

BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

# Understanding and improving crop root function

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# Introduction

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Recent decades have seen a dramatic increase in research on plant roots. A deeper understanding of the complex ways roots interact with soils is making it possible to 'design' roots to optimise nutrient and water uptake in low-input environments as well as deliver other benefits such as improved soil health and reduced nutrient leaching. This collection summarises the wealth of current research in this important area and how it can contribute to more ecologically sustainable and regenerative crop production systems.

Part 1 of this collection reviews recent research on understanding root system architecture and growth together with key interactions in the rhizosphere. Chapters cover topics such as modelling techniques, root architecture, root growth regulators, root anatomy and nutrient acquisition. Chapters also cover plant root interactions with rhizobacteria and the role of arbuscular mycorrhizal fungi in the nutrient cycle. Part 2 assesses how roots respond to biotic stresses such as parasites, root-feeding insects and nematodes. Part 3 summarises what we know about root uptake of water and key nutrients such as nitrogen and phosphorus. The final part of the book explores how this understanding can be used to improve root function. Chapters cover topics such as the genetics of plant root traits, the use of plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AM). Part 4 also discusses improving deep rooting in crop plants, the use of rootstocks to improve root function and crop nutrient-use efficiency and understanding and improving phosphorus acquisition by crop root systems.

## **Part 1 Analysing root system architecture, growth and interactions with the rhizosphere**

Chapter 1 reviews advances in root architectural modeling. Root system architectural (RSA) models have become important tools in root research and plant phenotyping for studying root traits, processes, and interactions with the environment. The models have been used to simulate how various root traits and processes influence water and nutrient uptake. At a more technical level, they have assisted the development of phenotyping technologies, particularly through the production of algorithms for segmenting root systems. Model complexity has also increased to cope with root functioning and contributions of root systems to plant nutrition. This chapter describes first the application of the models to questions in plant biology, breeding, and agronomy, and second the development of the models. It concludes with a short outlook suggesting that models need benchmarking and validation and that new developments

are likely to include better descriptions of root plasticity responses and focus on biological interactions among (soil) organisms, including mycorrhizal fungi.

The next chapter discusses the development of crop root architecture and optimization of nutrition acquisition, specifically focusing on rice. Root system architecture (RSA), the spatial configuration of a root system in the soil, is critical for water and nutrient acquisition. Rice generates a root system consisting of seminal, lateral, and crown/adventitious roots, whose growth and development are regulated by plant hormones and can be fine-tuned to meet adverse environmental conditions. Chapter 2 summarises original and more recent findings on genes and molecules identified so far to be involved in rice root development. It also discusses the cellular organization and function of rice roots, as well as the responses of RSA to the availability of water and nutrients.

Chapter 3 examines advances in understanding of plant root growth regulators. Global food production needs to increase by more than 60% by 2050 while concurrently reducing fertiliser applications to crops to reduce greenhouse emissions, production costs and environmental pollution. The chapter explores the role of hormones in nitrogen and phosphate uptake. In particular it focuses on auxin, cytokinin and strigolactones in various nutrient conditions and how they interact with each other to control root architectural responses. Past success with stay-green crop varieties, modified in cytokinin regulation of nitrogen remobilisation, demonstrates the real-world significance of a detailed understanding of hormone networks. The chapter also highlights current limitations in our understanding and exciting directions for the future.

Moving on from Chapter 3, Chapter 4 explores advances in understanding plant root anatomy and nutrient acquisition. The chapter summarises root anatomical traits and trait states, and nutrient acquisition mechanisms, along with some environmental issues affecting nutrient acquisition. Then, the whole range of adaptations of root anatomical traits, and its impact on nutrient acquisition are discussed. Combinations of anatomical traits lead to suggestions for root ideotypes potentially capable of supporting agricultural productivity under different edaphic constraints. Spatiotemporal aerenchyma formation in the various root types of maize under nitrate, phosphate or sulfate deprivation is discussed in a case study.

