

REVIEW ARTICLE

Root traits for Nutrient and Water Acquisition in the Quest for a Second Green Revolution: Exploring prospects and Assessing Limitations

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ABSTRACT

More than 200 years ago, Thomas Malthus predicted that a growing population of mankind would eventually be severely affected due to resource limitations. Today, the world faces challenges in providing food security for a growing population, despite efforts like the Green Revolution in the last century. While the Green Revolution focused on improving shoot biomass and seed yield, it failed to recognize the vital role played by the root system in nutrient and water uptake, anchorage, and interaction with symbiotic organisms. Recent research has highlighted the significance of root architecture and development in optimizing plant growth and crop yield. Changes in root structure and function can have a profound impact on plant productivity. Recognizing the importance of the "hidden half" of plants, current scientific discussions emphasize the need for a second Green Revolution that considers root system development and its potential for increasing crop yield. By integrating research on root architecture, nutrient uptake, and symbiotic relationships, it becomes possible to design crops that can better adapt to unfavorable conditions and optimize resource utilization. Moving forward, future agricultural innovations should not overlook the crucial role of the root system in plant growth and yield enhancement. By exploring strategies to improve root architecture, nutrient uptake efficiency, and stress tolerance, we can unlock the untapped potential of the root system and contribute to a more sustainable and productive agricultural system. A holistic approach that considers both the aboveground and belowground parts of plants is necessary to achieve optimal crop yields and ensure food security for a growing global population.

Key words: Population growth, green revolution, second green revolution, root system architecture, sustainable.

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INTRODUCTION

In 1798, Thomas Robert Malthus made a prediction that a continuously growing global population would inevitably encounter famine, disease, and widespread mortality [1]. Fast forward two centuries, and the world is currently grappling with the challenge of providing food security for an ever-expanding population, all while agricultural land continues to diminish [2]. The International Food Policy Research Institute's 2020 Vision Initiative was established with the objective of achieving sustainable food security worldwide by the year 2020 and reducing the number of chronically undernourished individuals on the planet by 50% by 2015 [2]. Regrettably, these ambitious goals have not been accomplished, emphasizing the urgent need for a solution to this escalating predicament. By the mid-20th century, food security in developing nations was under threat due to the inability of food production to keep up with population growth. Cereals, such as rice and wheat, had limited responsiveness to fertilizers and would easily collapse under high fertility conditions. To address this challenge, Norman Borlaug and his team [3], developed dwarf varieties of rice and wheat that could effectively respond to fertilizers without lodging. This breakthrough, known as the 'Green Revolution,' significantly increased grain production and prevented a potential disaster. This approach in the mid-20th century managed food production to keep pace with worldwide population growth [4] and is widely regarded as one of the most crucial agricultural innovations of the 20th century, saving countless lives, and ensuring food availability for millions. The Green Revolution was a series of initiatives and technological innovations aimed at increasing agricultural

productivity, which was primarily needed in the developing countries. Its main approach consisted of three key elements:

- improved seeds,
- synthetic fertilizers, and
- irrigation

Improved seeds, known as high-yielding varieties, replaced traditional crop varieties and offered resistance to diseases, pests, and adverse weather conditions. HYVs significantly increased crop yields and addressed the growing food demand. Synthetic fertilizers, containing nitrogen, phosphorus, and potassium, were used to enhance soil fertility and provide essential nutrients. Their application, combined with improved seeds, led to a substantial boost in crop productivity, although excessive use caused environmental challenges. Irrigation played a crucial role by providing water to crops in areas with inadequate rainfall. This enabled year-round cultivation, multiple cropping seasons, and higher agricultural productivity. However, irrigation projects also had environmental impacts, including water scarcity and community displacement. The Green Revolution focused on intensification, maximizing yields per unit of land rather than expanding agricultural areas. Despite the significant increase in grain production brought about by the Green Revolution through the use of fertilizers and improved cereal varieties, many of the world's neediest individuals were unable to benefit from these advancements due to various factors such as poverty, limited access to resources, credit, and markets, and the predominant reliance on crops other than wheat and rice in many developing agroecosystems. Statistics indicate that approximately 854 million people still suffer from malnutrition, and more than half of all childhood deaths in developing regions can be directly or indirectly attributed to malnutrition [5]. Cereal grains, including rice, wheat, maize, barley, sorghum, and millet, are vital staple food crops that sustain billions of people, accounting for over 50% of the global caloric intake derived from cereal consumption [6]. However, there is a substantial yield deficit for rice, wheat, and maize, estimated to range from 30% to 60% in several regions due to water and nutrient scarcity [7]. Moreover, projections indicate that cereal demand needs to increase by 60% to ensure food security by 2050 [8]. Various limitations further exacerbate the situation, such as edaphic constraints characterized by low phosphorus availability and soil acidity in large areas of the developing world, as well as extensive degradation of agricultural land (~40%) caused by human activities. Climate change poses additional challenges to plant growth and habitat, including water scarcity, soil degradation, soil pests, increasing salinity of groundwater, and the rising demand for biofuels, all of which must be addressed to achieve improved yields. According to [9,10] stress that in the past, crop improvement and agricultural techniques primarily focused on enhancing shoot biomass and seed yield. However, the classical approach of relying on increased water, fertilizers, and pesticides to boost yield has reached its maximum potential. Further attempts to increase yield through excessive use of these inputs will result in public health and environmental problems, ultimately undermining productivity [11]. Consequently, alternative solutions are necessary to address this persistent issue. Integrated nutrient management, which entails the judicious use of fertility inputs, practices to preserve and enhance soil fertility, and the utilization of adapted germplasm capable of thriving in low-fertility soil, could serve as one of the potential solutions. One of the most direct contributions to food security would be improved food production in developing nations, benefiting subsistence farmers, reducing food costs for the poor, and boosting rural incomes. A variety of approaches have been tried and tested to increase/maintain the food grain production. In this reference, continuation of some of the traditional agricultural techniques such as legume crop rotations for alternative fertilization have contributed considerably to the improvement of soil quality [12]. Developing crops that can deal with unfavorable edaphic and climate conditions, with improved root architecture, nutrient uptake efficiency, nutrient storage, and root-to-shoot transport, along with strategies to prevent soil erosion and resist pathogens and harsh conditions such as salt and drought, requires well thought-through research. Integrated approaches are needed to identify central regulators of nodes where genetic, developmental, and physiological pathways interact. To address these issues, the scientific community is stressing the need of a second green revolution [13] which could concentrate on some of the approaches referred above along with many others. It should address the food crisis and improve food security, particularly in developing nations. Improving plant yield will also be essential for using plants as a renewable energy source, and achieving the ideal food-population balance. However, environmental stresses such as drought, high salinity, nutrient deficiency, and adverse temperatures significantly affect plant growth and productivity. Previous approaches have stressed on increasing the shoot biomass and yield of seeds, and almost ignored the contribution of the hidden half of the plants (i.e., the roots). Recently, however, research has stressed the fact that the root system development is crucial for optimal plant growth and contributes significantly to crop yield [14,15,16]. The root system plays a

