

# Challenges of modifying root traits in crops for agriculture

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**Roots play an essential role in the acquisition of water and minerals from soils. Measuring crop root architecture and assaying for changes in function can be challenging, but examples have emerged showing that modifications to roots result in higher yield and increased stress tolerance. In this review, we focus mainly on the molecular genetic advances that have been made in altering root system architecture and function in crop plants, as well as phenotyping methods. The future for the modification of crop plant roots looks promising based on recent advances, but there are also important challenges ahead.**

## Crop root architecture and function

Roots provide the interface between plants and the complex soil environment. Their key function is to mine the water and nutrients contained in soils that are required for productivity. Many factors in soils lead to spatially and temporally heterogeneous conditions, including physical properties determined by weathering and erosion, mineral nutrient content, water content, biotic factors such as soil microbial populations, and the plant communities that inhabit particular locations. The spatial heterogeneity of soils makes studying roots under field conditions a complex problem. Despite the fact that roots are hidden and require considerable effort to characterize, they are some of the most important biological tissues in our biosphere because of their unique role in extracting both water and minerals from soils that are essential for plant and animal nutrition. This review will assess the current root research landscape and the challenges that lie ahead by addressing several aspects of crop plant roots, including architectural traits, advances in phenotyping technologies, and functional traits.

## Root architectural ideotypes

Crop root architecture is determined by genetics, edaphic conditions, planting density, plant size, intercropping patterns, agronomic practices and seasonal weather patterns [1]. Although a robust plant root system is an important factor for vegetative and reproductive fitness, progress in using root system architecture (RSA) as a trait to boost crop productivity [2] has been slow.

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Recent reviews address root ideotypes suitable for improving plant productivity by enhancing soil mineral resource capture [3–5] and by reducing root lodging [6] (Table 1). Another ideotype is disease-free roots that enable plants to forage through the soil for nutrients and water while balancing the metabolic cost of growing new roots with the cost of sustaining root function and activity. A steep–deep–cheap ideotype has been proposed to increase nitrogen and water use efficiency for crops grown under certain conditions. This model integrates root angles suitable for nitrate recovery, deep rooting for water and nutrient acquisition and a reduction of root cortical cells through the development of aerenchyma (RCA) to reduce the carbon cost of root maintenance [7]. To reduce the carbon cost of roots, another paradigm targets decreased root diameter, increased lateral root and root hair length, and increased root longevity over increased lateral root/root hair number and density [3,7]. The success of these ideotypes will be dependent on the farming systems being considered and the soil properties. For modern agriculture, high density planting is an important consideration where interplant competition may regulate root angle and root occupancy.

Root architecture ideotypes are comprised of complex, multicomponent, and interconnected traits. Root systems of various crop plants have different morphologies and these crops are cultivated under conditions with different limiting factors. Therefore, the strategies to alter architecture must be crop specific, making this a challenging task for biotechnological approaches, because a tool kit of many genes may be required. For example, corn (*Zea mays*) root systems are polymorphic and developmentally controlled (Figure 1). The post-embryonic root system consists of a primary root and variable number of branched seminal roots that predominate during the seedling stage. Other cereals such as rice (*Oryza sativa*) and wheat (*Triticum aestivum*) have a fibrous root system [8] (Figure 2). In contrast to monocot roots, dicots such as soybean (*Glycine max*) have a taproot system with the radical developing into the primary root, from which, multiple orders of lateral roots are formed (Figure 3). Although each crop has a unique RSA, the ontogeny of some root classes is conserved across plants. For example, the embryonically derived primary root develops from the radical, whereas the postembryonic lateral, crown, brace, and basal cluster roots develop from the pericycle derived founder cells near xylem poles [9,10] or from the stem cortical parenchyma cells close to the vasculature. In many cases, genes regulating root development

**Table 1. Desired modifications in root traits that will contribute to different important ideotypes that are hypothesized or demonstrated to improve root architecture and function**

Trait modification	Ideotype
Increased nodal root number	Root lodging resistance
Increased root diameter	Root lodging resistance
Reduced root turnover rate	Root lodging resistance
Seedling root vigor	Root lodging resistance and enhanced nutrient capture
Transporter modification	Improved root function
Rhizosphere pH	Improved root function
Enhanced root-microbe interactions	Potential for improved root function
Root proliferation	Enhanced nutrient capture
Root exudates	Enhanced nutrient capture
Increased lateral root number	Enhanced nutrient capture
Root angle and gravitropism	Steep, deep, cheap
Cortical aerenchyma	Steep, deep, cheap
Long root hairs	Steep, deep, cheap
Increased root hair longevity	Steep, deep, cheap
Increased root length density	Steep, deep, cheap
Long lateral roots	Steep, deep, cheap

