Root Architectural Plasticity in Changing Nutrient Availability

Prakhar Awasthi and Ashverya Laxmi

Abstract Plant roots have been an intriguing subject to plant biologists for a long time. Roots serve a wide range of functions in plants, including anchorage and absorption of water and nutrients. Roots are highly plastic in their development and directional growth to facilitate better absorption and assimilation of water and nutrients under different environmental conditions. Plasticity of root system architecture (RSA) confers different architecture in response to immediate soil-based and endogenous signals. Nutrient heterogeneity in the soil is a major factor determining RSA. Plants sense local nutrient availability and facilitates directional root development to enhance nutrient acquisition. Among the mineral nutrients, Nitrogen (N) and Phosphate (Pi) are major macronutrients important for plant development. N dissolves in water and accumulates in deep soil, thus compelling plants for producing deeper roots. Pi retains in topsoil and during pi deficiency, root system grows more laterally to enhance pi uptake. Thus, RSA is highly dynamic in nature which varies according to soil condition and nutrient availability and enhancing the plasticity of RSA will improve the nutrient uptake and use efficiency of crops. In this chapter, we are discussing how N and pi availability remodel different aspects of RSA in model plants and crops.

Keywords Ammonium · Lateral root differentiation · Lateral root primordia · Nitrate · Nutrient acquisition · Nutrient crosstalk · Nutrient use efficiency · Phosphate · Primary root growth · Root system architecture · Root plasticity · Root hairs · Root meristem · Soil heterogeneity · Topsoil foraging

Abbreviations

RSA	Root system architecture
N	Nitrogen

P. Awasthi · A. Laxmi (✉)
National Institute for Plant Genome Research, Aruna Asaf Ali Marg, New Delhi, India
e-mail: ashverya_laxmi@nipgr.ac.in

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Pi	Phosphate
NUE	Nutrient use efficiency
LRP	Lateral root primordia
PHR1	Phosphate starvation response
PSR	Phosphate starvation responses
LR	Lateral roots
PR	Primary root
P1BS	PHR1-binding sites
ARFs	Auxin-response factors
GWAS	Genome-wide association study
QTLs	Quantitative trait locus

1 Introduction

Roots played a crucial role in the evolutionary success of land plants. They search for minerals and water in the soil and supply it to the above-ground parts of the plant. Plants need mineral nutrients for optimal growth. Roots forage the soil to maximize nutrient acquisition. Plants require a range of essential nutrients, among them, nitrogen (N), phosphate (Pi), potassium (K) are required in large quantities. The inorganic forms of phosphate (HPO_4^-, Pi) and nitrate (NO_3^-) or ammonium (NH_4^+) are taken up from the soil (Bouain et al. 2019). The heterogeneous distribution of these nutrients in the soil limits their acquisition. Moreover the assimilation of pi in plant is also poor as inorganic phosphate reacts with iron (Fe_3^+), aluminum (Al_3^+), and calcium (Ca_2^+) ions present in soil to form an insoluble complex. Limitation of phosphate and nitrogen in the plant severely affects plant growth and productivity and nitrogen and phosphate are externally supplied to the crop in form of fertilizers to enhance productivity. Excessive input of fertilizers causes water and air pollution. Ongoing soil degradation, water pollution, and climatic changes negatively affect sustainable agriculture (Li et al. 2016). An increasing population and limited agricultural space aggravate this problem. One effort in mitigating the situation would be to improve nutrient use efficiency (NUE) of crop plants. Global agriculture demands nutrient efficient crops with improved nutrient uptake even under nutrient-deficient conditions. Plants employ multi-level pathways for nutrient uptake, such as modification of root system, enhancing the activity of nutrient transporters, releasing organic acids in soil, and developing symbiosis with fungi or bacteria (Chen and Liao 2017).