vital role in nutrient and water uptake, anchorage in the substrate, and interaction with symbiotic organisms. The impact of the “hidden half” on plant growth has become increasingly apparent, not only in model plant *Arabidopsis thaliana* but also in crops such as wheat, rice, maize, and legumes [14,15,16]. Recent simulations suggest that changes in root architecture can strongly affect yield, which might explain the maize yield trends in the USA Corn Belt [17]. This indicates that root growth and development represent an underexplored area for strategies to enhance crop yield. According to [18] plant roots play a vital role in reducing yield gaps and are fundamental to the success of the second Green Revolution aimed at meeting the increasing global food demand. They act as conduits for resource uptake from the soil and are of great importance for enhancing crop productivity on nutrient-deficient soils [19]. Additionally, roots are crucial in establishing symbiotic relationships with microbial organisms, making them a significant target for the second Green Revolution and essential for the production of high-yielding food grains like wheat and rice [20]. Fundamental analyses in model plants, such as *Arabidopsis*, model legumes, and certain crop species, including maize, rice, and soybean, can aid in designing plants that fulfill the requirements to contribute to an improved and more efficient root system. It is possible to improve root architecture, surface and nutrient uptake, along with fixation to achieve the set goals. A variety of approaches could be explored for increasing the yield of the plants, by augmenting the contribution from physiological, morphological, and architectural components of the plants. In the present review, we discuss some of these approaches, and the related trade-offs.

Root traits of the plants

The interaction between a plant's original developmental blueprint and information perceived from the surrounding environment influences the development of post-embryonic parts in plants. This developmental plan is capable of being modified in response to internal and external conditions. When environmental information is integrated into the organism's developmental plan, resulting in phenotypic changes, it is known as developmental plasticity [21] which carries significant ecological significance. The growth of new plant parts, including the root system, is driven by the need for efficient tissue production. The overall arrangement of different root types, such as the primary root, lateral roots, and crown roots, is encompassed by root system architecture (RSA), a term used interchangeably with RSA [21]. Two common types of root system morphologies have been identified. Allorhizic root systems, observed in plants like *Arabidopsis*, consist of a primary root (tap root) as the dominant component, producing lateral roots (LRs) capable of further branching. Adventitious roots may also emerge from the stem or hypocotyl due to wounds or other factors [22]. In contrast, monocots exhibit a root system dominated by adventitious roots, particularly in crops like maize and rice. These roots can be categorized based on their origin from shoot parts, such as crown roots or brace roots [23]. In maize, embryogenic roots known as seminal roots can develop from the scutellar node, contributing to the formation of new lateral branches [24]. This secondary homorhizic root system is characterized by a reduced importance to the primary root during the early seedling phase, unlike the allorhizic system. However, seminal roots in plants like maize retain importance in water uptake throughout the plant's life cycle [25]. Root architecture plays a critical role in soil resource acquisition by determining the deployment of roots foraging in distinct soil domains and the extent of competition for soil resources among roots of the same or neighbouring plants [26]. The economic paradigm of plant resource allocation suggests that the metabolic investment in root growth and maintenance, measured in carbon units, can be a significant drain on reproductive output, especially in low-fertility environments [27,28]. Thus, selection of genotypes with abundant root production in the context of crop breeding may not necessarily be beneficial, which is one of the trade-off that needs to be considered seriously. Multiple studies have provided evidence that the metabolic expenses associated with soil exploration by root systems can surpass 50% of daily photosynthesis and are of significant magnitude [29,30]. Hence, characteristics that improve the efficacy or efficiency of roots in obtaining soil resources would serve as more suitable targets for selection compared to focusing solely on root size.

