Chapter 12
Root Traits for Improving N Acquisition Efficiency

Hannah M. Schneider and Jonathan P. Lynch

Abstract Global agriculture requires the development of nutrient-efficient crops to improve food security while reducing environmental pollution. In developing nations, low soil nitrogen (N) availability and limited fertilizer usage is a primary limitation to crop production, while in developed nations, intensive N fertilization is a primary economic, energy, and environmental cost to crop production. In order to mitigate these risks, the development of crops with superior root traits enhancing N acquisition is essential. The development of crops with enhanced N capture would increase crop productivity, enhance sustainability, and reduce environmental pollution. There is substantial genetic variation for root phenes that have potential to improve N capture and reduce the N requirement of crops. In this chapter, we explore root phenes that enhance N acquisition that are urgently needed in global agriculture. Root ideotypes for enhanced N capture are predicted to pave the way for more productive and sustainable cropping systems.

Keywords Agriculture · Root · Phenotype · N

12.1 N-Efficient Crops are Needed in Global Agriculture

A major challenge for global agriculture is to improve crop productivity to feed a growing population while reducing the environmental impact. Sustainable crop production is an ever-growing challenge as the global population and food demand continue to rise. In agroecosystems, nutrient efficient crops are important for crop productivity as suboptimal nitrogen (N) availability is a primary limitation to crop growth. In low-input agricultural systems, nutrient deficiency is a primary limitation to crop productivity and therefore food security. In high-input agroecosystems, the energy and economic cost and pollution caused by intensive N fertilization is unsustainable. Chemical fertilizers are widely used to enrich soils with nutrients and improve plant production, however, add a significant cost to crop production and are

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a major source of environmental pollution. In addition, as little as 50% of applied fertilizer is captured by crop roots (Pask et al. 2012). The production of fertilizer requires finite fossil fuels and mineral reserves and therefore the dependency of fertilizers must be minimized to achieve food security. The key to development of nutrient efficient crops is harnessing genetic variation for root phenes (phene is to phenotype as gene is to genotype) (see Box 1) that enhance soil resource acquisition. Understanding the functional utility and genetic architecture of plant phenes that enhance soil resource capture is urgently needed for global food security.

Nitrogen, after carbon, oxygen, and hydrogen, is the most abundant mineral element in plants and is an important part of proteins, nucleic acids, and chlorophyll. Nitrogen is one of the most important inputs to agroecosystems as it is one of the primary limiting resources in agriculture production. Therefore, N acquisition is one of the most important crop breeding targets. Generally, soil N exists in three forms: organic N compounds and inorganic ammonium (NH_4^+) and nitrate ions (NO_3^-). Most of the potentially available soil N at any given time is in the form of organic N as plant and animal residues and soil organisms. Organic N compounds are typically not directly available to the plant but may be converted to plant available N forms (e.g. nitrate) by microorganisms. In agricultural systems, nitrate is generally the most abundant form of available N and acquired by crops in the greatest amounts. In modern agriculture, inorganic N fertilizers have become indispensable for crop production. Over the past 50 years, food production has increased nearly twofold which can largely be attributed to the use of N fertilizer. In high-input systems, the use of intensive N fertilization has the potential to increase crop production, however it comes at an environmental cost. Most of the applied N fertilizer is not taken up by the crop and the remainder is incorporated into soil organic matter or lost through erosion, leaching, surface runoff, or volatilization causing environmental pollution. In addition, the production of inorganic N fertilizers through the Haber-Bosch process is extremely energy intensive and has a large carbon footprint. Driven mainly by increases in fossil fuel prices, the price of inorganic N fertilizer has increased reducing profit margins in rich nations. In the developing world, where the majority of the global population lives, access to fertilizer is limited and farmers are often poor and cannot afford to buy fertilizers. The development of crop cultivars with enhanced soil resource acquisition is an important goal for global agriculture.

Improving N use efficiency (NUE) is an important strategy for boosting plant performance and yield in both high and low input agroecosystems. NUE, or the grain weight produced per unit of soil N is a result of N uptake and utilization processes including absorption, assimilation, and remobilization. The development of plants with improvement in both uptake and utilization efficiency is ideal. Efficient uptake of N is important as over half of applied N is lost from farmlands due to leaching and other factors. Roots are the interface between the soil and plant and provide important functions for the plant including resource uptake, storage, and soil anchorage. Therefore, roots have a substantial potential to improve N uptake. The great potential in improvement of NUE through plant uptake highlights the potential of root ideotype breeding to improve NUE. In this chapter, we discuss root phenes that enhance N acquisition, their genetic architecture, and potential deployment in crop breeding programs.

12.2 Physiological Mechanisms of N Uptake

Nitrogen is considered to be a mobile soil nutrient and moves through the soil primarily through mass flow. The process by which nutrients are transported to the root surface through water movement (e.g. percolation, transpiration, evaporation) is mass flow and the rate of flow determines the amount of nutrients transported to the surface of the root. Nitrate ions have a high solubility and therefore have greater uptake at peak plant transpiration (Lebot and Kirkby 1992). Nitrate solubility also influences its soil mobility as N is rapidly leached into deeper soil domains and groundwater, lost through surface runoff, or temporarily immobilized during periods of drought. Generally, N is more available in deeper soil domains, especially later in the growth season, due to crop uptake and leaching throughout the growth season.

Activity of high-affinity transport systems (HATS) and low-affinity transport systems (LATS) help crop plants acquire soil N, mainly in the form of nitrate. HATS activity may enhance N acquisition in suboptimal N through the upregulation of HATS-N in low-input agroecosystems. LATS activity is primarily constrained to high N concentrations and it may enhance N acquisition if the plant encounters patches and pulses of high N. However, the contribution of LATS to N uptake is typically negligible as in most agricultural systems the concentration of nitrate in the bulk soil solution is low. In the majority of agroecosystems, HATS and its kinetic parameters is the most meaningful component of the root nutrient uptake system as most systems have suboptimal N and fluctuating availability of N due to leaching, mineralization, and denitrification. The Michaelis Menten equation quantitatively describes the dynamics of N uptake. The Michaelis Menten equation has two key parameters: Vmax (the maximum velocity of uptake and measurement of the maximum uptake rate) and Km (the substrate concentration at which half of the maximum velocity is attained and measurement of the affinity of the uptake sites for the nutrient) (Fig. 12.1) (Griffiths and York 2020). Presumably, the type and number of transporters, assimilation machinery, and anatomical phenes influence uptake kinetics.

