

BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Understanding and improving crop root function

Edited by Emeritus Professor Peter J. Gregory
University of Reading, UK



Contents

Series list	xiii
Introduction	xx
Part 1 Analysing root system architecture, growth and interactions with the rhizosphere	
1 Advances in root architectural modeling	3
<i>Johannes A. Postma, Forschungszentrum Jülich, Germany; and Christopher K. Black, The Pennsylvania State University, USA</i>	
1 Introduction	3
2 Advances in the application of root system architectural (RSA) models	4
3 Advances in model development	16
4 Current challenges and future directions	23
5 Conclusions	24
6 Acknowledgements	24
7 Where to look for further information	24
8 References	24
2 The development of crop root architecture and optimization of nutrition acquisition: the case of rice	33
<i>Wei Xuan, Nanjing Agricultural University, China; Yuanming Xie, Nanjing Agricultural University, China and Ghent University and VIB-UGent Center for Plant Systems Biology, Belgium; and Tom Beeckman, Ghent University and VIB-UGent Center for Plant Systems Biology, Belgium</i>	
1 Introduction	33
2 Rice root architecture and cellular organization of the rice root	34
3 Hormone regulation of rice root development	38
4 Control of rice root development by other pathways	45
5 Adaptation of RSA to environmental conditions	49
6 Future trends in research	53

	7 Where to look for further information	55
	8 Acknowledgement	55
	9 References	55
3	Advances in understanding plant root growth regulators <i>Findimila Dio Ishaya and Amanda Rasmussen, University of Nottingham, UK</i>	69
	1 Introduction	69
	2 Auxin	72
	3 Cytokinin	76
	4 Strigolactones	79
	5 Using plant growth regulators to control root development for improved nutrient uptake	84
	6 Future trends in research	86
	7 Conclusion	89
	8 Where to look for further information	89
	9 References	91
4	Advances in understanding plant root anatomy and nutrient acquisition <i>Dimitris L. Bouranis and Styliani N. Chorianopoulou, Agricultural University of Athens, Greece</i>	99
	1 Introduction	99
	2 Root anatomical traits	99
	3 The nutrient acquisition mechanisms	101
	4 Environmental issues affecting nutrient acquisition	102
	5 Adaptations of root anatomical traits	103
	6 Impact of adapted root anatomical traits on nutrient acquisition	114
	7 Case study: root anatomy of maize under nutrient shortage	118
	8 Summary	121
	9 Future trends in research	121
	10 Where to look for further information	122
	11 References	123
5	Advances in understanding plant root hairs in relation to nutrient acquisition and crop root function <i>Timothy S. George and Lawrie K. Brown, The James Hutton Institute, UK; and A. Glyn Bengough, University of Dundee, UK</i>	127
	1 Introduction	127
	2 Root hair physiology and development	128
	3 Phylogenetic and genetic variation in root hairs	132
	4 Root hair interactions with the environment	138
	5 Trade-offs and interactions with other traits	147

6	Prospects for utilising root hairs	149
	7 Acknowledgement	150
	8 Where to look for further information	150
	9 References	151
6	Understanding plant-root interactions with rhizobacteria to improve biological nitrogen fixation in crops <i>Ulrike Mathesius, Australian National University, Australia; Jian Jin, La Trobe University, Australia and Chinese Academy of Sciences, China; Yansheng Li, Chinese Academy of Sciences, China; and Michelle Watt, Forschungszentrum Juelich GmbH, Germany and University of Melbourne, Australia</i>	163
	1 Introduction	163
	2 Understanding existing interactions of plants with nitrogen-fixing rhizobacteria	164
	3 Improvements and limitations to nitrogen-fixing associations and engineering new symbioses	173
	4 Conclusion	181
	5 Acknowledgements	183
	6 Where to look for further information	183
	7 References	184
7	Advances in understanding arbuscular mycorrhizal fungal effects on soil nutrient cycling <i>Haiyang Zhang and Jeff R. Powell, Western Sydney University, Australia</i>	195
	1 Introduction	195
	2 Current understanding of AM fungi and nutrient cycling	196
	3 AM fungal effects on soil fertility in an agronomic context	201
	4 Future research: functional linkages between roots and AM fungi	204
	5 Where to look for further information	206
	6 References	207
Part 2 Root response to biotic threats		
8	Advances in understanding plant root response to weedy root parasites <i>M. Fernández-Aparicio and D. Rubiales, CSIC, Spain</i>	215
	1 Introduction	215
	2 Host-parasitic weed interaction	216
	3 Host plant defence	218
	4 Future trends in research	222
	5 Where to look for further information	224

6	Acknowledgements	224
7	References	224
9	Advances in understanding plant root responses to root-feeding insects	231
	<i>Scott N. Johnson, Hawkesbury Institute for the Environment - Western Sydney University, Australia; and Ximena Cibils-Stewart, Hawkesbury Institute for the Environment - Western Sydney University, Australia and Instituto Nacional de Investigación Agropecuaria (INIA), Uruguay</i>	
1	Introduction	231
2	Root-feeding insects: an evolving research path	233
3	Changes in plant growth and physiology	234
4	Root defences against root herbivory	236
5	Root defence via fungal partners	240
6	Conclusion and future trends	249
7	Where to look for further information	250
8	References	252
10	Advances in understanding plant root response to nematode attack	267
	<i>Shahid Siddique, University of California-Davis, USA; and John T. Jones, The James Hutton Institute and University of St Andrews, UK</i>	
1	Introduction	267
2	Modes of parasitism	268
3	Plant-nematode interactions	271
4	Activation and suppression of plant defence responses	281
5	Resistance	283
6	Future trends	288
7	Where to look for further information	288
8	Acknowledgement	289
9	References	289
Part 3 Root uptake of nutrients and water		
11	Advances in the understanding of nitrogen (N) uptake by plant roots	303
	<i>Malcolm J. Hawkesford and William R. Whalley, Rothamsted Research, UK</i>	
1	Introduction	303
2	Nitrogen in the soil	304
3	Nitrogen uptake and NUE in agriculture	305