Resource foraging by roots

Recognition of the importance of root traits to increase food production and sustainability, are echoed with calls for a “Second Green Revolution” focused on roots [13]. The following part tries to highlight some of the challenges in developing fruitful strategies for enhanced resource acquisition in crops, with a focus on resource foraging, which is the process by which root system architecture (RSA) changes over time to acquire resources. While most studies on foraging in plants have focused on resource competition between wild species, using plants subjected to natural selection, not agricultural selection [31], they have been extremely useful to begin to identify the mechanisms and selective forces that shape adaptation and survival in natural environments [32,33]. A striking conclusion from these studies is the diversity of root behavior, including foraging, observed in different species, even in different accessions of

the same species, revealing its adaptive nature. Resource foraging is the process by which plants explore their environment to acquire resources that are differentially and non-uniformly distributed in space and time. Root behavior can be defined as the tropisms and growth activities that vary quantitatively over time, such as changes to growth rate, direction, and root density. While each of these parameters can impact foraging capacity, those that affect the behavior of lateral organs stand out because they define the capacity to exploit locally enriched resources. Resource perception likely occurs through processes localized in the root cap, which is involved in the perception and orchestration of responses to several environmental cues [34,35] and which is consistent with a requirement for pre-existing lateral root primordia (LRP) to be activated in the vicinity of resource patches, rather than de novo production of primordia. Recent research conducted on *Arabidopsis* has demonstrated that the detection of resources triggers the development of some lateral root primordia (LRP) as a response to environmental cues. However, there is an ongoing debate regarding whether plant roots actively search for resources, meaning they grow without prior knowledge of available resources, or if resource perception simply promotes growth behaviors that facilitate resource exploitation. The behavior of root growth exhibits significant variability (referred to as 'plasticity') regardless of the growth substrate. Numerous studies have highlighted substantial variations in the growth rates of individual lateral roots, even in seemingly "homogeneous" environments. Therefore, while progress has been made in comprehending the mechanisms involved in resource foraging, there are still challenges to overcome in devising effective strategies to enhance resource acquisition in crops [36,37]. To select for optimal nutrient and water uptake, the investigation of root system architecture (RSA) can be carried out using a combination of polygenic traits, including primary root length, total root length, root angle, root number, root thickness, root length density, root growth habit, and root surface area [38]. Currently, there remains a lack of comprehensive exploration into the phenotypic and genetic variations of root traits in cereal crops. It is crucial to acquire knowledge regarding the interactions between genes, hormones, signaling molecules, water, and nutrient availability in order to reshape RSA [39]. A deeper understanding of these interactions would enable the optimization of RSA for specific environmental conditions. Scientists have shown a growing interest in root system architecture (RSA) as a means to ensure future food security in the face of climate change. Among the environmental challenges affecting cereal growth and sustainable productivity, drought stands out as a major constraint [40]. Consequently, enhancing RSA to promote deeper root architecture, which facilitates nitrate capture and improves water-use efficiency, can enable plants to access water from greater soil depths and reduce the reliance on irrigation [17]. By modifying RSA in cereals, it becomes possible to enhance the plants' ability to efficiently acquire soil nutrients and water, ultimately leading to improved grain yield [41]. Additionally, such modifications can result in reduced dependence on applied fertilizer and irrigation. The manipulation of RSA traits is therefore crucial in increasing both grain yield and the plants' resilience to adverse growth conditions and climate extremes, thus playing a pivotal role in ensuring future food security [42,43].

Making use of plant hormones to modify RSA

There are different approaches to increase nutrient uptake. One approach is to directly interfere with auxin levels or auxin response mechanisms. This can modify the root architecture and enhance resource uptake. However, this approach has limitations in refining root growth. It often results in highly branched but superficial root systems. Simply increasing cell division does not guarantee more lateral roots or longer main roots. A better strategy involves a moderate increase in auxin levels and increased cell cycle activity, which could lead to more branching with only minor negative effects on main root growth. A fine-tuned control of cytokinin catabolism is another means to influence root branching and mass in both *Arabidopsis* and crops [44,45]. A balanced mixture of targeting several signaling pathways will be required to have an impact on all aspects of root growth and branching, from initiation to post-emergence growth [13,46,47].

Under limited nutrient availability

Low availability of nitrate and phosphorus is known to limit plant growth and productivity [48,49]. For example, under low phosphorus availability, plants may allocate resources to maintain root elongation at the expense of lateral branching and secondary growth [50,51]. In maize, smaller root diameter is associated with greater specific root length (SRL) of lateral roots, faster lateral-root growth, greater shoot growth, and phosphorus efficiency [49]. However, this strategy has some drawbacks, for instance, a smaller root diameter may also reduce the ability to penetrate hard soil and increase susceptibility to root herbivores and pathogens. A common response to suboptimal nutrient availability is an increase in the relative allocation of biomass to roots, typically resulting from a greater inhibition of shoot growth than root growth [52,53,54]. A portion of this apparent change is allometric, i.e. root: shoot ratios normally decline with growth, and since plants in infertile soils grow more slowly, their root: shoot ratios are

greater at a given plant age. However, when this factor is eliminated by comparison of allometric partitioning coefficients among plants grown at different phosphorus levels, phosphorus-efficient genotypes maintained a greater root: shoot ratio (greater allometric partitioning coefficient to roots), made possible by reduced respiratory costs of root growth [55]. Low phosphorus and nitrogen availabilities reduce leaf appearance, leaf expansion and shoot branching [53,56]. It has been reported that dicots exhibit a greater reduction in shoot growth compared to monocots when faced with phosphorus stress among annual plants. This difference in response may be attributed to difference in leaf morphology [57].

