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## Dynamic root growth and architecture responses to limiting nutrient availability: linking physiological models and experimentation

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### ABSTRACT

In recent years the study of root phenotypic plasticity in response to sub-optimal environmental factors and the genetic control of these responses have received renewed attention. As a path to increased productivity, in particular for low fertility soils, several applied research projects worldwide target the improvement of crop root traits both in plant breeding and biotechnology contexts. To assist these tasks and address the challenge of optimizing root growth and architecture for enhanced mineral resource use, the development of realistic simulation models is of great importance. We review this research field from a modeling perspective focusing particularly on nutrient acquisition strategies for crop production on low nitrogen and low phosphorous soils. Soil heterogeneity and the dynamics of nutrient availability in the soil pose a challenging environment in which plants have to forage efficiently for nutrients in order to maintain their internal nutrient homeostasis throughout their life cycle. Mathematical models assist in understanding plant growth strategies and associated root phenes that have potential to be tested and introduced in physiological breeding programs. At the same time, we stress that it is necessary to carefully consider model assumptions and development from a whole plant-resource allocation perspective and to introduce or refine modules simulating explicitly root growth and architecture dynamics through ontogeny with reference to key factors that constrain root growth. In this view it is important to understand negative feedbacks such as plant–plant competition. We conclude by briefly touching on available and developing technologies for quantitative root phenotyping from lab to field, from quantification of partial root profiles in the field to 3D reconstruction of whole root systems. Finally, we discuss how these approaches can and should be tightly linked to modeling to explore the root phenome.

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### 1. Introduction

Land plants live partly above- and partly below-ground, giving them the opportunity to use a relatively large and diverse pool of resources available in these two “worlds”. This unique feature implies that plants have to cope with the widely different environmental conditions on either side of the soil surface. Strategies to maximize resource capture and adaptations to stress factors are likely to be different belowground in comparison to those aboveground. The strong architectural, morphological and anatomical differences between shoot and root systems are an indirect indication of these different strategies. The aboveground strategies are better understood than the belowground ones. This is not only because it is easier to quantify experimentally key structural and functional parameters of shoots compared with those of roots but also because the number of resources and biotic interactions that

roots need to acquire and establish, respectively, is much greater. Aboveground the main goals ignoring reproduction are light and CO<sub>2</sub> capture for photosynthesis, and the biosynthesis of carbon skeletons while facing the main constraint that water loss must be kept within strict boundaries. Typical stress factors in diverse environments include light competition and photo-damage, exposure to prolonged and excessive heat, and mechanical stress due to wind and herbivore attacks. In contrast, resource acquisition belowground targets, in addition to water, at least fourteen essential nutrients and, most likely essential for survival and productivity in an agro-ecological context, and several other beneficial ones (Marschner, 2011). Stresses belowground include toxic levels of aluminum, manganese, sodium or chloride anions, low water potentials, low temperatures, herbivore damage and mechanical resistance to root penetration. Not only the soil physics and chemistry is relatively complex, but also the number of biotic interactions is larger as the belowground microflora and fauna has both greater biomass and biodiversity compared with the aboveground counterpart (De Deyn and Van der Putten, 2005; Watt et al., 2006). It may be argued that the spatial and temporal heterogeneities of natural and agricultural soils are also greater than in the aboveground gas phase since the CO<sub>2</sub> concentrations that leave experience are relatively uniform and the ensuing gradients, i.e. greater concentrations close to the soil surface and lower

*Abbreviations:* QTL, Quantitative Traits Loci; MLH, Multiple Limitation Hypothesis; MRI, Magnetic Resonance Imaging; CT, Computed Tomography.

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concentrations close to the photosynthetically active canopy, are well defined. Also, light has a clear directionality, which results in greater light intensities at the top of the canopy and lower intensities deeper down. In contrast, water and nutrient distributions in the soil are highly variable and the different resources, as we will discuss below in more detail, do not necessarily occur at the same location. The heterogeneity of soil resources also implies that plants growing at different locations need to have different strategies. Not only the changes in soil parameters occurring in space but also those that depend on time (e.g. temperature fluctuations, mineralization rates, and soil moisture) are of importance. How these variables relate to the dynamics of plant developmental programs has been the object of detailed experimentation (Schurr et al., 2006). It follows that understanding plant growth responses and how plant architecture relates to both resource acquisition and utilization are crucial but not trivial tasks.

During the past decades, simulation models have been useful to study the dynamics of plant growth. These models are mathematical descriptions of the concepts and theories that reside in the plant biology domain and allow us to test the quantitative logic and compute the consequences of these different theories. In this review we summarize both the theoretical background of models that address the dynamics of plant growth and discuss this knowledge in the context of available experimental results. We will focus specifically on modeling root growth on low fertility soils. Biomass production in most ecosystems is probably foremost limited by edaphic stresses and not by carbon gain through photosynthesis. This point is recognized in agricultural practices as farmers dedicate considerable efforts in minimizing edaphic stresses by soil preparation, fertilization and irrigation management. Nevertheless, current soil management practices in intensive agriculture are not always sustainable in the long-term and cannot be easily transferred to less developed parts of the world where fertilizer inputs are more expensive and less available, and the level of mechanization is generally low. Therefore there is a need for plants that produce more with fewer inputs. However, to assist plant breeding and continue crop improvement in this direction, a better understanding of plant growth, and especially the root phenome, is needed (de Dorlodot et al., 2007; Hirel et al., 2007; Lynch, 2007b, 2011; Lynch and Brown, 2012).