12.3 Root Ideotype for Improved Acquisition of N

Soil resources are spatially and temporally heterogeneous therefore adaptations to root systems are important for soil resource acquisition and therefore plant fitness. Root phenes have the potential to improve plant performance in suboptimal N availability by improving the metabolic efficiency of soil exploration. Metabolic efficient soil exploration can be achieved by optimizing the allocation of resources and thus

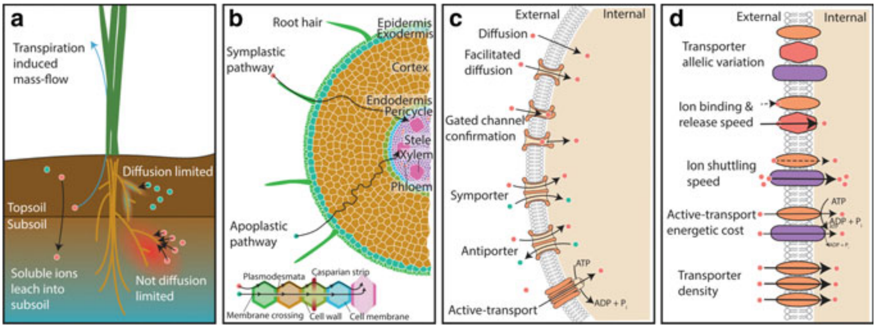

Fig. 12.1 Root uptake kinetics from the soil environment to transporter-level dynamics. **a** Mobility and bioavailability of soil nutrients determine the interception of nutrient ions with the root surface. **b** Nutrient ions may travel across the root through the apoplastic pathway (through the cell wall) or the symplastic pathway (through the cytoplasm) to reach the xylem for transport. **c** A variety of mechanisms exist for ions to enter the root through the soil solution. **d** Properties of transporters are presumably influenced by genetic variation and influence nutrient acquisition efficiency. From Griffiths and York (2020)

root foraging in specific soil domains. The construction and maintenance of root tissue requires an investment of resources (e.g. carbon and nutrients) by the plant. The reduction or elimination of unnecessary root tissue or investment in root tissues that are more metabolically efficient create roots with more efficient soil resource capture and greater plant performance in N stress. The metabolic cost (i.e. carbon and nutrient cost) of the root system is substantial and can exceed 50% of the daily photosynthesis (Lambers et al. 2002). The metabolic cost of soil exploration can significantly influence plant performance and yield under edaphic (soil-related) stress. Every unit of root growth requires each unit of leaf area to sustain relatively more non-photosynthetic tissue. Plants that are able to acquire N at a reduced metabolic cost will enable more metabolic resources to be available for further root growth and thus greater soil exploration, nutrient capture, and plant productivity. Strategic investment of plant resources results in more efficient root system function and resource capture.

An important ideotype in maize for the capture of soil N in both high input and low input agroecosystems is the ‘steep, cheap, and deep’ ideotype developed by (Lynch 2013) (Figs. 12.2 and 12.3). The ‘steep, cheap, and deep’ ideotype consists of several root architectural, anatomical, and morphological phenes that enhance N and water acquisition in maize by improving deep soil exploration at a reduced metabolic cost. The ‘steep’ component of the ideotype refers to the steep growth angle of nodal roots that increase root foraging in deep soil domains. The ‘cheap’ component of the ideotype refers to root anatomical and architectural phenes that reduce the metabolic cost of soil exploration therefore permitting further root growth in deeper soil domains. Significant natural genetic variation for ‘steep’ and ‘cheap’ root phenes that allow roots to explore ‘deep’ soil domains. Genetic variation for root phenes coupled with high throughput field phenotyping methods should enable