Although root growth has obvious importance for acquisition of soil resources, it is particularly important for the acquisition of immobile resources. Nutrients that are soluble in water are brought to the root primarily via transpiration-driven mass flow, whereas diffusion-limited nutrients, including phosphorus and potassium, must be acquired by roots (or root symbionts) in close proximity [58]. It is therefore not surprising that root growth is strongly regulated by phosphorus availability. Low phosphorus availability changes the distribution of growth among various root types. In bean, growth of primary- and basal-root axes is maintained under low phosphorus, whereas initiation of lateral roots is reduced, so that lateral-root density declines [51]. In phosphorus-starved maize, axile (seminal and nodal)-root elongation and lateral-root density were unaffected, but lateral-root elongation was first promoted slightly, then severely retarded, as phosphorus starvation proceeded [54]. Sustained elongation of axile roots in maize and bean could be interpreted as exploratory behavior, allowing these roots to encounter localized patches of higher phosphorus availability. When the main root of a phosphorus-deficient plant encounters a patch of higher nutrient availability, lateral roots may proliferate within the patch [59].

The response of the length and number of lateral roots to phosphorus stress varies substantially among maize genotypes, with some genotypes increasing and others decreasing lateral rooting [49]. Genotypes with increased or sustained lateral-root development under phosphorus deficiency had superior ability to acquire phosphorus and maintain growth. In bean, some genotypes respond to low phosphorus availability by preferentially increasing the production of adventitious roots, which have the advantages of low construction cost and location in the nutrient-rich topsoil [60].

Genetic differences in adaptation to low soil phosphorus availability among genotypes of maize and bean have been associated with the extent of topsoil foraging, which is an essential aspect of phosphorus acquisition in most soils [61,62]. Architectural traits linked to enhanced topsoil foraging include the following:

- shallower growth of basal roots,
- enhanced adventitious rooting, and
- greater dispersion of lateral roots.

Geometric modeling studies have shown that shallower root systems explored more soil per unit of root biomass than did deeper systems in soils with uniform phosphorus distribution [62]. Empirical studies with bean have demonstrated good correlation between basal-root growth angle and phosphorus uptake from low-phosphorus soil, yield in field trials in low-phosphorus tropical soils, and growth in a low-phosphorus field trial in Honduras [61,63]. Genetic mapping in bean has revealed co-segregation of quantitative trait loci (QTL) for root shallowness and phosphorus uptake in the field in Colombia [64]. In maize, genotypes with shallower seminal roots had superior growth in low-phosphorus soils in the field and greenhouse [65]. Adventitious rooting from subterranean hypocotyl or mesocotyl tissue is another element of topsoil exploration by the root system. Adventitious rooting may have several benefits for topsoil exploration, including greater specific root length and abundance of aerenchyma [66].

Exploiting root exudates

Root exudates receive considerable research attention since they are crucial for aluminum tolerance and phosphorus uptake from low-fertility soils, and unlike many other root traits, are under relatively simple genetic control. In the case of phosphatases, the trait is itself a gene product. The genetic simplicity of these traits is counteracted to some degree by the complexity of the fate of these compounds in the rhizosphere, particularly considering the microbial population of the rhizosphere and the significant variation in exudate production in different soils [67,68]. The increasing availability of sequence information for major genes controlling root exudates makes these traits attractive targets for genetic manipulation.

Carboxylate exudation plays an essential role in phosphorus solubilization in the rhizosphere.

Carboxylates chelate Al^{3+} , Fe^{3+} and Cu^{2+} , resulting in the mobilization of phosphate from bound forms and promoting anion exchange of phosphate from iron and aluminum oxide surfaces [69]. This activity is complemented in neutral and alkaline soils by rhizosphere acidification, which increases the solubility of

calcium phosphates [70]. The importance of carboxylate exudation for phosphorus mobilization in the rhizosphere has been extensively discussed [69,70].

Root exudates are also critical for the acquisition of micronutrient metals such as iron and zinc, which are poorly available in alkaline soils. Significant genetic variation exists for iron and zinc uptake from such soils [71], associated with metal mobilization in the rhizosphere via protons, phenolics, and organic acids in dicots and with phytosiderophores in cereals [72].

Since a considerable proportion of soil phosphorus may occur in organic forms, plants can increase phosphorus availability in the rhizosphere by secreting phosphohydrolases to mineralize phosphate from organic compounds [73]. Secreted acid phosphatases can be up-regulated under phosphorus deficiency [74]. Recent studies have demonstrated their significance for phosphorus nutrition under phosphorus-limiting conditions [74,75], although their importance seems to vary with species, cropping system, and forms of organic phosphorus in the soil [75,76].

