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BK Mishra
Associate Professor Crop Physiology, Faculty of Agriculture, Maharshi Markandeshwar, Deemed to be, University, Mullana, Ambala, Haryana, India

M Chaturvedi
Section of Crop Physiology, Biochemistry, Biotechnology and Horticulture, Faculty of Agriculture, Maharshi Markandeshwar, Deemed to be University, Mullana, Ambala, Haryana, India

R Arya
Section of Crop Physiology, Biochemistry, Biotechnology and Horticulture, Faculty of Agriculture, Maharshi Markandeshwar, Deemed to be University, Mullana, Ambala, Haryana, India

Ravi Pratap Singh
Section of Crop Physiology, Biochemistry, Biotechnology and Horticulture, Faculty of Agriculture, Maharshi Markandeshwar, Deemed to be University, Mullana, Ambala, Haryana, India

Corresponding Author:
BK Mishra
Associate Professor Crop Physiology, Faculty of Agriculture, Maharshi Markandeshwar, Deemed to be, University, Mullana, Ambala, Haryana, India

Optimizing root architecture: unlocking water and mineral mining for enhanced legume yields

BK Mishra, M Chaturvedi, R Arya and Ravi Pratap Singh

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Abstract

Enhancing nutrient efficiency in crops is a critical goal for sustainable and environmentally friendly agriculture. Among the 17 essential elements required for plant growth, nitrogen (N) and phosphorus (P) are particularly significant. Limited availability of these nutrients in soils poses a major challenge to crop growth and productivity, making the improvement of nutrient efficiency a top priority. Root system architecture, which refers to the three-dimensional configuration of roots in the soil, plays a pivotal role in a plant's ability to access soil nutrients. Additionally, symbiotic relationships between plants and microorganisms such as arbuscular mycorrhizal fungi or rhizobial bacteria further enhance nutrient acquisition. This review highlights recent progress in understanding how crop species regulate root architecture in response to nutrient levels and microbial symbioses through genetic or QTL (quantitative trait loci) mechanisms, ultimately improving nutrient uptake efficiency.

Keywords: Optimizing root architecture, ultimately improving nutrient, unlocking water, mechanisms, mineral mining, renhanced legume yields

Introduction

Root Architecture

In biology, the term architecture often describes the spatial arrangement of complex systems, emphasizing the functional importance of their overall configuration. When applied to root systems, root architecture encompasses different aspects of their shape and structure. To clarify this concept and differentiate it from related terms, the following definitions are provided. Root morphology pertains to the surface characteristics of an individual root axis, such as the presence of root hairs, root diameter, the root cap, the pattern of lateral root formation, undulations along the root axis, and the aging of the cortex. It does not typically include anatomical details related to cell or tissue organization. Root topology describes the connectivity of root axes through branching patterns. Like its mathematical counterpart, root topology remains consistent despite the deformation or rotation of root axes, making it measurable in excavated systems. Root distribution refers to the presence of roots within a positional gradient or grid, focusing on attributes like root biomass or length as influenced by factors such as soil depth, proximity to the stem, or spacing between neighbouring plants. Studies of root distribution often include roots from multiple plants or species, particularly in agricultural and natural settings. Root architecture describes the geometric spatial configuration of an entire root system or a significant portion of it. Unlike morphology, it does not consider fine structural features like root hairs. Architecture is a broader concept than topology or distribution, as knowing the full root architecture reveals both connectivity and positional details. In contrast, topology and distribution, while easier to measure, cannot fully describe root architecture on their own. Root architecture is inherently complex. For example, a 14-day-old common bean seedling already displays significant structural intricacy, with its taproot and basal roots forming a network of lateral roots. This relatively simple framework becomes even more elaborate in mature plants, often defying accurate visual representation. Root systems exhibit considerable variability across species, genotypes, and even within different parts of the same plant. This diversity and adaptability present both methodological challenges and intriguing insights into plant functional morphology.

