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# KEYNOTE: A critical role for root models in feeding $10^{10}$ people

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**Highlights:** There is an urgent need to develop crops with reduced nutrient and water requirements. The complexity of relevant processes overwhelms conventional empirical approaches. Structural-functional modeling of root systems has a unique role in providing important insights into the root phenome, which will focus empirical research on the most productive avenues, and inform crop ideotype development.

**Keywords:** root traits, modeling, food security

We confront a global crisis. Approximately 1B people are chronically hungry, soil and water resources are degrading, climate is changing, and the human population is expected to reach 10B in a few decades. The greatest challenge facing humanity today is the need to develop systems to sustainably support our species.

Food production requires water and nutrients. In rich nations the intensive use of fertilizers and irrigation are causing significant environmental degradation, while in poor nations drought and low soil fertility are primary limitations to crop yields, food security, and economic development. It is unrealistic to expect poor nations to adopt the input-intensive agriculture of rich nations for both economic and environmental reasons, as well as inherent limits to the supply of resources including fresh water and high grade phosphorus ore deposits. In both rich and poor nations, new crops and crop varieties with reduced water and nutrient requirements would have great value.

Fortunately, substantial genetic variation exists within crops for growth and yield in stressful soil environments. Much of this variation is related to root traits. However, we do not understand root/soil interactions very well, in large part because of the complexity of the problem. Root systems are highly dynamic, complex structures, interacting with the soil, which is a highly complex, dynamic, diverse, and opaque environment. It is very difficult to conceptualize how a root trait might affect crop growth in the context of this complexity. Structural-functional plant models therefore have unique value in helping us understand the acquisition of soil resources by plant roots. Such models have heuristic value in identifying knowledge gaps, key processes, and potential outcomes and interactions, that are useful for guiding empirical research. Empirical research is in turn useful in parameterizing and guiding model development.

An example of the application of root modeling for the improvement of crop stress tolerance is the search for root traits to improve water and N acquisition by maize.

An ideotype to optimize water and N acquisition by maize root systems is called "steep, cheap, and deep"; 'steep' representing architectural traits, 'cheap' representing anatomical traits that reduce the metabolic cost of soil exploration, and 'deep' representing the goal of placing roots deeper in the soil profile, where water and nitrate resources are often found under stressful conditions (Lynch, 2013). The ideotype includes 1) a large diameter primary root with few but long laterals and tolerance of cold soil temperatures, 2) many seminal roots with shallow growth angles, small diameter, many laterals, and long root hairs, or as an alternative, an intermediate number of seminal roots with steep growth angles, large diameter, and few laterals coupled with abundant lateral branching of the initial crown roots, 3) an intermediate number of crown roots with steep growth angles, and few but long laterals, 4) one whorl of brace roots of high occupancy, having a growth angle that is slightly shallower than the growth angle for crown roots, with few but long laterals, 5) low cortical respiratory burden created by abundant cortical aerenchyma, large cortical cell size, an optimal number of cells per cortical file, and accelerated cortical senescence, 6) unresponsiveness of lateral branching to localized resource availability, and 7) low Km and high Vmax for nitrate uptake. Some elements of this ideotype have experimental support, but most are hypothetical.

The structural-functional root model *SimRoot* has been very useful in assessing various aspects of this ideotype. *SimRoot* is a dynamic model that simulates the growth and development of root systems and nutrient acquisition from the soil (Lynch *et al.*, 1997; Postma and Lynch, 2011).

One application of *SimRoot* was to quantitatively evaluate the hypothesis that the formation of root cortical aerenchyma (RCA) is a useful adaptation to suboptimal availability of phosphorus, nitrogen, and potassium by reducing the metabolic costs of soil exploration. Empirical data shows that RCA formation reduces the respiration and nutrient content of root segments, but it was not known if these effects could significantly benefit plant growth, considering the spatiotemporal complexity of RCA expression, and the autocatalytic effects of reduced root metabolic costs on soil resource acquisition. *SimRoot* showed that RCA could increased the growth of simulated 40-d-old maize plants substantially under conditions of suboptimal nitrogen, phosphorus, or potassium, and that RCA could also reduce critical fertility levels in high-input systems (Postma and Lynch, 2011). The utility of RCA depended on other root phenes and environmental factors. In low-phosphorus soils, the utility of RCA was greater in plants with increased lateral branching density. In low-nitrate soils, the utility of RCA formation was greater in coarser soils with high nitrate leaching. These results were supported by field results showing that high RCA maize lines have greater rooting depth, better drought tolerance, and better growth under limited N.

*SimRoot* was also used to assess the potential value of several architectural phenes, including nodal root growth angle and branching. These results indicate that moderately steep nodal root growth angles are best for N acquisition, but that the magnitude of the benefit depends on the rate of nitrate leaching, which in turn depends on the soil texture, precipitation, and N fertility regime. Planting density also effects the optimal root branching angle by affecting interplant competition. Variation in lateral branching was also related to nitrate capture. Root phenotypes with few, long lateral branches had the best nitrate capture. However, for phosphorus capture, the best root phenotype had many, short lateral roots. This functional tradeoff is an example of the complexity that modeling can elucidate.

The 'steep, cheap, and deep' ideotype is composed of multiple architectural, anatomical, and physiological traits. Some of these traits have interactions with each other, including synergism (positive interaction) and antagonism (negative interaction). The possible combinations of these traits generates millions of potential root phenotypes, the utility of which will be affected by several environmental variables including precipitation, soil type, nutrient availability, soil temperature regime, etc. Simulation modeling is the only feasible way to explore this 'fitness landscape' and guide empirical research to the most promising avenues.

Root modeling has great value in helping us understand the complexity of the interactions between plant root systems and soil. Linking root modeling efforts with empirical research and crop breeding is more powerful than modeling in isolation. Currently the field is limited by inadequate research and training investment outside of the EU. This must change if we are to realize the benefit of this tool for improving global food security.

## LITERATURE CITED

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