The intricate three-dimensional web of roots in the soil is known as root system architecture (RSA) (Satbhai et al. 2015). Enhancing the resilience and plasticity of RSA is one of the ways to improve the nutrient uptake of crops. Root length, branching, angle, and surface area, are major tenets of RSA. The RSA of a plant is the cumulative product of genetic and environmental interaction (Lynch 2019). Plants sharing the same genotype might develop different root systems depending on the immediate requirement. This interaction of genome and environment provides plasticity to the plant roots system. Root plasticity is more advanced in higher plants to support much complex physiology (Satbhai et al. 2015). Phenotypic plasticity of roots shapes root system in response to local root environment which includes, soil texture and compactness, water and nutrient availability, soil fauna, and gravity (Satbhai et al. 2015). As nitrogen and phosphate both are involved in RSA remodeling in response to their availability in soil, but the phenotypical changes in roots are contrasting to each other in terms of primary root growth and lateral root formation. Plants faces deficiencies of multiple nutrients in soil at a time and in such combinatorial stress, a crosstalk between the nutrients signaling is required (Bouain et al. 2019). In this chapter, we will briefly discuss the idea of RSA in model and crop plant then we will move forward to study the role of nitrogen in mediating RSA. We will zoom into the molecular machinery of plant RSA in response to phosphate, and progress in utilizing the underlying machinery to improve the nutrient efficiency of crops.

2 RSA and Nitrogen Mediated Root Remodeling

Nutrient efficiency has been an important trait in the evolution of roots in land plants (Lynch 2019). Plants utilize the root system for the acquisition of mineral nutrients such as nitrogen and phosphate from the soil. Plants need to forage the soil in search of nutrients which varies from place, time, and depth of soil. Exploration of soil is mediated by roots in terms of root growth, branching, root hair formation, and microbial symbiosis. Dicots plants such as Arabidopsis have tap root system, which consists of the main primary root and several branched lateral roots along with root hairs (Satbhai et al. 2015). Monocots such as maize and rice develop fibrous roots primarily consisting of adventitious roots. Adventitious roots rising from any non-root tissue, such as junction roots, crown roots, etc. (Del Bianco and Kepinski 2018). Root system architecture (RSA) has been considered essential for soil exploration and NUE. Modifying the RSA for improving the nutrient acquisition of the plants is the most basic yet complicated trait for crop improvement.

In general, the distribution of nutrients in soil depends on the amount of nutrients, soil composition, nutrient solubility, etc. Nitrogen (N) is an essential structural and functional component of primary and secondary organic compounds. Limitation of nitrogen in plants constraints plant growth and development with subsequent reductions of plant productivity (Luo et al. 2020). Owing to Haber's process of artificial nitrogen fixation, the production of ammonium has increased (Jenkinson 2001). However, the high solubility of nitrate and ammonium in water causes nitrogen to leach out with the groundwater, causing poor nitrogen acquisition and environmental pollution. The most logical and accessible option to reduce wastage and pollution is to improve nitrogen utilization efficiency (Xu and Takahashi 2020). In dicots, such as model plant Arabidopsis, four methods of root remodeling have been studied in the presence of nitrogen, (i) presence of nitrate promotes localized elongation of lateral root growth, (ii) high tissue nitrate systemically inhibits the lateral root meristems, (iii) exogenously supplied L-glutamate inhibits primary root growth and promotes root branching, (iv) high carbon to nitrogen ratio inhibits the lateral root initiation (Zhang et al. 2007).

The effect of normal nitrate on primary root growth was either insensitive or modestly promoting the primary root growth (Forde 2014). Although moderately higher concentration of KNO_3 inhibited the primary root growth and this was mediated via the miR393/AFB3 regulatory module (Vidal et al. 2010). microRNA393 is induced by nitrate and it specifically cleaves transcripts of AFB3, an auxin receptor which has a role in auxin dependent root growth in response to nitrate (Vidal et al. 2010). L-glutamate, an amino acid when exogenously provided specifically inhibited the primary root growth (Forde 2014). Nitrate was seen to monitor the stem cell dynamics by regulating the cell division genes and differentiation of distal stem cells (Guan et al. 2017; Wang et al. 2017). TCP20, a component of nitrate signaling interacts with NIN-like proteins, NLP6 and NLP7, and upregulates the expression of nitrate-dependent genes and downregulates the G2/M cell cycle gene *CYCB1;1* in the root meristem (Guan et al. 2017).