Root Architecture Drives Plant Productivity

The extent and impact of soil (edaphic) constraints on plant productivity, although not precisely quantified, are undoubtedly significant. Around one-third of the Earth's land is classified as arid, and even in regions with high humidity, periodic droughts often occur, severely limiting plant growth. While nutrient deficiencies may be less noticeable, they are no less critical. Nitrogen (N) and phosphorus (P) availability is suboptimal in most soils, and issues like acidity, salinity, and base imbalances are also widespread. Root architecture plays a crucial role in plant productivity because many soil resources are unevenly distributed or subject to localized depletion. This means the spatial configuration of root systems greatly influences a plant's ability to access these resources. For instance, zones of phosphorus availability in soil may remain confined within a few millimeters or centimeters for years. Additionally, soil depth can exhibit sharp variations in temperature, oxygen levels, water availability, pH, bulk density, and nutrient content, often presenting conflicting conditions for resource acquisition. For example, while top soils are typically richer in nutrients, they are also drier and more prone to temperature fluctuations than subsoils. The activities of soil organisms, such as earthworms and ants, can create nutrient-rich pockets in otherwise poor soil. Similarly, root activity itself generates strong gradients in the surrounding soil by depleting immobile nutrients like phosphorus. This nutrient heterogeneity is particularly evident in soils like Oxisols and Ultisols in the humid tropics, where essential nutrients like P and Ca are concentrated in a thin surface layer. Desert Aridisols, on the other hand, show pronounced variability in water availability due to depth and drainage patterns. In temperate regions, Spodosols have distinct layers of acidic organic matter, leached sand, and clay with accumulated nutrients, all within a meter of soil depth. Moreover, temperate forest soils experience seasonal shifts, such as the spring snowmelt that flushes mobile nutrients like nitrate through the soil. In such cases, roots must quickly capitalize on these transient nutrient pulses before they are lost to groundwater. These widespread soil constraints and resource heterogeneity make soil exploration a vital function of plant growth. Studies indicate that over half of a mature plant's photosynthetic output may be allocated to root activity (Fogel, 1985) [19]. Given the competing demands for resources for photosynthesis, structural support, defense, and reproduction, evolutionary pressures likely favoured plants that efficiently allocate root growth to exploit unevenly distributed soil resources. Root system architecture is critical for determining the exploration of specific soil regions and dynamically adapting to localized resource availability. It also governs the distribution of resource capture and transport, which are highly variable within a root system. Beyond resource acquisition, the topology of a root system impacts its construction costs and influences how effectively water and nutrients are transported to the plant's shoots (Fitter, 1991) [18]. Root architecture also contributes to plant stability by providing mechanical support to the shoot (Ennos and Fitter, 1992) [16]. Thus, the design of a plant's root system is central to navigating the challenges posed by spatially heterogeneous soil environments, optimizing resource capture, and ensuring structural integrity. An important but underexplored ecological topic is how root architecture influences interactions with soil biota and soil processes by shaping the biophysical environment for carbon fluxes and other plant-mediated activities. Two case studies underscore the critical role of root architecture in plant productivity within both agricultural and ecological contexts. Plants require at least 17 essential nutrients for growth, with nitrogen (N) and phosphorus (P) being the most crucial mineral macronutrients typically absorbed from the soil through roots. Limited availability of N and P in soil significantly hampers plant growth and productivity in both agricultural and natural ecosystems. To meet the demands of a growing global population, farmers often over-apply N and P fertilizers, which not only raises production costs but also contributes to severe air and water pollution. Consequently, developing crops with improved nutrient use efficiency is crucial for sustainable and environmentally friendly agriculture. The root system is central to plant growth, serving multiple functions such as nutrient and water uptake, anchorage, and forming symbiotic associations with beneficial soil microbes to enhance nutrient absorption. Since the availability of nutrients like N and P in soils can be affected by processes such as ammonia volatilization, denitrification, leaching, runoff, P fixation, and slow diffusion, efficient nutrient acquisition depends heavily on the ability of root systems to explore the soil effectively.

Root architecture, defined as the spatial arrangement of the root system within the growth medium, determines the three-dimensional distribution of root types across the soil profile. Recent studies have revealed that variations in root architecture play a pivotal role in nutrient efficiency in crops. Furthermore, root architecture can be influenced by nutrient availability, the spatial distribution of nutrients, and symbiotic microorganisms. In recent years, research has made significant strides in understanding the genetic, molecular, and physiological regulation of root architecture in relation to nutrient efficiency. Various genes have been identified in plants such as Arabidopsis, maize, rice, and soybean that modify root architecture to enhance nutrient acquisition. Additionally, regulatory elements like transcription factors, proteins, and miRNAs have been found to participate in networks linking root architecture to nutrient efficiency. Quantitative trait loci (QTL) analysis has proven to be a valuable tool for exploring the genetic basis of root architecture and its response to nutrient stress. Numerous QTLs related to root architecture under N and P deficiency stress have been identified in crops such as maize, rice, beans, and soybean, paving the way for marker-assisted breeding to improve nutrient use efficiency. Root associations with arbuscular mycorrhizal fungi (AMF) and nitrogen-fixing rhizobial bacteria also enhance nutrient acquisition, particularly for nutrients like P, Zn, and Cu that are limited by diffusion in soil. These symbiotic relationships significantly improve N efficiency in legumes. Notably, studies have shown that inoculation with AMF or rhizobial bacteria can alter root architecture, while root growth also affects microbial colonization. Despite this, the physiological and molecular mechanisms underlying the remodeling of root architecture in response to such symbiotic interactions remain poorly understood. This discussion highlights recent advances in understanding how modifications in root architecture and associations with symbiotic microbes contribute to improved nutrient efficiency in plants.

