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Environmental Control of Root System Biology

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Abstract

The plant root system traverses one of the most complex environments on earth. Understanding how roots support plant life on land requires knowing how soil properties affect the availability of nutrients and water and how roots manipulate the soil environment to optimize acquisition of these resources. Imaging of roots in soil allows the integrated analysis and modeling of environmental interactions occurring at micro- to macroscales. Advances in phenotyping of root systems is driving innovation in cross-platform-compatible methods for data analysis. Root systems acclimate to the environment through architectural changes that act at the root-type level as well as through tissue-specific changes that affect the metabolic needs of the root and the efficiency of nutrient uptake. A molecular understanding of the signaling mechanisms that guide local and systemic signaling is providing insight into the regulatory logic of environmental responses and has identified points where crosstalk between pathways occurs.

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1. INTRODUCTION

The atmosphere and soil domains of our planet are bridged by plants. The evolution of photosynthesis, first in bacteria and then through the adoption of endosymbionts in early plants, transformed the atmosphere by capturing carbon dioxide and generating oxygen (54). However, it was not until plants developed the ability to survive on land during the Devonian period 360–400 million years ago that the second transformation, of the soil itself, began in earnest (5, 10). Rhizoids and then roots infiltrated the virgin soils on land and changed their physicochemical properties and capacity to maintain life (60, 115). With the invasion of plants onto land, the soil and atmosphere became more intimately connected. Through the activity of roots, plants direct the redistribution of water from the soil through the shoot to the atmosphere and significantly affect the flux of water in the hydrological cycle (56). In the other direction, carbon dioxide is chemically fixed through photosynthesis in shoots and sent down into the soil, where microbial activity and root-derived metabolites generate an organization at micro- and macroscales that helps make soil the leading store of carbon on the planet (15, 112). Thus, the root system represents an important interface through which plants act on (and are acted on by) the environment, which has local and global implications.

20.2 Rellán-Álvarez • Lobet • Dinneny



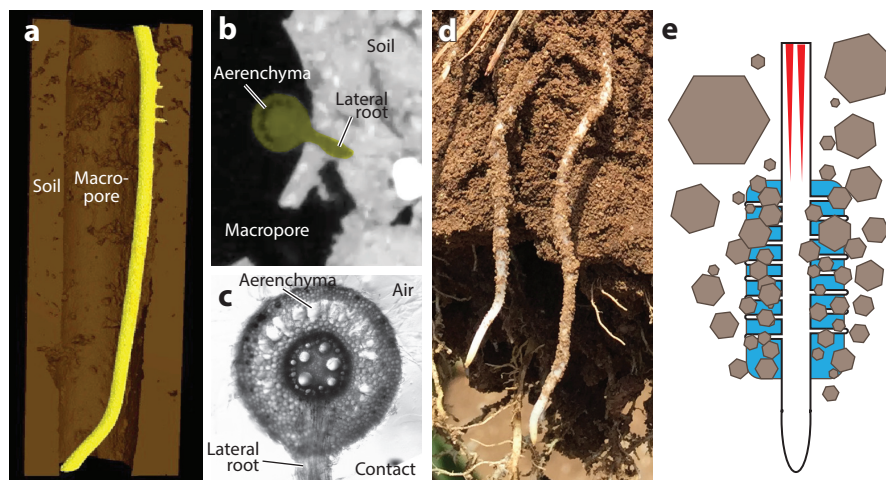


Figure 1

The biology of roots in soil. (a) X-ray micro-computed tomography (micro-CT) three-dimensional rendered image of a maize root (yellow) growing through a macropore of field soil (brown). Note the development of lateral roots on the side of the primary root contacting the soil. Image courtesy of Craig Sturrock and Sacha Mooney, Hounsfield Facility, University of Nottingham. (b) Cross section of the root in panel a, showing the development of a lateral root toward the contact side as well as air pockets (dark region), termed aerenchyma, in the cortical tissues of the air side. Image courtesy of Craig Sturrock and Sacha Mooney, Hounsfield Facility, University of Nottingham. (c) Bright-field image of a maize root cross section, showing aerenchyma development on the air side and lateral root initiation on the contact side. Image courtesy of Neil E. Robbins II, Stanford University. (d) A shovelomics-excavated root crown of maize, showing nodal roots with a rhizosheath surrounding the root. (e) Diagrammatic representation of the rhizosheath. Soil particles (brown hexagons) adhere to a matrix of mucilage (blue) and root hairs. Red stripes indicate the region of the root where mature xylem cells enable rapid water uptake, which correlates with a loss of rhizosheath integrity.

Root systems are complex physical networks, and their intricate form has inspired systems biology work to identify the various molecular components that determine this form (8). Form, however, is not the only property of this system that defines function. Roots provide conduits for the uptake of nutrients and water and alter the rhizosphere through the exudation of various metabolites (139). These functions are spatially and temporally differentiated in the root, though our understanding of this aspect remains poor (88). The environment that surrounds plants is as complex as the plant itself, if not more so. The interface between the environment and plants is multifaceted, with temporally and spatially dynamic processes affecting the signals that cells perceive (88). Research in the molecular biology of plant-environment interactions has often assumed a simple interaction, in which changes in a single environmental variable are perceived by the plant in isolation—an approach driven largely by the use of experimental systems in which a single variable can be altered with precision (138). However, changing a variable in a plant's environment may also have wide-ranging effects, only some of which are anticipated. Even a simple medium such as agar can interact with the plant in complex ways. Work in the Dinnyeny laboratory has shown that roots growing on the surface of an agar medium experience two remarkably different environments across the circumferential axis (3), creating a bias in the patterning of root tissues (Figure 1a–c). This spatial acuity in a root's response to the local environment mirrors the scale at which such stimuli vary in soil.

In this review, we define aspects of the multidimensional biology of root systems and establish a framework that may help guide future studies aimed at developing a holistic understanding of

Macropore: a channel formed in soil through the activity of roots or animals; macropores facilitate water and air flow as well as new root growth

Rhizosheath: a region of a root that tightly binds soil and forms a specialized microenvironment through root exudates and mucilage

root-environment interactions. We first describe the nature of the soil environment and how important properties of the soil vary at the microscale, macroscale, and global scale. We then discuss the architectural properties of root systems and how mathematical and computational approaches to modeling root systems is enabling a systems-level understanding of the functional properties of these organs. Finally, we define the biological context in which root-environment interactions act, providing an overview of the root types, tissues, and molecular pathways involved in controlling root growth and environmental responses to nutrients and salinity.