Local patches of nitrate promote preferential lateral root growth (Mounier et al. 2014). Nitrate being the major source of nitrogen has an intrinsic role as a nutrient and signaling molecule perceived by plant nitrate transporter 1.1 (*NRT1.1*) (Maghiaoui et al. 2020b). This nitrate-dependent lateral root growth is the outcome of nitrate transporter/sensor NRT1.1 (also known as *NPF6.3* or *CHL1*) and auxin interaction (Krouk et al. 2010). NRT1.1 regulates lateral root growth by orchestrating the basipetal transport of auxin out of lateral root primordia (LRPs) (Krouk et al. 2010). In a recent study, it was found that NRT1.1 also regulates the auxin biosynthesis (Maghiaoui et al. 2020a), NRT1.1 negatively regulated the expression of auxin biosynthetic gene, TAR2 and auxin influx carrier, LAX3 to reduce acropetal transport of auxin in LRPs (Maghiaoui et al. 2020a). Interestingly, the supply of NH_4^{+a} a preferential source of nitrogen for crops, stimulate lateral root branching (Lima et al. 2010; Jia and von Wirén 2020). In Arabidopsis, it was found that local NH_4^+ promoted branching with the help of NH_4^+ transporter AMT1;3. This branching was found absent in quadruple mutant of *AMMONIUM TRANSPORTER* (*amt1;1, amt1;2, amt1;3, amt2;1*), reconstituting the expression of *AMT1;3* in quadruple mutant restored the branching (Lima et al. 2010). Ammonium uptake releases protons in the apoplast, this acidification of apoplast modifies the auxin mobility which in turn increased the lateral root density (Meier et al. 2020; Pélissier et al. 2021). A detailed overview of nitrogen-dependent lateral root formation is published recently (Pélissier et al. 2021).

Along with local signaling, systemic signaling also regulates root architecture in foraging soil nitrogen. Systemic signals of nitrogen deficiency shape the root architecture by modulating the phytohormones such as auxin, cytokinin, and Brassinosteroids (Kiba et al. 2011). The *steep, cheap, and deep* roots in crops attain root architecture exploring deeper sections of soil in search of mobile nitrate (Lynch 2019). This architecture includes *steep* lateral growth angle, fewer branching of root or *cheaper* in carbon units, and *deeper* roots in foraging nitrogen. Several reports in maize and rice support *steep, cheap, and deep* root ideotype of crops in low nitrogen condition (Lynch 2013; Trachsel et al. 2013; Ju et al. 2015; Chen and Liao 2017; Lynch 2019). Recent studies have suggested an integration of phosphate and nitrate signaling in plant root development (Medici et al. 2015, 2019a; Bouain et al. 2019). GARP type transcription factors, HRS1 and NIGT1.2 both have been shown to involved in nitrate and phosphate signaling (Medici et al. 2015; Wang et al. 2020). A crosstalk between Nitrate receptor NRT1.1 and PHOSPHATE STARVATION RESPONSE1 (PHR1) was observed (Medici et al. 2019a). PHOSPHATE2 (PHO2) integrated the N availability into the phosphate starvation responses (PSR). Nitrogen mediated PSR were significantly affected in *pho2* mutants (Medici et al. 2019a).