4 Genetic variation in NUE and roots	306
5 Transporters involved in nitrogen uptake	308
6 Root responses to nitrogen availability	310
7 Effects of soil conditions and structure on root N-uptake and proliferation	310
8 Future trends for crop improvement	313
9 Acknowledgements	314
10 Where to look for further information	314
11 References	315
12 Advances in understanding plant root uptake of phosphorus	321
<i>Jiayin Pang, The University of Western Australia, Australia; Zihui Wen, The University of Western Australia, Australia and China Agricultural University, China; Daniel Kidd and Megan H. Ryan, The University of Western Australia, Australia; Rui-Peng Yu, Long Li and Wen-Feng Cong, China Agricultural University, China; Kadambot H. M. Siddique, The University of Western Australia, Australia; and Hans Lambers, The University of Western Australia, Australia and China Agricultural University, China</i>	
1 Introduction	321
2 Root architecture and morphology associated with phosphorus (P) uptake	322
3 Root biochemistry associated with P uptake	325
4 Arbuscular mycorrhizal fungi (AMF) and fine root endophytes	337
5 Trade-offs in traits	341
6 Microbially-mediated efficient P acquisition in species-diverse systems	343
7 Farming-management practice in P acquisition at the intensive agricultural system level	344
8 Breeding to improve P acquisition	347
9 Case study: mobilisation of phosphorus and manganese in cluster roots of <i>Lupinus albus</i>	349
10 Conclusion	351
11 Future trends in research	352
12 Where to look for further information	354
13 Acknowledgement	355
14 References	355
13 Advances in understanding plant root water uptake	373
<i>Mutez Ali Ahmed, University of Bayreuth, Germany; Doris Vetterlein, Helmholtz Centre for Environmental Research-UFZ, Germany; and Andrea Carminati, University of Bayreuth, Germany</i>	
1 Introduction	373
2 Principles of water flow in soil and plants	375

3 Rhizosphere processes relevant for root water uptake	382
4 Conclusion and future trends	386
5 Acknowledgements	387
6 References	387

Part 4 Improving root function

14 Understanding and exploiting the genetics of plant root traits	395
<i>Roberto Tuberosa, Elisabetta Frascaroli, Marco Maccaferri and Silvio Salvi, University of Bologna, Italy</i>	
1 Introduction	395
2 Mapping loci for root traits	396
3 Fine mapping and cloning of loci for root traits	420
4 Genomics-assisted breeding for root traits	425
5 Conclusion and future trends	433
6 Where to look for further information	437
7 References	438
15 The use of plant growth-promoting rhizobacteria (PGPR) to improve root function and crop nutrient use efficiency	467
<i>Melissa M. Larrabee and Louise M. Nelson, University of British Columbia, Canada</i>	
1 Introduction	467
2 The effect of plant growth-promoting rhizobacteria on root function	469
3 The effect of plant growth-promoting rhizobacteria on plant mineral nutrition	477
4 Future trends in research	482
5 Conclusion	485
6 Where to look for further information	485
7 References	486
16 The use of arbuscular mycorrhizal fungi to improve root function and nutrient-use efficiency	493
<i>Tom Thirkell, Grace Hoysted, Ashleigh Elliott and Katie Field, University of Leeds, UK; and Tim Daniell, University of Sheffield, UK</i>	
1 Introduction	493
2 Mycorrhizal nutrient acquisition	495
3 AMF effects on root architecture	501
4 Barriers to AMF utilisation in agriculture	503
5 Adapt, replace, restore (or ignore?)	506
6 Conclusion	512
7 Future trends in research	513
8 Where to look for more information	514
9 References	515

17	Using systems agronomy to exploit deep roots in crops <i>John Kirkegaard and Julianne Lilley, CSIRO Agriculture and Food, Australia</i>	531
	1 Introduction	531
	2 Wheat-based farming systems in south-eastern Australia - a brief overview	532
	3 Unused subsoil water	535
	4 Improving root systems to capture subsoil water	537
	5 Increasing the depth of roots	539
	6 Capturing more subsoil water - manipulating the system rather than the soil	542
	7 Genetic improvements to rooting depth and density	548
	8 Accounting for legacy effects	549
	9 Scaling up to whole farm benefits	550
	10 The future - using more of the soil and more of the season	552
	11 Conclusions	553
	12 Where to look for further information	553
	13 References	554
18	Rootstocks to improve root function and resource-use efficiency <i>Francisco Pérez-Alfocea, CEBAS-CSIC, Spain; Stephen Yeboah, CSIR-Crops Research Institute, Ghana; and Ian C. Dodd, Lancaster Environment Centre, UK</i>	561
	1 Introduction	561
	2 Nutrient relations	563
	3 Water relations	570
	4 Phytohormones	573
	5 Case study: Tomato rootstocks as a viable strategy to overcome abiotic stresses in Ghana	576
	6 Conclusion	578
	7 Future trends	578
	8 Where to look for further information	579
	9 Acknowledgements	579
	10 References	580
19	Delivering improved phosphorus acquisition by root systems in pasture and arable crops <i>Richard J. Simpson and Rebecca E. Haling, CSIRO Agriculture and Food, Australia; and Phillip Graham, Graham Advisory, Australia</i>	589
	1 Introduction	589
	2 Options for improving phosphorus acquisition by roots in pastures and arable crops	591