2. UNDERSTANDING THE ENVIRONMENT SURROUNDING ROOTS AT THE MICRO- AND MACROSCALES

2.1. Root-Relevant Soil Properties at the Microscale

Many soil properties that affect root growth and physiology arise from the microscopic details of soil structure (15). Soils are generally classified based on their relative proportions of sand, silt, and clay. Particle size is an important feature of these components because it determines the pore space between the particles: Soils with smaller particles have less pore space and bind water more tightly owing to capillary forces. This effect is quantified by the soil matric potential, which is affected by compaction and drying. Sandy soils allow water to flow readily but dry more quickly compared with clay soils, which have a higher capillarity. As a consequence, although root systems are generally able to extract water more easily from sandy soils, they may suffer more from a water deficit as the soil dries and the channels available for water movement become filled with air.

Strong heterogeneity in soil conductance can arise in the immediate environment of the roots, modifying the path of least resistance for water flow. Water uptake sites shift from the dry to the wet portion of the root system, leading to what is termed a compensatory uptake mechanism (58, 126). Thus, uptake dynamics are not driven solely by plant hydraulic architecture; they are also strongly influenced by the soil properties (27). An extreme example of this compensatory mechanism occurs when roots undergo a process known as hydraulic lift, in which water can flow out of the root into soil at night when root pressure is high (19). This has been proposed to be important for enabling root growth in dry regions of soil and for aiding in nutrient uptake.

At a higher spatial scale, structural features such as cracks and macropores affect soil properties (88, 96). Wetting and drying cycles in soil cause swelling and shrinking, respectively, which induce cracks that can extend deep into the soil. Macropores are small channels in the range of 30 μm to 3 mm and can vary in length, width, and tortuosity (**Figure 1a,b**). Macropores are also generated by animals such as earthworms or roots themselves and are important avenues for root growth. Their effect on roots is in part a consequence of the lower resistance they provide for growth and the movement of air and water. Roots also affect the structure of soil through the formation of rhizosheaths, which are regions of roots that tightly bind soil and form specialized microenvironments (142) (**Figure 1d,e**). Rhizosheath structure is dependent on root mucilage (139), which is made up of complex polysaccharides exuded by the root cap that form hydrated gels (hydrogels) and bind soil particles (142). These exudates may affect the colonization of the root by microorganisms, which themselves contribute to the complex composition of rhizosheath organic matter. Rhizosheaths in maize form proximal to the root tip in regions where xylem maturation has not yet been completed and water uptake is limited (89, 95, 142). The relationship between water availability and rhizosheath formation was identified by Watt et al. (142), who measured parameters of this structure in roots exposed to local water deficit. Interestingly, the diameter of rhizosheaths and their structural integrity are highest in regions of soil with lower water availability, suggesting that rhizosheaths may be important under drought conditions. Indeed,

North & Nobel (95) found that root segments of cactus with rhizosheath formation maintained contact with soil particles better than parts of the root without rhizosheath formation.

Rhizosheaths tend to be absent from more mature regions of the root. In maize, these regions correspond to places where water uptake is likely highest (89). The rhizosheath may act as a domain that facilitates several processes that must be coordinated for effective nutrient uptake, including hydration of soil particles, contact of the root with the soil, and, perhaps, enhanced microbial activity caused by the prevalence of exuded fixed carbon (66). Thus, the rhizosheath represents a structure dependent on both the root and soil systems, with developmental and environmental parameters determining the nature of the rhizosheath as well as its likely function. Which genetic pathways are responsible for rhizosheath formation and whether selection for germplasm with improved rhizosheath formation would benefit root system efficiency are unknown.

X-ray micro-computed tomography (micro-CT) and magnetic resonance imaging (MRI) are being applied to study the root system architecture in natural soils and enable the measurement of microscopic features of soil (91). The development of computer vision algorithms for semiautomated extraction of root architecture provides the opportunity to study root growth in natural field soil (85). Although not frequently applied together with quantification of root growth, micro-CT has been used to characterize soil structure and the effects of compaction on pore space (133). Tremendous opportunities exist for fine-scale quantification of water, air, soil particles, and roots; however, algorithms must also be developed for characterizing the function of soils based on these data. Models of soil chemical and physical properties (such as matric potential, hydraulic conductance, and hardness) need to be designed that enable prediction of such properties based on image data (134). These data can be integrated into plant physiological models such as SimRoot to predict the effects of the soil environment on root physiology (108).

Root system architecture:

the three-dimensional assembly of the different root types that compose a root system

2.2. Root-Relevant Soil Properties at the Macroscale

The architecture of roots is of general importance because the distribution of nutrients and water is not uniform in soil at the macroscale (83). Thus, the position of roots within the soil column determines, in part, the efficiency with which a root system captures these valuable resources. The distribution of water is generally determined by gravity; however, the porosity of the soil and the presence of hardpans and macropores influence the rate of bulk flow (15). Some nutrients, such as nitrogen, follow similar principles as water because they do not bind tightly to clay particles in soil. Phosphorus is present at very low levels in about 70% of agricultural soils and in chemical forms that are unavailable to the plant (79). The decomposition of organic litter in the topsoil typically leads to higher levels of phosphorus in these upper tiers. In contrast to nitrogen, inorganic phosphorus moves slowly through soil as it binds to clay, iron, and aluminum oxides. Root proliferation in regions of soil with higher phosphorus and the production of root hairs promotes uptake of this resource (83). In addition, acidification of the soil through the action of proton-ATPases mobilizes phosphorus and increases its availability to the root (143).

Because of the varying distributions of nutrients and water, root systems that are optimized to take advantage of one resource may be suboptimal for others. Postma et al. (108) have utilized the SimRoot mathematical model to simulate the functions of root systems with varying densities and lengths of lateral roots. Root systems optimized for nitrogen uptake had longer and more sparsely spaced lateral roots, whereas root systems optimized for phosphorus uptake had shorter and more densely spaced lateral roots. An important finding of this work was that a high local lateral root system density may become disadvantageous if resources are highly mobile and lateral roots compete with one another for nutrients. These computationally derived root architecture ideotypes inform breeding efforts to identify genotypes best suited for particular agricultural



lands. Importantly, however, the potential trade-off of optimizing root systems for particular nutrient stresses is not clear in the field. Plasticity in root architecture traits as a consequence of environmental stress has been described but has not been well investigated as a trait in itself, and many questions remain: Is it possible to select for certain architectural responses to nutrient deficiencies and stress rather than static ideotypes? How much variation in nutrient uptake exists in species independent of root architecture? Do developmental and physiological differences among root types and developmental stages constitute an untapped source of phenotypic variation in root function?