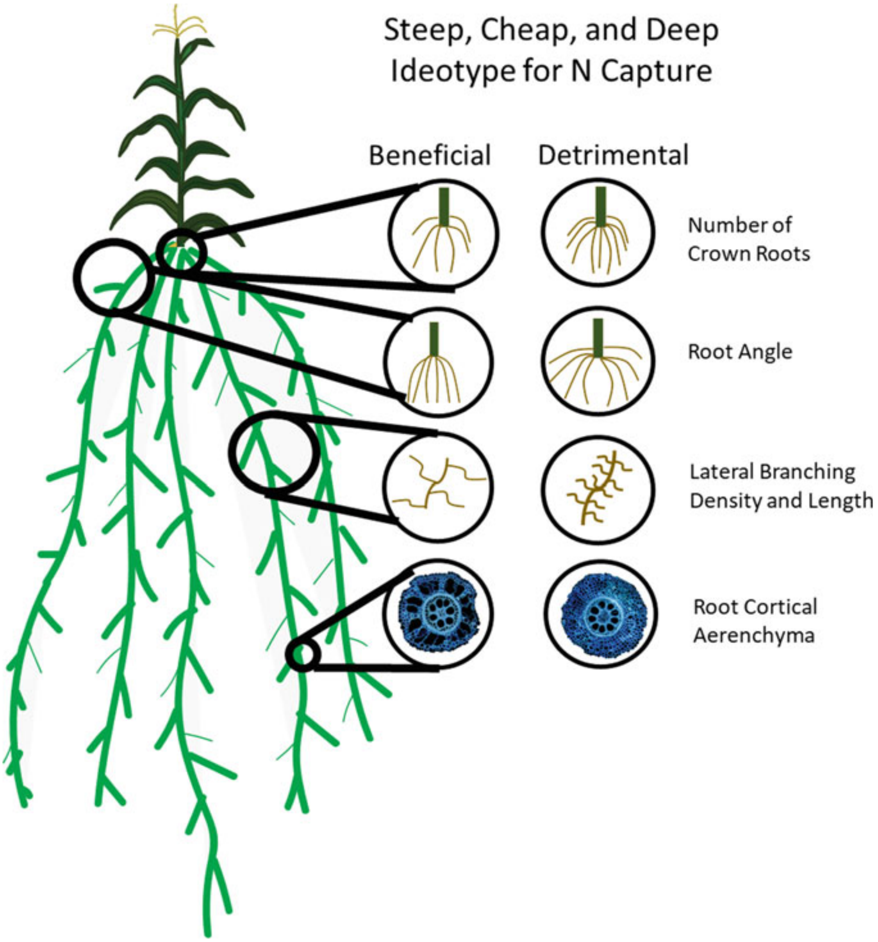

Fig. 12.2 The ‘steep, cheap, and deep’ ideotype for enhanced plant performance in N stress. In N stress, few nodal roots with a steep angle, few long lateral branches, and root cortical aerenchyma formation are adaptive responses for stress tolerance. Modified from Schneider and Lynch 2020

the understanding and deployment of improved root ideotypes into crop improvement programs. Understanding the fitness landscape of phenes, interactions between phenes, plastic responses of phenes, and their genetic control will lead to enhanced N acquisition and therefore more productive crops in both low and high-input systems. In the sections below we will briefly discuss some of the phene components of the ‘steep, cheap, and deep’ ideotype.

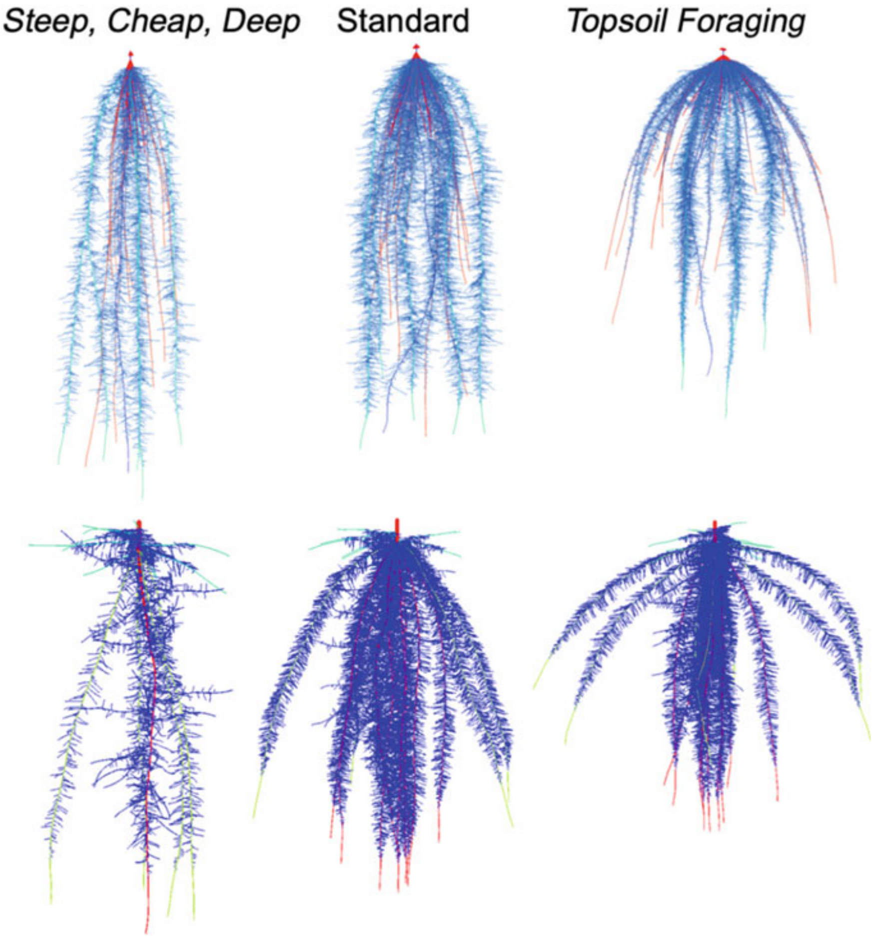

Fig. 12.3 The 'steep, cheap, and deep' and 'topsoil foraging' ideotypes in maize (upper panel) and common bean (lower panel). Root systems are simulated to 42 d after germination by OPENSIM-ROOT. Root systems in the center represent standard maize and common bean phenotypes. The maize root system represents a non-tillering monocot root architecture and the common bean root system represents an annual dicot root architecture. The 'steep, cheap, and deep' ideotype enhances subsoil resource acquisition and is beneficial for the capture of N. In contrast, the topsoil foraging phenotype is useful for the capture of topsoil resources including phosphorus, potassium, calcium, magnesium, and recently mineralized nitrate. From Lynch 2019

12.4 Root Architecture Ideotype for Improved Acquisition of N

Root architecture is the spatial configuration of the root system within the soil matrix. Root phenes have important roles in soil resource capture, particularly in environments with low nutrient availability. Root phenes determine the spatial and temporal placement of roots in specific soil domains and thus the capture of nutrient resources. As N is more available in deeper soil domains, root phenes that place roots deep in the soil profile at a reduce metabolic cost to the plant will be beneficial for N acquisition.

Root system architecture in monocots and dicots differs significantly (see Box 2), however many root phenes that confer enhanced N acquisition are similar. For example, in maize, root angle has an important role in N acquisition (Fig. 12.4). The angle which roots penetrate the soil influences plant depth and a steeper growth angle results in deeper rooted plants. Deeper roots enable the capture of N in deep soil domains and therefore had enhanced plant performance (Trachsel et al. 2013). Similarly in dicots, plants with a steep or fanned angle phenotype performed better under N stress when compared to plants with a shallow angle phenotype (Rangarajan et al. 2018). In maize, nodal root growth angles commonly are shallow in older nodes and steeper in younger nodes in maize. The emergence of roots with progressively steeper growth angles establishes a root architecture that initially is shallow, which coincides with greater availability of N in the topsoil during seedling establishment. The emergence of steeper growth angles in younger nodal roots over time coincides with the greater availability of N in deeper soil strata as the season progresses through leaching and crop uptake (York and Lynch 2015).