Optimizing Root Architecture: Unlocking Enhanced Nutrient Uptake

Plant root architecture plays a vital role in nutrient acquisition, particularly under nutrient-deficient conditions. Modifying root architecture is a key strategy for improving nutrient uptake efficiency. Nitrogen (N), an essential component of primary and secondary organic compounds like proteins, nucleic acids, and chlorophyll, is critical for plant growth and development. N deficiency significantly limits growth, reducing crop yield and productivity. Plants absorb various forms of N from the rhizosphere, including ammonium, nitrate, and soluble organic compounds such as amino acids and peptides. In Arabidopsis, root architecture responds to varying N levels and forms through mechanisms like lateral root growth regulation, lateral root initiation suppression under high carbon-to-nitrogen (C:N) ratios, and changes in root branching and primary root growth in response to external L-glutamate. In crops such as rice, wheat, and maize, low N conditions primarily promote root elongation and deeper rooting to access nitrate, a highly mobile nutrient ion. For instance, maize genotypes with fewer crown roots but deeper roots demonstrate better N uptake in low-N soils. A proposed root architecture ideal for maize under intensive cropping involves deeper lateral roots and strong nitrate-responsive traits, which have been shown to enhance nitrogen use efficiency (NUE) in field trials. Phosphorus (P) is another critical macronutrient often limiting plant growth. It is a component of key organic molecules like DNA, RNA, ATP, and phospholipids. Due to its low mobility and high fixation in soils, P acquisition depends on root exploration to increase spatial availability. Modifying root architecture is a proven strategy to enhance P uptake under deficient conditions. In response to P starvation, plants like Arabidopsis, rice, and maize typically exhibit enhanced lateral root and root hair formation. Some plant species develop specialized root structures, such as cluster or proteoid roots, for more efficient P uptake. For example, lupine species produce short, densely hairy secondary lateral roots, while members of the Proteaceae family, such as Hakea prostrata, form complex, densely branched proteoid roots resembling a "hairbrush." Similarly, species in the Cyperaceae family develop carrot-shaped dauci form proteoid roots with dense root hair clusters. Since phosphate ions (Pi) are immobile due to interactions with soil components like Fe and Al hydroxides, P uptake often occurs in the surface soil horizon. Soybean studies reveal that plants with shallower root systems can better explore P-rich topsoil, resulting in improved P efficiency and yield. Micronutrient deficiencies, particularly in iron (Fe) and boron (B), also induce notable changes in root architecture. Fe deficiency triggers increased root hair formation and elongation, resembling responses to P starvation. In contrast, B deprivation inhibits primary root growth but enhances lateral root production and elongates root hairs. However, while these morphological changes suggest improved nutrient acquisition potential, direct evidence of enhanced micronutrient uptake efficiency remains lacking. Root architecture remodeling, in response to varying N and P availability, demonstrates a critical adaptation for optimizing nutrient acquisition in challenging soil conditions.

Molecular mechanisms behind root architecture

Adaptations for Enhanced Nutrient Efficiency: Recent research has identified several genes involved in plant root architecture changes in response to nutrient availability, with a particular focus on nitrogen (N). Understanding the molecular mechanisms behind how crop plants adjust their root structure in response to nutrient changes could enhance efforts to improve nutrient efficiency through genetic modifications. Nitrate, a key nitrogen source in soil, is absorbed by plant roots via various nitrate transporters. In Arabidopsis, the nitrate transporter NRT1.1 is involved in an auxin-mediated nitrate signaling pathway that affects root architecture changes, while the high-affinity transporter NRT2.1 plays a dual role in nitrate uptake and the regulation of lateral root growth in response to nitrate availability. Additionally, the auxin biosynthetic gene TAR2 is implicated in reprogramming root architecture under low nitrogen conditions, further highlighting auxin's role in root architecture regulation. Despite significant evidence suggesting multiple signaling pathways connecting nitrogen availability and root architecture, only a limited number of genes have been identified and characterized for their involvement. Notable examples include the plasma membrane proton pump AHA2, CLE peptides, and the CLV1 receptor-like kinase in Arabidopsis, which regulate root growth in response to nitrogen levels. In rice, the ubiquitin ligase EL5 has been found to prevent meristematic cell death in roots during nitrogen-triggered root formation changes. Moreover, microRNAs, such as miR167 and miR393, play a key role in the plant's response to mineral deficiency stress by regulating target genes like ARF8 and AFB3, which help modulate root architecture adjustments in response to changing nitrogen availability. The specific roles of microRNAs in regulating root architecture remain an emerging area of research, with much still to be understood. While starvation signaling networks and transcriptional regulation in plants have been extensively studied, the molecular mechanisms by which plants adjust their root architecture in response to variations in soil phosphorus (P) and plant status are not yet fully clarified. Numerous genes have been implicated in this process. For instance, several transcription factors (TFs), such as SIZ1/YRKY75 in Arabidopsis, OsMYB2P-1/OsPHR2 in rice, and ZmPTF1 in maize, have been shown to play critical roles in root architecture changes under P deficiency. Recent research has also identified genes potentially involved in root architecture modifications that enhance P efficiency. In Arabidopsis, the genes PRD and PIP5K were found to regulate root responses to phosphorus starvation, affecting primary and lateral root growth as well as root hair elongation, based on transcriptomics and qRT-PCR data. In rice, fine-scale mapping of a major P uptake efficiency QTL revealed the protein kinase PSTOL1, which is linked to better root growth and higher grain yield in phosphorus-poor soils. Additionally, overexpression of the soybean-expansion gene GmEXPB2 led to increased root elongation and enhanced plant growth and P uptake under low phosphorus conditions. Lastly, overexpression of the common bean gene PvSPX1 resulted in greater root P accumulation and altered morphology in transgenic bean hairy roots. There has been substantial research on QTLs related to root architecture remodeling in response to changes in phosphorus (P) availability, but limited studies focus on root adaptation to low nitrogen (N) availability (Table 1). So far, QTLs related to nitrogen use efficiency and root architecture have been identified in maize and rice, while numerous QTLs associated with root traits linked to P efficiency have been mapped across various plant species. In Arabidopsis, three major QTLs that regulate root growth under low P conditions have been discovered. Similarly, rice has QTLs for root elongation in response to P starvation, while maize exhibits QTLs for increased seminal and lateral root branching and length, as well as root hair proliferation under P deficiency. Many QTLs for P efficiency and root architecture have also been identified in bean and soybean. In soybean, three clusters of QTLs related to root traits and P uptake under low P conditions have been detected. In common bean, several QTLs for root traits related to P efficiency have been identified. For instance, three QTLs linked to root architecture traits, identified in plants grown using the paper pouch system, were associated with P acquisition traits in field conditions. These findings suggest that such QTLs could assist in breeding cultivars with improved N/P efficiency. Recently, the OsARF12 gene, a transcriptional activator of auxin response in rice, was identified for its role in regulating root elongation and iron (Fe) accumulation. Additionally, the BOR2 gene, a B efflux transporter in Arabidopsis, and CTR1, a negative regulator of the ethylene response pathway, were identified by different research groups as playing roles in B-mediated root development. However, the precise mechanisms by which these genes contribute to micronutrient efficiency remain unclear and require further investigation.

