

ROOT ARCHITECTURE AND RHIZOSPHERE DYNAMICS IN VEGETABLE CROPS: IMPLICATIONS FOR NUTRIENT USE EFFICIENCY AND PRODUCTIVITY

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ABSTRACT

Restricted ability to acquire nutrients deeply in the soil may be due to the use of shallow-rooting systems, high input of fertilizers, and the multiple irrigation cycles used in the production of vegetables. In varied subsurface soil moisture conditions, root system architecture and the related physiological processes help determine vegetable crops ability to acquire, translocate, and utilize nutrients. There are differences in the ability to acquire the three major nutrients i.e. nitrogen, phosphorus and potassium, due to root length density, the presence of laterals, root hairs, and the distribution of roots in the soil. Different crops (leafy, fruiting, and root) behave differently and have different strategies and fertilization requirements, therefore, distinct nutrient foraging patterns in the root system. The uptake of nitrogen is the result of the synergistic action of transporters and the allocation of carbon to the roots, while the acquisition of phosphorus is, the result of expanded root surface area and the ability of the root system to adapt to low phosphorus availability. Under intensive management, potassium uptake is essential for osmotic regulation, activation of enzymes, and stress tolerance. A concerted understanding of both the physiological and architectural elements on root systems, can provide ways to improve nutrient use efficiency, and at the same time, lower reliance on fertilizers. The ability of root systems in vegetable crops is understudied, and the relationships between root systems and productivity is poorly understood. Selection for root traits in breeding and management has the greatest untapped potential in the production of vegetables.

KEYWORDS: root system architecture; nutrient uptake; vegetable crops; root hairs; nitrogen transport; phosphorus efficiency; potassium dynamics

1. INTRODUCTION

While vegetable crops are vital to the food system and dietary nutrition, the production systems associated with them tend to have low nutrient utilization efficiency while still requiring high fertilizer input. Depletion of potassium reserves, fixation of phosphorus in the soil, and leaching and volatilization of nitrogen are significant and widely reported losses in intensive vegetable production (Tilman et al. 2011; Zhang et al. 2015). These losses also further contribute to environmental degradation. Therefore, to help solve the problem, targeted research to better understand the traits of the plant which help with the acquisition of nutrients, rather than increased dependency on fertilizers will be required.

Water and mineral nutrients are acquired through the roots which form the primary interface of the soil. Traits associated with roots, however, remain poorly studied in research on vegetable crops. Instead, emphasis is placed on the above-ground traits associated with yield and quality. As a result of the nutrient dependence of the top soil layer, most vegetable crops tend to develop highly plastic, and relatively shallow, root systems (Swiader & Ware 2016). A shallow rooting habit will increase nutrient stress under supply fluctuating conditions as well as limit access to the nutrient reserves in the sub soil. The architecture in root systems determines how roots are organized within soil and how far a plant can explore nutrient-rich areas. Some of the most important features are the density of roots, branching structures, growth angle, and the presence of fine roots and root hairs. These features control the volume of soil and root-soil interface, which are critical zones for nutrient acquisition, especially for immobile nutrients such as phosphorus. Plants often exhibit plastic responses to nutrient deficiency. This includes the formation of more lateral roots and the elongation of root hairs, which help in more efficient nutrient foraging (Chen et al. 2020).

The roots' physiological mechanisms, along with active transport, further control nutrient acquisition through membrane transport, ion transport channels, and metabolic mechanisms. Effective nitrogen assimilation involves a functional interplay between the systems for the transport of nitrates and ammonium, which is also associated with root growth and the allocation of carbohydrates (Xu et al. 2012). The acquisition of phosphorus is reliant on the presence of low-affinity phosphate transporters, whose activity increases in response to low external concentrations of phosphate, and this is associated with a higher root surface area and altered rhizosphere (Shen et al. 2011). The uptake of potassium is beneficial for maintaining cell osmotic pressure, activating enzymes, and improving tolerance to stress, especially in cases of drought and salinity, which are common in vegetable production (Wang & Wu 2013).

Different vegetable types have different root structures and ways of acquiring nutrients. Leafy vegetables form a lot of fine roots because they receive nutrients often, while fruiting vegetables have deeper and more widespread roots for longer perforated periods of growth. However, some root storage crops have tap roots for nutrients, storage, and root modification. Because of the variation relating to the root structure, and the way it affects the uptake of nutrients and the utilisation of fertilisers, high regards should be given to it when the optimised management practices are required.

Root phenotyping, imaging, and molecular biology have progressed, ensuring that the studies of root traits in situ, and the linking of structures to uptake become more prolific and possible. When these techniques are blended to agronomic practices, the development of root traits to fashioned edaphic configurations should be possible. Promising pathways for defining the soil nutrient balance and the energetic resources include the greater root length density in the top soil, the deeper roots penetrating into the soil for nitrate, greater root hairs in nutrient scanty conditions, and the improved nutrient efficiency.

This review compiles information on root system architecture and physiological mechanisms of nutrient uptake in vegetable crops, specifically focusing on the uptake of nitrogen, phosphorus, and potassium. It aims to integrate root structural and functional components with nutrient use efficiency and provide guidance on the achievable balance between crop productivity and fertiliser input reduction.

2. Root System Architecture in Vegetable Crops

Current understanding of root system architecture in vegetable crops shows the considerable variation due to individual plant group growth patterns, life cycles, and the history of crop domestication. Vegetables in the leafy category, including lettuce, spinach, and cabbage, develop more fibrous and highly root-dense systems in the top layers of the soil. While this configuration is beneficial for rapid and efficient absorption of nutrients through surface fertilisation, or surface fertigation, this root system architecture also limits the crop's access to deeper soil layers. The root systems of these crops often are so comprised of fine roots that the crop system becomes inadequate to handle rapid growth, or the crop poses a risk to the growing system through a rapid and excessive biomass increase. Such fibrous root systems also make crops more sensitive to changes in available nutrients and moisture and more hydroponic systems (Swiader and Ware, 2016).