3 Rhizosphere modifications that improve phosphorus acquisition	597
4 Understanding the agronomic context in which improved phosphorus acquisition by roots can deliver benefits	600
5 Critical phosphorus benchmarks for soil phosphorus management	604
6 Case study: improving the phosphorus efficiency of sheep and beef grassland farming in southern Australia	606
7 Conclusion and future trends in research	628
8 Where to look for further information	629
9 Acknowledgements	631
10 References	631
Index	649

Introduction

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

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

Chapter 1

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

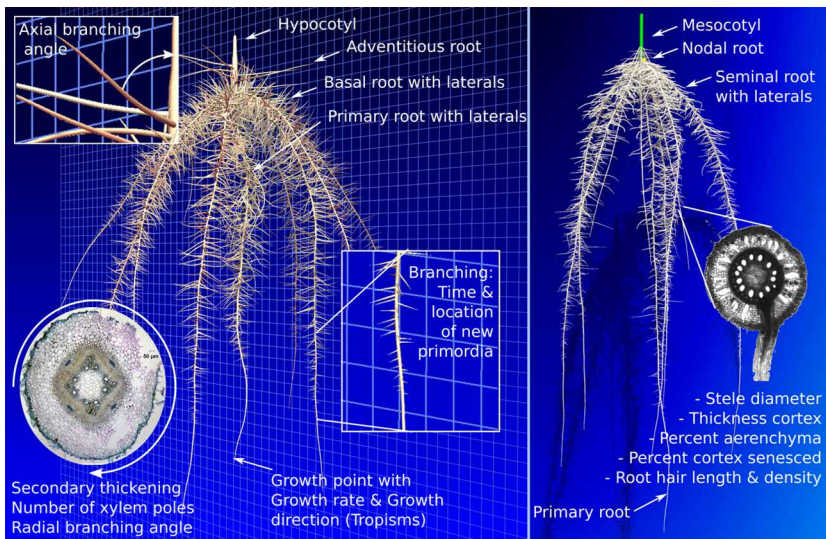


Figure 1 Rendering of a simulated bean and maize root system with indication of various root traits. Simulations were run with OpenSimRoot and rendering was done with Paraview. Figure was reproduced with permission from Postma et al. (2017).

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

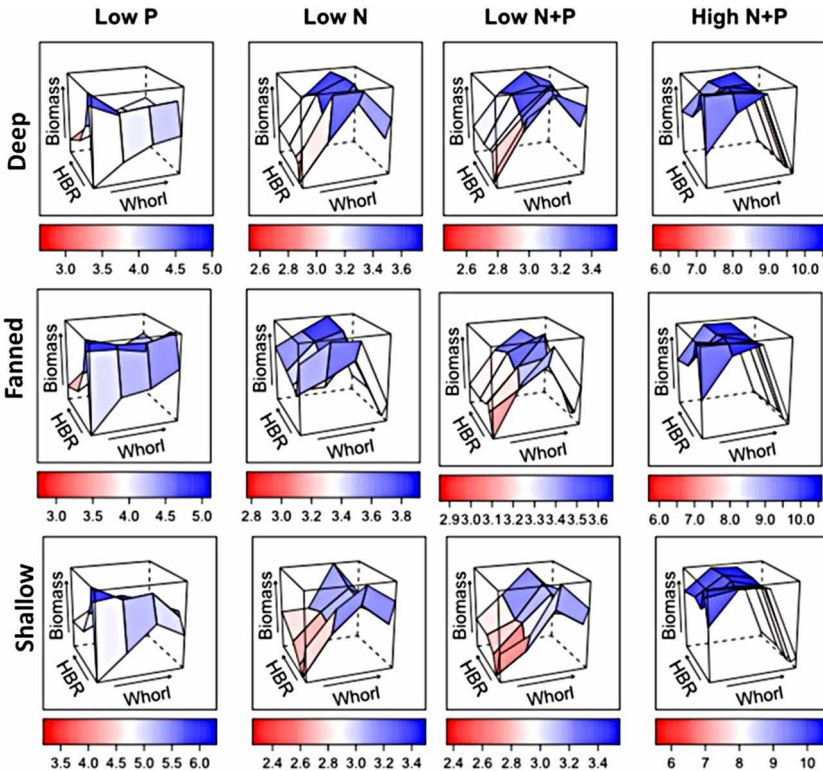


Figure 2 Simulated shoot biomass of 40-day-old bean plants as a function of basal root whorl number (BRWN), number of hypocotyl born roots (HBR), basal root angles type (deep, fanned, shallow), and nutrient availability (low P, low N, low N+P, high N+P). Figure reproduced with permission from Rangarajan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

Index

Note: Page numbers in italics denote figures.