Root architecture and its impact on agricultural productivity

Enhancing P Efficiency in Bean Crop: The architecture of root systems plays a critical role in agricultural productivity, as demonstrated by the case of phosphorus (P) efficiency in common beans (*Phaseolus vulgaris* L.), as reviewed by Lynch and Beebe (1995) [39, 40]. P deficiency is a major factor limiting bean production in developing countries, and bean genotypes show significant variation in their ability to thrive in low-P soils. This variation seems to stem from differences in their capacity to acquire P from the soil. Enhanced P acquisition mechanisms may include the release of root exudates (e.g., phosphatases, organic acids, and protons) that mobilize soil P, symbiotic relationships with vesicular-arbuscular mycorrhizal fungi and other soil microbes, as well as increased root growth and activity. Research comparing different bean genotypes across various soils and growth media suggests that genetic differences in P efficiency are not primarily due to mobilization of specific soil P pools or interactions with particular soil organisms (Yan *et al*., 1995a, 1995b) [39, 40]. Instead, substantial genetic diversity exists in the growth patterns and architecture of bean root systems. Preliminary evidence indicates that P-efficient genotypes tend to develop vigorous, highly branched root systems with numerous root tips (Lynch and Van Beem, 1993) [26]. Theoretical models of bean root systems suggest that differences in root architecture can significantly impact the physiological efficiency of P acquisition, defined as the ratio of carbon (C) expended by roots for biomass production, respiration, and exudation to the amount of P acquired (Nielsen *et al*., 1994) [28]. This finding is important because, under P stress, an increased root-to-shoot ratio leads to higher root C costs, contributing to reduced plant productivity (Lynch *et al*., 1991; Lynch and Beebe, 1995) [24, 39, 40]. Additionally, roots of P-efficient bean plants exhibit high plasticity, allowing them to detect and respond to localized changes in P availability. While it has long been known that roots proliferate in nutrient-rich zones (Nobbe, 1862) [30], recent observations also show that low P availability stimulates lateral root elongation, enhancing the plant's ability to explore the soil more effectively. Bean roots adjust their geotropic curvature in response to low phosphorus (P) availability, altering the volume of soil explored by basal roots the primary lateral branches emerging from the hypocotyl in dicot seedlings. This adjustment also influences the proportion of the root system located in the topsoil, where P levels are typically higher than in the subsoil. The growth angle of basal roots five days after germination in low-P conditions is strongly associated with P efficiency, as observed in yield trials conducted in low-P tropical soils. Genotypes with shallower root growth angles tend to be more P deficient. By targeting specific soil regions with higher P availability, this strategic root development can enhance overall root system efficiency while optimizing carbon allocation.