Soil constituents can also have negative effects on plant growth. Salinity affects soils throughout the globe, most prevalently in arid regions of Australia, Africa, Latin America, and the Near and Middle East (15). Salinity is caused by the accumulation of solutes that arise from the weathering of minerals as well as fossil deposits. Salts are dissolved in all supplies of water and are usually deposited in low-lying flatlands as a result of water flow from higher elevations. Groundwater may also be a source of salinity, with rising levels bringing solutes to the surface of soil through capillary action and evapotranspiration. Because all sources of water used in agriculture include dissolved salts, irrigation without proper drainage often leads to salinization. Indeed, history provides strong examples of civilizations where salinization led to agricultural disaster. The farmers in the Fertile Crescent of the twelfth century utilized irrigation to increase productivity without providing sufficient drainage to remove accumulated salts (15), and as a consequence, large swaths of land in southeastern Iraq were abandoned and are still useless for cultivating crops today. More recently, an estimated 10% of agricultural land is abandoned each year because of high salinity, which is similar to the amount of land brought under cultivation through the introduction of irrigation (39).

Salinity is also influenced by proximity to the coast, with sea spray and the influx of seawater onto land being important contributors (15, 77). Natural variation in the salt tolerance of *Arabidopsis* correlates with proximity to the coast, which led to the identification of a specific allele of the sodium/proton antiporter gene *HIGH-AFFINITY K⁺ TRANSPORTER 1;1* (*HKT1;1*) as a determinant for this phenotypic variation (6). More recently, common garden experiments have shown that *Arabidopsis* accessions collected near the coast are generally more fit when grown near the coast, whereas inland accessions show reduced fitness when grown near the coast (17).

At a smaller spatial scale, salinity can vary with soil depth in complex ways; higher sodium concentrations often occur deeper in the soil as a consequence of groundwater stores, but they can also occur in the surface layers owing to seepage and evaporation (15, 145). It will be interesting to determine how the structure of the root system may contribute to differences in salt tolerance and whether root architecture ideotypes exist that provide advantages in saline environments, as they do for nutrients (61).

3. METHODS FOR CAPTURING THE MULTIDIMENSIONAL NATURE OF ROOTS THROUGH METRICS AND MODELS

Environmental conditions affect the structure and physiology of the root system in complex ways, and understanding this process requires quantification and classification schemes that capture the multidimensional properties of the system. Because of the recent advances in root phenotyping, it is particularly timely to carefully consider the theoretical nature of the phenotypes that researchers assay and the strategies used for capturing and sharing such data. These approaches affect how researchers communicate the results of their experiments and their ability to model such phenomena using quantitative approaches.



3.1. The Theory of the Phenotype: Traits, Phenotypes, and Cryptotypes

Root system complexity calls for multiple phenotyping strategies of varying granularity. Global traits, such as rooting depth and width, total root surface, and convex hull area, are simple yet effective ways to quantify root systems. They usually summarize the general shape and soil exploration efficiency of the root system in a few metrics. These traits can be computed automatically from root images [e.g., with GiA Roots (General Image Analysis of Roots) (41)] and have been used frequently in quantitative genetic studies (36, 127, 132, 146). However, one drawback of using global traits is that they are often the result of a combination of several other, more fundamental traits. For instance, root system width is influenced by the lateral root gravitropic set-point angle, changes in lateral root gravitropism, and/or lateral root growth. Therefore, looking for a precise genetic basis for root system width is likely to be difficult.

For this reason, Lynch and coworkers (79, 81, 144) recently proposed that quantification of root traits should focus on phenotypes, which are defined as the smallest quantifiable phenotypic elements that cannot be divided further. Although the definition of a phenotype is conceptually simple, its practical application is not always straightforward. The gravity response of a root could be considered a phenotype because it cannot be defined by any other macroscopic variable. However, plant phenomics are not restricted to measurement of the physical properties of an organism and can also encompass its chemical composition (40, 84). Thus, because gravitropism is influenced by the expression level of several genes, such as *AUXIN RESISTANT 1 (AUX1)* (9) and *PIN-FORMED (PIN)* (120), the expression levels (mRNA composition) themselves could then be considered phenotypes.

Depending on the scale considered, the plant physiological age, the resolution of the measurement method used, and/or the questions at hand, researchers might consider and measure different phenotypes. Because a measured phenotype will always be a subset of the complete plant phenotype, or holophenotype, the phenotype can be considered, by definition, infinite (21, 84). In line with this observation, Chitwood & Topp (21) proposed the concept of the cryptotype (where *crypto* means “hidden,” as opposed to *pheno*, which means “show”). They defined the cryptotype as the set of traits (multivariate phenotype) that best separates classes (such as genotypes, treatments, and time points) chosen a priori. The cryptotype is therefore unknown (hidden) until the experiment reveals it. Again, the cryptotype is subjective by definition and strongly depends on the investigated question and the methods used to interrogate the system. In the end, researchers will aid understanding of root function if their studies focus on characterizing processes that directly affect root physiology, rather than doing so through indirect proxies; the most useful terminology should aid in understanding functional connections in biological systems.

Phenotyping exercises often fail to explicitly measure local environmental conditions and instead focus on plant traits aggregated at the organism scale. This is particularly true of root systems, for which even a subset of the roots might be sufficient to retrieve statistically meaningful information (e.g., root diameter classes) (35). However, aggregating metrics at the organism level partially hides how individual roots respond to their local environment. Because the soil environment may change dramatically during a plant’s lifetime, intrinsic root plasticity can be an important feature for plant survival (80, 105). Understanding the mechanisms underlying plasticity requires measuring attributes of the root system in both space and time in order to build quantitative response curves. From these response curves, a selected number of parameters can be extracted (e.g., the slope and intercept) for which genetic determinism can be found. This approach has already been used to quantify cavitation in xylem vessels (135), but it has been seldom applied to roots. Jukowska et al. (61) successfully applied a similar methodology with ROOT-FIT. The authors were interested in the root response to different levels of salt stress, and instead of comparing

Soil exploration efficiency: soil area depletion divided by root area (see 144)

Gravitropic set-point angle: the angle, relative to the gravity vector, at which organ (root or shoot) growth is maintained as a consequence of gravitropism (see 22)

Phenotype: the building block of the phenotype; it is unique and indivisible into any other phenotypic element

Holophenotype: the complete plant phenotype, which can be considered infinite by definition

Cryptotype: the set of phenotypes that best separates a priori classes



Tree: a subset of a mathematical graph (set of connected objects); trees can be either directional (parent/child relationship) or acyclic

Functional-structural plant model: a model that links an explicit representation of the plant architecture with physiological processes (e.g., uptake, production, and transport)

the root length at different time points, they synthesized the measurement in one quadratic root growth curve parameter for each plant. Although these curves did not directly incorporate environmental conditions, this example shows that more integrative metrics can be obtained.

The way researchers represent root systems and their environment has a strong influence on how they consider the whole system. Reducing the root system to a few metrics conceals its complexity. Similarly, excluding the environment from the analysis leaves out half of the reality. Although these simplifications are often necessary, today's technical advances call for a more complete and integrative way of representing the soil-root system.