Chapter 5 assesses advances in understanding plant root hairs in relation to nutrient acquisition and crop root function. Root hairs are found on most terrestrial flowering plant species. They form from epidermal cells at a predetermined distance behind the growing root tip in three main patterns. Their presence, pattern, length, density and function are genetically controlled and numerous genes are expressed solely in root hairs. Their growth and proliferation are attenuated by the environment and root hairs growing in soil are generally shorter and less dense than those in laboratory studies. The chapter begins by discussing root hair physiology and development, followed

by a review of phylogenetic and genetic variation in root hairs. It also examines root hair interactions with the environment, then goes on to review trade-offs and interactions with other traits. A discussion on the prospects for utilising root hairs is also included.

Chapter 6 reviews our understanding of plant root interactions with rhizobacteria to improve biological nitrogen fixation in crops. Plant roots have evolved with the presence of rhizobacteria that can colonise the surface or interior of the plant. Some of these rhizobacteria are actively recruited by the plant and carry out particular functions, in particular in nutrient acquisition. Nitrogen-fixing bacteria form associations with many plant species, either as external associations or as symbiotic endophytes. The chapter highlights our current understanding of the molecular determinants of legume nodulation as well as challenges for improvements of biological nitrogen fixation in legumes and non-legumes. There is a need for connecting our knowledge of the molecular regulation of nodulation with field-based studies that take into account the interaction of nodulation with multiple biotic and abiotic constraints. In addition, current approaches for engineering new symbioses are discussed.

The final chapter of Part 1 considers advances in understanding arbuscular mycorrhizal fungal effects on soil nutrient cycling. Arbuscular mycorrhizal (AM) fungi assist with plant acquisition of nutrients, with most studies focussing on the nutrient forms taken up and translocated to the host. Recent studies have focused on how extraradical fungal hyphae can affect nutrient transformations, leaching and movement. However, it is still unclear the extent that nutrient cycling is influenced in agricultural contexts. Chapter 7 summarises how AM fungi can influence specific soil nutrient processes, then focuses on AM fungi in crop production systems and examples of (in)compatibilities in these systems. These research areas are then contextualized with new approaches to understand AM fungal roles in nutrient acquisition and utilisation, which the authors propose will lead to applications in improving nutrient use efficiency of agroecosystems.

## **Part 2 Root response to biotic threats**

The subject of Chapter 8 is advances in understanding plant root response to weedy root parasites. The chapter begins by reviewing host-parasitic weed interactions, focusing specifically on seed dispersal and germination and the possibility of host infection as a consequence of germination. The chapter then moves on to discuss host plant pre-penetration and post-penetration defence mechanisms. It concludes by emphasising the importance of developing management strategies for parasitic weed management.

Chapter 9 assesses the advances in understanding plant root responses to root-feeding insects. The chapter presents an overview of the interactions between plant roots and root-feeding insect herbivores, focussing on changes in growth and physiology and crucially how roots are defended against insect attack. Several previous reviews have covered the ecology and management of insect root herbivores, together with their interactions with the abiotic and biotic soil environment. Therefore, this chapter focuses particularly on advances in our understanding of how plant mutualistic fungi may affect root-herbivores. This is an emerging area of research, with many attendant knowledge gaps, but this is an important component of how plants resist attack by belowground insect herbivores.

The final chapter of Part 2 reviews advances in understanding plant root response to nematode attack. Plant parasitic nematodes are damaging pests on all crops grown across the world. They exploit plants using a range of strategies, ranging from simple browsing ectoparasitism to highly complex biotrophic endoparasites. Chapter 10 begins by highlighting the different modes of parasitism, which is then followed by a review of plant-nematode interactions. The chapter also examines activation and suppression of plant defence responses and discusses how natural resistance can be used to control plant nematodes.

### **Part 3 Root uptake of nutrients and water**

Part 3 begins with a chapter on advances in the understanding of nitrogen uptake by plant roots. Efficient use of nitrogen (N) by plants and particularly crops, is of global importance. In agriculture, high crop yields and protein content depend upon extensive N-inputs, but fertilizer N is costly to the farmer, and overuse can be damaging to the environment. A critical component of optimised usage is efficient capture by crop root systems. Chapter 11 focuses on principal mechanisms of uptake and factors influencing efficiency. Genetic variation in root architecture and in an array of transporters known to be involved in nitrogen capture is detailed. The impacts of abiotic stress factors such as soil structure are described. Finally, prospects and opportunities for crop improvement are discussed.