Use of ion transporters

Ion transporters play a crucial role in the transport of ions and water across biological membranes and are mediated by proteins [77]. The manipulation of ion transporters has gained considerable attention due to modern techniques in molecular and cellular biology, and the potential for improving plant adaptation to soil constraints. Several research studies have been conducted on this topic, including those by [78,79,80,81].

Manipulation of ion transport properties can improve the acquisition of nutrients carried by mass flow of water to the root, including nitrate, calcium, and magnesium [58,82,83]. Increasing the copy number of nitrate transporters can enhance nitrate acquisition by changing the V_{max} of nitrate transport at the root surface [58]. Production of crop genotypes with increased nitrogen efficiency is of interest to the agricultural biotech industry as the cost of intensive crop production is related to the production and use of nitrogen fertilizers. Selection of crops with superior calcium and magnesium transport characteristics is useful in acid soils of the humid tropics, and ion transporters can also improve the acquisition of metals like iron, zinc, and manganese in low concentrations in certain soils [72,84]. Manipulation of ion transporters can also enhance crop tolerance to salinity by improving exclusion or compartmentalization of toxic ions [85].

The approach appears quite promising but nevertheless has some limitations. It is important to note that ion transport across membranes is not always the limiting factor in nutrient acquisition. Specifically, the uptake of nutrients such as ammonium, phosphate, and potassium, whose movement in the soil is usually restricted by diffusion, leads to the formation of depletion zones near the root. These zones result in reduced nutrient availability [58]. Mechanistic models predict that increasing the number of transporters or their substrate affinity should have little effect on net acquisition of these nutrients over time because the activity of the transporters is limited by the slow process of diffusion [58]. Besides, the activity of ion transporters may also be limited by the bioavailability of their substrate in the soil, especially for phosphate, which may be intercepted by many living and non-living soil constituents before it arrives at the root surface. In such cases, altering ion transporters without improving substrate bioavailability through means such as exudates is unlikely to improve net uptake. Additionally, leakage of acquired ions from the root back into the soil may occur, particularly when an ion faces an unfavorable electrochemical gradient for uptake across the plasma membrane [86]. For instance, in maize roots, phosphate efflux is up to 80% of phosphate influx at realistic phosphate concentrations [87]. Therefore, aggressive re-acquisition of leaked ions by modified transporters may only waste metabolic energy.

In conclusion, although manipulating ion transporters is technically feasible, it may have limited utility in the Second Green Revolution due to the various factors discussed above.

Dealing with the symbionts

Most higher plant species have mycorrhizal symbioses with fungi that assist nutrient acquisition [88]. Ectomycorrhizas enhance phosphorus acquisition by mobilising sparingly soluble phosphorus, and both ectomycorrhizas and arbuscular mycorrhizas, common in many annuals and hardwood species, increase the volume of soil explored beyond the depletion zone surrounding the root for phosphorus acquisition. In exchange for phosphorus, the plant provides the fungal symbiont with reduced carbon.

Mycorrhizal symbiosis was thought to be superior to root traits when it came to phosphorus acquisition, leading researchers to believe that root traits were of secondary importance or insignificant in comparison to the assistance provided by fungi. However, it has been discovered that mycorrhizal symbiosis is not as promising as initially believed. Strong correlations have been observed between phosphorus uptake and root traits like root-hair length [89], root branching [90] and root diameter [91]. In addition, different plant species exhibit distinct root traits that are likely to affect their mycorrhizal associations, indicating that root traits and mycorrhizal symbioses may interact in complex ways.

Therefore, while mycorrhizal symbioses are reported to be important for plant phosphorus acquisition, root traits should not be disregarded as irrelevant factors. Instead, root traits and mycorrhizal symbioses could be considered together as key components of the plant's strategy to acquire phosphorus from soil.

One often overlooked aspect of the analysis of this association relation is the fact that the carbon cost of mycorrhizal symbioses can be a significant component of the metabolic cost of phosphorus acquisition. Mycorrhizal colonisation increased root phosphorus acquisition in beans, but the increase in shoot photosynthesis did not result in increased plant growth due to greater root respiration [29]. At high phosphorus supply, mycorrhizal colonisation reduced the growth of citrus seedlings due to a greater root carbon cost [92].

The cost of the mycorrhizal symbiosis in various herbaceous and woody species ranges from 4 to 20% of daily net photosynthesis [29,93,94]. Mycorrhizal fungi may play a non-beneficial or even parasitic role in agroecosystems due to the greater metabolic burden of mycorrhizal roots [95].

Under scarcity of water

According to [96] the problem of water scarcity is a significant factor leading to worldwide crop losses. The author predicts that this issue will exacerbate further as a result of climate change and growing competition for water resources among urban, industrial, and agricultural sectors. Various countries have experienced severe droughts at different times. In the United States, for instance, droughts have resulted in around 67% of crop losses over the past 50 years, with the 2012 drought being the most severe in six decades. As a result, there is a growing interest in the development of drought-tolerant crops. Drought tolerance refers to the capacity of plants to maintain their productivity even in drought conditions, as defined by [97]. This can be achieved through different mechanisms, such as drought avoidance or prevention of desiccation, matching crop water use with available water, and recovering growth after rehydration, as discussed by [98].