The production of fine roots (e.g. lateral roots) also plays a role in soil resource acquisition. Greater root length can be achieved with a fixed proportion of assimilates through reducing root diameter i.e. specific root length or the length of root per unit root mass. Reducing the construction and maintenance costs per unit root length enables a larger volume of soil exploration at a reduced metabolic cost. The length of lateral roots and the density at which they emerge from the main root axes plays a role in N capture and plant performance. In maize, fewer but longer lateral roots emerging from crown root axes are beneficial in N stress (Zhan and Lynch 2015) (Fig. 12.5). Similarly in common bean, a reduction in lateral root branching density enabled plants to accumulate a greater shoot biomass in low N environments (Rangarajan et al. 2018). Fewer lateral roots reduce competition for nutrients between different roots of the same plant (i.e. intra-root competition) and between roots of different plants (i.e. inter-root competition). Fewer, longer lateral roots reduce the metabolic cost of soil exploration and enable further root growth in deep soil domains and therefore improve plant performance and yield in low N environments.

The number of axial roots also influence soil N acquisition. In a field study, maize genotypes that had fewer crown roots had greater rooting depth, greater capture of deep soil N, and therefore greater plant growth and yield in low N environments (Fig. 12.6a). The emergence of fewer crown roots enables deeper soil exploration and the capture of deep N that has been leached into deeper soil domains throughout the growth season. Maize plants with fewer nodal roots, increase N capture and therefore plant performance through reallocation of carbon and resources to the growth of lateral roots, embryonic roots, and first node crown roots that grow in deep soil domains to increase soil foraging efficiency (Saengwilai et al. 2014b). Similarly in dicots, a smaller number of basal root whorls and fewer hypocotyl-borne roots increased root depth and enabled better N capture (Rangarajan et al. 2018). The

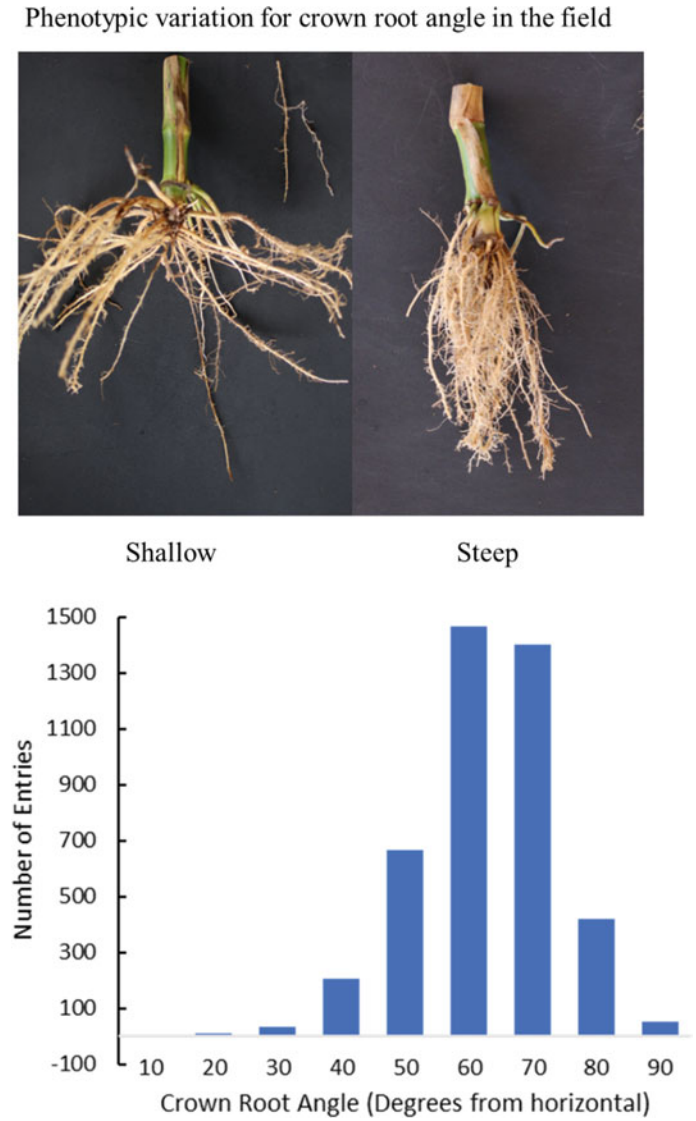

Fig. 12.4 Root growth angle influences the capture of N. Crown root angle in maize has a wide range of natural genetic variation in the field and greenhouse. Maize plants with steep crown root angles have greater root depth and plant growth in N stress