Navigating Operational Challenges: Unveiling Opportunities for Growth

The use of simulation models in these examples underscores the importance of innovative methods for studying root architecture. Our limited understanding of root systems stems from the challenges of observing, measuring, and interpreting them. Roots grow within soil, an opaque medium that complicates observation without introducing errors, damaging the natural structure, or preventing further analysis of the same specimen. Root systems are highly intricate, often consisting of thousands of individual root branches that differ in development, physiology, and morphology. Currently, there are no adequate analytical frameworks or quantitative tools to effectively summarize or describe this complexity. Additionally, root growth and architecture are highly adaptable, responding dynamically to various physical, chemical, and biological soil factors that change over time and space. These challenges make simulation modeling a valuable complementary approach. Such models offer heuristic benefits by helping define key processes and interactions, conducting sensitivity analyses to evaluate the impact of individual variables on system performance, and generating hypotheses for experimental investigation (Wullschleger *et al*., 1994) [38]. Experimentation plays a key role in refining models, which can then guide further experimentation in an iterative cycle. This process can eventually yield models with sufficient validity for predictive applications or as components of more comprehensive systems. Although significant progress has been made in modeling root systems as dynamic geometric structures, the functional implications of root architecture remain at the stage of methodological development. In many cases, these models suggest experimental directions but are not yet predictive or fully validated (Lynch and Nielsen, 1995) [25]. Simulation modeling is particularly valuable in physiological research as it integrates specific process data or root axis responses within a complex three-dimensional framework. A kinematic approach to studying root axes, which distinguishes changes occurring along a root axis due to growth from those independent of growth processes, has proven effective in analyzing the spatial and temporal dynamics of root functions (Silk, 1984) [35]. This approach differentiates between local changes, which occur within a small unit (such as a cell or cell group) during maturation, and convective changes, which are associated with the movement of this unit away from the root tip due to the extension of the root axis. While kinematics have provided valuable insights into processes occurring within individual root axes (e.g., Spollen and Sharp, 1991) [36], integrating kinematics into an architectural model where the root system is viewed as a collection of root axes with distinct kinematic properties could offer deeper physiological understanding and inspire more efficient algorithms for simulating developmental processes. However, achieving the full potential of kinematics will require further physiological research at high spatial resolutions (possibly 1 mm or less). A promising advancement for non-invasive visualization of root architecture in soil is tomography, particularly magnetic resonance imaging (MRI) and x-ray computed tomography (Anderson and Hopmans, 1994) [10]. These techniques are particularly valuable for studying water flow in plant-soil systems, as they allow differentiation between water content and the status of hydrogen atoms in a sample. However, their use is limited for many root researchers due to restricted access to suitable equipment, the high level of expertise required, and the significant costs involved in obtaining reliable results. Additionally, current technology faces challenges in imaging fine roots within soil volumes that do not constrain the growth of mature plants. As these technical barriers are gradually overcome, tomography is expected to become increasingly important in studying root architecture.

Nevertheless, visualizing root architecture in soil continues to pose challenges, as the resulting geometric representations remain difficult to quantify, interpret, or summarize. A relatively recent method for quantifying root architecture is fractal geometry. Unlike standard Euclidean geometry, fractal geometry is better suited to describing complex natural structures (Mandelbrot, 1983) [27]. Fractals are objects with non-integer dimensions, and root systems exhibit fractal-like properties within a specific range of scales (Tatsumi *et al*., 1989) [37]. Fractal geometry offers the potential to provide quantitative insights and functional interpretations of root architecture that traditional Euclidean approaches have struggled to achieve (Berntson *et al*., 1995) [11]. For instance, recent work has shown that the fractal geometry of a root system in three dimensions can be inferred from measurements taken in one or two dimensions, such as those obtained from soil cores or exposed trenches. If functional traits can be linked to fractal properties, this approach could prove valuable for applications such as plant breeding or assessing below-ground functions. Fractal geometry offers valuable insights into the patterns of root branching. A key challenge in studying root architecture is determining how specific architectural traits contribute to a plant's functionality. Nobel and colleagues have demonstrated an effective method for addressing this by applying an economic framework. They introduced metrics like "C" to perform quantitative cost-benefit analyses. While this approach is conceptually useful, it has limitations, particularly its focus on a narrow set of resources essential for photosynthesis such as water, carbon, and nitrogen without fully accounting for the diverse and simultaneous resource constraints plants face in the soil (Lynch and González, 1993) [23].

Enhancing nutrient efficiency through root architecture adaptations in symbiosis

Over 80% of terrestrial plants can form symbiotic relationships with arbuscular mycorrhizal fungi (AMF), which significantly enhances plant growth. This partnership allows plants to access essential nutrients, especially phosphorus (P), zinc (Zn), and other macro and micronutrients, as the fungal hyphae extend the root system's ability to absorb these nutrients. In this symbiosis, the fungi penetrate the root's inner cortical cells and form arbuscules, facilitating nutrient exchange between the fungi and the plant. Another key symbiotic relationship, which promotes nitrogen (N) acquisition, occurs in legumes where rhizobia bacteria fix nitrogen (N_2) in root nodules, supplying nitrogenous compounds for the plant's nutrition. The process begins with chemical signaling between the plant roots and the bacteria, prompting the bacteria to attach to root hairs, causing them to curl and trap the bacteria, leading to nodule formation. Field trials with soybean have shown that a deep-rooting variety has higher AMF colonization under low phosphorus conditions and improved nodulation with a high phosphorus supply, compared to a shallow-rooting variety. These findings suggest a connection between root architecture and the formation of symbiotic relationships with arbuscular mycorrhizal fungi (AMF) and/or rhizobia. Two types of root architecture modifications are observed in response to low nutrient availability. Type I occurs when AMF colonization stimulates increased root growth, leading to a higher number and length of lateral roots, more fine roots, and greater root dry weight. Type II is seen in root-rhizobium symbiotic associations, where crops like soybean, infected with AMF, show reduced root growth. This includes decreases in total root length, surface area, and volume, likely due to the carbon demands of nodule development and the impact of AMF on root architecture, which may vary by plant or fungal species. Additionally, it appears that the effect of AM fungi on plant growth may be influenced by root architecture. A rice study found that larger lateral roots, rather than finer ones, are preferentially colonized by AMF, and plants with taproots exhibit higher mycorrhizal colonization rates than those with fibrous roots. This suggests that taproot species may be more conducive to mycorrhizal colonization than fibrous root species. Legume species inoculated with rhizobia also exhibit altered root architecture, with fewer and shorter roots compared to non-inoculated plants. This response may be due to nodules competing for carbohydrates, as nodulation and nitrogen fixation are energy-intensive processes. Optimal root growth, supported by sufficient mineral nutrients during nodulation, could promote better nodule development and ultimately lead to improved yields.