Chapter 12 looks at the advances in understanding plant root uptake of phosphorus. At a global scale, phosphorus (P) deficiency comprises a large area of cropland, while P has also been used in excess of crop requirements in many other regions. Improved crop P-acquisition efficiency would allow lower target critical soil P values and provide savings in P-fertiliser use. At the same time, it would reduce P lost through erosion, leaching and/or soil sorption. The chapter summarises the progress in research on root traits associated with P acquisition, including root morphology, architecture, biochemistry,

colonisation by arbuscular mycorrhizal fungi, and fine root endophytes, and the trade-offs among all these traits. Farming-management practices to improve P acquisition under current intensive agricultural systems are also discussed. The chapter summarises breeding progress in improving P-acquisition efficiency on soils that are both P deficient and P replete through legacy applications, and suggests future directions to improve P acquisition in five key areas.

Part 3 of the book concludes with an examination of advances in understanding plant root water uptake. Water deficit is one of the primary limitations to crop production. Chapter 13 reviews the role of root and rhizosphere hydraulic processes that affect the ability of a plant to extract water from the soil. Prominent features of rhizosphere hydraulic properties are: root shrinkage, alteration of pore geometry in the rhizosphere, effect of mucilage on water retention, hydraulic conductivity and water repellency, root hairs, and mycorrhiza connecting the root surface to the soil matrix. Although our understanding of the mechanisms related to these factors has advanced significantly in the last ten years, the relative importance of these rhizosphere processes for the ability of crops to extract water from the soil and better tolerate drought is still largely unclear. The authors propose that the next research step is to investigate the implications of these rhizosphere processes on crop growth and water use economy and to use this knowledge to grow more resilient crops that match to their environment.

## **Part 4 Improving root function**

The final part of the book opens with a discussion on understanding and exploiting the genetics of plant root traits. Chapter 14 illustrates how genomics and other -omics approaches coupled with new-generation sequencing (NGS) platforms have been deployed to dissect the genetic make-up of RSA traits and better understand their functions, particularly under environmentally constrained conditions that commonly occur in most farmed soils. The major emphasis is devoted to studies during the past two decades in crops with occasional reference to the vast literature from RSA studies conducted in *Arabidopsis* and other model plants. The chapter also provides examples on how, in some cases, this knowledge is already benefiting farmers and how it can help in reducing the environmental impact of agriculture worldwide.

Chapter 15 focuses on the use of plant-growth-promoting rhizobacteria (PGPR) to improve root function/crop nutrient use efficiency. Bacteria that colonize plant roots and promote plant growth and development, plant growth-promoting rhizobacteria (PGPR), can contribute to more sustainable intensification of agriculture while minimizing detrimental impacts associated with excessive fertilizer applications. The chapter reviews recent research on the use of PGPR as biofertilizers to enhance root function and improve nutrient

uptake. PGPR alter root architecture, root metabolism, nutrient use efficiency and enhance plant tolerance to abiotic stresses such as salinity and drought by a variety of mechanisms that are not yet well understood. Beneficial effects observed in the laboratory are not always seen consistently in the field due to varying environmental and complex biotic interactions, limiting the widespread application of PGPR in agriculture. The chapter highlights new research approaches that will facilitate our understanding of this complex community at the molecular level and from a holistic perspective. Applied research to facilitate registration and commercialization of biofertilizers is also considered.

The next chapter examines the use of arbuscular mycorrhizal fungi to improve root function and nutrient use efficiency. Arbuscular mycorrhizal fungi (AMF) form endosymbiosis with over 70% of land plants, including most crops including cereals. These symbioses facilitate resource exchange between partners and can significantly increase plant nutrient uptake and growth, among other benefits. AMF ubiquity in agricultural soils, in addition to the many roles they are known to play in soil health, demands we consider them when discussing crop function. Chapter 16 discusses how AMF are capable of increasing crop acquisition of macro- and micronutrients. It examines further impacts that AMF have on root system architecture, and how this relates to nutrient acquisition. The chapter also highlights reasons why potential benefits of the symbiosis are often not realised and how this influences current perspectives on the utility of AMF. It also discusses aspects of modern agronomy practice which are deleterious to mycorrhizal functioning. Strategies are suggested by which mycorrhizas might be exploited in future highlighting future research priorities.