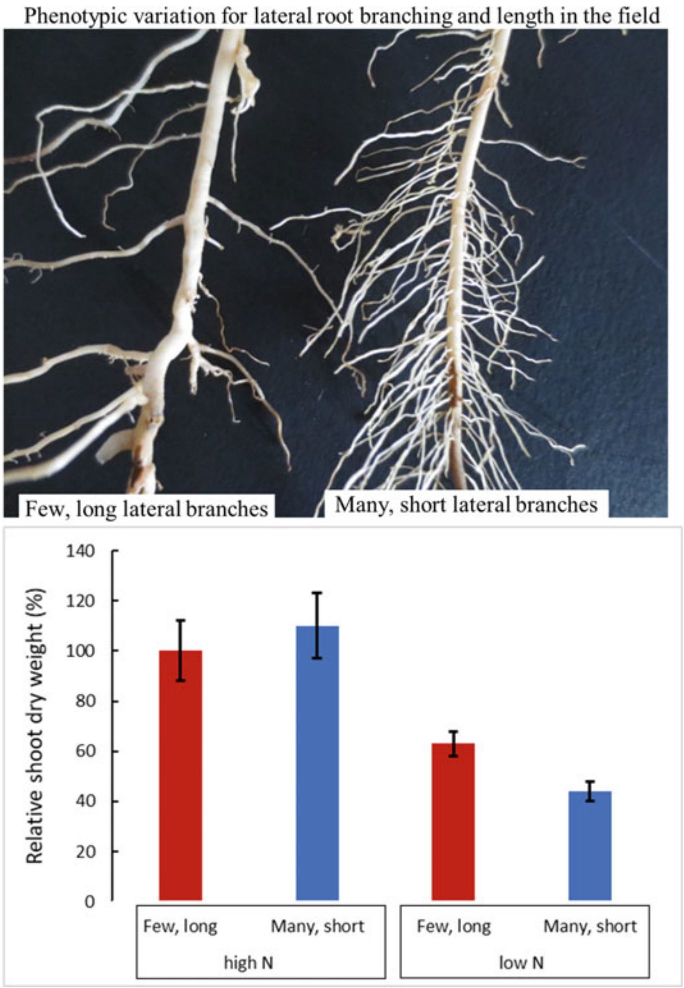

Fig. 12.5 Lateral root branching density and length is associated with N stress tolerance. Maize displays genetic variation for the density and length of lateral roots. In N stress in the field and greenhouse, maize lines with few, long lateral branches had 35% greater growth compared to lines with many short lateral branches Modified from Zhan and Lynch 2015

construction and maintenance of fewer axial roots enable further root growth of established axial roots into deeper soil domains.

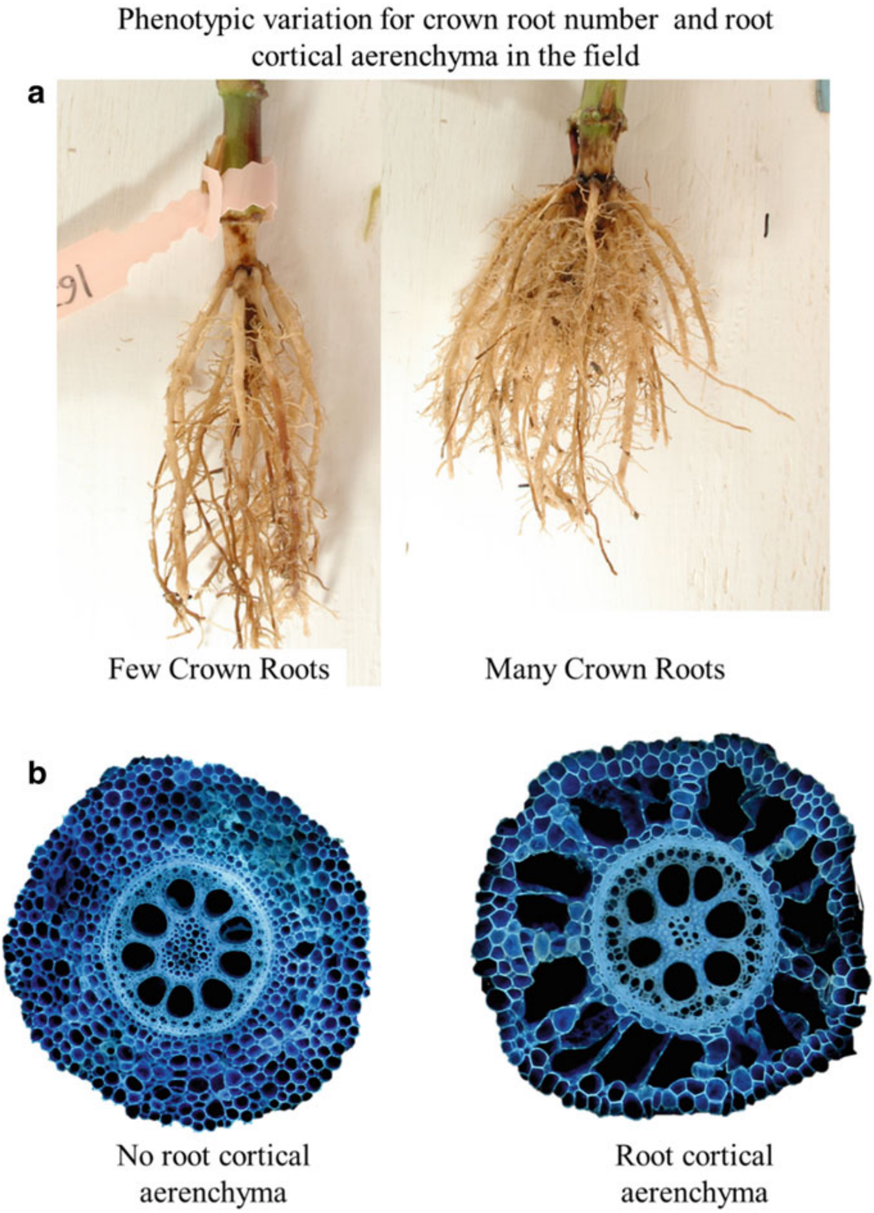

Fig. 12.6 Natural genetic variation exists for the formation of **a** the number of crown roots and **b** root cortical aerenchyma (RCA). Fewer crown roots and root cortical aerenchyma formation improve N capture

12.5 Root Anatomical Ideotype for Improved Acquisition of N

Root anatomical phenes can influence the metabolic cost of root tissue. Several anatomical phenes reduce the amount of living cortical tissue. A reduction in living cortical tissue therefore reduces root respiration and nutrient content, thereby permitting greater resource allocation to other plant processes including growth and reproduction. The change in ratio between respiring and non-respiring tissue reported in various anatomical phenes have been shown to have large effects on the metabolic cost of the root. For example, the formation of root cortical aerenchyma (RCA) replaces living cortical aerenchyma with air spaces (i.e. lacunae). Morphological, anatomical, and architectural phenes that reduce the metabolic cost of root tissue have the potential to enhance N acquisition.

Root cortical aerenchyma is primarily known for increased oxygen transport in hypoxic conditions, however RCA formation is induced by suboptimal availability of N, phosphorus (P), sulfur, and water. The formation of RCA converts living cortical parenchyma tissue into large intercellular spaces (i.e. lacunae) by programmed cell death. In low N environments, the formation of RCA in maize increased rooting depth in deep soil domains, increased leaf N and chlorophyll content, and increased plant biomass and grain yield through a reduction in the metabolic cost of root tissue (Fig. 12.6b). Similarly to RCA, root cortical senescence (RCS) involves the senescence of root cortical cells in temperate small grains through programmed cell death. RCS reduces the respiration and nutrient content of root tissue and the reduced metabolic costs associated with RCS can be attributed to enhance plant performance in low N environments.