Tomato, brinjal, and capsicum (with chillies and capsicums) are categorized as fruit-bearing vegetables, and develop root systems more like what is described in the previous paragraph. However, in contrast to leafy vegetable crops, fruit-bearing vegetables develop lateral roots and deeper penetrating roots. Compared to leafy root crops, the described rooting systems/habits extend the crop's root system further/allow these crops to utilize a larger soil volume, or give the crop root system a larger soil surface volume. Such changes also allow the crop to maintain more stable nutrient supply for the crop, or root system, during long growing/harvest cycles. Root plasticity is also observed in these crops, in their ability to adapt to, or utilize, the nutrient spatial contingency described in of the soil. For example, the lateral root system described above is also often the result of low nitrogen (N) conditions and leads to the development of root systems as described above. Also in low P soils, there are increased root hairs and top soil foraging increased in P to create a better nutrient supply (Lynch, 2019; Chen et al, 2020).

Carrots, radishes, and beetroots are examples of storage root crops. They possess distinct architectural characteristics that include the presence of a dominant primary taproot that acts both as storage organ and nutrient uptake conduit. The development of the taproot is associated with the formation of secondary roots, as well as with cambial activity that influence nutrient acquisition and assimilate partitioning. The dual function of the primary taproot presents particular challenges constraining root architecture in that excessive branching could limit the storage function of the roots and insufficient branching could limit the nutrient uptake. For this reason, enhancing the storage taproot is essential when aiming at high yields in storage root crops.

Root hairs are an essential feature of nutrient acquisition because they increase the effective root surface area and enable the root system to contact more soil particles. This is especially important for phosphorus acquisition because this nutrient is largely immobilized in the soil. It is well documented that roots growing in phosphorus deficient conditions often develop longer and more numerous root hairs as a key adaptive trait to increase the phosphorus acquisition efficiency of the root system (Shen et al. 2011). Root exudation, as well as morphological influences, further impacts nutrient availability and uptake and is a means of silencing the rhizosphere.

The soil's spatial distribution of roots determines the ability to exploit gradients in soil nutrient distribution. Surface-rooted systems capture nutrients from frequent surface applications, while deep-rooted systems can exploit soil layers that contain leached nitrates. Comprehending these architectural strategies is crucial for optimizing the integration of fertilizer placement, irrigation, and root distribution.

Crop group	Root type	Rooting depth	Zone of highest root length density	Root hair development	Dominant nutrient capture strategy	Key nutrient use efficiency implication	Reference
Leafy vegetables	Fibrous, highly branched fine roots	Shallow (mostly within top 20–30 cm)	Topsoil, concentrated near fertiliser placement and irrigation zone	High under low P conditions	Rapid uptake of readily available nutrients from surface layers; efficient	High recovery of applied nutrients but low access to subsoil reserves;	Lynch (2019); Fageria et al. (2011)

					exploitation of frequent fertigation	sensitive to nutrient fluctuations and leaching losses	
Fruit vegetables	Moderately deep taproot with extensive lateral branching	Medium to deep (30–60 cm or more depending on soil conditions)	Topsoil and mid-soil with active lateral proliferation in nutrient-rich patches	Moderate to high, responsive to nutrient stress	Exploration of larger soil volume; capture of mobile nutrients such as nitrate; adaptive proliferation in fertigation zones	Improved nitrogen recovery and yield stability; better tolerance to variable nutrient supply	Lynch (2013); White & Kirkegaard (2010)
Storage root vegetables	Dominant taproot with secondary laterals	Medium depth with strong vertical penetration during early growth	Upper and mid-soil; balance between storage organ development and fine root proliferation	Moderate; functionally important for early P uptake	Dual function of nutrient acquisition and assimilate storage; efficient early nutrient capture followed by allocation to storage organ	Nutrient supply during early stages critical; excessive branching may reduce storage yield	Gregory (2006); Fageria et al. (2011)
Legume vegetables	Taproot with nodulated laterals	Medium depth with active lateral nodulation zone	Topsoil and nodulation zone around root crown	Moderate; enhanced under P deficiency	Symbiotic nitrogen fixation combined with soil nutrient uptake; increased reliance on P for nodulation	Reduced dependence on external N fertiliser; improved system-level NUE and soil fertility benefits	Graham & Vance (2003); Lynch (2019)

Table 1. Comparative RSA traits and nutrient acquisition strategies

The roots of leafy vegetables are shallow and fibrous and have a high root length density in the upper horizons of soil, aiding in the rapid uptake of nutrients that are applied on a frequent basis. In contrast, fruiting vegetables have more deeply situated roots that are more highly branched, and that may allow for the exploration of a greater volume of soil and capture of more mobile nutrients, such as nitrate. Root storage crops tend to develop a dominant taproot with laterals that must balance the roles of the root in the acquisition of nutrients and in the storage of those nutrients. Root hairs are reportedly more developed in all groups of vegetables under conditions of phosphorus deficiency, and this phenomenon supports the acquisition of phosphorus more efficiently.

3. Physiological Mechanisms of Nutrient Uptake

Root nutrient uptake happens through a series of complex, coordinated physiological mechanisms, including membrane transporters, ion channels, and a source of metabolic energy. Primary nitrogen uptake occurs in the form of ammonium and nitrate through high- and low-affinity transport systems located in the root epidermis and root cortex. These transporters are expressed and their activity is regulated by available external nitrogen, internal nitrogen, and the root carbon allocation, in order to regulate the synchronisation of nutrient supply and in-planta demand (Xu et al. 2012). Nitrate uptake is often coupled to increased root elongation and the formation of lateral roots, suggesting a strong integrated signalling system of nitrogen and root systems.

Phosphorus uptake is performed through high-affinity phosphate transporters which are highly effective below a certain threshold. Due to the low mobility of phosphates in the soil, plants often develop modified strategies such as enhanced root hair formation and more Acid-Root-Systems (ARS) to enable more effective phosphorous (P) acquisition in nutrient

poor conditions. The excretion of protons and organic acid leads to an increase in dissolved phosphates in the soil and increases the uptake of these nutrients (Shen et al. 2011). These responses and adaptations are especially important in vegetable systems due to the frequent banding and basal dosing of phosphorus fertilisers.

Potassium absorption involves both passive and active transport and is essential for osmotic balance, regulation of stomata, and activation of certain enzymes. Improved potassium nutrition strengthens plants' resistance to abiotic stresses like drought and salinity, which are prevalent in intensive vegetable farming. The control of potassium transporter proteins is inextricably linked to the hydration and metabolism of the plant and stresses the need for proper integration of nutrient and irrigation management (Wang & Wu 2013).