Chapter 17 focuses on using systems agronomy to exploit deep roots in crops. The chapter reviews strategies to capture benefits from deeper rooting, taking the example of the semi-arid southern Australian wheat belt. The chapter also focuses on the theme of better capturing deep subsoil water with deeper and more effective root systems, and looks at ways of increasing rooting depth, the role of agronomic techniques as well as genetic improvement methods. A discussion on the legacy effects of deeper roots and utilisation of deep soil water is also included, which is then followed by a review of the benefits of scaling up to the whole farm level, specifically large farms in Australia.

The subject of Chapter 18 is the use of rootstocks to improve root function and resource use efficiency. Grafting, a technique to attach genetically different shoots and roots (scions and rootstocks) allows 'designer root systems' to enhance agricultural productivity and sustainability. Rootstocks improve plant nutrient relations by increasing nutrient capture and/or nutrient use efficiency, by multiple mechanisms including altered root morphology. Moreover, rootstocks can enhance water uptake and/or diminish water loss according to changes in root form and function, and root-to-shoot phytohormonal signalling. The

chapter begins by focusing on nutrient and water relations to rootstocks, then moves on to discuss how when triggered, changes in phytohormone status can affect rootstock hormone status and in turn, affect shoot processes in plants. A case study on using tomato rootstocks as a viable strategy to overcome abiotic stresses in Ghana is also included.

The final chapter of the book focuses on delivering improved phosphorus acquisition by root systems in pasture and arable crops. Improving the low efficiency of phosphorus (P) use in agriculture is an imperative because P is one of the key nutrients underpinning sustainable intensification of food production and the rock-phosphate reserves, from which P fertilisers are made, are finite. Chapter 19 describes key soil, root and microbial processes that influence P acquisition with a focus on factors that can be managed to ensure optimal use of fertiliser, and development of root systems for improved P acquisition. A case study describing grasslands in southern Australia where the P-balance efficiency of production is very low, mainly because soils are P deficient and moderately to highly P-sorbing, is also included. Progress towards improved P efficiency using pasture legumes with high P-acquisition efficiency is outlined, followed by a discussion on the development of a 'whole-of-system' understanding for effective P acquisition by roots.

# Part 1

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**Analysing root system architecture,  
growth and interactions with the  
rhizosphere**

# Chapter 1

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## Advances in root architectural modeling

*Johannes A. Postma, Forschungszentrum Jülich, Germany; and Christopher K. Black, The Pennsylvania State University, USA*

- 1 Introduction
- 2 Advances in the application of root system architectural (RSA) models
- 3 Advances in model development
- 4 Current challenges and future directions
- 5 Conclusions
- 6 Acknowledgements
- 7 Where to look for further information
- 8 References

### 1 Introduction

Mathematical models of plant roots are formulations that quantitatively describe the morphology, size, growth, or physiology of plant roots. These models have a long history of development, and different root models have been presented in the literature. Among the different models, root system architectural (RSA) models are distinguished from other model types by their specific concern for which roots of what types are where in space, and they give arguably the most explicit and detailed representations of the root system (Table 1). The first RSA models were developed at the end of the 1980s (Fitter, 1987; Diggle, 1988; Pagès et al., 1989). At that time the simulated root systems were relatively small and the simulations were mainly concerned with representing the geometric aspects of root architecture. Since those early beginnings, these models have been developed further and the range of applications has expanded. The models have added physiological aspects of root growth and functioning, and thereby in effect have become what we now call functional structural plant models (Vos et al., 2010), albeit with the focus belowground, not aboveground. The functionality and application of RSA models were reviewed by Dunbabin et al. (2013). Since then new model codes have been released and many model studies have been published. The RSA models have been coupled to soil and shoot models, and have acquired more detail and functionality. Significant effort went into improving the code, and the model development typically expanded

**Table 1** List of cited models

Model software	Citation
ArchiSimple	Pagès et al. (2014)
CRootBox	Schnepf et al. (2018b)
DigR	Barczy et al. (2018)
Grolmp	Henke et al. (2014)
OpenSimRoot	Postma et al. (2017)
RSWMS	Javaux et al. (2008)
RootBox	Leitner et al. (2010)
SimRoot	Postma and Lynch (2011b)
SPACSYS	Wu et al. (2007)

from single researchers to development teams. In this chapter, we aim to describe the advances of these models during the last decade (2010–2020) and how the simulation exercises contributed to our scientific understanding of root and plant functioning.