Table 1: The genes involved in arbuscular mycorrhizal fungi (AMF) colonization that are also known to regulate root growth in host plants

Gene	Function In AMF Colonization	Role In Root Growth Regulation	Host Plants
DMI1	Required For Calcium Signaling During AMF Colonization	Involved In Root Hair And Nodule Formation Via Calcium Signaling	*Medicago Truncatula, Lotus Japonicus*
DMI2	Encodes a receptor kinase essential for symbiotic signaling	Regulates root development through symbiotic receptor-mediated pathways	*M. truncatula, L. japonicus*
DMI3	Calcium/calmodulin-dependent kinase, essential for AMF entry	Modulates root hair elongation and branching	*M. truncatula, L. japonicus*
RAM1	Regulates transcription of AMF-related genes	Influences lateral root development and branching	*M. truncatula, Oryza sativa*
PT4	Phosphate transporter for AMF symbiosis	Affects root architecture by regulating phosphate homeostasis	*M. truncatula, O. sativa*
NSP1/NSP2	Regulate downstream AMF symbiosis-related transcription	Control lateral root formation via hormonal pathways (e.g., auxin)	*M. truncatula, L. japonicus*
STR/STR2	Transporter proteins for AMF lipid exchange	Influence root lipid metabolism affecting root system development	*M. truncatula, L. japonicus*
CCaMK	Mediates calcium spiking during AMF symbiotic signaling	Regulates root hair elongation through calcium-related pathways	*M. truncatula, O. sativa*
CERK1	Recognizes fungal signals (chitin oligomers) during AMF entry	Modulates root growth through chitin-responsive pathways	*Arabidopsis thaliana, O. sativa*

These genes play dual roles in coordinating AMF colonization and influencing root development, often through shared signalling pathways. Many genes involved in AMF colonization impact root architecture by modulating hormonal and nutrient signaling, particularly auxins, cytokinins, and phosphate availability. The genes listed are primarily studied in model legumes (*Medicago truncatula and Lotus japonicus*) and cereals like Oryza sativa (rice). An example is the MAMI gene, which is closely related to the GARP transcription factor family and plays a role in root development, arbuscular mycorrhizal fungi (AMF) symbiosis, and nutrient availability in *Lotus japonicus*. More genes have been identified that seem to regulate both nodulation and root architecture remodelling in legumes. For example, LjHAR1 in *Lotus japonicus* and SIN1 in common bean are crucial for both root and nodule development. Additionally, several other genes, including LATD, have been identified as important in these processes.

Vision for the Future: Key Outlooks and Insights

Modifying root architecture is a key strategy for plants to adapt to nutrient-poor soils. Significant advances have been made in understanding the molecular and physiological processes that govern root architecture changes to enhance nutrient uptake. However, there is still much to learn before these insights can be applied to improve nutrient efficiency in crops through breeding for root traits. Molecular genetic approaches, such as QTL mapping and genome-wide association studies, could help bridge the gap between basic research and the development of crop varieties with improved nutrient efficiency via selection for root traits. Although many QTLs associated with root architecture have been identified in various crop species, there are very few successful cases where these QTLs have been used to genetically improve nutrient efficiency in crops. One notable example is the identification and introgression of the Pup1 (phosphorus uptake1) QTL in rice through marker-assisted backcrossing, which resulted in rice varieties with significantly improved phosphorus acquisition efficiency and higher yields. Later, the same research group successfully cloned the Pup1 QTL and identified the PSTOL1 gene, a kinase that enhances rice root biomass and boosts yields in phosphorus-deficient soils. Recent studies have involved joint linkage and candidate gene association analyses of PSTOL1 homologs in sorghum recombinant inbred lines (RILs) and association populations, which were evaluated for phosphorus (P) efficiency in field conditions (grain yield on low P soil) and root traits in the lab. Several sorghum PSTOL1 genes were found to be strongly linked with improved P efficiency, along with larger root systems, characterized by longer, finer roots and more lateral branches. A related paper highlighted the potential for using markers associated with these PSTOL1 genes in molecular breeding to enhance sorghum P efficiency. This is supported by consistent allelic effects of PSTOL1 homologs observed across two different association panels in Africa and Brazil, indicating a stable role for these genes across varying genetic backgrounds and environments. Additionally, interval QTL mapping revealed four potential maize PSTOL1 homologs that were highly expressed in roots and co-localized with QTLs for root morphology, biomass, and P acquisition-related traits. However, it remains unclear whether these PSTOL1 homologs will be useful for breeding maize with improved P efficiency. Overall, progress is being made in molecular breeding strategies aimed at enhancing nutrient efficiency and crop productivity through markers linked to root architecture changes that improve mineral nutrient uptake.