Over the past 100 years, agricultural inputs and management practices have dramatically changed in rich nations from low fertilizer inputs and low planting densities to intensive fertilization and dense plant populations. Modern maize lines have a shallower root growth angle, fewer nodal roots, and a greater distance between nodal root emergence to lateral root emergence when compared to older maize lines. RCA formation increased in greater population densities. These changes in root architecture and anatomy have the potential to increase maize shoot growth by 16% in high N environments with a high planting density (York et al. 2015). The evolution of maize root anatomical and architectural phenes over the past century is consistent with greater N capture.

12.6 Root Phene Synergisms for N Capture

Root architectural and anatomical phenes do not function in isolation. Ideotype, or trait-based breeding, is a strategy to combine phenes that each would contribute to increased yield. Ideotype breeding not only considers phenes in isolation, but also the relationship between phenes as the integration of phenes determines how the whole plant functions. Phene synergisms (i.e. when the plant performance response of the interaction of multiple phenes is greater than the expected additive effect) are most effective between root phenes that affect the placement of roots in the soil profile and those that reduce the metabolic cost of root tissue. For example, in common bean the utility of root hairs is influenced by the root growth angle as the root angle determines the placement of root hairs in the soil profile (Miguel et al. 2015). Phene synergisms exist between RCA and the formation of lateral roots. Greater lateral root length branching density permits greater soil exploration and therefore the capture of soil resources. However, increased lateral branching length and density increases the metabolic demand of the root and due to competing sinks this could influence the growth of other root classes. This trade-off can be alleviated by decreasing the metabolic demand of the root through the formation of RCA. At an intermediate level of N, plants with RCA in lateral roots had 220% greater shoot biomass that was attributed to RCA formation (Postma and Lynch 2011). RCS had greater utility for resource capture and plant performance in plants with fewer tillers. Plants with RCS and few tillers had 20% greater shoot growth in suboptimal N availability. The growth of tillers coincides with the growth of nodal roots associated with tillers. In suboptimal N availability, nodal roots from tillers depleted limited soil nutrient resources faster and subsequently plant growth was reduced as soil resources became limiting in later growth stages. Therefore, a reduction in the number of tillers, and therefore nodal root development, reduced intra-root competition and enhanced plant growth in suboptimal N. Similarly, in low N environments, plants with RCS had 12% greater shoot growth when they also had a fewer lateral branches due to decreased intra-root and inter-root competition (Schneider et al. 2017). Understanding the fitness landscape of phene interactions is an important consideration for ideotype breeding.

12.7 Dimorphic Root Phenotypes for N Capture

In the field, plants may be exposed to dynamic or multiple, simultaneous stresses. For example, in low-input agroecosystems, availability of deep (i.e. N and water) and shallow (i.e. P and potassium (K)) resources are often co-limiting in crop production. The ‘steep, cheap, and deep’ ideotype may optimize the capture of mobile resources like N, however, may be maladaptive for the capture of shallow resources. For example, in common bean, plants with a steep or fanned root growth angle and fewer nodes of basal roots had enhanced N uptake, however the phenotype was maladaptive for phosphorus uptake. A root system optimized for phosphorus uptake has increased root length in shallow soil domains achieved through a shallow growth angle and a greater number of basal and hypocotyl-borne roots to enhance topsoil exploration (Rangarajan et al. 2018) (Fig. 12.3). An increased number of roots in shallow soil domains results in an increased metabolic cost of the root system and therefore a reduced root depth and trade-offs for N acquisition.

Dimorphic root phenotypes capable of effectively acquiring both deep and shallow soil resources would be beneficial in co-optimizing the capture of N, P, K, and water in environments where the availability of all soil resources is suboptimal (e.g. low-input systems). For example, a successful dimorphic root phenotype in common bean is a plant with an increased number of basal root whorls. A greater number of basal root whorls results in a greater range of growth angles and therefore a greater vertical range of root distribution and soil exploration which improves foraging in both the topsoil and deep soil domains (Rangarajan et al. 2018). Simulation modeling studies have demonstrated that numerous combinations of anatomical and architectural phenes could generate ideotypes for the capture of multiple, dynamic stresses. Integrated phenotypes optimized for the capture of soil resources are likely to differ between monocots and dicots.

12.8 Root Phenes Have Plastic Responses to N

Phenotypic plasticity is the ability of an organism to alter its phenotype in response to the environment (see Box 3). Soil is often heterogeneous and resource availability is spatially and temporally dynamic which often alters the expression of root phene states. For example, in suboptimal N environments, maize root angles became steeper enhancing soil exploration in deep soil domains and subsequently N capture (Trachsel et al. 2013). The formation of RCA increased in N deficit, enabling metabolic resources to be directed towards deeper root length, biomass, and reproduction (Saengwilai et al. 2014a). Similarly, nutrient deficiency, including suboptimal N availability, accelerated the rate of RCS formation. Enhanced RCS formation and the subsequent reduction in the metabolic cost of the root, enabled additional root growth in deep soil domains and enhanced the capture of N (Schneider et al. 2017).

In variable environments, phenotypic plasticity may be advantageous. However, in high input environments, with intensive fertilization and monoculture growth systems, phenotypic plasticity may be maladaptive. The evolution of crops took place in environments with biotic and abiotic stress and root growth and function evolved strategies for soil resource capture. However, in high input environments, constraints for soil resource acquisition are mitigated as crops are fertilized and irrigated. In most agricultural systems, root phenes, whether plastic or not, that contribute to the exploration of deep soil domains enhance N capture (Lynch 2019). The fitness landscape of phenotypic plasticity is dependent on specific environments and management practices. The genetic architecture of phenotypic plasticity is complex and highly quantitative. Before we integrate phenotypic plasticity into breeding programs, we first need to understand the utility of root phenes and interactions between root phenes in order to better understand adaptive or maladaptive plasticity under specific edaphic stresses.