Figure 1. Root nutrient uptake pathways and transport processes

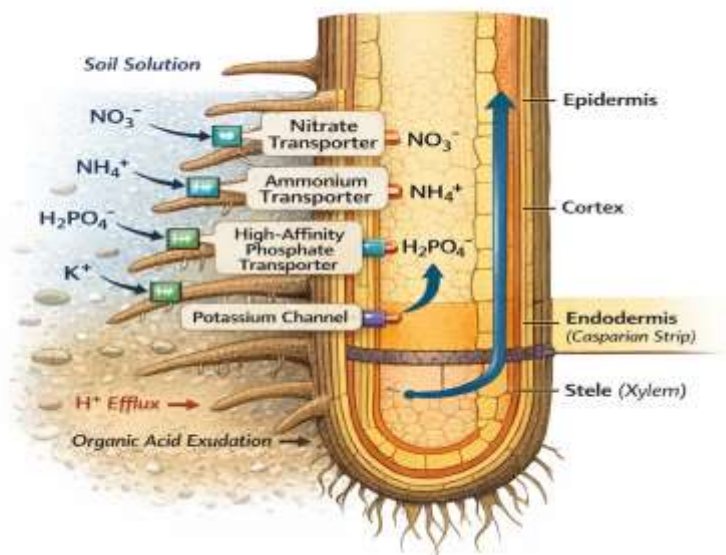


Figure 1. Root nutrient uptake pathways and transport processes

A conceptual representation showing nitrate and ammonium transport systems, high-affinity phosphate transporters, potassium channels, and their integration with root growth and carbon allocation. (Marschner (2012))

4. Rhizosphere Dynamics in Vegetable Production Systems

The rhizosphere is a very dynamic area of the interaction of plant roots, soil and microorganisms. There are biological and physicochemical processes that create and control the processes that govern the availability and uptake of nutrients. In system-based production of vegetables, this area becomes very important due to the shallow and dense patterns of rooting that cause concentration of activity in the upper horizons of the soil. The practices of intensive fertilization and irrigation modify the conditions of the rhizosphere by causing changes in the soil pH, redox potential, and microbial composition, which in turn affect the processes of transformation of nutrients and the efficiency of plant uptake of nutrients (Philippot et al. 2013).

The process of root exudation is one of the most important initiators of rhizosphere processes. Root exudation by vegetable crops contains a wide variety of low molecular weight compounds, which include sugars, amino acids, organic acids, phenolics, and mucilage, which provide a source of carbon to microorganisms and alter the chemical composition surrounding the root. These root exudates are able to help improve solubility, especially for phosphorus and certain micronutrients, through processes of chelation and acidification. For instance, in soils that have low concentrations of phosphorus, organic acids (such as citrate and malate) that are able to provide a source of phosphate in insoluble forms (Dakora & Phillips 2002). The quantity and composition of exudates from roots vary from one vegetable species to the other and are influenced by the nutrient status, the developmental stage, and the environmental conditions.

The movement of carbon from roots to rhizosphere boosts the growth and activity of microbes, which stimulates enzymatic processes that lead to the mineralization of nutrients. The transformation of organic nutrients into inorganic forms that plants can utilize is known to be facilitated by dehydrogenases, ureases, and phosphatases, among others. In vegetable systems, especially those that incorporate large amounts of organic matter from compost/manure, these processes of enzymatic activity become important in the cycling of Nitrogen and Phosphorus. Increased activity of microbes in the rhizosphere, therefore, can enhance the availability of nutrients, as well as the competition between plants and microbes for the nutrients (Richardson et al. 2009).

The modification of rhizosphere pH is yet another impactful mechanism that controls nutrient availability and distribution. The rhizosphere can become more acidic as a result of proton extrusion from the uptake of ammonium, and this can result in the increased availability of soluble phosphorus and other micronutrients. The uptake of nitrate can result in increases of alkaline pH, thus, in calcareous soils, can reduce the availability of phosphorus. Vegetable crops differ in their ability to alter rhizosphere pH, which can affect how fertilizers and nutrients are applied (Hinsinger et al. 2009).

The soil's nutrient distribution heterogeneity oversees the processes occurring in the rhizosphere. Roots respond to localized nutrient distribution by increasing the number of lateral roots and increasing root exudate production in those

nutrient-rich zones to improve the capture of those nutrients. Such plastic response to the environment is particularly important in vegetable production systems that employ fertigation as it offers nutrient vertical gradients along the soil profile in the root zone. The capacity of roots to utilize these vertical gradients is influenced by rhizosphere flow as well as root system architecture.

Different soil moisture and texture combine to modulate rhizosphere activities. Sufficient soil moisture supports diffusion of nutrients towards the roots and also facilitates the activities of microbes. However, waterlogging creates anaerobic conditions that can alter the transformation of nutrients such as denitrification, and anaerobic transformation of iron and manganese. On the contrary, dry conditions limit the activities of microbes, the diffusion of nutrients, and, subsequently, the uptake of these nutrients, even when they are present in the soil in adequate amounts (Nannipieri et al. 2012).

The use of organic amendments such as farmyard manure, compost, and crop residues in vegetable cultivation systems positively influence the soil environment around the plant roots (rhizosphere) by providing essential carbon substrates for microbial proliferation as well as improving the structural and hydrological properties of the soil. Such amendments stimulate increases in microbial biomass and enzyme production, which accelerate the mineralization of soil nutrients and which improve the synchronicity between nutrient supply and plant demand. Mulching also positively influences the soil around the plant roots by improving soil temperature and moisture, which improves root growth and microbial activities. The overall effectiveness of the plant's ability to gather nutrients is determined by the interaction of root structure and the processes of the rhizosphere. Plants with root systems that are more developed than average stimulate the activities of a greater volume of soil than non developed root systems; the activities of fine roots and hairs stimulate microbially mediated nutrient exchange and colonization; thus in this regard, the rhizosphere is most optimally viewed as a functional component of a root system rather than a soil zone devoid of structure and function roots. Such an understanding enables the improvement of nutrient placement, irrigation systems, and organic manure strategies in the cultivation of vegetables.