## 2 Advances in the application of root system architectural (RSA) models

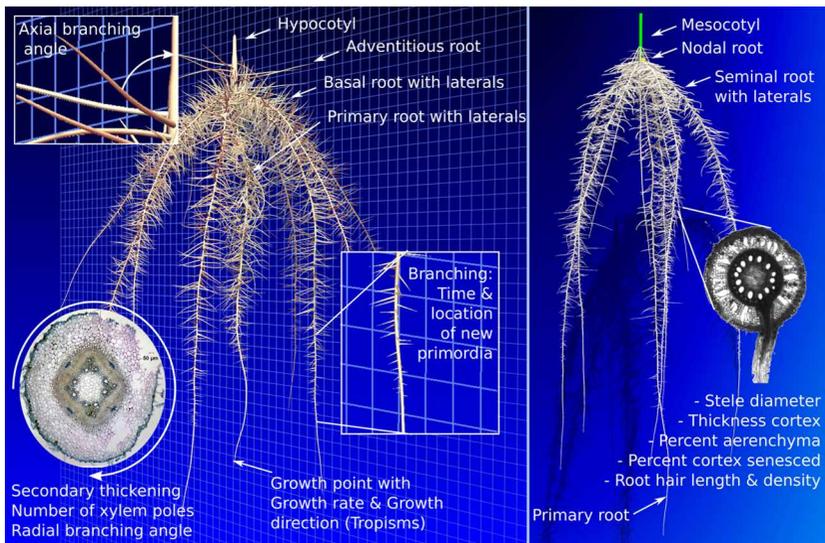
During the last decade, RSA models have been applied to study an increasing number of plant species, root traits, and plant physiological processes. The models have been coupled to increasingly more complex simulations of the (soil) environment (see Section 3) and many papers focus on the interaction between environment and phenotype. This has led to applications in the area of breeding, agronomy, and ecology, although these fields are strictly speaking at a higher scale than single plant models. Currently, our understanding of the function of phenotypic root traits is still fairly limited, but the RSA model studies that we highlight here have demonstrated the complexity of, and provided insights into, phenotype by environment interactions.

### 2.1 Root traits studied

RSA models contrast with root length density models by explicitly simulating the placement of each root, whereas root length density models typically assume homogeneous distribution of roots within a given soil layer (Postma et al., 2008). Simulating competition for nitrate among different species (maize, bean and squash) (Postma and Lynch, 2012) showed that a homogeneous root distribution gave much greater nitrate uptake than a root distribution determined by root architecture. We can conclude from this that root architecture restricts the foraging capacity of the root. This immediately raises the question

as to what the optimal architecture is for the acquisition of various nutrients. Several studies were published in which the sensitivity of nutrient uptake for root architectural parameters was tested. These parameters are usually directly translated to root architectural traits. In many cases, the sensitivity depended on the simulation environment and nutrient simulated, giving some insight into the complex interactions between the environment and root architecture. Additionally, the studies suggested some trade-offs exist for optimizing root architecture toward the acquisition of different nutrients.

