specific root cell types also play important roles in stress resilience. In this issue, Cornelis and Hazak (2022) review the function and regulation of root xylem development under environmental stress. Given that the xylem is the main route for transporting water and stress signals from root to shoots such new knowledge is urgently needed to underpin the design of climate-resilient crops. For example, drought has a major impact on root xylem patterning and hence water transport rate, yet knowledge of the underlying regulatory mechanisms (which appear to be ABA-dependent; Ramachandran et al., 2018) are still in their infancy in model systems like Arabidopsis and almost unknown in crop species. This represents an area for urgent attention which promises to deliver a major impact in terms of improving water use efficiency in crops. Other root cell types like root hairs have recently also been linked with water stress resilience. Carminati et al., 2017 showed that barley mutants deficient in root hair formation struggle to maintain water uptake in drying soils (Carminati et al., 2017). In this issue, Kohli et al. (2022) review evidence that root hairs help to maintain nutrient and water uptake in drying soil conditions by extending the physiological radius of crop roots. A role for root hairs in water uptake raises questions about the behaviour of water in drying soils: is it more characteristic of mass flow or does the patchiness of water availability make its accessibility more similar to diffusion-limited resources? Root hairs appear to provide an invaluable pathway for water movement during soil drying, maintaining flow rates across a larger soil volume and sustain water uptake. These examples clearly reveal the importance of including anatomical scale phenotypes (Figure 1) when selecting future crop varieties with improved water stress resilience. Kohli et al. (2022) also highlight the key role of root hairs during nutrient stress conditions, particularly for immobile elements like P. The authors review evidence gathered for multiple crops that selecting for longer root hairs improves P foraging. Intriguingly, rice plants appear to have gone one step further and developed novel 'macro' root hair-like lateral roots. This unique form of lateral root, termed an S-type (for short), is determinate and does not branch but contains many root hairs. In this issue, Kuppe et al. (2022) propose that the development of S-type lateral roots has enabled upland rice to adapt to strongly P sorbing soils. The authors developed a novel rhizosphere model that integrated key rice root architectural (e.g., different root classes) and physiological (e.g., P solubilisation) parameters. Model simulations predict that to maximize P uptake root systems need to position laterals beyond the P depletion-zone but within their solubilization zone. Short and hairy S-type laterals appear to be the key root parameter to achieve increased P uptake. This study provides an elegant example of how model-driven phenotype predictions can help inform researchers and breeders about which root traits should be prioritized for selection. In this specific case, the recent identification of regulatory genes determining S-type versus L-type lateral root identity (Kawai et al., 2022) enables marker-assisted (as well as phenome) based selection approaches to be accelerated.

7 | STRATEGIES FOR AVOIDING AND TOLERATING SOIL TOXICITIES

Root systems can also adapt their growth and development to *reduce* uptake of selected compounds. For example, salt represents a major (and increasing) challenge to global agriculture (FAO Food and Agricultural Organization of the United Nations, 2021). In this issue, Zou et al. (2022) review dynamic root growth strategies in response to salinity. The authors describe how moderate and high levels of salt (75–150 mM) negatively impact root growth through reductions in primary and lateral root lengths as well as numbers and lengths of root hairs (Dinneny et al., 2008). However, when exposed to a salt gradient, roots exhibit an avoidance mechanism termed halotropism, growing away from the area of high salt (even when counter to the direction of gravity). This salt-specific tropic response (which is distinct from hydrotropism) employs several auxin components in common with gravitropism including the auxin efflux carrier PIN2 (Galvan-Ampudia et al., 2013). Nevertheless, PIN2 re-localization to lateral walls of expanding epidermal cells is specific to salt and depends on the function of the phospho-lipase D gene PLDζ1 (Korver et al., 2020). Hence, plant roots have developed an adaptive growth avoidance mechanism (capable of reversing the direction of a lateral auxin gradient normally associated with gravitropism) when exposed to a salt gradient. Salt also triggers adaptive changes in root architecture (Kitomi et al., 2020; Li et al., 2021). In this issue, Zhao et al. (2022) report how a cell wall-related protein termed OsHyPRP06/R3L1 regulates RSA and salt tolerance in rice. The R3L1 gene belongs to the hybrid proline-rich proteins (HyPRPs) gene family which is targeted for regulation by salt. R3L1-OE lines exhibit increased LR formation, but shorter root length and enhanced salt tolerance, whereas r3l1 mutants showed greater salt sensitivity and reduced LR formation. The authors report that OsR3L1 regulates RSA and salt tolerance by controlling peroxidases and apoplastic ROS (H_2O_2) metabolism. Hence, OsR3L1 represents a promising new tool to develop salt-tolerant crops.

Micro-nutrients like iron can also reach toxic levels under selected environmental circumstances, necessitating crop roots to employ a range of mechanisms to ameliorate their effects. In this issue, Kirk et al. (2022) review the range of root and rhizosphere adaptations of irrigated rice to iron toxicity which represents a major constraint to its production in highly weathered, nutrient-depleted soils rich in iron oxides in sub-Saharan Africa. Iron toxicity is associated with submerged soils, because exclusion of O_2 from the soil leads to accumulation of reduced, soluble Fe(II), whereas in well-aerated soils, insoluble Fe[III] is the dominant form of iron. Crown root growth and branching are inhibited by iron toxicity, leading to a smaller surface area that will restrict nutrient uptake. Root tolerance mechanisms described to date include exclusion of Fe(II) by oxidation, membrane selectivity, and retention of iron in roots. However, high concentrations of Fe(II) at the root surface can suppress the uptake of macronutrients like potassium (Wu et al., 2019). The authors propose that future breeding programmes should be based on molecular markers for iron toxicity tolerance traits. However, to date none of the studies have identified loci with large enough effects to be utilized in applied breeding, limiting progress to develop crops resilient to iron toxicity. Other macronutrients like ammonium when elevated are toxic to most plant species, yet conifers are tolerant to ammonium. In this issue, Ortigosa et al. (2022) employ transcript profiling approaches to reveal that high levels of ammonium potentially regulate the development of pine roots by modifying hormonal crosstalk and the expression of selected transcription factors. However, validating insights about the key candidate genes and mechanisms identified awaits the development of a genetically amenable model conifer system.