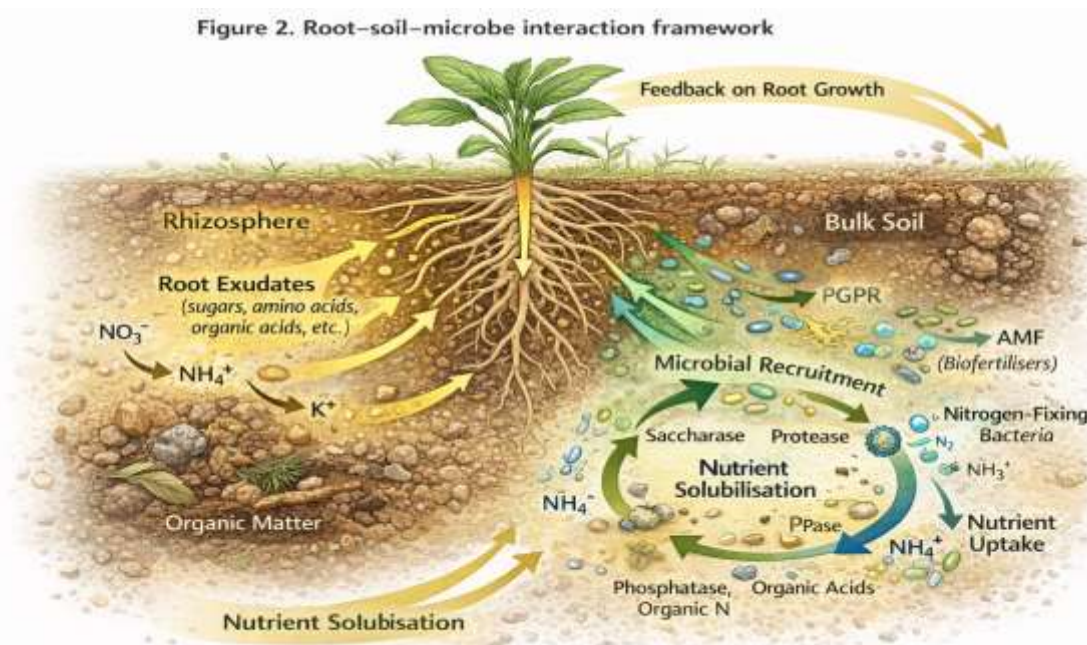


Figure 2. Root–soil–microbe interaction framework

A conceptual framework illustrating root exudation, microbial recruitment, enzymatic mineralisation, nutrient solubilisation, and feedback effects on root growth and nutrient uptake. (Richardson et al. (2009))

5. Root–Microbe Interactions and Biofertiliser Efficiency

Microbe-root relationships are vital to plants' overall health and systems. They are situated in the rhizosphere and interact with the roots of vegetables and other plants to help advance or in some cases hinder plants through positive or negative relationships. Beneficial microorganisms improve the health of plants by reducing stresses given to plants and by encouraging the growth of roots. Because of the aforementioned factors, it contributes to plant nutrient use efficiency and overall plant productivity.

Vegetable systems primarily utilize and study plant growth-promoting rhizobacteria (PGPR). These bacteria help plant growth by enhancing the processes responsible for nutrient acquisition. These processes include biological nitrogen fixation, phosphate solubilisation, and potassium mobilisation. Within these factors, phytohormone production occurs. Examples of plant growth promoting rhizobacteria (PGPR) are auxins, and cytokinins. The production of indole-3-acetic acid (IAA) of some PGPR stimulates the growth of lateral roots (hairs) which are responsible for the absorption of nutrients (Lugtenberg & Kamilova 2009). Furthermore, some PGPR secrete siderophores that, in addition to promoting plant growth, increase nutrient availability to the plants and control the growth of iron-reducing pathogens.

Arbuscular mycorrhizal fungi (AMF) associate symbiotically with the roots of most vegetables, expanding the effective root system via hyphal networks that reach greater soil volumes than the root depletion zone. These networks help in the uptake of less mobile nutrients, particularly phosphorous and zinc. Mycorrhizal colonization also facilitates the uptake of water and enhances the ability of plants to tolerate drought and saline conditions, which are typical in vegetable production (Smith & Read 2008). Level of dependency on mycorrhizae differs among vegetable species which include some crops where responses to low phosphorous conditions were significant.

Biological nitrogen fixation is a significant process that occurs in legume vegetables such as peas and beans, where symbiotic associations with Rhizobium species provide a significant proportion of the nitrogen the plant requires. This process lessens the necessity of using synthetic nitrogen fertilizers and increases soil fertility for subsequent crops. In the case of non-legume vegetables, associative nitrogen-fixing bacteria are able to provide small, but important, quantities of nitrogen, particularly in low-input systems (Giller 2001).

Phosphate-solubilising microorganisms, such as Bacillus, Pseudomonas, and Aspergillus, improve phosphorus accessibility through the secretion of organic acids and phosphatases that transform phosphate to orthophosphate (plant-available phosphorus). The soil type, organic matter of the soil, and association with the host plant can enhance or limit the effectiveness of the microorganisms. In vegetable systems that exhibit significant phosphorus fixation, the introduction of phosphate-solubilising biofertilisers can enhance phosphorus use efficiency and optimise the fertiliser requirement. (Richardson et al. 2009).

Root exudates provide primary compounds that influence beneficial microbial interactions, and act as selective signals to guide the recruitment of specific microorganisms. The vegetable species exhibits unique root exudates that shapes different compositions of rhizosphere microbial communities. Therefore, this trait can be used to breed crops that have improved ability to recruit beneficial microorganisms. The performance of microbial inoculants in the field can be influenced by native microbial populations, environmental factors, and increasing plant growth, which leads to the rapid recruitment of the exudate microbial population.

Combining biofertilisers with conventional fertiliser use provides improved nutrient use efficiency in vegetable crops. The joint application of plant growth-promoting rhizobacteria (PGPR) and fertiliser reduction improves crop yields and helps to reduce the environmental impact of production. Mycorrhizal inoculation also improves early root growth and nutrient uptake, particularly in phosphorus-deficient soils, when carried out in the nursery or at the time of transplantation.

The uptake of biofertilisers in vegetable cultivation is inevitably constrained by inconsistent efficacy, absence of formulations tailored to specific crops, and an underdeveloped comprehension of soil–plant–microbe interactions. It is recommended that future research concentrates on compatible microbial consortia, advanced carrier and application method technologies, and the combination of microbial inoculants with precision fertiliser technologies.