3 Root System Architecture in Response to Phosphate (Pi)

Phosphate (HPO_4^-, Pi) is another essential nutrient required for plant growth and development. Being a component of DNA, protein, and cell membrane, it is requisite along with carbon and nitrogen for optimal growth. The acquisition of phosphate in plants is also inefficient, which is supported by the fact that only 10–25% of applied phosphate is taken up by the plant (Crombez et al. 2019). Limitation of pi in soil affects plant growth and reduces plant productivity. Unlike nitrogen, the sources of phosphorus are non-renewable and has been predicted to deplete in the next few decades (Lynch 2013, 2019). The predominant form of phosphorus in soil is orthophosphate (HPO_4^-), which reacts with cations such as Mg^{2+} and Ca^{2+} (Chen and Liao 2017). Low mobility of orthophosphate or pi in the soil makes the topsoil rich in phosphate. To increase the uptake of pi, plants forage the topsoil (Lynch 2019). Topsoil foraging in crops generally reorganizes the root system architecture with more production of axial roots, shallower axial root angle, greater lateral root density, and longer and denser root hairs (Lynch 2019). In Arabidopsis shallow root system is optimized with reduced primary root length, increasing lateral root length and density, and producing denser root hairs (Fig. 1) (Huang and Zhang 2020).

3.1 Primary Root Growth Under Pi Deficiency

Inhibition of primary root growth in low phosphate is orchestrated in a coordinated fashion, by arresting cell division, inhibiting the cell elongation, and stimulating the cell differentiation (Péret et al. 2014). Numerous genetic screenings identified the role of several mutants in regulating the root meristem under pi deficiency. In Arabidopsis, LOW PHOSPHATE ROOT 1 (LPR1) and PHOSPHATE DEFICIENCY RESPONSE 2 (PDR2) appeared in regulating the meristem activity (Ticconi et al. 2009; Müller et al. 2015). *PDR2* encodes a single P5-type ATPase which supports the expression of Scarecrow (*SCR*) in maintaining root patterning (Ticconi et al. 2009). *LPR1* (Ferroxidase) and *PDR2* both works together under pi deficiency to arrest root apical meristem (RAM). LPR1-PDR2 module promotes iron deposition specifically in the cell wall of RAM. Accumulation of Fe stimulates callose deposition which interfere the cell to cell communication and inhibiting transport of SHORTROOT

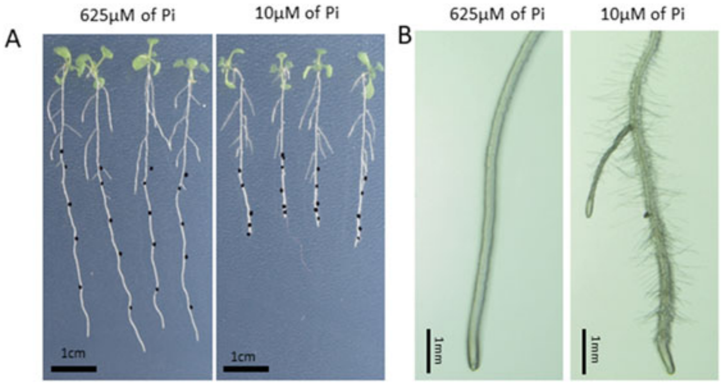

Fig. 1 RSA of Arabidopsis wildtype in phosphate deficient (10 μM) and sufficient medium (625 μM). 7 DAG old Col-0 subjected to pi deficiency for five days showed inhibition of primary root growth, an increase in lateral root density (panel **a**), and root hair (panel **b**). Dots represent the primary root growth kinetics for a period of five days