Root system size, properties, and distribution are critical factors that determine plant access to water, which ultimately limits shoot functioning [99,100]. As a result, there is a growing interest in developing root traits that improve water foraging efficiency and help maintain productivity under water deficit conditions. However, it is still unclear which root traits are most effective and under what conditions.

Previous breeding endeavors aimed at cultivating crops suitable for water-limited environments have primarily concentrated on targeting specific traits tailored to particular crops and drought conditions [101]. Hence, comprehending the growth strategies employed by individual crops and the unique drought conditions they encounter becomes imperative for the triumph of breeding programs. Moreover, to accommodate diverse plant traits and growth strategies demanded by distinct environments and management practices, breeding efforts must incorporate the genotype by environment by management ($G \times E \times M$) interaction [98,102].

The complexity of root systems in both ligneous and herbaceous plants is often overlooked despite its crucial role in their functions. It is important to acknowledge that the root system comprises not just a single organ, but rather two, and sometimes three, main types of root organs. In ligneous plants, the coarse woody roots mirror the aboveground stems and fulfil various functions, including providing perennial structures, anchorage, carbohydrate and nutrient storage during the season, as well as facilitating nutrient and water transport. Conversely, the fine roots of ligneous plants are confined to the terminal two root segments, known as first and second branch orders, counting back from the root tips. These fine roots transiently explore underground resources [103,104].

According to [105] in herbaceous plants, encompassing both crops and non-crops, the root system consists of coarse and fine roots, which can be likened to the tap and lateral roots in a tap root system or seminal and nodal roots versus lateral roots in a fibrous root system. In a similar manner to the woody plants, herbaceous plants also exhibit a noticeable increase in the diameter of roots between the terminal two root orders and the remaining root system. In herbaceous plants the coarse roots fulfill vital functions such as providing anchorage and controlling the overall architecture of the root system. They play a significant role in determining the maximum depth of rooting and the plant's ability to penetrate compacted soil layers [106]. In addition to the coarse seminal roots, herbaceous plants also develop nodal roots (or brace roots in maize) from the lower sections of the stem. These nodal roots contribute to late-season precipitation absorption and exhibit distinct responses to soil water conditions compared to the primary root system [107]. Lastly, the fine (or lateral) roots display the highest activity in terms of water uptake and account for the majority of the length and surface area in both herbaceous and woody plants [108,109].

The size of a plant's root system plays a crucial role in acquiring soil resources, particularly when considering its relationship with the rest of the plant, such as leaf area, shoot, or overall plant size. Changes in allometric patterns (measuring root to shoot relationships) and shoot structure can

compensate for water scarcity. These adjustments, along with alterations in stand densities, enable the maintenance of stomatal conductance at levels comparable to mesic conditions, even under xeric conditions [110].

Allometry is commonly evaluated by the root-to-shoot ratio of dry mass. However, when biomass is used, a more robust measure for quantifying the relative size of root systems is the root biomass per total plant biomass, also known as root mass fraction (RMF). Despite its statistical advantages, RMF has been less frequently utilized [111].

In terms of functionality, ratios such as root-to-leaf surface area (AR:AL) or root length-to-leaf area ratio provide a more descriptive representation. They serve as proxies for water uptake capacity relative to light interception, and also indicate the surface area available for water uptake versus transpiration loss. These functional ratios are considered more informative than mass fractions when characterizing tissues [110,111].

Diverse environments are involved in rice cultivation, and specific cropping systems have been developed for deep-water, rain-fed lowland, upland, and irrigated conditions [112]. Rice has been extensively studied in genetic and genomic research and is considered a model organism for monocot crops, similar to how *Arabidopsis* is for dicots [16,113]. The classification of drought environments in rice is based on the duration of the wet season and the severity of water stress during different growth stages, such as the early planting season, tillering to flowering stages, intermittent stress, and late flowering to grain filling [114]. The impact of rice roots on crop productivity has been extensively investigated, with rice root research being more advanced compared to other crops [115]. Rice possesses a well-defined fibrous root system, typical of monocots, consisting of seminal, nodal, and lateral roots, which have been thoroughly explored through morphometric, anatomical, and genetic studies [116,117,118]. Researchers strive to understand the role of roots in enhancing nutrient and water uptake and increasing grain yield in rice breeding, regardless of the targeted ecosystem.

According to [119] tropical japonica rice varieties are known to have fewer tillers and deeper root systems compared to other rice ecotypes such as indica, aus, and rayada. Significant variations in root thickness, depth, and root mass have been observed among different rice cultivars, with documented genetic diversity for root morphological traits in response to drought, as highlighted by [120]. However, the full understanding of this variation and its impact on the water uptake function of rice crops under drought conditions is still incomplete, as noted by [120]. Breeding programs targeting an ideal rice plant and implementing direct selection for yield under drought are currently underway, supported by physiological research on rice root function, including investigations into root hydraulic conductance, anatomy, and aquaporin expression, as mentioned by [115]. To date, comprehensive trait assessments have shown no inherent differences between upland and lowland rice types. Indica types, mainly grown in lowland areas, exhibit thinner and shallower roots, while aus types, commonly cultivated in upland regions, demonstrate intermediate diameter roots similar in length to japonica varieties, which encompass upland Asian and temperate cultivars [115].