Microbial group	Representative genera	Target nutrient process	Mechanism of action	Vegetable crop response	Nutrient use efficiency outcome	Reference
Plant growth-promoting rhizobacteria (PGPR)	Azospirillum, Pseudomonas, Bacillus	Nitrogen uptake, phosphorus solubilisation, potassium mobilisation	Biological N fixation (associative), organic acid production, phytohormone synthesis, siderophore release	Enhanced root length, lateral branching, and root hair development; improved vegetative growth	Higher nutrient recovery, reduced fertiliser requirement, improved yield stability	Vessey (2003); Richardson et al. (2009)
Arbuscular mycorrhizal fungi (AMF)	Glomus, Rhizophagus, Funneliformis	Phosphorus and micronutrient uptake	Hyphal extension beyond depletion zone, increased absorptive surface area, improved water uptake	Increased biomass, improved nutrient status, greater tolerance to drought and salinity	Enhanced P use efficiency, improved water–nutrient coupling, reduced P fertiliser demand	Smith & Read (2008); Smith & Smith (2011)
Rhizobium symbiosis (legume vegetables)	Rhizobium, Bradyrhizobium	Biological nitrogen fixation	Nodule formation and conversion of atmospheric N ₂ into plant-available forms	Improved growth and protein content in pea, bean and other legumes	Substitution of synthetic N fertiliser, improved system NUE and soil N balance	Graham & Vance (2003)

Phosphate-solubilising microorganisms	Bacillus, Pseudomonas, Aspergillus, Penicillium	Phosphorus availability	Secretion of organic acids and phosphatases that convert insoluble phosphates into orthophosphate	Improved root growth and P uptake, especially in low-P soils	Increased P recovery from native and applied sources, reduced P fixation losses	Richardson et al. (2009)
Potassium-mobilising bacteria	Bacillus, Frateuria	Potassium release from mineral forms	Production of organic acids and chelating compounds that weather K-bearing minerals	Improved K uptake, better osmotic regulation and stress tolerance	Enhanced K use efficiency, improved fruit quality and stress resilience	Basak & Biswas (2010)

Table 2. Microbial inoculants and their effects on nutrient use efficiency

Certain types of bacteria, known as plant growth-promoting rhizobacteria, can promote greater uptake of nutrients by fixing nitrogen, solubilising phosphate, mobilising potassium, and producing phytohormones that promote greater root growth and nutrient uptake. Additionally, arbuscular mycorrhizal fungi can improve the phosphorus and some micro nutrient uptake and water assimilation by extending the functional root system through hyphal networks. The symbiosis of Rhizobium in legume vegetables provide biologically fixed nitrogen and contribute to the fertility of the soil. In addition, some soil phosphate-solubilising bacteria and fungi can enhance availability of the otherwise insoluble phosphorus by producing organic acids and then enzyme in that process. When these microbial inoculants are integrated with lesser quantities of fertilisers, nutrient use efficiency and crop productivity can be enhanced.

6. Environmental and Agronomic Factors Influencing RSA and Rhizosphere Functioning

Environmental factors and agricultural management approaches highly influence the root system architecture and rhizosphere activities of vegetable crops. Most vegetable species have relatively shallow and flexible root systems. As a result, they frequently respond to alterations in soil physical characteristics, moisture distribution, nutrient distribution, and organic matter inputs. Such alterations influence root systems morphology and distribution, and the activities of the soil microorganisms, and the soil nutrients in the rhizosphere.

Root penetration and branching patterns are determined by soil texture and structure. In coarse-textured soil, there is a lower mechanical resistance to root penetration which allows deeper root penetration. However, this condition often leads to poor water and nutrient retention, which in turn decreases the root length density in the topsoil. In fine-textured soils, particularly those that are clay rich, root elongation is restricted by high bulk density. As a result of poor aeration, root concentration occurs near the soil surface. Soil compaction is a common phenomenon in intensively cultivated vegetable fields. It increases mechanical resistance and further limits root growth. Layers of soil that are compacted limit the development of deep roots and is associated with low diffusion of oxygen, reduced activity of soil microorganisms, and low nutrient uptake which poor functioning of the rhizosphere (Bengough et al. 2011).

The moisture level of soil significantly influences the growth of roots and the diffusion of nutrients. Sufficient moisture improves the movement of nutrients to the root surface and enhances the activity of microorganisms important for the nutrient-adding process. During drought, limited nutrients, and microbial activity, as well as a decrease in the elongation of roots, results in less nutrient acquisition, even if soil nutrients (fertilizers) are high. For soil moisture, sufficient roots and nutrients levels are important for microbial activity. Furthermore, excessive moisture and waterlogging lead to anaerobic (without oxygen) root conditions. The microbial community changes, and continued activity of certain microorganisms (denitrifying microorganisms) reduces nitrogen (Nannipieri et al. 2012). The moisture sensitivity of vegetable crops highlights the need for coordinated irrigation as roots develop and as nutrients are drawn.

Fertiliser placement, coupled with irrigation practice, impacts the moisture and the root zone distribution. With regard to drip irrigation, commonly used in vegetables, the moist zone results in localized zone root concentration along the emitter(s) at high root density. This set-up increases the efficiency with which nutrients are absorbed when fertiliser is also applied through the irrigation system (i.e., fertigation). However, the moisture and root zone outside the wetted area may be missed. On the other hand, with furrow or sprinkler irrigation, soil moisture is distributed uniformly resulting in root and moisture zones being uniformly distributed which may also be timed with root moisture zones resulting in increased leaching (particularly nitrate) outside the zones. Therefore, to enhance nutrient absorption, it is important to synchronize irrigation with the root distribution and fertiliser placement.

The practices used to manage nutrients impact the way roots develop and how the rhizosphere becomes active. For example, high levels of nitrogen that is easy to access often result in decreased root elongation and, consequently, decreased root-to-shoot ratios. This results in a decreased ave. dependence on the soil for exploration and an increased dependence on a continuous supply of fertilizer. However, a moderate level of nutrient, especially initiates root development and increases the number of root hairs, which improves soil nutrient capture. Root proliferation in a fertilized zone is increased with banded phosphorus application, while lower root density and soil nutrient capture are associated with less localized root proliferation from phosphorus in the zone (Lynch 2019). This illustrates the necessity of matching fertilizer application and root development.