3.2. Mathematical Concepts Applied to Root Systems

Despite their complexity, root systems can be easily described using well-known mathematical formalisms. The use of mathematical formalisms facilitates the archiving of root system data and their analysis. Such formalisms also enable the use of computational models to describe root system shape and function.

3.2.1. Root systems as trees. From a mathematical point of view, root systems are trees: The entire system is organized as a binary hierarchical structure, comprising nodes (branching points), branches (connections between two branches), and leaves (terminal branches). Root system topology is physiologically relevant, as it determines preferential fluxes of water, nutrients, and sugars between the different organs of the plant.

In the late 1980s, Fitter (37) proposed simple topological metrics for the analysis of root systems. They were designed to provide a collection of topological descriptors able to discriminate species, genotypes, and treatments. Although some of these descriptors correlated with more classical variables, such as root exploration (38), they are seldom useful in root research owing to two major bottlenecks. First, complete topology is often difficult to acquire, especially at a high throughput (73). Second, topology can be seen as the result of several traits, such as lateral root branching density, maximal branching order, and root growth rate. These individual metrics have often been preferred to topological ones because they are more directly related to the developmental processes that lead to the emergent topological features.

Nevertheless, topological representation has been used for decades in root models (49, 78) because it is the most natural way of representing root systems, both from a mathematical and a biological point of view. The current models fall broadly into two groups. First, models describing the root system architecture alone have been used to understand the building mechanisms of the root networks (49, 71, 78, 102, 103). Second, functional-structural plant models have been created to explore the crosstalk between root systems and their soil environment (for a review of current models, see 30). As with the first group of models, functional-structural plant models represent the whole root architecture explicitly. In addition, each element of the root system can interact with its exogenous (e.g., the soil) and endogenous (e.g., the neighboring roots) environment. These models are often coupled with soil models to simulate realistic environmental conditions (47) and allow researchers to test hypotheses *in silico* before testing them experimentally.

Functional-structural plant models can be used to dissect processes that cannot be easily separated *in vivo* in order to investigate their individual contributions. For instance, SimRoot (82) has been extensively used to analyze which root system architecture traits have the most important effect on phosphorus and nitrogen uptake and whole-plant physiology. By varying individual root traits, Lynch and coworkers showed that root gravitropism (43), root insertion angle (52), root cortical aerenchyma (109, 110), and lateral root density (108) have a substantial influence on these processes. Functional-structural plant models are also effective for studying complex, multilayered

processes, such as root water uptake dynamics. R-SWMS (Root-Soil Water Movement and Solute Transport) is a simulation tool that links a model of tridimensional water flow in the soil domain to a root architectural model (59). It is presently the only model that explicitly simulates water movement in the whole soil-root domain, and it has been used to vary specific properties of the soil-plant system in order to understand their contributions to the overall water uptake process. In particular, it has been used to investigate the effect of root hydraulic architecture (27), soil salinity (124), and long-distance chemical signaling (55) on root water uptake dynamics. The model also highlighted the predominant influence of the soil on the water uptake dynamics in drying soil (27).

The major bottleneck in the use of functional-structural plant models remains the lack of quantitative data sets to parameterize them. Although most physiological studies are based on qualitative data, very few have produced quantitative measurements that can be directly used in modeling platforms. Response curves showing how different processes change with a plant's environment are needed.

3.2.2. Root systems as densities. Representing the root system as a tree is not always appropriate. First, a complete topological map of the root system may be unavailable or only partially available; for plants grown in rhizotrons, for instance, only a fraction of the root system is visible, though this visibility can be improved substantially with expression of reporter genes such as luciferase (114). Second, root systems at late stages of development might be too complex for topological analysis (114). Finally, simulating explicit models of a mature root system can be computationally demanding, in which case representing the root system as a set of distribution functions may be more convenient (32). These functions can represent the distribution of root branches (31), root meristems, or even root orientations (33, 114). Such models can reconstruct realistic root architectures from simplified data sets. In addition, such methods summarize the different root properties by soil volume units (31), making it more closely related to the representation of a three-dimensional soil structure (32). This opens the door to more efficient soil-root interaction models that can be used on a larger scale (e.g., a field) than typical functional-structural models.

3.3. Root System Markup Language: Toward a Cross-Platform Descriptive Language for Roots

The past few years have seen an increase in the number of tools for characterizing root system architecture, including root phenotyping setups (26, 70, 87, 114), the extraction of root information from digital images (18, 114, 129), the analysis of root architecture data (12, 61), and the modeling of root processes (20, 71, 74). The advent of so many tools reflects the fact that none of them is universal. Instead of one tool, the root research community has adopted a diverse toolbox, each component of which matches a specific need based on the imaging modality used and the complexity of the root system analyzed. But as with any toolbox, a minimal level of standardization is necessary to ensure cross-compatibility among different tools and the data sets generated.

Lobet et al. (75) recently proposed the Root System Markup Language (RSML) as a standard format to store any type of root architecture data. Based on the eXtensible Markup Language (XML) formalism, the RSML format was designed to store three levels of information (graphically represented in **Figure 2**). First, the structure of the file (the relative placement of the different elements) reflects the topology of the root system. Second, each root is individually defined by its geometry (a polyline describing the position of the root in space). Finally, different functions can be superposed on top of the geometry to describe local properties (such as root diameter, root

Rhizotron: a flat container with at least one transparent side, used to grow plants; root growth is recorded on the transparent side(s)