(SHR) from stele into the quiescent center (Müller et al. 2015). Inhibition of primary root growth in pi deficiency was completely abolished in *lpr1lpr2* double mutant. In contrast, the primary root of *pdr2* mutant was hypersensitive to pi deficiency (Müller et al. 2015). Phosphate-dependent callose deposition in RAM was due to enhanced reactive oxygen species (ROS) production in stem cells, which increased in pdr2 mutant (Müller et al. 2015). Reduced cell elongation and stimulation of cell differentiation are two other very important characteristics of pi-mediated inhibition of PR growth. STOP (SENSITIVE TO PROTON TOXICITY1) and ALMT1 (ALUMINUM-ACTIVATED MALATE TRANSPORTER1) module coordinate the cell expansion in Arabidopsis (Balzergue et al. 2017). STOP is a transcription factor that controls the cell elongation by modulating the expression of its direct target gene, *ALMT* which codes for malate channel. Together they mediate cell wall stiffening with the help of iron and peroxidase (Balzergue et al. 2017). SIZ1 a SUMO E3 ligase regulates PSR, *siz1* mutant exhibited reduced primary root and extensive lateral root and root hair development in pi deficient conditions (Miura et al. 2005).

In crops, the effect of primary root growth inhibition in pi deficiency is less pronounced (Péret et al. 2014). Different crops and cultivars showed a different response to primary root growth under pi deficiency (Péret et al. 2014). Crop plants favor proliferation of adventitious roots in pi deficiency. Maize genotypes with more crown roots and lateral root branching have higher topsoil foraging, growth, and a better yield under low pi conditions (Jia et al. 2018; Lynch 2019). In addition to that, different plant families such as Proteaceae and Leguminosae develop denser lateral roots in cluster are known as proteoid roots in response to low pi (Li et al. 2016). Pi deficiency in plants stepwise coordinates the reduction in primary root growth to mobilize the carbon allocation from the primary root to lateral root density and root hair formation.

3.2 *Lateral Root Growth in Pi Deficiency*

Lateral roots in plants have an important role in the acquisition of pi from the topsoil by increasing the total surface area (Waidmann et al. 2020). In pi deficiency, plants have to minimize the resources allocation as well as it has to explore the soil. As a result, the primary root growth needs to be reduced along with the elongation of lateral roots and the formation of higher-order LRs (Waidmann et al. 2020). A repertoire of genes gets differentially activated in response to lateral root formation. These genes are majorly involved in auxin biosynthesis, transport, and signaling (Banda et al. 2019; Crombez et al. 2019). Systemic responses of phosphate sensing and signaling are largely managed by the transcription factor PHR1 (Rubio et al. 2001; Gutiérrez-Alanís et al. 2018). PHR1 binds on PHR1-binding sites (P1BS) and regulates the expression of phosphate starvation responses (PSR) genes (Fig. 2) (Rubio et al. 2001; Castrillo et al. 2017). Auxin signaling interacts with phosphate signaling in response to lateral root formation and elongation.

Lateral root initiation begins from the cells present in the pericycle known as lateral root founder cells (LRFCs). Auxin is known to mark the pre-branch site for future lateral roots (Banda et al. 2019). Pi starvation increases auxin level and sensitivity in root tip and lateral root primordia of Arabidopsis. Auxin receptor *TRANSPORT INHIBITOR RESPONSE1* (*TIR1*) expression increases under pi deficiency, causing the degradation of AUX/IAA proteins, which overall increases the auxin sensitivity in pi deficiency (Pérez-Torres et al. 2008). *TIR1* expression in low phosphate was found to be directly regulated by PHR1 (Castrillo et al. 2017). Auxin-response factors (ARFs) are downstream to the auxin signaling controlling various aspects of auxin signaling. ARF7 and ARF19 play important role in lateral root priming, lateral root