- ABA. *see* Abscisic acid (ABA)
- ABCG. *see* G subfamily ATP-binding cassette (ABCG)
- Abscisic acid (ABA) 43–44, 376, 572, 573
regulation, of canopy growth and water use 574
- ACC. *see* 1-Aminocyclopropane-1-carboxylic acid (ACC)
- Aerenchyma formation 7
- AgResearch New Zealand 244
- AMAPsim 19
- AMAPstudio 19
- Amaranthus hypochondriacus* 481
- AMF. *see* Arbuscular mycorrhizal fungi (AMF)
- Amino acid metabolism 46
- 1-Aminocyclopropane-1-carboxylic acid (ACC) 470
regulation, of nutrient stress responses 575–576
- Ammonium transporters 309
- Anchorage, of root hairs 139–140
- AOI. *see* Autoregulation of infection (AOI)
- Aphelenchoides besseyi* 268
- Apoplastic pathway 101, 103
- AQP. *see* Aquaporins (AQP)
- Aquaporins (AQP) 377
- Arabidopsis* spp. 37, 38, 46, 49, 52, 54, 72, 75, 79, 85, 275, 280, 288, 308, 309, 336, 396, 398, 400–402, 432
- Arabidopsis thaliana* 136, 138, 306, 469, 470, 478
- Arbuscular mycorrhizal fungal effects, on soil
nutrient cycling 195–196, 202
current understandings
nutrient uptake and transfer 196–197
soil nutrient processes 197–201
morphological and nutritional linkages
between root and hyphal traits 204–206
soil fertility and 200–201
interactions among agronomic practices 201–204
- Arbuscular mycorrhizal fungi (AMF) 147–148, 240, 337–341, 385, 481, 494–495, 622–623
in crop micronutrient uptake 500–501
effects on root architecture 501–502
exploiting genetic diversity in plant interactions with 506–507
field inoculation with 507–508
inoculum production 508–509
inoculant outcomes reliability 509–511
AMF as target of efforts 511–512
future trends in research 513–514
mycorrhizal nutrient acquisition
symbiotic fungi, improving
phosphorus assimilation in crops 495–497
root-associated soil fungi, in crop N nutrition 497–500
phosphorus acquisition and 596
root defence and 241
utilisation in agriculture, barriers to 503
crop growth responses to symbiotic fungal colonisation 503–505
agricultural management detrimental effects 505
- ArchiSimple model 15, 21
- AtNRT1.1 73, 309
- AtNRT2.1 71
- AtNRT2.2 71

- Atrichoblasts 131
 Autophagy and autophagy-like processes 110
 Autoradiographs 129, 130
 Autoregulation of infection (AOI) 167
 Auxin 84, 276–278, 469
 biosynthesis, transport, and signalling 72–73
 manipulation of 84–85
 nitrogen and 73–75
 phosphate and 75–76
 rice root development and 39–41
Avena sativa 474
 Axiom®CicerSNP array 423
 Axiom®HD wheat genotyping array 423
Azospirillum spp. 470

Bacillus spp.
 B. amyloliquefaciens 472
 B. cereus 476, 481
 B. firmus SW5 474
 B. megaterium 472, 477
 B. subtilis Y16 476
 B. thuringiensis (Bt) 239, 477
 B. velezensis 478
 KAP6 482
 Y14 476
Beaufort rootstock 564, 565, 569, 571, 573
Beauveria bassiana 246–248
 Bioengineering 240
 Biofertilization 477–478, 482
 Biological nitrogen fixation 163–164, 197–198
 improvements and limitations
 legume nitrogen fixation 173–176
 nodulation molecular aspects and soil complexity uncertainties 176–178
 non-legumes and nitrogen-fixing symbioses 178–181
 rhizobacteria and 164–173
 significance of 181–183
Bradyrhizobium japonicum USDA 110 476
Brassica napus 314, 333, 470, 534
 Brassinosteroids 44
Bromus spp. 617
 Broomrapes 215, 218
 BSR-Seq 435
 ‘Building up and maintenance’, concept of 354
Bursaphelenchus xylophilus 267

 Cadenza0900 mutant 411–412
 Calreticulin 283

Capsicum spp.
 C. annuum 565
 C. chinense 565
 Carbon exudation and resource uptake 141–145
 Carboxylates
 in intercropping systems 331–333
 leaf manganese as proxy of belowground, for plant breeding 333–334
 role in P uptake 325–326
 root exudation and 328–329
Carex korshinskyi 334
 Casparian strips 103–104, 117, 308
 Cavitation 377–378
 CCFN. *see* Cortical cell file number (CCFN)
 CCS. *see* Cortical cell size (CCS)
 Cf-2 gene 286
 Chickpea. *see* *Cicer arietinum*
Cicer arietinum 330, 350, 431–432, 436
Citrullus lanatus 567, 570
Citrus spp.
 C. limonia 574
 C. sinensis 574
Cladosporium fulvum 286
 Compaction 385, 502
 Companion cells 281
 Compensatory root growth 236
 Core microbiomes 483
 Cortex, protection to 104–108
 Cortical area, adapting 108–109
 Cortical cell file number (CCFN) 100
 plasticity in 109
 Cortical cell size (CCS) 101
 plasticity in 109
 Cortical senescence 7–8
Costelytra zealandica 245
Creonte rootstock 569
 CRISPR 87
 Critical soil test phosphorus benchmarks
 confidence, for pasture production 614
 CRootBox model 14, 16, 20, 21
 ‘Crops in Silico’ project 20
 Crops Research Institute (CSIR) 577
 Crosstalk 43
 of legume nodulation programme 167–171
 CrossTalk SPFS 19
 CSIR. *see* Crops Research Institute (CSIR)
Cucumis spp.
 C. melo 567
 C. sativus 501