eXtensible Markup Language (XML): a hierarchical markup text format



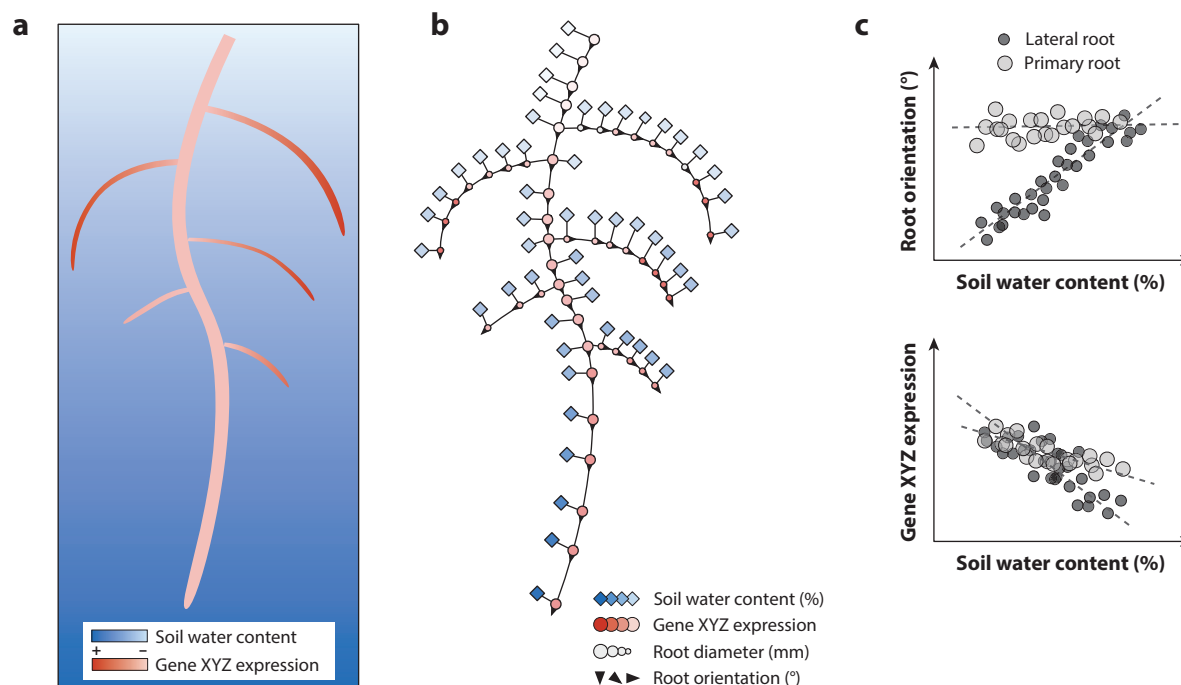
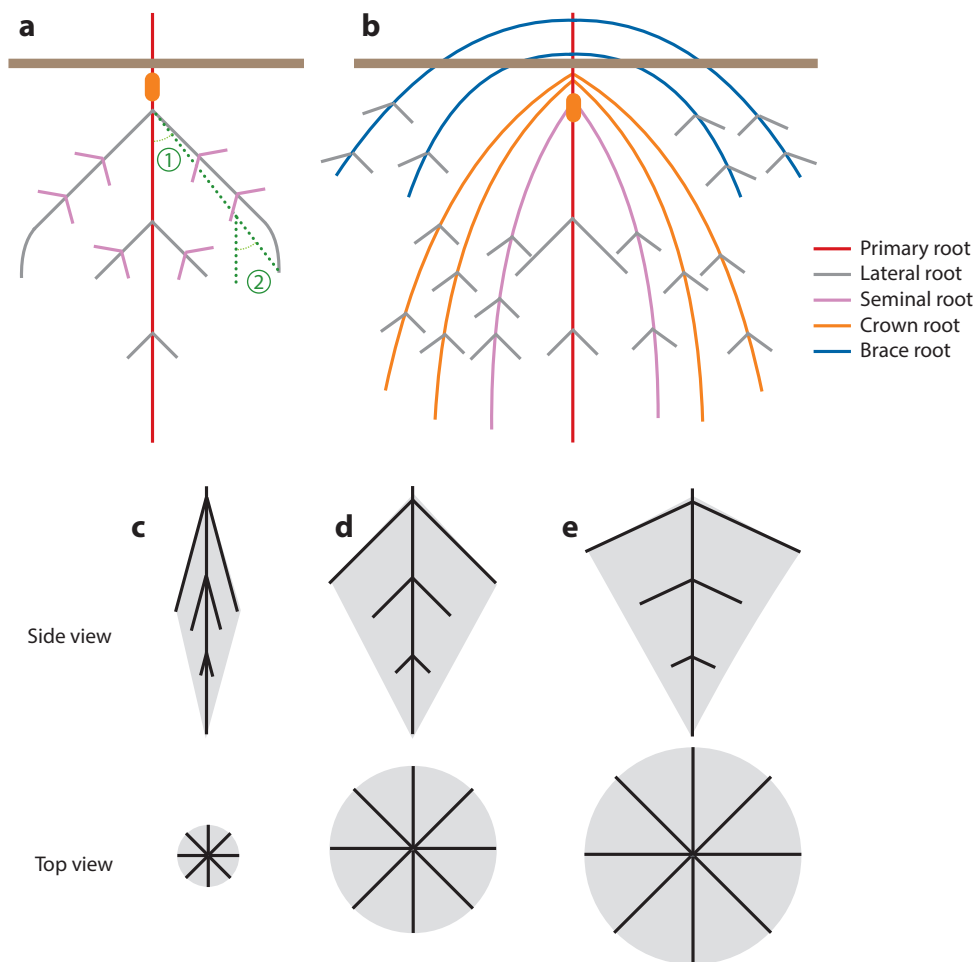


Figure 2

Representation of a root system and its environment. (a) Schematic representation of a root system growing in soil. Blue indicates the soil water content (with lighter colors indicating a lower content), and red indicates the expression level of a hypothetical gene XYZ (with lighter colors indicating a lower expression level). (b) Graphical representation of the information stored in the corresponding Root System Markup Language (RSML) file. The RSML format enables the storage of the root topology and morphology as well as any local attributes. In this example, the RSML file contains local information about the soil water content, gene expression level, root diameter, and root orientation. (c) Two examples of root response curves generated from the rich information contained in an RSML file.

orientation, and soil water content). Used in combination with a multidimensional phenotyping platform such as GLO-Roots (Growth and Luminescence Observatory for Roots) (114), RSML files can also store local gene expression information (**Figure 2b**). Explicit links between the different functions (all mapped on the same root morphology) enable the establishment of response curves at the plant level. The modularity of RSML allows users to either compute response curves directly from the raw data (**Figure 2c**) or store the curve parameters in the file for faster meta-analysis.

Although the tree-like structure of RSML is ideal for storing root system information, it is not the best choice for soil information. Indeed, soil elements are connected not as a network but as a three-dimensional matrix, with each voxel in continuous exchange with its neighbors. Topological links are useless for understanding the matrix dynamics. So although the information contained in an RSML file indicates how the root elements react to changes in their environment, it does not show the influence of the root system on the soil system. Fully understanding how root system development influences soil processes requires linking the experimental data with modeling tools. To do so, experimental data (encoded as an RSML file) can serve as input for compatible modeling platforms [such as R-SWMS (59) or RootBox (71)]. The modeling platform enables access to data that are difficult to access experimentally (e.g., the actual water flow in the soil domain).

**Figure 3**

(a,b) Diagram showing the basic architecture and different root types of taproot (panel a) and fibrous (panel b) root systems. The lateral root gravitropic set point and root tip angles are labeled as ① and ②, respectively. (c-e) Side and top views of root systems with lateral root angles of 15° (panel c), 45° (panel d), and 65° (panel e). The potential root foraging area is shaded in gray.