12.9 Genetic Variation for Root Phenes and Breeding Strategies

Few genetic loci have been identified for anatomical phenes including root stele and xylem vessel diameter in rice (Uga et al. 2008, 2010), xylem vessel phenes in wheat (Sharma et al. 2010), and RCA in *Zea* species (Mano et al. 2005, 2007). In maize, genetic loci for the areas of cross section, stele, cortex, aerenchyma, and cortical cells, root cortical aerenchyma, and cortical cell file number have been identified through quantitative trait loci (QTL) mapping of recombinant inbred lines (Burton et al. 2014). In addition, genetic loci associated with root cross-sectional area, area of the stele and cortex, root cortical aerenchyma, lateral branching density and length, root angle, size of cortical cells and the number of cortical cell files in maize have been identified through genome-wide association mapping (Schneider et al. 2020a, b). However, the integration of these phenes into breeding programs is complex due to the highly quantitative nature of root phenes.

A large number of genetic loci each contribute small effects to the expression of a single phene. The genetic control of root phenes is further complicated by the distinct genetic control and expression of root phenes in abiotic stress and their plastic response to those stresses. Highly quantitative traits can pose a challenge for conventional breeding programs that use single-trait breeding strategies and marker assisted selection. The use of conventional tools would require the stacking of hundreds of genes for the development of desirable root ideotypes. Modern breeding methods, including genomic selection enable the selection of multiple loci. Genomic selection methods should include phenes and integrated phenotypes, not just selection for yield. Selection for individual root phenes has advantages compared to brute-force yield selection for edaphic stress. Landraces and wild germplasm may be an important source of phenotypic variation for ideotype development and in crop improvement programs. Genomic selection training sets must also consider wild and landrace germplasm, which presumably express more combinations and greater extremes of root phenes. Crop breeding programs must not only include expertise in genetics, plant pathology, and agronomy, but also soil science, plant nutrition, and ecophysiology in order to guide the development of crop ideotypes with enhanced N capture. We need to make a concerted effort to train and support scientists capable of working across disciplines to develop more N efficient crops.

Although the integration of plant phenes in breeding programs has been limited, there are a few notable examples. In wheat, breeding for smaller diameter xylem vessels has been employed as a means for improving water use efficiency. Plants with narrow xylem vessels had 3–11% greater grain yield when compared to the control in drought environments (Richards et al. 1989). In addition, the suberin content in the cortical exodermis has also been examined as a potential breeding target for Phytophthora resistance in soybean (Ranathunge et al. 2008). The ‘Topsoil foraging’ ideotype for improved phosphorus acquisition, which includes longer, denser root hairs and several architectural phenes that position more root foraging in shallow soil domains with greater phosphorus bioavailability (Lynch 2019), has been used to breed new varieties of common bean with substantially improved productivity in low fertility soils of Africa (Burridge et al. 2019). The continued development of root phenotyping platforms and the identification of genes associated with root phenes should facilitate the integration of root phenes in crop breeding programs.

12.10 Future Perspectives

The development of nutrient efficient crops has the potential to address urgent global challenges. Understanding plant evolution and biology requires the understanding of plant adaptation to nutrient constraints. However, this topic receives very little attention in basic and applied plant biology. The scientific community has made great progress in understanding and manipulating the plant genome, however most root phenes are genetically and physiologically complex and do not readily align with the gene-centric paradigm that dominates plant biology. Phenotypic plasticity and heterogenous soil environments complicate the identification of highly quantitative genes associated with root phenes through genome-wide association mapping. Future work must focus on understanding the fitness landscape (i.e. how root phenes affect cop performance in an array of environments and phene combinations). The fitness landscape of root phenes and their plastic responses is poorly understood. Differences in growth between controlled and field environments are often overlooked. Controlled environments (e.g. greenhouse, growth chamber) often do not represent the heterogeneous field environment (e.g. planting density, light, temperature, soil bulk density, nutrient distribution) and therefore are challenging to identify and understand plant phenes and their responses. Field phenotyping is often a bottleneck in crop physiology and breeding programs and high-throughput phenotyping often does not allow for the measurement of complex phene states. Field environments are usually heterogeneous and dynamic and difficult to replicate, measure, and monitor. In silico biology enables the study of complex interactions of the root fitness landscape that are not possible empirically and many environment and phenotype combinations that do not exist in nature. The study of the utility of root phenes for enhanced N capture requires many disciplines including ecology, physiology, development morphology, genetics and in silico biology.

12.11 Conclusion

In summary, there is great potential for the development of N efficient crops. Several high-throughput methods can be used to rapidly phenotype important root phenes for N capture. As discussed above, many root phenes for N capture have been well characterized and genetic loci have been identified enabling ideotype breeding. Root phenes important for N capture express significant genetic variation. Multiple phenes, each under distinct genetic control, interact with each other and the environment to determine the fitness of the root system. However, further research is needed to understand phene synergisms, trade-offs associated with other plant functions, and how phenes interact to influence plant fitness in different environments and management practices. The development of N efficient crops may allow farmers in low-input systems to increase crop productivity and climb out of the poverty trap of low input and low yields. N efficient crops may be easily adoptable in low-input systems as they have relatively few barriers for implementation and have the potential to have large effects on crop yields. In high-input systems, the development of N efficient crops may reduce environmental pollution and increase agricultural sustainability.

Box 1. What is a phene?

A phene is to phenotype as gene is to genotype. A phene is a distinct element of an organism's phenotype. A collection of distinct phenes comprise the phenotype, as a collection of distinct genes comprise the genotype. Genes have variants called alleles and similarly, phenes have variants called phene states. An example of a root phene is root growth angle. Root angle has at least two phene states: 'steep' and 'shallow'. The utility of soil resource acquisition is dependent on the phene state. For example, the 'steep' phene state is important for N acquisition in leaching environments.

Box 2. Root Classes

In annual crops, generally the root system of monocots consists of three major root classes: primary, seminal (or seed-borne) and nodal (shoot-borne) roots which all produce lateral (root-borne) roots of the first and second order. Nodal roots that emerge below ground are referred to as crown roots and nodal roots that emerge above ground are called brace roots. The root system of a dicot is distinct from that of a monocot. For example, a bean root system consists of a primary root, hypocotyl-borne roots, and basal roots which all produce lateral roots.