Root traits also play important roles negating the impact of toxic metals and metalloids. In this issue, Podar and Maathuis (2022) review how roots and rhizosphere processes provide tolerance to toxic metal(loid)s like arsenic, cadmium, mercury, and zinc in crops. The authors describe the key root processes that confer metal(loid) tolerance, ranging from modified uptake, efflux, and long-distance transport to altering microbial populations in the rhizosphere and exploiting root plasticity. Given the myriad mechanisms described it was surprising to learn very few mechanisms proved effective to improve crop metal(loid) tolerance after translation from lab to field. Successes included work by Tang et al. (2017) who exploited genome editing to disrupt rice NRAMP5, a plasma membrane transporter for Mn and Cd uptake, which resulted in up to a 30-fold reduction in grain Cd levels but also lowered Mn. Surprisingly, transgenic rice lines overexpressing NRAMP5 were able to block grain Cd accumulation without impacting Mn levels (Chang et al., 2020). Arsenic is another toxic metalloid that represents a substantial threat to human health and environmental risk. In this issue, Frémont et al. (2022) report that white lupin is able to tolerate high levels of As by secreting in root exudates phytochelatins, major intracellular metal-binding detoxification oligopeptides, not previously reported to have an extracellular role. Metal-polluted soils often contain more than one metal, yet few studies have investigated the impact mixtures of toxic metals have on plants. In this issue, van Dijk et al. (2022) compiles data for changes in RSA to Cu, Cd, and Zn stress, following single or multimetal exposure of the model plant *Arabidopsis thaliana*.

8 | SERVICES PROVIDED BY OTHER ORGANISMS

In addition to improving root traits in new varieties to improve their resilience to environmental stresses, future crops will also rely on other organisms to facilitate their field performance. In this issue, Griffiths et al. (2022) review how cover crops are playing an increasingly important role to provide critical ecosystem services. These services include soil structural remediation, such as using taprooted plants like forage radish to penetrate and break up compacted subsoil and leave soil biopores; capture of soil resources, where "catch" cover crops convert residual soil nutrients into plant biomass that will be released to later crops after cover crop termination; and improving organic content, through the release of root exudates which have a strong positive effect on soil carbon dynamics. The authors make a compelling case that, like cash crops, cover crop roots merit the attention of phenotyping technologies and breeding strategies to aid agricultural sustainability.

Non-plant species also deliver critical functions to field-grown crops such as arbuscular mycorrhizal (AM) fungi. In this issue, Chen et al. (2022) report how manipulating root-mycorrhizal interactions can improve tomato performance. The authors identify an AM-induced GH3 gene, termed SlGH3.4, that encodes a putative IAA-amido conjugating enzyme, which negatively regulates mycorrhization. Loss of *SlGH3.4* function increased free IAA and arbuscule incidence. The authors' results reveal there is a positive correlation between IAA content and mycorrhization level, and identify a promising target for genome editing in crops. The review by Ndoye et al. (2022) also refers to mycorrhizal associations as a key trait for water saving in rice systems. Fungi (like many other rhizosphere organisms) release signals into the rhizosphere to manipulate root traits. In this issue, Li et al. (2022) report how the volatile molecule cedrene from the plant-beneficial fungus *Trichoderma guizhouense* is able to modulate Arabidopsis root development. The authors identify sesquiterpenes as the main volatile compounds produced by *Trichoderma* and show that disrupting their biosynthesis ameliorates the fungus' plant-beneficial effects. Intriguingly, cedrene-mediated promotion of lateral root branching was dependent on the auxin transport and canonical response machinery. Exactly how cedrene does this remains unclear. Nevertheless, it illustrates the exchange of signals taking place between plants and microbes within the rhizosphere which serves to stimulate root growth (and resources to symbiotic partners) and improve resilience. The root-microbe interaction might also induce pathways that offer cross-protection against various stress factors. In their review on root responses to heat stress, Tiwari et al. (2022) point to microbial species including *Trichoderma* as triggering priming effects that are important in protecting plant root growth against heat stress.

9 | OUTLOOK

This Special Issue of *Plant, Cell and Environment* showcases the enormous breadth of the questions, research, and insights into the role of root phenotypes for plant performance under environmental stress. The compiled articles highlight the fact that root responses to the environment are not confined to an individual phenotypic scale. Multi-scale approaches including the whole plant/agroecosystem, root architecture, the root surface, root cells, anatomy, and the rhizosphere must be integrated to address key environmental constraints to plant growth. A promising perspective arising from the collection of studies in this Special Issue (Figure 1) is that one given root strategy may be beneficial to multiple environmental conditions; for example, root hairs, hormones/crosstalk, and microbial associations stood out as having the potential to benefit plant growth under a range of stresses. Furthermore, an increasing number of the genes that are directly responsible for several root phenotypes are being identified, which will facilitate the deployment of key root strategies in breeding. Finally, along with these multi-scale approaches comes the need for multi-disciplinary efforts and strong collaborations to effectively address many of the global challenges to plant growth and crop production. The array of disciplines featured in this special issue can serve as an example of the types of collaborative research necessary to ensure impact for future environmental adaptation strategies.

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