4. ENVIRONMENTAL CONTROL OF ROOT ARCHITECTURE AND CELLULAR ANATOMY

4.1. Root System Architecture Subtypes

Root systems comprise distinct root types that show characteristic responses to environmental cues and give rise to a physical network with diverse functionality. In the angiosperms, root systems fall broadly into two types: (a) taproot or allorhizic systems, which are characteristic of eudicots, and (b) fibrous or homorhizic root systems, which are characteristic of monocots (**Figure 3b**). For reviews describing the differences between these root systems in detail, we refer readers to References 53, 100, 101, and 121.

Taproot systems (**Figure 3a**) are composed of a primary root (the taproot) and lateral roots that emerge from this primary root. The depth of the primary root; the periodicity of lateral root patterning (93); and the gravitropic set-point angle (22), growth rate, and root tip angles of the lateral roots define the potential volume of soil that can be explored and foraged for resources by the root system (**Figure 3c–e**). All of these factors controlling lateral root development are highly plastic and are modulated under different environmental conditions (see below).

Fibrous root systems (**Figure 3b**), which are typical of grass species, can be divided into embryonic and postembryonic roots. Embryonic roots are divided into primary and seminal roots and emerge from the seeds; they are important during the establishment of the seedling and the early stages of plant development. Postembryonic roots are divided into shoot-borne roots (which develop from the nodes of the shoot) and lateral roots (which develop from lower-order roots) and take on a prominent role in later stages of development (99). Shoot-borne roots that emerge belowground are known as crown roots, which are organized in different levels of whorls and constitute most of the root system biomass in adult plants. The number, depth, and angle of crown roots are highly plastic traits that can adjust to different environmental conditions and play a fundamental role in water and nutrient acquisition (see below). In maize, the *Teosinte branched 1* (*Tb1*) locus, which was fundamental for the domestication of modern maize from wild teosinte (25), controls the number of tillers and the number of crown roots (42). In some species (including maize), brace roots, which emerge from the aboveground part of the shoot, play an important role in providing anchorage and preventing lodging (53).

The root types described above constitute the basic scaffold of root system architecture. However, most of the total root system length is made up of fine roots (secondary and higher-order roots). Because of their small size, fine roots can increase root surface contact with soil and reach into soil micropores, defining the effective volume of soil that is actually foraged for nutrients and water. Fine roots also constitute the largest number of root tips in the root system (88).

4.2. Root Architectural Changes Involving Gravity Responses

Root system architecture plasticity is defined as the ability of a root system to adjust its architecture to different physicochemical soil cues. This plasticity is based largely on the different root-type developmental programs and unique physiological responses to soil conditions (131). One of the most obvious differences between primary roots and lateral roots is their different sensitivities to gravity: Primary roots are generally more gravitropic and establish the depth at which lateral roots develop (80, 136). The gravitropic set-point angle can vary between related species. For example, the tomato wild species *Solanum pennellii*, which originates from dry areas with rare precipitation events, has a primary root angle of approximately 60°, whereas the cultivated variety *Solanum lycopersicum* var. M82 has an angle of only 10° (118). Shallow roots may be an adaptation to certain environments where rapid capture of water from recent precipitation events is important.

The gravitropic set-point angle of lateral roots is controlled by the auxin pathway. The application of external auxin causes lateral roots to become more vertically oriented (120), whereas pharmacological inhibition of auxin synthesis (120) or genetic knockout of the auxin receptor gene *TRANSPORT INHIBITOR RESPONSE 1* (*TIR1*) leads to a marked lateral root agravitropic response (114, 120).

Recent work in the Dinneny laboratory has shown that lateral roots grow at a steeper angle under simulated drought conditions and that this change in gravitropic set-point angle is dependent on auxin perception (114). Interestingly, this process is independent of hydrotropism, which directs growth toward regions of soil with higher relative moisture (94). Although hydrotropism generally acts in opposition to gravity responses, drought-induced changes in root growth may

act by enhancing the gravity response. Loci affecting the auxin pathway may also be important for variation in the lateral root gravitropic set-point angle. In rice, the *DEEPER ROOTING 1 (DRO1)* quantitative trait locus confers a higher yield under water deficit stress conditions and positively regulates gravitropism (136).

4.3. Architectural Changes in Response to Stress Through Root-Type-Specific Growth Control

Nutrient bioavailability is a major factor controlling the growth dynamics and physiology of different root types. The molecular pathways controlling the effect of phosphorus deficiency on root system architecture have been extensively studied (for recent reviews, see 46, 51, 76). Changes in root system architecture in response to phosphorus deficiency generally lead to a greater root density in the top layers of soil, where phosphorus tends to be released by the degradation of organic matter (144). The strategies used by plants to achieve this higher topsoil exploration vary across species. In *Arabidopsis* primary roots, growth stops (128) and lateral root growth is stimulated by a modulation in auxin sensitivity that depends on the auxin receptor TIR1 and the auxin response factor ARF19 (106). Bean varieties with a shallow basal root growth angle (92) and maize varieties with a larger number of crown roots and associated lateral roots (7) are more efficient at acquiring phosphorus. Highly phosphorus-efficient species, such as members of the Fabaceae and Proteaceae families, have developed specialized types of roots, known as proteoid or cluster roots (68), that form dense clusters of lateral roots. Proteoid roots are generally ephemeral but have a high metabolic activity and generate bursts of organic acid exudates and phosphatases (68).

Work in the Dinney laboratory has shown that the responses of primary and lateral roots to salinity are distinguished at the level of growth and hormonal signaling. Live imaging of *Arabidopsis* seedlings after transfer to salt stress revealed that both root types show dynamic changes in growth but do so at very different timescales: The primary root enters a growth quiescence period for several hours before recovery, whereas lateral roots enter this quiescence period for days (29, 45). The different responses resulted from different effects of abscisic acid on growth during salt stress and the timing of such signaling. Interestingly, in both types of roots, abscisic acid signaling in the endodermal tissue layer was critical for growth control during salt stress, highlighting the important functions of this cell layer in regulating growth and sodium uptake under inhospitable conditions (23, 117).

4.4. Environmental Acclimation Through Changes in Cellular Anatomy

The radial cellular organization of roots is typified by several layers of concentrically organized specialized tissues (86). The functions of these tissues and their organization in the root can change depending on environmental conditions and can affect the pathway by which water and nutrients are transported (86). Thanks to the development of techniques that allow root cell type-specific transcriptional profiling and gene activation/knockdown, studies in the last few years have begun to elucidate the developmental programs, hormonal signaling, and environmental stimuli unique to the different root cell types (16, 24, 45).