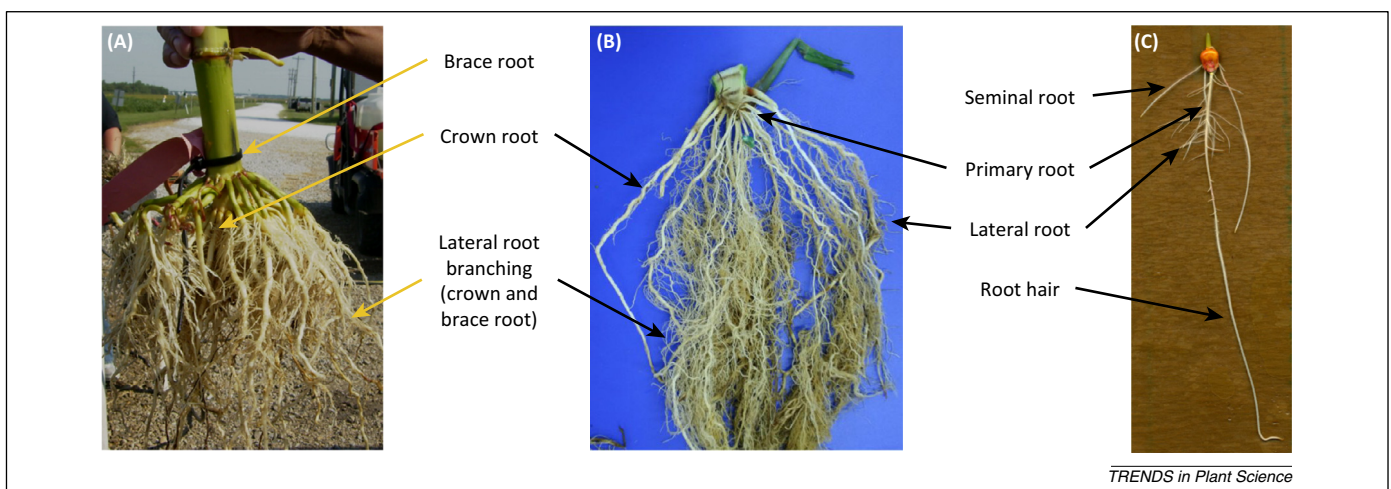
are conserved and may be used across multiple species, even though having a large toolbox of genes may ultimately be necessary to overcome crop specific bottlenecks in improving RSA.

### Genetics of root system architecture

Research to characterize genes and describe the genetic control of RSA has advanced in rice, corn, wheat, and soybean, but is still an area ripe for future discovery. The known genes whose genetic manipulation via overexpression or targeted suppression modifies root architecture in crops are summarized in Table 2. Additional insights can be made from the wealth of mutant studies in both corn and rice. In corn, this includes an auxin responsive LOB domain transcription factor *Rootless* concerning Crown and Seminal root (*RTCS*) and its downstream target Auxin Response

Factor (*ARF34*), which control nodal root formation in monocots [11], the root hair mutants such as Hair Less 1 (*RTH1*), which codes for a yeast *sec3* homolog, *RTH3*, which encodes a glycosylphosphatidylinositol anchor COBRA-like protein affecting root hair elongation [12], and *RTH5*, which encodes a monocot-specific NADPH oxidase [13]. The short lateral roots 1 and 2 (*slr1*, *slr2*) and lateral root 1 (*lrt1*) loci are reported to control lateral root development in maize; however, the underlying genes have not been cloned [14]. The *RUM1* locus encoding an Aux/IAA response regulator modulates seminal root and lateral root initiation in maize [15]. There are also multiple root architecture quantitative trait loci (QTLs) reported in maize, which control architecture and yield stability across multiple genetic backgrounds and different water regimes [16]. Other major QTLs in maize control root length, number, and dry weight, as well as root length/area co-localized with grain yield [17]. Cloning of the genes that underlie these QTLs will reveal the additional molecular mechanisms that control RSA.

Rice root architecture is controlled by many genes including: the auxin regulated Adventitious and Crown Rootless *ARL1*; *CRL1*, which encodes a LOB domain transcription factor conserved across monocots and dicots [18]; *OsCAND1*, which encodes a ubiquitin ligase homologous to *AtCAND* [19]; *CRL4/OsGNOM1*, which encodes a guanine nucleotide exchange factor [20]; *CRL5*, which encodes an AP2/ERF transcription factor [18]; the auxin biosynthetic *OsYUCC1* [21]; and the highly conserved *OsmiR393* regulatory RNA [22]. The loci regulating root elongation include *GNA1*, which encodes a glucosamine-6-P acetyltransferase, *OsCYT-INV1* (an alkaline/neutral invertase) [8,23], *Osglu3-1* (a putative membrane-bound endo-1,4- $\beta$ -glucanase [24]), *OsRPK1* (a  $\text{Ca}^{2+}$ -independent Ser/Thr kinase [25]), and other candidates such as WUSCHEL-related homeobox 3A (*OsWOX3A*), and *OsARF16* (an integrator of phosphate starvation and auxin response [26,27]), which control lateral root development. Thus far, the majority of these genetic loci have not been targeted for transgenic manipulation, and in a few cases, the effects on RSA were accompanied by pleiotropic effects [22] (Table 2). These findings suggest the need for precision in transgene



**Figure 1.** Photographs of maize root systems from (A) the field, (B) growth chamber, and (C) young seedlings grown on germination paper. The photos illustrate the different types of roots found in maize along with changes that occur over the course of root system development. The post-embryonic root system of corn is initially dominated by the seminal or primary root and then as the plant ages the root system becomes dominated by crown or nodal roots. (Photos courtesy of Monsanto.)

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