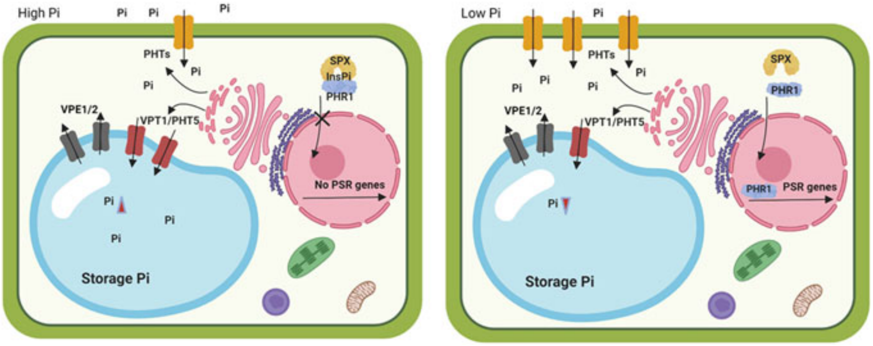

Fig. 2 Phosphate signaling in plant cell. Phosphate (pi) is taken up by phosphate transporters present on the cell membrane (PHTs). Vacuolar efflux transporters situated on tonoplast controls cytosolic pi concentration by transporting the pi in and out of the vacuole. PHOSPHATE STARVATION RESPONSE (PHR) is sequestered by SPX domain harboring proteins in the presence of Inositol Phosphate (InsPs). In the deficiency of phosphate SPX allows PHR to bind to cis-regulatory elements P1BS to regulate the expression of phosphate starvation-response (PSR) genes. Image created in BioRender.com

initiation, patterning, and initiation (Banda et al. 2019; Crombez et al. 2019). Interestingly, expression of PHR1 was also positively regulated by ARF7/19, and the impairment of lateral root growth in *arf7arf19* double mutant was also rescued by overexpressing the PHR1 (Huang et al. 2018). PIN-FORMED (PIN) transporters of auxin and several ARFs are also possible targets of PHR1 (Castrillo et al. 2017). Along with auxin several other mutants such as *lpr1, pnp, plt1;1plt1;4, alf3, siz1,* and *wrky75* showed differential regulation of lateral roots in low pi (Niu et al. 2013). (Huang and Zhang 2020) recently reviewed the role of different phytohormone in pi deficiency.

The response to low pi conforms to differential root growth in crops. Crop plants such as maize and rice have a fibrous root system that is generally deeper and shallower than the taproot system of Arabidopsis, and bean. Several genes have been identified in maize, rice, tomato, and bean that showed robust remodeling of root in varying pi conditions (Yang et al. 2007; Zhou et al. 2008; Dai et al. 2012; Postma et al. 2014; Zhou et al. 2014; Jia et al. 2018; Gonçalves et al. 2020). Simulation modeling of *Zea mays* roots using SimRoot suggested densely spaced but shorter lateral roots were more optimal to phosphorus acquisition (Postma et al. 2014). Maize with greater lateral root branching outperformed others in terms of phosphate acquisition and crop productivity. Higher uptake of phosphate led to 14% greater grain yield than control maize plants (Jia et al. 2018). Considering the above-mentioned studies of lateral root growth in pi deficiency, lateral roots show a promising role in battling pi deficiency. Branching of lateral roots overall improves the phosphate uptake and thus the growth of the plant.

3.3 Role of Root Hairs in Pi Deficiency

Root hairs are specialized tubular epidermal cells of plant roots that play a significant role in nutrient and water absorption (Salazar-Henao et al. 2016). The presence of root hairs near the root tip is considered a hotspot for pi assimilation as root hairs can be responsible for up to 90% of phosphate uptake by the plants (Brown et al. 2013). Restricted cell elongation in the primary root is the prerequisite for increasing root hair frequency (Salazar-Henao et al. 2016). Pi deficiency-induced callose deposition inhibits the cell to cell signaling in epidermal cells leading to shorter epidermal cells and increased expression of ENHANCER OF TRY AND CPC 1 (ETC), which results in a higher frequency of hairs per unit root length (Savage et al. 2013; Salazar-Henao et al. 2016b). Auxin has a significant role in root hair initiation and elongation (Knox et al. 2003; Salazar-Henao et al. 2016a; Bhosale et al. 2018; Giri et al. 2018). Pi deficiency-induced root hair growth is determined by bHLH transcription factor ROOT HAIR DEFECTIVE 6-LIKE 4 (RSL4). RSL4 protein synthesis increases in low pi and initiates the hair elongation and it gets gradually degraded by 26S proteasomal pathway. The amount of RSL4 synthesized directly determines the final size of differentiated root hair cells (Datta et al. 2015). Rise in auxin level ultimately promotes downstream ARFs. ARF19 induction in root apex shown to induce RSL4 in the root differentiation zone (Bhosale et al. 2018). Notably, AXR3/IAA17 and SHY2/IAA3 module are also involved in root hair initiation and elongation (Knox et al. 2003).