The epidermis is the first layer of contact with the rhizosphere. Epidermal cells initiate contact with symbiotic bacteria, such as nitrogen-fixing rhizobia, to form an infection thread that transmits the bacteria to inner cell layers (98). The length and density of root hairs also play roles in determining the efficiency with which phosphorus is extracted from soil (92). In some species, an exodermis develops from the outermost cortical cell file and may act as a hydraulic barrier against water loss (116). Further inside, the cortex constitutes one-to-many cell layers of the root



Hydropatterning:

a bias in the patterning of tissues in the root resulting from local variation in water availability (see 3)

and acts as an important center for metabolism (57) and colonization by fungal endophytes (125). Cortical tissues can also undergo programmed cell death or cell-cell separation processes that lead to air spaces in a tissue, known as aerenchyma. Aerenchyma may promote the ability of oxygen to diffuse into the hypoxic soil environment and facilitate aerobic metabolism. Aerenchyma also enhances root growth under macronutrient deficiency conditions, likely because of the reduced metabolic costs of this tissue type (123). Because water moves slowly through air, aerenchyma may also provide a hydraulic barrier to water loss (116).

Internal to the cortical layers, the endodermis (44, 117) acts as a hydrophobic diffusion barrier that regulates water and nutrient passage, among other functions. Endodermal cells develop a Casparian strip made of lignin that limits the diffusion of molecules into the stele. In maize, the radial expansion of the Casparian strip is increased, which may enhance the barrier function (62). A similar increase occurs in *Arabidopsis*, and genes associated with Casparian strip formation are transcriptionally induced by salt (45). Pfister et al. (107) recently showed that the integrity of the Casparian strip is necessary to maintain nutrient homeostasis.

Internal to the endodermis is the pericycle cell layer, which maintains meristematic activity and is the site for the development of lateral root primordia (137). The specification of lateral root founder cells in the pericycle is generally thought to be resistant to environmental control; however, recent discovery of the hydropatterning response (see below) and characterization of the local effects of water deficit suggest that these early events may be targets of water-associated stimuli (2, 3).

At the core of the root, xylem and phloem vessels transport and distribute water and nutrients from the root to the shoot and photoassimilates from the shoot to the root. Plants under nutrient deficiency upregulate expression of the transporters involved in xylem loading of nutrients (50) or molecules (34) involved in long-distance nutrient transport (113).

4.5. Hydropatterning May Optimize Root Architecture and Histology for Efficient Water Uptake

The particulate nature of soil and the effects of gravity and evaporation cause microscale spatial variation in the distribution of water and air. The spatial scale at which roots sense such variation was not understood until Bao et al. (3) defined a novel plant response they termed hydropatterning. This study showed that the roots of a diverse set of plant species are able to sense the local distribution of available water and use this as a positional cue to pattern root branching and the local differentiation of root hairs and aerenchyma (**Figure 1a–c**). The authors defined the properties of water that control root branching and showed that hydraulic conductivity is likely the key environmental variable affecting this process. Developmental analysis of root patterning showed that water biases the positioning of founder cells that later form lateral roots and that these responses occur at the root tip. Characterization of the signaling pathways regulating hydropatterning showed that these pathways exert local control over auxin biosynthesis and transport, which transmits patterning information downstream of moisture. Hydropatterning illustrates that environmental signaling can affect the development of the root at the suborgan level to influence organ system-level and histological patterning processes.

5. ENVIRONMENTAL SIGNAL INTEGRATION AT THE ROOT SYSTEM AND WHOLE-PLANT LEVEL

Root and shoot growth must be coordinated because both of these organ systems depend on the products of photosynthesis and soil-based resources. Systemic signals are an important

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mechanism by which shoot and root organ systems communicate limitations in the availability of such resources. In this section, we highlight recent studies elucidating the molecular mechanisms that communicate and integrate environmental cues at the local and whole-plant level.

5.1. Local and Systemic Integration of Nutrient Signals

The ability of root systems to sense and respond to local heterogeneity in the distribution of nutrients in the soil environment has been studied since the early work of Drew (28), which showed a higher proliferation of roots in areas of soil with high concentrations of nitrate. These experiments suggested a possible long-distance signaling mechanism at the whole-plant level that modulates local and root system-wide growth dynamics. In recent years, several studies have shown that nutrient transporters such as the nitrate transporter NRT1.1 can also function as sensors of their substrate, providing a possible mechanism for nutrient level-dependent regulation of root growth (72). At low nitrate concentrations, NRT1.1 can also transport auxin and repress lateral root growth by enhancing basipetal transport of auxin out of the root tips (13, 67). Roots also synthesize small peptides such as C-TERMINALLY ENCODED PEPTIDE 1 (CEP1) (97) and the CLAVATA 3/ESR-RELATED (CLE) small peptide, which is sensed locally by the leucine-rich-repeat receptor kinase CLAVATA 1 (CLV1) (1) and inhibits lateral root emergence (**Figure 4**).

How do root systems balance local signaling cues for nitrogen with whole-plant nutritional demands? Cytokinin is partly involved in the long-distance regulation of growth in root systems exposed to spatially heterogeneous levels of nitrogen (122). In addition, local nitrogen deprivation induces CEP1, which travels to the aerial part of the plant, where it binds to at least two leucine-rich-repeat receptor kinases (130). An unidentified signaling molecule is then thought to mediate shoot-to-root communication that induces growth in parts of the root system with high nitrogen but not in nutrient-deficient regions, where local mechanisms act primarily to limit growth (1, 67, 97). This regulatory system allows a fine modulation of root growth dynamics in soil patches with different nutrient concentrations (11, 130) (**Figure 4**).

Small RNA molecules constitute a molecular mechanism for long-distance signal transmission that directly affects gene expression (63, 64). Endogenous phosphorus levels are sensed in the aerial part of the plant—where phosphorus is needed to form phospholipids in the chloroplast membrane, among other functions—by SPX DOMAIN GENE 1 (SPX1), a phosphate sensor that binds to PHOSPHATE STARVATION RESPONSE 1 (PHR1) under high phosphorus levels but not under low levels (111, 140). Under low phosphorus levels, PHR1 upregulates the expression of several genes involved in the phosphorus deficiency response, including microRNA 399 (miR399). Grafting experiments using shoots overexpressing miR399 demonstrated that the processed small RNA can move from shoots to roots, where it downregulates the expression of its target transcript PHOSPHATE 2 (PHO2) (104), an E2-conjugating ubiquitin enzyme that, under sufficient-phosphorus conditions, facilitates the degradation of PHO1, the xylem phosphate-loading transporter that also controls root system architecture (4, 119) and other phosphorus uptake transporters. This mechanism enables miRNA-mediated long-distance communication of phosphorus levels in the shoot, leading to modulation of phosphorus uptake mechanisms in the root.