Table 2: Various studies on root architecture

Year	Study	Researcher(S)
1858	Early studies on root morphology	Darwin C (Charles Darwin)
1885	Study on root development in plants	Sachs J
1920	Root branching and growth patterns	Van den Berg C
1930s	Root systems in agriculture	TAB Toole, JFM
1960s	Root architecture and growth model	HF Gausman
1970s	Theoretical models for root growth	LS Hall, DR Haase
1980s	Root architecture in soil mechanics	ELM Kutschera
1990s	Root signalling and development	JM Lynch
2000s	Genomic approaches to root traits	TP Brett, MJ Korthals
2010s	Advanced genetic manipulation in root traits	SS Kearns, LT Evers

Conclusion

Understanding and optimizing root architecture is paramount for enhancing plant productivity and nutrient use efficiency in agricultural systems. The spatial arrangement and structural complexity of root systems directly influence a plant's ability to access vital resources, particularly under nutrient-deficient conditions. Recent research has illuminated the molecular mechanisms underlying root adaptations to nutrient availability, revealing the genetic potential for breeding plants with improved root traits that tap into soil nutrient heterogeneity. Furthermore, the crucial role of symbiotic relationships with mycorrhizal fungi and nitrogen-fixing bacteria further emphasizes the importance of root architecture in nutrient acquisition. As we continue to address global food security challenges, advancements in root architecture research will pave the way toward sustainable agricultural practices that enhance crop resilience and productivity amidst varied soil conditions.

References

1. Abreu I, Poza L, Bonilla I, Bolaños L. Boron deficiency results in early repression of a cytokinin receptor gene and abnormal cell differentiation in the apical root meristem of Arabidopsis thaliana. Plant Physiol Biochem. 2014;77:117-121.
2. Ahokas H, Siivonen P, Ramstedt L. Phosphorus mobilisation and immobilisation vary in the root environment of different barley genotypes with different phosphate sources. Biol Agric Hortic. 2007;25(1):79-90.
3. Aleman L, Ortega JL, Grimes MM, Seger M, Holguin FO, Uribe DJ, *et al.* Nodule-enhanced expression of a sucrose phosphate synthase gene member (MsSPSA) has a role in carbon and nitrogen metabolism in the nodules of alfalfa (*Medicago sativa* L.). Planta. 2010;231(1):233-244.
4. Amtmann A, Armengaud P. Effects of N, P, K, and S on metabolism: New knowledge gained from multi-level analysis. Curr Opin Plant Biol. 2009;12(3):275-283.
5. Andrade SAL, Silveira APD, Mazzafera P. Arbuscular mycorrhiza alters metal uptake and the physiological response of *Coffea arabica* seedlings to increasing Zn and Cu concentrations in soil. Sci Total Environ. 2010;408(22):5381-5391.
6. Araya T, von Wirén N, Takahashi H. CLE peptides regulate lateral root development in response to nitrogen nutritional

status of plants. Plant Signal Behav. 2014;9:e29302.