- Cucurbita* spp.
C. maxima 567, 569–571
C. moschata 567, 569, 570
C. pepo 570, 571
- Cupriavidus taiwanensis* 168
- Cyclocephala* spp. 250
- Cyst nematodes 271, 273–277, 282
 resistance against 285–286
- Cytokinin 41–42, 276, 278
 biosynthesis, transport, and signalling 76–77
 manipulation of 85–86
 nitrate and 77–78
 phosphate and 78–79
 regulation, of canopy senescence 575–576
- Cytoplasmic Ca 131
- Dactylis glomerata* 628
- Damage-associated molecular patterns (DAMPs) 281, 282
- DAMPs. see Damage-associated molecular patterns (DAMPs)
- Deep rooting, significance of 6, 10, 53, 311, 374, 416–417, 424, 624; see also Systems agronomy, for deep roots in crops
- Defence priming 242
- Defensive proteins 238
- DEG. see Differentially expressed genes (DEG)
- De Moraes model 11–12
- Denitrification 199
- Dermolepida albohirtum* 232
- Diabrotica virgifera virgifera* 232
- Differentially expressed genes (DEG) 421
- Differentiation zone 35
- Diloboderus abderus* 247, 248
- Doussan's equations, significance of 9–10
- DRO1* gene 417–418, 423, 427
- Drought 476–477
- Durinta* 573
- ECDs. see Extracellular domains (ECDs)
- Echium plantagineum* 133
- Effector triggered immunity (ETI) 281
- E-IR. see *Epichloë* endophyte mediated-induced resistance (E-IR)
- Elongation zone 34–35
- Endodermis 105–108
- Enterobacter* sp. C7 472
- Enterobacter* sp. Fs-11 478, 481
- Entomopathogenic fungi, as endophytes 246–249
- Entomopathogenic nematodes (EPNs) 234, 240
- ENTs. see Equilibrative nucleoside transporter (ENTs)
- Epichloë* endophyte mediated-induced resistance (E-IR) 245
- Epichloë* endophytes 240, 241, 243–244
 and grass associations 244
 and root herbivory 245–246
- Epichloë* hyphae 244
- EPNs. see Entomopathogenic nematodes (EPNs)
- Equilibrative nucleoside transporter (ENTs) 77
- eSTOMP model 12
- Ethylene 42
- ETI. see Effector triggered immunity (ETI)
- Exodermis 108
- Exopolysaccharides 168
- Expansigeny 111
- β -Expansin genes 138
- Extracellular domains (ECDs) 282
- Fertiliser application and AMF 505
- Fick's first law of diffusion 591
- Fine root endophytes (FRE) 340–341
- Flavonoids 165
- Florida 47 564, 565
- FRE. see Fine root endophytes (FRE)
- FSPM. see Functional structural plant models (FSPM)
- Functional structural plant models (FSPM) 8, 17
- Funneliformis mosseae* 201, 501
- Gaeumannomyces graminis* 544
- GatB 46
- Gene ontology (GO) 280
- Genetics, of plant root traits 395–396, 398–408
 fine mapping and cloning of loci and 420–425
 future trends 433–437
 genomics-assisted breeding and 425–426
 rice 426–429
 wheat 429–431
 pulses 431–433
 mapping loci and 396–397
 mutants 397, 400–402, 409–412
 QTLome and 412–413

- linkage mapping with biparental populations 413-419
 association mapping with diversity panels 419-420
- Genome-wide association studies (GWAS) 347, 351, 420
- Genomic selection 436
- Genomic sequences 422
- Giant cells 271, 277-278
 cytoskeleton changes in syncytia and 278-280
 metabolism and nutrient delivery in syncytia and 280-281
- Gibberellic acid 44-45
- Globodera* spp.
G. pallida 273, 284, 285, 287
G. rostochiensis 283-286
- Glycine max* 333, 595
- GmACP1* gene 348
- GmPAP4* gene 336
- GO. *see* Gene ontology (GO)
- Gossypium hirsutum* 575
- Gpa2* R gene 282
- Grazed fields, factors influencing phosphorus accumulation in 616-619
- Greyback canegrub 232
- Grolmp 19
- 'Growth Grammar' 19
- G subfamily ATP-binding cassette (ABCG) 77
- GWAS. *see* Genome-wide association studies (GWAS)
- Hakea prostrata* 333
- Haustorium penetration, in roots 218, 219, 222
- Heterodera* spp.
H. glycines 287
H. schachtii 285, 286
- Heterogeneous inbred family (HIF) 421-422
- Hevea brasiliensis* 344
- HIF. *see* Heterogeneous inbred family (HIF)
- Holcus lanatus* 499
- Hordeum vulgare* 552, 597
- Horizontal gene transfer, in plant-parasitic nematodes 272-273
- HORVU7Hr1G030250* gene 410
- Host defences, suppression of 283
- Hydroponics 417, 425
- Hypocreales 246
- ILL. *see* Introgression library line (ILL)
- Indole 3-acetic acid (auxin) treatments 84
- Initial syncytial cell (ISC) 274
- Inorganic nitrogen 196-197
- Inorganic phosphorus 197
- Interprocess communication, through message-passing 20
- Intrinsic water-use efficiency (WUEi) 572
- Introgression library line (ILL) 419
- ISC. *see* Initial syncytial cell (ISC)
- Jaguar* 567
- Japanese beetle grubs 232
- JA-production 241-242
- Jasmonic acid 44, 45
- Karrikins 80
- Kennedia* spp. 342
- Klebsiella* spp. 474
- Lacunae formation
 in cortex 110-111
 by targeted cell elimination processes 111-113
- Lagenaria siceraria* 567, 570, 571
- LASAP2* gene 336
- Lateral root branching density 6-7
- Lateral root number (LRN) 433
- LCA. *see* Living cortical area (LCA)
- LCOs. *see* Lipochitin oligosaccharides (LCOs)
- lcrn1* gene 48-49
- Leaf water potential 375-376
- Legume-rhizobia symbioses, requirements for 164-166
 autoregulation of nodulation (AON) 166-167
- Leymus chinensis* 334
- Lipochitin oligosaccharides (LCOs) 165
- Living cortical area (LCA) 100
 plasticity in 108
- Lolium perenne* 324
- Long coleoptile trait, significance of 547
- Longidorus* spp. 269
L. elongatus 269
- Loose coupling 17, 18, 19
- Lotus* spp. 329
L. corniculatus 330
- LRN. *see* Lateral root number (LRN)
- L-systems 19
- Lupinus* spp.
L. albus 325, 326, 332, 333, 599, 600, 628
 phosphorus and manganese mobilisation in cluster roots of 349-351