The root systems of rice are significantly influenced by environmental factors and water management practices. [121] found that intermittent irrigation has a positive impact on root length density and total root mass. Furthermore, the size of the roots is closely associated with available growing space, root impedance, and the presence of competitor plants [122]. In comparison to lowland varieties, upland rice develops longer root systems due to specific environmental conditions in upland ecosystems [123]. Upland areas characterized by well-drained soils facilitate water movement and enhance oxygen diffusion, thereby promoting rice root elongation [124]. Conversely, anaerobic flooded fields with inadequate soil drainage restrict oxygen supply and impede root growth, resulting in shallow root systems. Hence, it is essential for farmers to effectively manage irrigation and drainage systems to optimize rice root growth and development, ultimately leading to improved crop yield and quality.

Assessment and integration of genetic diversity

The primary method employed by humans to domesticate plant species during the past 10,000 years primarily involved the careful examination and deliberate selection of above-ground structures such as stems, leaves, flowers, and fruits. However, there was minimal focus on the investigation of below-ground structures, such as roots, except in cases where the root served as a storage organ for food and was directly selected for [125]. On the other hand, the domestication of animals entailed the observation and selection of the entire organism. The significance of roots for providing stability, as well as for the absorption of water and nutrients from the soil solution, is widely acknowledged among most plant scientists [125].

The genetic bottleneck resulting from domestication or subsequent selection has been recognized as a cause for reduced diversity in crop species, potentially leading to a loss of beneficial alleles [126]. The

significance of enhancing root systems has often been underestimated, with root traits being no exception [127]. Notably, advancements in genotyping techniques and understanding of root architecture have been made possible by research conducted on model species such as *Arabidopsis* [128], rice [15] and purple false brome (*Brachypodium distachyon*) [129]. These model systems offer various advantages. Firstly, the comparative mapping of identified quantitative trait loci (QTL) in related species serves as a starting point for identifying candidate genes and potential utilization in marker-assisted selection (MAS) programs [130]. Secondly, the utilization of cloned genes from model systems enables the manipulation of trait expression in the species of interest through transgenic breeding approaches [131].

Bread wheat, scientifically known as *Triticum aestivum*, is an allohexaploid plant with the genome formula BBAADD. It originated from the hybridization between domesticated tetraploid wheat and diploid weedy goat grass [132]. The green revolution in wheat during the mid-20th century, primarily driven by the selection of above-ground organs, was extensively documented by Dr Norman Borlaug [133]. Unlike above-ground organs, breeding programs focused on wheat roots received little attention from breeders in the CIMMYT or national programs [133]. The first scientist to excavate and illustrate the root system of bread wheat and rye was [134]. Furthermore, [135] reported the variances in root growth among seven cultivars of Canadian spring bread wheat.

By gaining a deeper comprehension of root traits and their genetic makeup, it becomes possible to enhance root systems by harnessing the existing diversity within modern cultivated germplasm [131]. Notably, modern cultivars of wheat possess a comparable amount of untapped genetic variation that contributes to stress tolerance, just like landraces (primitive varieties) of wheat [136]. Additionally, cultivated varieties of rice may harbor alleles that promote more extensive root growth and distribution, surpassing those found in wild species, as suggested by observations of container-grown plants [137]. The introduction of alleles from modern varieties mitigates the negative effects of linkage drag caused by the use of wild species and landraces [138]. However, certain landrace varieties for specific species also hold potential for integrating genetic diversity into modern varieties. It should be noted that not all landrace varieties or wild accessions are expected to exhibit abiotic stress tolerance. Nevertheless, successful utilization of this approach can be observed in crops such as barley [139], wheat [136] and pearl millet [140].

Breeding for better nutrient acquisition and growth

Routine field screening of large numbers of genotypes for low-fertility adaptation is generally noisy, costly, slow and unproductive [141]. There are several reasons for this, some of which are mentioned here in after:

1. large spatial variation in soil properties, especially when the topography is not completely flat,
2. subsoil acidity and compaction, which can restrict root growth,
3. the fact that most experiment stations are located on fertile soil,
4. confounding effects of past management practices on soil fertility, especially residual effects of lime and phosphorus application,
5. confounding effects of environmental interactions, including light and precipitation that can influence stress severity (effects which are especially problematic for manganese toxicity),
6. the difficulty of isolating specific edaphic stresses from other co-occurring stresses, as is the case for example with the acid soil complex, where aluminum toxicity is difficult to separate from deficiency of phosphorus, calcium, magnesium and potassium,
7. confounding effects of biotic stresses, especially those that affect roots such as nematodes and root rots,
8. the difficulty of directly evaluating root phenotypes in the field and
9. the statistical improbability of identifying genotypes possessing useful traits in a setting in which the possession of many distinct, yet interacting, traits is necessary for organismal success.

This last point is especially relevant considering that much of the crop breeding that has occurred in the past 50 years has focused on yield traits and disease resistance, selected under high fertility. Most of the elite lines that are now being used as parents in crossing programs may therefore have little adaptation to low-fertility soils. In contrast, landraces have undergone centuries of selection with low inputs, and may have many useful traits, but may lack disease resistance, local adaptation, high yield, grain marketability or other traits that are important for success in field trials. For example, a genotype possessing root traits enabling superior phosphorus acquisition but that cannot efficiently mobilize that phosphorus to grain because of indeterminacy or late maturity will not be identified as a source of useful traits in a yield trial.