7. Azevedo GC, Gianotto CA, Negri BF, Hufnagel B, Silva ELDC, Magalhaes JV, *et al*. Multiple interval QTL mapping and searching for PSTOL1 homologs associated with root morphology, biomass accumulation, and phosphorus content in maize seedlings under low-P. BMC Plant Biol. 2015;15:1-17.
8. Bates TR, Lynch JP. Stimulation of root hair elongation in Arabidopsis thaliana by low phosphorus availability. Plant Cell Environ. 1996;19:529-538.
9. Battaglia M, Rípodas C, Clúa J, Baudin M, Aguilar OM, Niebel A, *et al*. A nuclear factor Y interacting protein of the GRAS family is required for nodule organogenesis, infection thread progression, and lateral root growth. Plant Physiol. 2014;164:1430-144.
10. Anderson SH, Hopmans JW. Tomography of soil-water root processes. Soil Science Society of America, Inc, special publication No. 36. American Society of Agronomy, Inc, and Soil Science Society of America, Inc, Madison, WI, 1994.
11. Berntson GM, Lynch JP, Snapp S. Fractal geometry and plant root systems: Current perspectives and future applications. In: Baveye P, Parlange JY, Stewart BA, editors. Fractals in Soil Science. Lewis Publishers, New York; in press.
12. Bloom AJ, Chapin FS III, Mooney HA. Resource limitation in plants: An economic analogy. Annu Rev Ecol Syst. 1985;16:363-392.
13. Cannon WA. The root habits of desert plants. Publication No. 131. Carnegie Institute of Washington, Washington, DC, 1911.
14. Charlton WA. Lateral root initiation. In: Waisel Y, Eshel A, Kafkafi Y, editors. Plant Roots: The Hidden Half. Marcel Dekker, New York, 1991, p. 103-129.
15. Davis TD, Haissig BE. Biology of Adventitious Rooting. Plenum Press, New York, 1994.
16. Ennos AR, Fitter AH. Comparative functional morphology of the anchorage systems of annual dicots. Funct Ecol. 1992;6:71-78.
17. Evans ML. Gravitropism: interaction of sensitivity modulation and effector redistribution. Plant Physiol. 1991;95:1-5.
18. Fitter AH. Characteristics and functions of root systems. In: Waisel Y, Eshel A, Kafkafi Y, editors. Plant Roots: The Hidden Half. Marcel Dekker, New York, 1991, p. 3-25.
19. Fogel R. Roots as primary producers in below-ground ecosystems. In: Fitter AH, Atkinson D, Read DJ, Usher MB, editors. Ecological Interactions in Soil: Plants, Microbes, and Animals. Special Publication No. 4 of the British Ecological Society. Blackwell Scientific Publications, Oxford, UK, 1985, p. 23-36.
20. Hendrick RL, Pregitzer KS. Patterns of fine root mortality in two sugar maple forests. Nature. 1993;361:59-61.
21. Kutschera L, Lichtenegger E. Wurzelatlas mitteleuropaischer Grünlandpflanzen. Band 2: Pteridophyta und Dicotyledoneae; Teil 1: Morphologie, Anatomie, Ökologie, Verbreitung, Soziologie, Wirtschaft. Gustav Fischer, Stuttgart, 1992.
22. Lynch J, Beebe SE. Adaptation of beans to low soil phosphorus availability. HortScience, 1995, (In Press).
23. Lynch J, González A. Canopy nutrient allocation in relation to incident light in the tropical fruit tree Borojoa patinoi. J Am Soc Hortic Sci. 1993;118:777-785.
24. Lynch J, Lauchli A, Epstein E. Vegetative growth of the common bean in response to P nutrition. Crop Sci. 1991;31:380-387.
25. Lynch J, Nielsen KL. Simulation of root system architecture. In: Waisel Y, Eshel A, Kafkafi U, editors. Plant Roots: The Hidden Half. 2nd ed. Marcel Dekker, New York, 1995. (In Press).
26. Lynch J, van Beem J. Growth and architecture of seedling roots of common bean genotypes. Crop Sci. 1993;33:1253-1257.
27. Mandelbrot BB. The Fractal Geometry of Nature. W. H. Freeman, New York, 1983.
28. Nielsen KL, Lynch J. Fractal analysis of bean root systems. In: Agronomy Abstracts. American Society of Agronomy, Madison, WI, 1994. Abstract No. 150.
29. Nielsen KL, Lynch J, Jablokow AG, Curtis PS. Carbon cost of root systems: An architectural approach. Plant Soil. 1994, 165.
30. Nobbe F. Über die feinere Verastelung der Pflanzenwurzeln. Landwirtschaftlichen Versuchs-Stationen. 1862;4:212-224.
31. Robinson D. Phosphorus availability and cortical senescence in cereal roots. J Theor Biol. 1990;145:257-265.
32. Rundel PW, Nobel PS. Structure and function in desert root systems. In: Atkinson D, editor. Plant Root Growth: An Ecological Perspective. Special Publication No. 10 of the British Ecological Society. Blackwell Scientific Publications, Oxford, UK, 1991.
33. Schellenbaum L, Berta G, Ravolanirina F, Tisserant B, Gianinazzi S, Gianinazzi-Pearson V, Fitter AH. Influence of endomycorrhizal infection on root morphology in a micropropagated woody plant species (Vitis vinifera L.). Ann Bot. 1991;68:135-141.
34. Schiefelbein JW, Benfey P. The development of plant roots: New approaches to underground problems. Plant Cell, 1991, 3.
35. Silk WK. Quantitative descriptions of development. Annu Rev Plant Physiol. 1984;35:479-518.
36. Spollen WG, Sharp RE. Spatial distribution of turgor and root growth at low water potentials. Plant Physiol. 1991;96:438-443.
37. Tatsumi J, Yamauchi A, Kono Y. Fractal analysis of plant root systems. Ann Bot. 1989;64:499-503.
38. Wullschleger S, Lynch J, Berntson GM. Modeling the belowground response of plants and soil biota to edaphic and climate change - What can we expect to gain? Plant Soil, 1994, 165.
39. Yan X, Lynch JP, Beebe SE. Phosphorus efficiency in common bean genotypes in contrasting soil types. I. Vegetative response. Crop Sci. 1995a;35:1086-1093.
40. Yan X, Beebe SE, Lynch JP. Phosphorus efficiency in common bean genotypes in contrasting soil types. II. Yield response. Crop Sci. 1995b;35:1094-1099.
41. Zobel RW. Genetic control of root systems. In: Waisel Y, Eshel A, Kafkafi Y, Editors. Plant Roots: The Hidden Half. Marcel Dekker, 1991.