Box 3. Phenotypic Plasticity

Phenotypic plasticity is the ability of an organism to change its phenotype in response to the environment. Phenotypic plasticity may involve changes in physiology, morphology, anatomy, development, or resource allocation and it is phene specific, not a characteristic of an organism as a whole. The plastic response of an organism may be adaptive, maladaptive, or neutral in regard to its fitness. An example of an adaptive plastic response is the response of root angle in suboptimal N. In low N environments, maize plants had steeper growth angles that were able to explore deep soil domains and enhance N capture.

References

Burridge JD, Findeis JL, Jochua CN, Mubichi-Kut F, Miguel MA, Quinhentos ML, Xerinda SA, Lynch JP (2019) A case study on the efficacy of root phenotypic selection for edaphic stress tolerance in low-input agriculture: common bean breeding in Mozambique. Field Crops Res 244:107612

Burton AL, Johnson J, Foerster J, Hanlon MT, Kaeppler SM, Lynch JP, Brown KM (2014) QTL mapping and phenotypic variation of root anatomical traits in maize (Zea mays L.). Theor Appl Genet 128:93–106

Griffiths M, York LM (2020) Targeting root ion uptake kinetics to increase plant productivity and nutrient use efficiency. Plant Physiol 182:1854–1868

Lambers H, Atkin OK, Millenaar FF (2002) Respiratory patterns in roots in relation to their functioning. In: Waisel Y, Eshel A, Kafkaki K (eds) Plant roots, hidden half, third edit. Marcel Dekker Inc, New York, pp 521–552

Lebot J, Kirkby E (1992) Diurnal uptake of nitrate and potassium during the vegetative growth of tomato plants. J Plant Nutr 15:247–264

Lynch JP (2019) Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture. New Phytol 223:548–564

Lynch JP (2013) Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. Ann Bot 112:347–357

Mano Y, Omori F, Muraki M, Takamizo T (2005) QTL mapping of adventitious root formation under flooding conditions in tropical maize (Zea mays L.) seedlings. Breed Sci 55:343–347

Mano Y, Omori F, Takamizo T, Kindiger B, Bird RM, Loaisiga CH, Takahashi H (2007) QTL mapping of root aerenchyma formation in seedlings of a maize × rare teosinte “Zea nicaraguensis” cross. Plant Soil 295:103–113

Miguel MA, Postma JA, Lynch J (2015) Phene synergism between root hair length and basal root growth angle for phosphorus acquisition. Plant Physiol 167:1430–1439

Pask AJD, Sylvester-bradley R, Jamieson PD, Foulkes MJ (2012) Field crops research quantifying how winter wheat crops accumulate and use nitrogen reserves during growth. F Crop Res 126:104–118

Postma JA, Lynch JP (2011) Root cortical aerenchyma enhances the growth of maize on soils with suboptimal availability of nitrogen, phosphorus, and potassium. Plant Physiol 156:1190–1201

Ranathunge K, Thomas RH, Fang X, Peterson CA, Gijzen M, Bernards MA (2008) Soybean root suberin and partial resistance to root rot caused by phytophthora sojae. Biochem Cell Biol 98:1179–1189

Rangarajan H, Postma JA, Lynch JJP (2018) Co-optimisation of axial root phenotypes for nitrogen and phosphorus acquisition in common bean. Ann Bot 122:485–499

Richards RA, Passioura J (1989) A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. Crop Pasture Sci 40:943–950

Saengwilai P, Nord EA, Chimungu JG, Brown KM, Lynch JP (2014a) Root cortical aerenchyma enhances nitrogen acquisition from low-nitrogen soils in maize. Plant Physiol 166:726–735

Saengwilai P, Tian X, Lynch JP (2014b) Low crown root number enhances nitrogen acquisition from low nitrogen soils in maize (Zea mays L.). Plant Physiol 166:581–589

Schneider HM, Lynch JP (2020) Should root plasticity be a crop breeding target? Front Plant Sci 11:546. https://doi.org/10.3389/fpls.2020.00546

Schneider H, Klein S, Hanlon M, Brown K, Kaeppler S, Lynch J (2020a) Genetic control of root anatomical plasticity in maize. Plant Genome In Press

Schneider H, Klein S, Hanlon M, Nord E, Kaeppler S, Brown K, Warry A, Bhosale R, Lynch J (2020b) Genetic control of root architectural plasticity in maize. J Exp Bot In Press

Schneider H, Postma JA, Wojciechowski T, Kuppe C, Lynch JP (2017) Root cortical senescence improves growth under suboptimal availability of N, P, and K. Plant Physiol 174:2333–2347

Sharma S, Demason DA, Ehdaie B, Lukaszewski AJ, Waines JG (2010) Dosage effect of the short arm of chromosome 1 of rye on root morphology and anatomy in bread wheat 61, 2623–2633

Trachsel S, Kaeppler SM, Brown KM, Lynch JP (2013) Maize root growth angles become steeper under low N conditions. F Crop Res 140:18–31

Uga Y, Okuno K, Yano M (2008) QTLs underlying natural variation in stele and xylem structures of rice root. 14:7–14

Uga Y, Okuno K, Yano M (2010) Fine mapping of Sta1, a quantitative trait locus determining stele transversal area, on rice chromosome 9 9, 533–538

York LM, Galindo-Castaneda T, Schussler JR, Lynch JP (2015) Evolution of US maize (Zea mays L.) root architectural and anatomical phenes over the past 100 years corresponds to increased tolerance of nitrogen stress. J Exp Bot 66:2347–2358

York LM, Lynch JP (2015) Intensive field phenotyping of maize (*Zea mays* L.) root crowns identifies phenes and phene integration associated with plant growth and nitrogen acquisition. J Exp Bot 66:5493–5505

Zhan A, Lynch J (2015) Reduced frequency of lateral root branching improves N capture from low N soils in maize. J Exp Bot 66:2055–2065

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