- L. angustifolius* 326, 327, 350
L. cosentinii 326, 350
L. luteus 326, 327, 350
 Lysigeny 110
 Lysine motif (LysM) proteins 169

 M.9 rootstock 572-573
 Machine-learning methodologies 423
 MAGIC. see Multi-parent advanced generation intercrosses (MAGIC)
 MAMPs. see Microbial-associated molecular patterns (MAMPs)
Manihot esculenta 344
 Marker-assisted backcrossing (MAS-BC) 431
 Marker-assisted selection (MAS) 348, 426, 428, 430, 431
 MAS. see Marker-assisted selection (MAS)
 MAS-BC. see Marker-assisted backcrossing (MAS-BC)
 Maxifort rootstock 565
 Medicago spp. 606
 M. sativa 336, 544, 606
 M. truncatula 336, 502
 Meloidogyne spp. 268, 277, 284
 M. incognita 273, 283
 M. javanica 283
 Meristematic zone 34
 Mesocotyl 120
Metarhizium anisopliae 246, 247
Methylobacterium oryzae 477
 MFRE. see Mucoromycotina fine root endophyte (MFRE)
 Mi-1 gene 284-285
 Michaelis-Menten kinetic parameters, significance of 9
 Microbial-associated molecular patterns (MAMPs) 168
 Microbial-induced systemic tolerance (MIST) 476
 Migratory ectoparasites 269
 Migratory endoparasites 269
 M-IR. see Mycorrhiza mediated-induced resistance (M-IR)
 MIST. see Microbial-induced systemic tolerance (MIST)
 Mitscherlich equation 327
 Mixed aerenchyma 111
 MM.111 rootstock 572
MtPHY gene 336
MtPT4 gene 201
 Mucilage 383-385
 Mucoromycotina fine root endophyte (MFRE) 495, 498-501, 505

 Multifort rootstock 564
 Multi-parent advanced generation intercrosses (MAGIC) 414
Musa acuminata 344, 472
 Mycorrhiza 148, 385-386
 Mycorrhizal pathway 503-504
 Mycorrhiza mediated-induced resistance (M-IR) 241-242

 NAC4 transcription factor 74
 NAM. see Nested association mapping (NAM)
 1-Napthalenacetic acid (NAA) treatments 85
 NARK. see Nodulation Autoregulation Receptor Kinase (NARK)
 NB-LRR. see Nucleotide-binding site leucine-rich repeat (NB-LRR)
 N-deprivation 119
 Near-isogenic lines (NILs) 427
 Necrosis 112
 Nematode attack. see Plant-parasitic nematodes (PPN)
 Nematode feeding sites (NFS) 270, 280
 Nested association mapping (NAM) 413, 414
 New generation sequencing (NGS) 422, 435
 NFS. see Nematode feeding sites (NFS)
 NGS. see New generation sequencing (NGS)
Nicotiana tabacum 336
 NILs. see Near-isogenic lines (NILs)
 Nitric oxide (NO) 83
 Nitrogen availability and uptake 70-71
 Nitrogen fixation. see Biological nitrogen fixation
 Nitrogen nutrition 49-51
 Nitrogen uptake 303-304; see also Nitrogen use efficiency (NUE)
 in agriculture 305
 future trends for crop improvement and 313-314
 nitrogen in soil and 304-305
 root proliferation and soil condition effects and 310-313
 root responses to nitrogen availability and 310
 traits and 306
 transporters involved in 308-310
 Nitrogen uptake efficiency into plant (NUpE) 304, 305, 307
 Nitrogen use efficiency (NUE) 9, 304
 in agriculture 305
 genetic variation in, and roots 306-307
 Nitrogen utilisation efficiency in terms of production (NUE) 304, 305