The development of root architectural models has aided the study of the root phenome (Dunbabin et al., *in press*). Generally, these models simulate root architecture in three (spatial) dimensions, usually in conjunction with shoot growth. They typically simulate photosynthesis and carbon gain, water and nutrient uptake processes, and may include different growth responses to low nutrient availability and selected soil parameters characterized by a heterogeneous distribution. This makes it possible to study the root phenome from a functional perspective. These models have been used to scale up small-scale processes to the whole plant and to study root trait interactions (Dunbabin et al., 2006; Postma and Lynch, 2011a,b). In addition, they can simulate plant–plant competition and complementarity effects between plants (Collet et al., 2006; Dunbabin, 2007; Postma and Lynch, 2012). Crucial for linking genome and phenome, including genetic information in these models is possible as the modeling environment parameterization can be coupled directly to Quantitative Traits Loci (QTL) or genes and alleles that are associated to root phenotypes (Baldazzi et al., 2012; Hoogenboom and White, 2003; Letort et al., 2008). Even without considering gene-based modeling approaches, model development and parameterization is tightly linked to root phenotyping methodologies. New technologies for root phenotyping (Cobb et al., 2013; Fiorani and Schurr, 2013) make it possible to discover new traits, understand the function of these phenes and the level of environmental and genetic control. We provide examples of how these technologies may be exploited together with the development of plant models towards a better understanding of specific root traits and the phenome with particular reference to the goal of

achieving greater and sustainable crop production on low fertility soils and reduced input systems.

There may be three complementary strategies for nutrient acquisition and use efficiency (Richardson et al., 2011). The first strategy involves co-location of roots with nutrients and is linked to architectural traits that influence the placement of roots in the soil such that plants grow relatively more roots in horizontal and vertical soil domains characterized by sufficient nutrient availability. The second one involves efficient rhizosphere depletion of soil resources. This strategy is complementary to the first one and involves traits such as root hairs, uptake kinetics or rhizosphere manipulation through exudates. The third strategy consists in efficient nutrient utilization that usually translates into high biomass production and yield per unit of nutrients taken up, or in a form of metabolic efficiency expressed as the amount of nutrient or carbon invested per unit of nutrients taken up. However, describing nutrient acquisition and utilization in terms of these three strategies has the risk of potentially overlooking three important aspects that are central to the development of plant growth models and for assessing the utility of root traits in our view. These three aspects are: 1) what limits root growth; 2) dynamic changes accompanying plant developmental processes, and 3) intra- and inter-individual root competition. We give these aspects special attention in this review.

## 2. Maximizing root growth

Closed crop canopies capture over 90% of the available light. However, agriculture is apparently much more wasteful with nutrients. Typical fertilizer use efficiency lies below 50% for all the major nutrients (Baligar et al., 2001). Therefore, increased nutrient acquisition strategies are desirable in high-input agricultural systems to increase fertilizer use efficiency while in low-input ones increased root growth might be desirable to increase productivity. The simplest way to increase nutrient uptake might be by increasing root growth and biomass. In this respect, numerous studies have reported QTL as the basis of breeding for larger root systems (Cai et al., 2012; Chloupek et al., 2006; de Dorlodot et al., 2007; Gerald et al., 2006; Kaeppler et al., 2000; Liu et al., 2008; Price and Tomos, 1997; Tuberosa et al., 2002; Zhu et al., 2005b). Taking into account shoot growth, this may mean that a single plant has simply a lower shoot-to-root ratio, while at the crop level increased root growth would lead to greater root length density ( $\text{cm cm}^{-3}$ ). However, maximizing uptake through increasing the size of the root system is not as straightforward as it might appear. We first need to understand what the relationship between root size and uptake is. Secondly, we need to consider which processes actually restrict root growth. Both aspects are important for setting up modeling frameworks.

A comparatively greater root length density at a given time during development will result in faster depletion of nutrients but not necessarily in greater total nutrient uptake if these dynamics approach the limit of total available nutrients. In other words depletion of nutrients will result in a negative feedback such that further investment into root length will have a diminishing return. Models can simulate nutrient depletion by roots in different soil domains and can thereby be used to estimate to what degree roots compete for nutrients. Additionally, it can be estimated what percentage of roots has to be exposed to high nitrate concentrations in order to meet the nitrogen demand of the plant. These estimates are well below 20% (Burns, 1980; Robinson et al., 1991). Leaching and depletion of nitrate requires continued growth into previously unexplored soil domains. In contrast, uptake of less mobile nutrients such as phosphorus is closely related to root length duration ( $\text{cm day}$ ), i.e., the residence time of roots within a certain soil volume. Consequently, a comparatively larger root system would increase phosphorus uptake. The optimal root length density for phosphorus is probably much greater than for nitrate. Consequently, predictions of how additional root length would increase uptake will

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