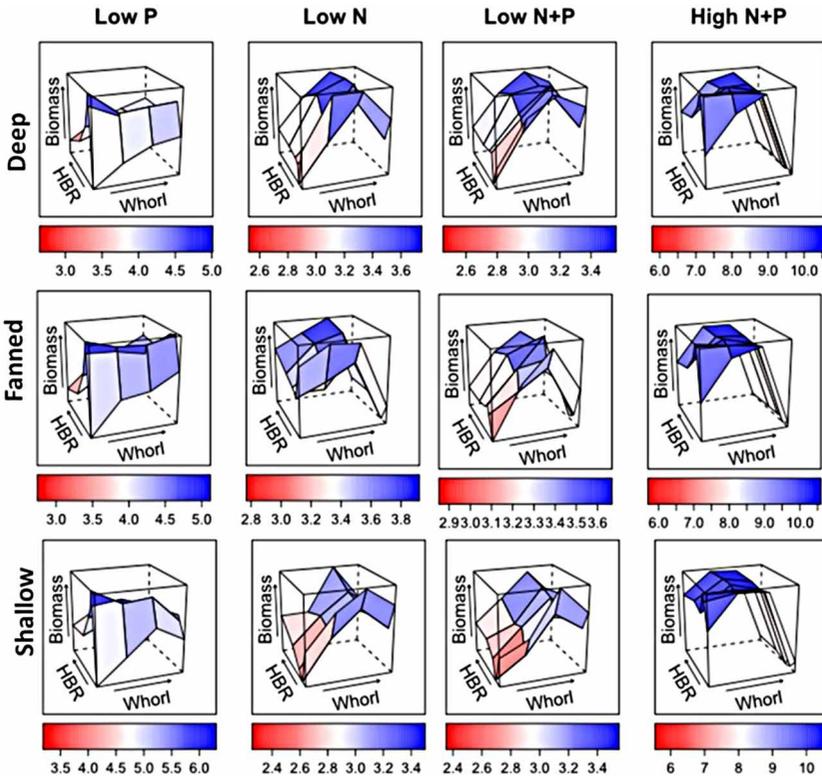
A relatively simple way to understand trait is root growth angle of branch- or adventitious roots (Fig. 1). Although various angles might be measured during phenotyping, including insertion angles, set-point angles, and the rate of the gravitropic response (Freschet et al., 2020), the overall angle causes the root system to be either shallower or steeper. Dathe et al. (2016) simulated steeper and shallower root growth angles in maize and showed that the optimum for nitrate uptake depended on the rate of nitrate leaching, with fanned phenotypes (larger variation in root growth angle) achieving relatively good performance in many environments. Already in 2001, Rubio et al. (2001) showed that shallow root growth angles may be advantageous for P uptake by basal roots in bean, and this work was recently followed up by a much larger set of simulations including mechanistic simulation of P uptake and simulating phenotypes that varied both in root growth angle and the number of basal roots (Rangarajan et al., 2018). The study gives support for the existence of



**Figure 1** Rendering of a simulated bean and maize root system with indication of various root traits. Simulations were run with OpenSimRoot and rendering was done with Paraview. Figure was reproduced with permission from Postma et al. (2017).

phenotypic variation in both traits, as the optimum is strongly dependent on the environment simulated. Nevertheless, the overall picture is that plants are faced with a trade-off between shallow and deep placement of roots through a change in root growth branching angle and that the trade-off determines the relative uptake of shallow (P) and deep (nitrate) resources. Experimental papers confirming the relation between P and nitrate uptake and root growth angle include greater P uptake by bean phenotypes with shallow basal root growth angles (Miguel et al., 2015) and greater N uptake by deep-rooting maize (Trachsel et al., 2013).

Phenotypic variation in the number of root axes was studied in several papers. We already mentioned the simulation study of Rangarajan et al. (2018) (Fig. 2), in which two or three whorls of basal roots were both the most frequently observed phenotype and the optimal number in many simulation scenarios. Lateral root branching density, which is the inverse of the interbranching



**Figure 2** Simulated shoot biomass of 40-day-old bean plants as a function of basal root whorl number (BRWN), number of hypocotyl born roots (HBR), basal root angles type (deep, fanned, shallow), and nutrient availability (low P, low N, low N+P, high N+P). Figure reproduced with permission from Rangarajan et al. (2018).

distance, has been studied experimentally in many species (Pagès, 2019; Freschet et al., 2020). Postma et al. (2014a) simulated observed phenotypic variation for this trait and predicted a trade-off between phenotypes with many short and few long lateral roots. The many short phenotypes would be advantageous for P uptake, whereas the few long phenotypes would benefit nitrate uptake. Experimental confirmation of the results came from two papers studying the same set of genotypes under P deficiency (Jia et al., 2018) and N deficiency (Zhan and Lynch, 2015). With a semi RSA model, Heppell et al. (2015) concluded that higher branching in the topsoil and lower branching in the subsoil could increase P uptake by 42%. In another simulation study, dense root systems were beneficial to quickly capture in-season rainfall but not for exploiting water stored before the growing season (Tron et al., 2015). Recently, Muller et al. (2019) took the concept of branching a step further and distinguished randomness in branching from structured variation. RSA models will be well-suited to simulate these various kinds of variation in branching and might estimate the utility of the different phenotypes in various soil environments. The lateral root branching density not only interacts with the environment but also with other traits. For example, Postma and Lynch (2011a) simulated a positive interaction between the number of branches and the amount of root cortical aerenchyma (discussed further below).