- NO. *see* Nitric oxide (NO)
- NodD transcription factor 164–165
- Nod factors 169–170
- Nodulation Autoregulation Receptor Kinase (NARK) 167
- Non-legumes, rhizobacteria contribution to nitrogen fixation for 171–173
- nPCD. *see* Nutritional PCD (nPCD)
- NPF family transporters 308–309
- NRT1.1 70, 73–74
- NRT1.2 70
- NRT2.1 71, 74
- NRT2.2 71
- NRT3.1 74
- Nucleotide-binding site leucine-rich repeat (NB-LRR) 282
genes 285–286
- NUE. *see* Nitrogen use efficiency (NUE)
- NUPE. *see* Nitrogen uptake efficiency into plant (NUPE)
- Nutrient acquisition; *see also* Root anatomy adapted root anatomical traits on 114–117
environmental issues affecting 102–103
mechanism 101
- Nutrient leaching 200
- Nutrient uptake 9
- Nutrient use efficiency 9, 69, 72, 86, 196, 201, 202, 203, 204, 206, 396, 481–482, 569; *see also* arbuscular mycorrhizal fungi (AMF); Plant growth-promoting rhizobacteria (PGPR)
- Nutritional PCD (nPCD) 119, 120
- OpenAlea 19
- OpenSimRoot model 5, 14, 16, 20, 21, 23, 122
- Optimum phosphorus fertility development and maintenance 611–614
- Organic nitrogen 197
- Organic phosphorus 197
- Ornithopus* spp. 329, 617, 621–625, 628
O. compressus 621, 624, 627
O. sativus 330, 621, 627
- Orobanche* spp. 215, 216, 218, 221
O. crenata 219, 220
O. cumana 219, 223
radicle and xylem vessels 220
- Oryza* spp.
O. rufipogon 429
O. sativa. *See* Rice root architecture
- Os07g39940* gene 411
- Os07g39940-OX* gene 411
- OsABI5-Like1* 44
- OsABIL2* gene 43
- OsAIM1* gene 46
- OsARF1* regulator 48
- OsARF16* 75
- OsARF12* 75
- OsARFs* genes 40
- Osarl1/Osclr1* gene 48
- OsAUX1* 52, 75–76
- OsAUX1* gene 40
- OsbHLH120* gene 53
- OsCAND1* regulator 48
- OsCASP1* 37
- Osclr6* gene 48
- OsCRD1* gene 49
- Osclr4* gene 48
- OsCRL5* regulator 43, 48
- OsCYP2* regulator 47
- OsCYT-INV1* gene 45–46
- OsDOF15* regulator 43
- OsEXPA8* gene 46
- OsFIB*. *see* *OsFISH BONE (OsFIB)*
- OsFISH BONE (OsFIB)* 39
- OsGLR3.1* gene 46
- OsGLU3* gene 46
- OsIAA13* gene 39
- OsIAA1* gene 39
- OsIAA23* gene 40
- OsIPK2* regulator 47
- OsJAZ1* gene 53
- OsNAL1* gene 48, 53
- OsNLA1* 52
- OsORC3* gene 47
- OsPHY1* gene 336
- OsPINs* genes 40
- OsPSTOL1* gene 428
- OsRHC* gene 411
- OsSAPK10* gene 43
- OsSLL1* gene 47
- OsSPL3* gene 49
- OsTOP1* regulator 46
- Ostrinia nubilalis* 247
- OsTryptophan Deficient Dwarf1 (TTD1)* 39
- OsYUCCA1* gene 39
- OsZFP* protein 47
- Paenibacillus polymyxa* E 681 471
- PAMPs. *see* Pathogen-associated molecular patterns (PAMPs)
- Pangenome 422

- Paraburkholderia* spp. 481
Parasponia andersonii 164
 Pathogen-associated molecular patterns (PAMPs) 281
 Pattern-triggered immunity (PTI) 281–283
 PBE. *see* Phosphorus Balance Efficiency (PBE)
 PBI. *see* Phosphorus Buffering Index (PBI)
 PCD. *see* Programmed cell death (PCD)
 P-deprivation 119
 PEcAn. *see* Predictive Ecosystem Analyzer (PEcAn)
 Penetrometer resistance 311–312
 PGPR. *see* Plant growth-promoting rhizobacteria (PGPR)
Phalaris aquatica 617, 628
Phaseolus vulgaris 595, 596
Phelipanche spp. 215, 216, 218
P. aegyptiaca 219
 Phenotypic variation 5–7, 11
 Phosphate availability and uptake 72
 Phosphate deficiency 142
 Phosphate nutrition 51–52
 Phosphorus acquisition 589–590
 agronomic context 600–601, 602
 agricultural fields with low to very low phosphorus-sorbing soils 601, 603
 agricultural fields with moderate to high phosphorus-sorbing soils 603–604
 critical phosphorus benchmarks for soil phosphorus management and 604–606
 future trends 628–629
 increasing, by rhizosphere management 599–600
 options to improve, in pastures and arable crops 591
 phosphate diffusion management 592
 plant root system absorptive surface increase 593–596
 root growth constraints alleviation 597
 phosphorus efficiency improvement
 sheep and beef grassland farming in southern Australia 606
 farming system context 606–607
 fertiliser practices on grassland farms 607–614
 pitfalls impeding progress 614–616
 progress towards next step-change 616–623
 soil phosphorus fertility management 623–624
 edaphic requirements 624
 yield and persistence 624–625
 opportunities identification for fertiliser use efficiency 626–627
 knowledge and tools development 627
 legumes identification and farming system P efficiency 627
 rhizosphere modifications and 597–600
 Phosphorus Balance Efficiency (PBE) 601
 Phosphorus banding 608–610
 Phosphorus Buffering Index (PBI) 614
 Phosphorus-efficient grazing system, development of 619
 Phosphorus-efficient pasture
 legumes 619–621
 Phosphorus uptake 321–322, 337–341
 acquisition, breeding to improve 347–349
 case study 349–351
 and farming-management practice, at intensive agricultural system level 344–347
 future trends in research 352–354
 microbially-mediated acquisition, in species-diverse systems 343–344
 root architecture and morphology associated with 322–325
 and root biochemistry associated with 325–326, 331–334
 root exudate research practical applications 326, 328–330
 phosphatases in phosphorus acquisition 334–336
 fertiliser-use efficiency 336–337
 trade-offs in traits and 341–343
 Phosphorus uptake efficiency (PupE) 425
 Phosphorus use efficiency (PUE) 425
 Phytases 335
PIN3 expression 278
PIN4 expression 278
 Plant density 346–347
 Plant growth-promoting rhizobacteria (PGPR) 236, 467–469
 effect on plant mineral nutrition 477–478, 481–482
 nutrient uptake 478, 481
 effect on root function 469