Roots and rhizosphere function are also affected in many ways by organic amendments like green manure, composts, and manures. These materials also make the soil less dense and increase the soil's ability to hold and retain water, which encourages the development of roots that go deeper and have greater density. Adding natural organic materials in the soil also increases the number of microorganisms and the enzymes they produce. This leads to more nitrogen and phosphorus to be available and improves the alignment of nutrients to the needs of the plant (Richardson et al. 2009). In vegetable systems, organic inputs are used consistently, and in these systems the soil health and nutrient use efficiency are increased by these influences.

Soil temperature variability and soil moisture are two factors that can be manipulated through mulch application. Modified soil temperature and moisture can have an effect on root and microbial growth. Part of the mulch soil temperature and moisture modification is dependent on the mulch material used to cover the soil. Root growth can be increased with the use of plastic mulch compared to organic mulch. Root growth with organic mulch will be slower because it promotes more microbial growth and thus more root growth is not as needed. All of these factors affect nutrient availability in the soil and root uptake.

Protected cultivation such as polyhouses and greenhouses offer different soil conditions compared to open field conditions. These soil conditions can be further altered with the use of irrigation and nutrient injections. These methods have the potential to increase root growth limiting soil conditions. In the case of soilless systems, the soil volume that the roots can expand into can be very slight and cause nutrient conditions to be unbalanced. In the case of modified soil conditions, the roots and the soil can be influenced in a number of ways specific to the nutrient solution.

How environmental elements combine with particular root characteristics will determine the efficiency of nutrient-acquisition. Management strategies that encourage root growth and increase activity within the rhizosphere, which leads to enhanced uptake of nutrients, are those that improve the structure of soil, are able to hold water/moisture at the “just right” level, and are able to supply nutrients at the “just right” level. On the other hand, strategies that cause soil compaction, supra-optimal nutrient supply, and water stress will, at best, reduce the growth of roots and at worst, reduce the functional ability of the rhizosphere. The knowledge of the interaction of these components must be incorporated into the production systems of vegetables to achieve sustainability in nutrient management.

7. Root Traits for Improving Nutrient Use Efficiency

In order to improve nutrient use efficiency in vegetable crops, it is necessary to improve root traits that allow for a greater range of nutrient acquisition in varying soil and management situations. These traits include increased root length and depth, lateral branching, increased root hairs, and greater root plasticity to tackle varying soil nutrient conditions. An important feature of root length that has a significant impact on nutrient uptake is root-soil contact. Operatively, root length is a dominant factor in determining contact with, and therefore uptake of, phosphorus within soil. Therefore, vegetable crops that contain a high root length density in an upper soil horizon are more suited to low phosphorus soil situations, particularly in cases where there is a high root density surface level phosphorus fertilizer application. Nonetheless, a high root length density may reduce the potential for above surface vegetative growth. Therefore root growth must be carefully balanced with shoot growth. Rooting depth is another critical trait, especially in relation to the capture of nitrogen. Nitrates are very mobile in soils and can leach below the topsoil. Vegetable crops that have deeper roots can intercept nitrate in the subsoil, decreasing nutrient loss and increasing the efficiency of nitrogen use. Additionally, deeper roots provide access to moisture, which may enhance nutrient supply and the joint uptake of water and nutrients during dry periods. Therefore, selection for deeper roots in fruiting vegetables with longer growing periods can be an effective way to improve nutrient efficiency. The role of lateral roots is important in the exploration of soil micro-sites, which enhances the ability of the plant to tap into localized nutrient ‘pockets’. When lateral roots proliferate into nutrient-rich areas, nutrient uptake is achieved with less investment in the elongation of primary roots. This response is particularly advantageous in fertigation where nutrients are provided in discrete concentrations. Since primary root branching is driven both by hormonal cues and nutrient status, there is scope for tailoring genetic improvements in this area.

Root hairs are involved in phosphorus acquisition through increasing root surface area and contact with soil. Phosphorus-deficient plants that increased root hair length and density were better phosphorus-uptake plants and improved in growth. In low-input vegetable crop systems, selection for positive root hair traits has been suggested as a cost-effective way to enhance phosphorus use efficiency (Shen et al. 2011). Root hairs are also a component in the formation of rhizosheaths, which help stabilise soil aggregates and encourage growth of soil microbes. A root's ability to sense and respond to its environment is given as architectural plasticity, and is a fundamental characteristic for nutrient foraging in heterogeneous systems. Located root proliferation, altered root growth angle or increased root growth in a nutrient rich zone are all examples of plasticity that help a plant optimise nutrient acquisition. Vegetable species with high plasticity/architectural plasticity adapt to dynamic and heterogeneous nutrient availability better and are more efficient with low fertiliser inputs. Newer methods for root trait phenotyping, such as high-throughput root imaging, rhizotrons, and root molecular markers, have made it easier to measure root traits and correlate them with root absorption and overall plant productivity. These advancements have also made it easier to establish molecular markers associated with root phenotypes and nutrient absorption efficiency, which are critical for developing nutrient-efficient cultivars. Root trait integration into breeding programs has historically been associated with the limited and difficult measurement of roots in situ, but recent advancements are alleviating these obstacles. Root trait management through novel management practices such as controlled nutrient supply, strategic placement of fertilizers, and the addition of organic matter have proven to increase root growth and ultimately improve nutrient utilization efficiency (NUE). Increased early root growth is critical in short cycle vegetable crops as it allows for adequate nutrient capture in certain growth matrices of the plant.

Figure 3. Root ideotype for high nutrient use efficiency (NUE)