5.2. Toward an Understanding of How Root Systems Integrate Complex Nutritional Signals

Most of the work done so far to understand the effects of environmental cues such as salinity and nutrient deficiency has been limited to controlled changes in a single environmental parameter, which is far from what occurs in a natural soil environment. In the last few years, several studies have started to explore interactions between different environmental cues and how these interactions are

Leucine-rich-repeat receptor kinases: transmembrane proteins that recognize extracellular ligands (such as small peptides) and trigger downstream signaling pathways through their intracellular kinase domain



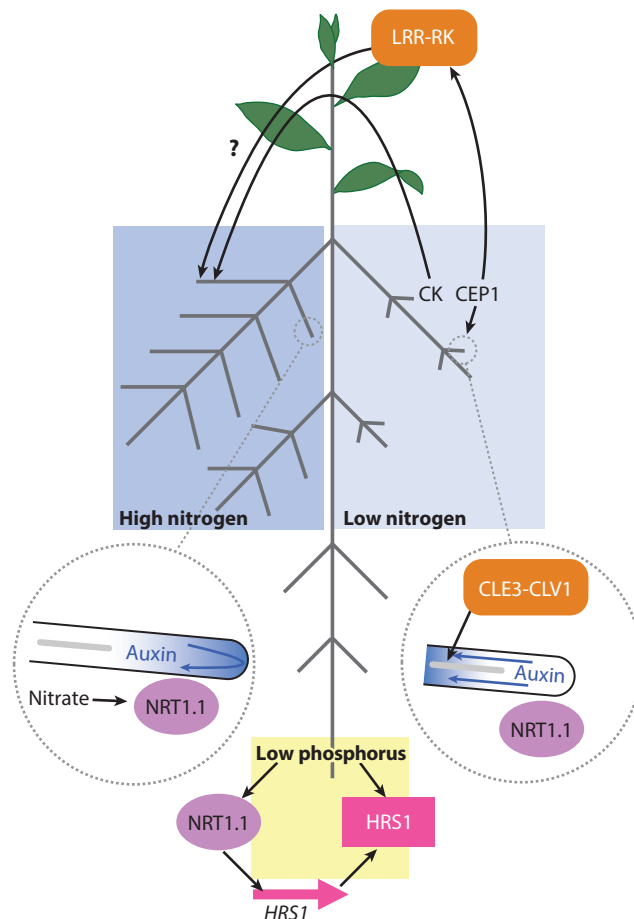


Figure 4

Diagrammatic view of local and long-distance signaling of heterogeneous distributions of nitrogen and the associated effects on root growth. Under low-nitrogen conditions, small peptides can repress root growth locally and travel to the aerial part of the plant, where they bind to leucine-rich-repeat receptor kinases (LRR-RKs), which then trigger a long-distance signal that induces growth in high-nitrogen areas. The nitrate transporter NRT1.1 can also transport auxin basipetally and reduce growth. Under low-phosphorus conditions, primary root growth is also reduced, but only if sufficient concentrations of nitrogen are present. This process is regulated by HYPERSENSITIVITY TO LOW PI-ELICITED PRIMARY ROOT SHORTENING 1 (HRS1). Additional abbreviations: CEP1, C-TERMINALLY ENCODED PEPTIDE 1; CLE3, CLAVATA 3/ESR-RELATED 3; CLV1, CLAVATA 1; CK, cytokinin.

regulated at the transcriptional level to affect root system architecture. Nutrient crosstalk is, in part, explained by the chemical interactions that occur in the rhizosphere between the nutrients. For example, iron and phosphate form insoluble precipitates that are not available to plants, inducing the activation of both phosphorus and iron acquisition machinery. Thus, under low phosphorus, iron acquisition is upregulated and can lead to iron toxicity, which suppresses primary root growth (141). *PHR1*, a master regulator of the phosphorus deficiency response, physically interacts with the *AtFER1* ferritin promoter and regulates its expression (14).

As mentioned earlier, differences in the mobility of phosphorus and nitrogen in soil require distinct architectural responses (108). A recent report has provided evidence of the molecular

crosstalk between phosphorus and nitrogen at the transcriptional and posttranslational levels (90). The authors discovered HRS1, a nitrate-inducible, NRT1.1-controlled transcription factor that, together with its homolog NIGT1, represses primary root growth under phosphorus deficiency, but only if nitrate is available (90).

Gruber et al. (48) have systematically studied changes induced by different nutritional levels in root system architecture and evaluated root plasticity in terms of a multivariate analysis of different traits, thus providing a framework to understand the common effects of different nutrients. By using binary combinations of different nutrients and analyzing their effects on root system architecture traits, Kellermeier et al. (65) showed that transcriptionally coregulated clusters of nutrient-responsive genes in roots and ionome composition in leaves could be assigned to root architecture traits in nitrogen/phosphorus/potassium binary combinations. The idea of using proxy traits such as shoot ion content as a readout of root system architecture or root function traits is of interest to root biologists and is already being explored, with very promising results (69).

6. CONCLUSIONS

Studies of root biology bring challenges and opportunities to understand the intimate interaction between plants and their environment. The biology of the shoot is also under tremendous pressures from the environment, and many of the considerations in analyzing the multidimensional nature of roots likely apply to the aboveground organ systems as well. How an organism that lacks a centralized information processing center, such as the nervous system in metazoans, integrates environmental information across a vast physical network and coordinates responses is a grand challenge in plant biology and will likely reveal principles of organization that are different from those of animal models. In the case of plants, understanding such processes at a quantitative and predictive level may enable efficient control over plant growth for sustainable agriculture.

SUMMARY POINTS

1. Soil physicochemical properties can vary at the different spatiotemporal scales that define a highly heterogeneous environment.
2. The complexity of soil-root interactions calls for the use of computer models to help integrate the different processes.
3. Linking models with quantitative data remains challenging. The development of common formalisms for root system architecture characterization will facilitate such integration.
4. Root systems are composed of different root types that perform specialized roles in root soil exploration. Root function and developmental programs enable acclimation to soil conditions that vary at the micro- and macroscales.
5. Root systems use a variety of mechanisms to adjust growth dynamics to local conditions, such as patchy distributions of nutrients and water. These signals are integrated using different systemic signals at the whole-plant and root system levels to adjust root and plant growth accordingly.

FUTURE ISSUES

1. Identification of root system ideotypes for important abiotic stress conditions such as salinity is necessary to facilitate breeding efforts focused on root traits.
2. More studies are needed of perennial roots, which not only are interesting from the perspective of basic biology (e.g., regeneration), but also could have a huge impact on agricultural practices.
3. Understanding how plants integrate signals from different nutrients at different concentrations and locations within the root system will require developing new methods to capture these complex interactions.
4. Transgenic approaches targeting specific root architecture and functional traits such as lateral root growth or exudate production could be deployed in the field to address specific challenges.

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