Improving RH density is an important agronomic trait (Brown et al. 2013). In rice and *Brachypodium*, overexpression of ROOT HAIR DEFECTIVE SIX-LIKE (RSL) class I bHLH transcription factor improved the root hair length (Kim et al. 2017; Zhang et al. 2018). Genome-wide association study (GWAS) of desi chickpea, maize, common bean identified several genetic loci associated with RH length (Yan et al. 2004; Zhu et al. 2005; Kohli et al. 2020). These QTLs analysis will help in modifying the surface area of root system architecture to improve crop productivity.

4 Conclusion and Future Perspective

Root system architecture is the underground three-dimensional arrangement of roots. RSA of a plant is the cumulative output of genomic and the immediate environmental conditions. Root plasticity reorganizes the RSA in response to water, mineral, microorganisms present in the soil. Nutrients are present in a heterogeneous manner in the soil. The limitation of nutrients in plants drastically affects the yield of the plant. Plants adapt to local patches of nutrients in the soil by proliferating the root growth for greater nutrient acquisition. Nitrogen and phosphorus are two essential nutrients that employ differential root systems for respective nutrient absorption. Deeper RSA with longer primary root and sparsely spaced lateral roots favor nitrogen uptake, while shorter primary root with higher lateral root branching with denser root hairs promotes phosphate acquisition. Molecular integration of nitrate and phosphate signaling also affected the RSA. Expression of nitrate transporter *NRT1.5* was strongly induced by Pi starvation, while its mutants observed an significant increase in primary root and reduced lateral roots in pi deficiency (Cui et al. 2019). Inhibition of cell division in phosphate deficiency is largely determined by the Fe-stimulated callose deposition in the root meristem. Promotion of lateral root increases the root surface that assists in topsoil foraging. Also, while increasing the foraged soil volume, the higher number of lateral roots also leads to a greater number of root tips. Root tips along with the root hairs are hotspots for pi uptake (Brown et al. 2013; Crombez et al. 2019). Integration of various nutrient signaling the in response to combinatorial stress project to develop the smart and sustainable agriculture.

Most studies done in Arabidopsis have been carried out under the artificial system by adding and reducing exogenous nutrient to “mimic” natural environmental conditions. These conditions are much more informative than the studies done in natural conditions. However, such studies propose the question of translation efficiency of nature mimicked studies to the natural conditions (Shahzad and Amtmann 2017). Buffered delivery of phosphate to Arabidopsis roots showed a non-canonical phenotype of pi deficiency. Phosphate buffered with Al_2O_3 particles supplied realistic low phosphate to plants. This buffered pi delivery resulted in smaller plants with reduced lateral root branching density, longer root hair, and differential expression of canonical phosphate starvation genes (Hanlon et al. 2018). This inefficient translation of the lab generated information to the field calls for much robust and updated experimental design.

An interconnected hub underlies RSA remodeling, wherein different phytohormone, signal peptides, and nutrient signals integrate to regulate primary root, lateral root, and root hair formation and elongation. Several reports have identified genes and QTLs to develop a smart root system. Different nutrients interact with each other in the remodeling of the root system (Bouain et al. 2019; Medici et al. 2019a, b). In future scientists need to consider a much practical soil conditions with multiple nutrient deficiency. Our challenge would be to develop a smarter network root system to coordinate mineral nutrient homeostasis and root growth.

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