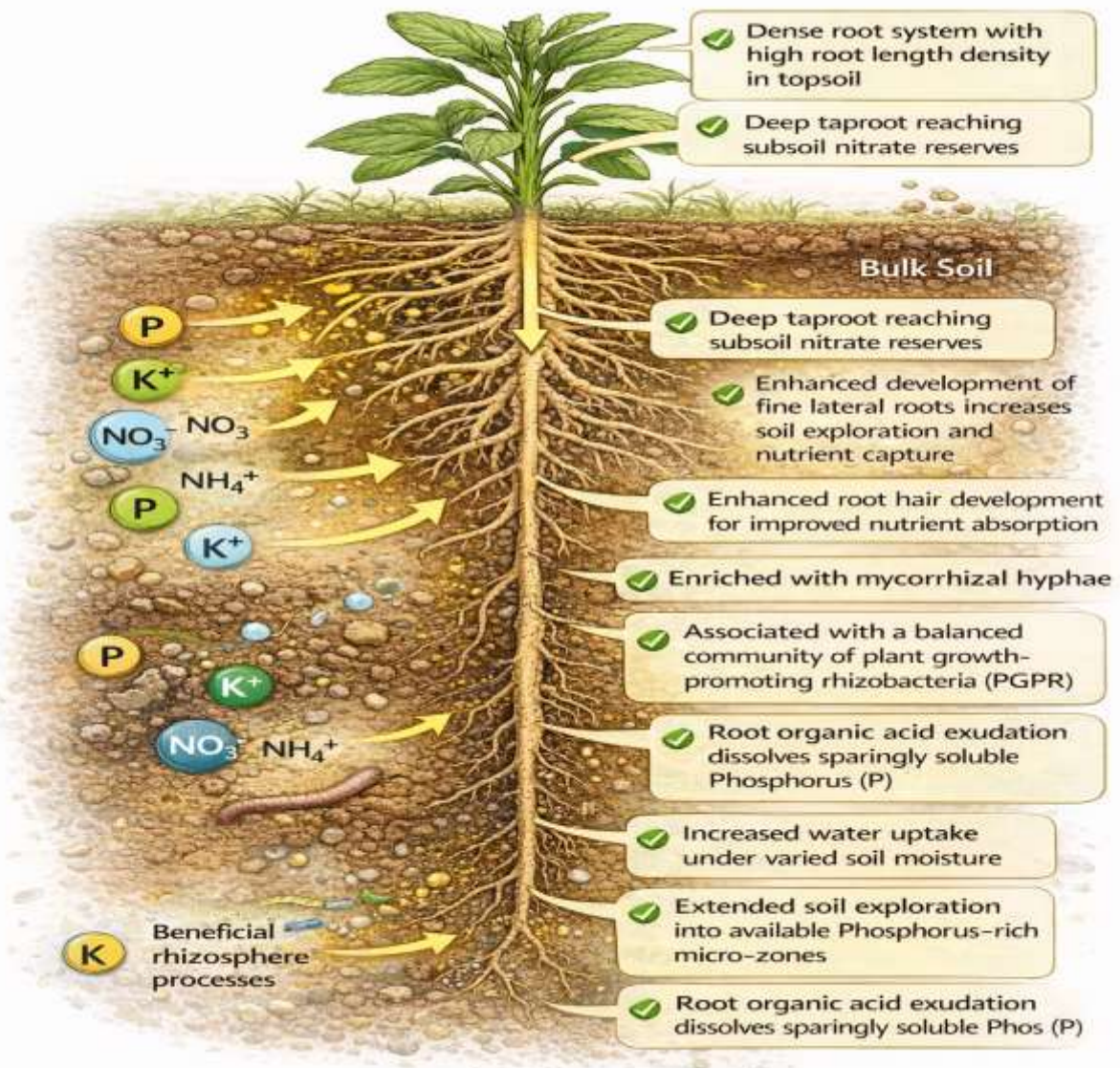


Figure 3. High-NUE root ideotype for vegetable crops

An idealized design should capture nitrate with a moderately deep primary root, capture phosphorus with a high root length density within the topsoil, and include abundant laterals for the exploration of nutrient heterogeneity, enhanced root hairs for increased absorptive surface area, and improved associations with beneficial microorganisms in the rhizosphere for improved nutrient uptake, reduced fertiliser retention, and increased productivity across a broad range of management practices. (Lynch (2019))

8. Implications for Productivity and Nutrient Use Efficiency

The functionality of the rhizosphere and architecture of the root system directly influence the productivity of vegetable crops. This is due to the fact that the acquisition of nutrients is directly correlated to the accumulation of biomass, formation of the yield, and the quality traits. In intensive vegetable cropping systems, shortened crop cycles and high nutrient-demanding crops rely on the coordination of root system development and nutrient availability to optimize the conversion of applied fertilisers to sellable yield. Improved photosynthetic capacity, enhanced rapid canopy expansion, and increased nutrient acquisition that sustains these traits, is the result of improved retention of nutrients and root systems, among other factors.

The depth of roots and the timing of root growth are critical determinants of nitrogen use efficiency. Improved retention of nitrates that are prone to leach and increased nitrogen uptake are hallmarks of vegetable crops with deeper and persistent roots. Increased nitrogen uptake has positive influence on the development of leaf area and on the chlorophyll content which facilitates increased photosynthetic activity and biomass accumulation (Xu et al. 2012). Increased uptake of nitrogen also has an impact on the quality of the produce as it reduces the vegetative growth and the accumulation of excess nitrates in the edible parts, which is particularly important in leafy vegetables.

The efficiency of phosphorus (P) in utilization is directly linked to the topsoil root length density, root hair formation, and modification of the rhizosphere. Due to the limited mobility of phosphorus, the greater the soil-dense fine root and root hair networks, the more soil phosphorus is obtained. Greater soil P accessibility furthers energy transfer, root proliferation, and development of the generative plant parts, thus increasing the yield and improving the fruit set of vegetable crops

(Shen et al. 2011). In phosphorus (P) deficient soils, the ability of roots to acidify the rhizosphere is of great significance in the unblocking of P and sustaining productivity.

Potassium (K) plays a key role in controlling osmotic regulation, enzyme activation, and stomatal behavior, and the efficient uptake of K is linked to improved water use efficiency and stress tolerance. Under adequate K nutritional status, the translocation of photosynthates from leaves to developing fruits and to the storage organs is enhanced, thus improving the yield and quality of fruit and root vegetables. Crops with root systems that can sustain K uptake even with alternating soil moisture levels are more suited to intensified production systems with alternate irrigation cycles.

The rhizosphere's microbial community and roots' interaction affects the efficiency and productivity of nutrient utilization. As noted by Vessey in 2003, Beneficial microorganism promotes root growth, and improve plant tolerance to abiotic stresses. This leads to an increase in recovery of nutrients and stability of yields. Mycorrhizal associations improve the acquisition of phosphorous and extend the effective root system. Additionally, plant growth-promoting rhizobacteria, improve the absorption of nitrogen and root and subsequently promote the development of hormones. All of these interactions contribute to a system that is more sustainable and reduces reliance on synthetic fertilizers.

Improvement of root and rhizosphere conditions increases the efficiency of nutrient utilization in vegetable production. For example, band placements of phosphorous organic fertilizers close to the root zone increases the local root proliferation and the absorption of phosphorus. With respect to root development and the subsequent acquisition of nutrients, the moderate soil temperature and moisture with mulching and conservation tillage. Enhanced microbial activity leads to improved nutrient mineralization and root development. Additionally, the use of soil organic amendments that improve the structure and microbial activity of the soil enhance root development.