A better strategy is to follow the proven methods used in breeding for tolerance of biotic stress, which are to evaluate a wide range of germplasm for the expression of specific tolerance traits to specific disease/pest organisms, in many cases specific races or variants of pathogens. Once genotypes that have

useful traits for specific stresses are identified, they are incorporated into a crossing program to integrate these traits with other desirable traits such as high yield, marketability, and so on, for specific regions. Similarly, trait-based selection for specific edaphic stresses is much more likely to be successful than simple screening of elite lines for growth or yield in infertile soil. Although some traits such as aluminum tolerance have manifold benefits for nutrient capture by sustaining root growth, many other traits of interest may only have value for specific stresses. For example, manganese tolerance involves leaf antioxidant mechanisms [142] that have little direct impact on aluminum tolerance or phosphorus acquisition.

Root traits for soil adaptation are useful in competitive environments, in subsistence agroecosystems usually in mixed stands with diverse taxa, and in commercial agriculture typically in high-density genetic monocultures. Traits influencing soil adaptation will affect plant productivity, and thereby competitive performance, under edaphic stress. An example of this is the positive effect of root hairs on plant competitiveness in mixed stands of *Arabidopsis* at low phosphorus but not at high phosphorus availability [143]. Traits influencing nutrient acquisition can also directly affect interplant competition by removing soil resources that could be accessed by competitors. For example, bean genotypes with shallow basal roots outcompete genotypes with deep basal roots in low-phosphorus fields [144], because of enhanced topsoil exploitation and reduced competition (i.e. reduced overlap of phosphorus-depletion zones) among roots of the same plant [144].

At the population level, competition among root systems can be important in determining the utility of root traits for nutrient acquisition. This appears to be the case for plasticity of basal-root shallowness, for which genetic variation exists; i.e. some genotypes respond to phosphorus stress by becoming more shallow, whereas others are unaffected or become deeper [61,63]. Modelling showed that interplant competition could be important in determining an optimal balance of plastic and non-plastic root phenotypes under conditions of phosphorus stress and combined phosphorus and water stress [145]. This suggests that genetic mixtures or multilines may have better performance in low-phosphorus agroecosystems than do genetic monocultures, especially in drought-prone environments.

The development of crops with superior growth in low-fertility soil and with better responsiveness to applied fertilizer inputs would have tremendous value in many developing countries, where yields are limited by low soil fertility and fertilizer use is minimal [91]. Since genotypic variation for nutrient acquisition efficiency is much larger than variation for nutrient use efficiency in crop plants, it is likely that nutrient-efficient crops will have greater nutrient acquisition than do conventional genotypes. Although such genotypes would extract more nutrients from the soil than conventional genotypes, they may actually enhance soil fertility in the long term through beneficial effects on soil erosion and nutrient cycling, as well as benefits they accrue to farm income and thereby the use of fertility amendments [91]. This is especially true for legumes, since enhanced growth of legumes benefits the cropping system by increasing biological nitrogen fixation.

Dealing with Aluminium toxicity

Aluminum toxicity is a major constraint to crop production in acid soils with $\text{pH} < 5.2$ [146]. Soluble aluminum hinders root elongation and reduces the uptake of essential nutrients such as phosphorus, calcium, magnesium, and potassium, which are already poorly available in most acid soils. Many studies have demonstrated considerable genetic variation in aluminum tolerance [146,147]. The production of root exudates, particularly carboxylates like malate and citrate, has been identified as a key tolerance mechanism [148]. These organic anions can chelate trivalent aluminum ions, thereby protecting the root tips from aluminum toxicity. Carboxylate exudation is relatively simple and is governed by one or two genes in several species, which enhances the prospect of transgenic approaches or direct genotype selection for improving aluminum tolerance [147]. Overexpression of enzymes responsible for organic acid production in roots improves plant growth in soils with excess aluminum or deficient phosphorus [148]. Aluminum tolerance has substantial benefits for nutrient (and water) acquisition and therefore could be a critical component of the second Green Revolution.

CONCLUSION

Research works the world over has established clearly that any further attempt to improve the productivity of plants to feed the growing world population, cannot ignore the significance of the roots in exploration and acquisition of the soil resources (nutrient elements and water) essential for plant growth. The way roots are structured has a crucial role in acquiring soil resources. It determines how roots spread out to search for resources in different areas of the soil and the competition for resources among roots of nearby plants. The allocation of resources in root growth and maintenance, which requires a significant amount of carbon, can negatively impact the reproductive output, particularly in environments

with low fertility. Numerous studies have shown that the energy spent on exploring the soil by root systems can exceed 50% of the daily photosynthesis and is of considerable magnitude. As a result, traits that enhance the effectiveness or efficiency of roots in obtaining soil resources should be prioritized. Learning from the experience with the green revolution of the last century, the future approach has to take into account the utility of root traits which can explore, acquire and transport the essential resources for the optimal growth of the plant. The approach has to be holistic, as selective stress on a single trait is less likely to be sustainable in the long run.

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