RSA models have also been used to investigate anatomical traits. So far the function of these has been difficult to study, so RSA models have been used to pose and simulate hypotheses on how anatomical traits influence nutrient uptake and plant physiology. Root cortical aerenchyma, the formation of air spaces in the root in this case through programmed cell death, is an interesting example. Aerenchyma formation is negatively correlated to both root respiration and root nutrient content ( $\text{mol cm}^{-3}$ ) and was hypothesized to reduce the metabolic cost of roots, allowing new root growth and thereby greater nutrient uptake (Fan et al., 2003; Postma and Lynch, 2011a,b). The simulation studies suggest large benefits from a metabolically more efficient root system, especially in maize where aerenchyma formation covers a relatively large percentage of the cortex as opposed to bean where aerenchyma formation is much less prevalent and is in part replaced by the loss of the whole cortex (cortical senescence) due to secondary growth. Variation in secondary growth itself, however, may be a form of metabolic efficiency that can be achieved when stressed plants with smaller shoots have reduced water requirements (Strock et al., 2017). Loss of the whole cortex also occurs in barley and several other Poaceae due to programmed cell death rather than secondary growth (Schneider et al., 2018). Cortical senescence is not only associated with reduced respiration and nutrient content but also associated with reduced water uptake and nutrient uptake (Schneider et al., 2017b). Simulating these processes showed that cortical senescence is beneficial when it occurs in the major root axes, but not

in the lateral roots (Schneider et al., 2017a). Indeed, cortical senescence in lateral roots was not observed.

One of the most studied anatomical traits in plant nutrition is the formation of root hairs. Different approaches to simulate the function of root hairs have been published. Zygalkis et al. (2011) presented a dual-porosity model for root hairs in which they take account of the interaction between root hair geometry and soil particle geometry. The model simulated greater uptake from P in micropores and showed that the uptake was less sensitive to soil moisture content than previously simulated. Leitner et al. (2010) took a different approach and used homogenization, a mathematical procedure, to derive an analytical solution for the uptake of nutrients by root hairs. Such analytical solutions can compute much faster and thereby be useful when simulating 100 000+ root segments.

Thus far we have treated the architectural traits as static traits, but in reality, many of these traits are influenced by the environment. Simulation models currently include some of this root growth plasticity, even though much about the mechanisms and regulation of root growth plasticity is still unknown. The models often include empirically derived relations between environmental conditions, plant status, and root growth responses (Dunbabin et al., 2011; Tournier et al., 2015; Postma et al., 2017). Root responses are typically defined in terms of tropisms (change in the growth direction), branching (change in the rate of primordia formation), or elongation rate. These empirical relations may be sufficient to study root growth plasticity as a functional trait. Henke et al. (2014) concluded that root growth plasticity in a heterogeneous soil would enhance N uptake. Similarly, Chen et al. (2013) produced a simulation study with root proliferation in response to P banding, which suggested large benefits from the proliferation response.

## **2.2 Root processes studied**

Functional structural plant models (FSPM) not only simulate structure, but also the relevant processes associated with that structure. In this respect, RSA models advanced strongly as they were coupled to models of plant metabolism, nutrient and water uptake. Besides the interactions between structure and environment, the mechanics of the structure and soil were explored.

To simulate plant metabolism, RSA models were coupled to shoot models, albeit not often coupled to geometric shoot models (see Section 3). This coupling allowed simulation of nutrient and carbon balances and source-sink relations, which play an important role in many simulations. The models typically restricted the total carbon consumption to the carbon available from photosynthesis and carbon storage. Carbon consumption is restricted by reducing the growth rate of the root system. Several conclusions resulted from

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