The economic and environmental impacts of improved efficiency of nutrient use are considerable. Efficient use of nutrients and reduction of fertilizer use as an input in production and as a cost of the production process reduces nutrient losses to the environment, which decreases the potential for contamination of ground water and the potential for increased greenhouse gas emissions. Improved recovery of nutrients can enhance the sustainability of vegetable production systems by better sustaining soil fertility and lowering the need for external inputs. From an economic standpoint, enhancing the optimal expression of certain root traits and processes in the rhizosphere allows the crop to maximize productivity at lower levels of nutrient inputs.

The dynamics of nutrient uptake can also affect vegetable quality traits, including nutrient levels, shelf life, and sensory attributes. An effective root system allows for better acquisition of nutrients and, hence, better concentration of vitamins, minerals, and other bioactive compounds. On the other hand, poor root uptake in combination with excessive fertilization may cause nutrient imbalances and lower the quality and increase the postharvest losses of vegetables. Therefore, the use of root-based strategies in conjunction with improved nutrient management can impact the quality of vegetable production in addition to enhancing yield.

9. Research Gaps and Future Directions

While the significance of root system architecture and rhizosphere activity in vegetable crops is gaining attention in recent years, their integration into breeding and management strategies is hampered by a number of knowledge gaps. One of these include the lack of root phenotyping data for a majority of vegetable species. For cereals, there are root trait databases that provide root length density, rooting depth, branching, and root hair data. On the contrary, for vegetables, this information is usually incomplete, and for the most part, available data comes from controlled settings. The absence of data from field environments leads to the limited understanding of root traits that promote better nutrient use efficiency.

The understanding of the genetic basis of root traits in vegetable crops is also very limited. Whilst in some model species' root architecture, molecular markers and quantitative trait loci have been established, this is not the case for the majority of vegetable species, particularly in the breeding process. The genetic control of root system development and its interactions with the environment will help in designing breeding strategies for developing root improved cultivars. Recently developed methods in genomics, transcriptomics, and phenomics can be used to identify genes and networks that regulate root development and nutrient absorption.

The relationship between root system architecture and the microbes in the soil needs more research. While the positive effects of some plant growth-promoting root bacteria and mycorrhizal fungi have been documented, their impacts in field studies are often unreliable. Soil type, existing microbes, and management practices can either support or hinder the introduced microorganisms. The literature offers little information regarding specific combinations of microbes and plants, and more research is needed regarding specific consortia of microbes introduced to support individual crops.

Nutrient management practices in vegetable farming are primarily reliant on factors visible above the soil. The integration of root architecture into management practices can allow for the more accurate placement and timing of nutrient inputs, enhancing the synchrony of nutrient supply and plant demand. The development of decision support systems that model root growth, soil nutrient levels, and the surrounding environment will support more efficient nutrient management. Root systems and the surrounding soil ecosystems in vegetable systems will likely face new challenges as the climate changes. Changes in temperature, the frequency and intensity of drought versus flooding, and the timing and amounts of precipitation are all likely to impact root growth, the activity of microbes, and the cycling of nutrients in soil. Understanding how specific root characteristics can enhance the system's resilience to these changes is necessary to design adaptive systems for producing vegetables under climate change.

Recently emerging technologies such as non-invasive root imaging, stable isotope tracing, and high throughput phenotyping allow for new possibilities to study root functions in situ. These technologies can help describe root uptake, root turnover, and process within the rhizosphere at field scale. These technologies integrated within modeling frameworks can describe nutrient acquisition under varying management practices.

Future works must also consider the construction of root ideotypes for particular vegetable crops and their production systems. These ideotypes would incorporate architectural features that favour root foraging, i.e. lateral root branching, with physiological attributes that improve nutrient uptake and assimilation. The incorporation of such traits in breeding, alongside enhanced practices in agronomy and microbial stewardship, is crucial for the sustainable intensification of vegetable production.

10. CONCLUSIONS

In vegetable cropping systems, root system architecture and rhizosphere dynamics are key elements for understanding nutrient acquisition, productivity, and systems sustainability. Root systems, and their configurations, determine potential soil volume explored. Physiological processes are responsible for the uptake and translocation of the macronutrients (N, P, K) while interactions with microorganisms in the rhizosphere enhance the availability of nutrients and the overall performance of the plant. The aforementioned factors determine the efficiency (NUE) and effectiveness of applied fertilizers.

There is substantial heterogeneity in root systems of vegetable crops, which is in part a product of differing growth habit and management practices. Leafy vegetables have shallow and dense root systems, as opposed to fruit and storage root crops, which have deeper root systems that are more specialized to store nutrients during extended growth cycles. These varying root architectures inform the design of fertiliser strategies and irrigation practices that are tailored to the root system and the stage of growth of the vegetable crop.

Root systems and rhizosphere processes are shaped by a combination of environmental factors and agronomic practices. The responses of root systems to soil structure, soil moisture, and the placement of nutrients, particularly in combination with organic materials, are critical to the ability of root systems to proliferate and aid in nutrient uptake. Nutrient dependent management practices that improve the health of soil and enhance the supply of nutrients may, in turn, foster root and microbial growth, improving NUE.

Identifying and using specific traits of roots that are responsible for proficient nutrient acquisition can yield improved productivity and decreased dependence on fertilizer. Efficient nutrient uptake and yield stability are aided by increased rooting for nitrate, improved root hair development, and beneficial root-symbiotic microorganism associations. Breeding and management of these traits will help achieve more sustainable vegetable production.

The combination of root data that is mostly absent from the field, the incomplete knowledge of the genetics behind root traits and the inconsistency of results from microbial inoculants continues to be a challenge. This type of research would cross root biology, soil science, microbiology and agronomy. The development of methods to quantify root function and create crop-specific root ideotypes will be aided by advancements in phenotyping and molecular biology.

The overall improvement of nutrient use efficiency, environmental impact, and the yield/quality of vegetable crops will be achieved by shifting the attention to root strategies and away from input nutrient management. To achieve sustainable efficiency in vegetable production, root systems and rhizosphere mechanics must be considered in research, breeding, agronomy, and root system engineering.

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