- root architecture 469-471
 - plant metabolism 471-473
 - abiotic stress 473-477
 - future trends in research 482-485
- Plant hydraulic conductance and components 376-378
- Plant-novel endophyte association 244
- Plant-parasitic nematodes (PPN) 267
 - control 283-284
 - future trends 288
 - parasitism modes 268-271
 - plant defence responses activation and suppression and 281-283
 - plant-nematode interactions
 - invasion and migration 271-273
 - morphological changes and syncytium development 273-277
 - giant cells 277-278
 - cytoskeleton changes in syncytia and giant cells 278-280
 - metabolism and nutrient delivery in syncytia and giant cells 280-281
 - resistance 283-286
 - by novel mechanisms 286-287
 - contemporary resistance breeding 287-288
- Plant secondary metabolites 238
- Polymorphic genes 422
- Popillia japonica* 232
- Postembryonic root system 118
- PpeDRO1* gene 417
- Pratylenchus* spp. 269
 - P. coffeae* 269
- Predictive Ecosystem Analyzer (PEcAn) 22-23
- Programmed cell death (PCD) 111-113, 119, 120
- Pseudomonas* spp.
 - P. fluorescens* 344, 470, 472
 - P. putida* 476, 482
- PTOL1* gene 348, 423, 428, 429
- PTI. *see* Pattern-triggered immunity (PTI)
- PUE. *see* Phosphorus use efficiency (PUE)
- Pup1* gene 348, 429
- PupE. *see* P-uptake efficiency (PupE)
- PUPs. *see* Purine permeases (PUPs)
- Purine permeases (PUPs) 77
- QC. *See* Quiescent center (QC) cells
- QSS. *see* Quorum-sensing signals (QSS)
- QTL. *see* Quantitative trait loci (QTL)
- QTL-Seq 435
- Quantitative trait loci (QTL) 51, 53, 128, 136, 223, 347-349, 396, 397, 416-422, 426-427, 430-435
 - root traits and 412-413
- Quiescent center (QC) cells 40
- Quorum-sensing signalling 165
- Quorum-sensing signals (QSS) 165
- qWT_Gm03* gene 432
- QYld.osu-1BS* allele 418
- QYld.osu-1B S* QTL 418
- Radial water flow, from soil to root surface 379-382
- Rahnella aquatilis* 197
- Ralstonia solanacearum* 168
- RCA. *see* Root cortical aerenchyma (RCA)
- RCc3* gene 412
- RCS. *see* Root cortical senescence (RCS)
- Receptor-like kinases (RKs) 282
- RenSeq. *see* Resistance gene enrichment sequencing (RenSeq)
- Residual heterozygosity (RH) 421
- Resistance gene enrichment sequencing (RenSeq) 287
- Resource sequestration 237
- RGA. *see* Root growth angle (RGA)
- RH. *see* Residual heterozygosity (RH)
- Rhamphicarpa fistulosa* 219
- Rhg1* gene 286, 432
- Rhg4* gene 286, 287, 432
- Rhizobium leguminosarum* (LR-30) 477
- Rhizobium leguminosarum* *bv. trifolii* 171
- Rhizophagus irregularis* 507, 509-511
- Rhizopines 180
- Rhizosheath 135-136
 - sampling 328
- Rhizosphere
 - development, and root hairs growth, in soil 138-139
 - root hairs and 145-147, 382-383
 - root water uptake and 382-386
- Rht* gene 430
- Rice root architecture 33-34, 35
 - adaptations 49-53
 - anatomy 35-37, 36
 - control by pathways 45
 - seminal root elongation 45-46
 - lateral root formation regulation 47
 - crown root formation regulation 48-49
 - crown/adventitious root formation 38
 - future trends in research 53-54

- hormone regulation 38-45
- lateral root formation 37-38
- morphology 34
- tissue organization 34-37
- RKs. *see* Receptor-like kinases (RKs)
- RLD. *see* Root length density (RLD)
- Root-ABA1 QTL 416
- Root anatomy 99, 100; *see also* Nutrient acquisition
 - future trends in research
 - root phenotypes for improved nutrient capture 121
 - root anatomical traits, software, and modelling 122
 - of maize, under nutrient shortage 118-121
 - traits 99-101
 - adaptations of 103-117
- RootBox model 11-13, 15
- Root cortical aerenchyma (RCA) 111-113
 - plasticity in 113
- Root cortical senescence (RCS) 113, 116
- Root-feeding insects; *see also* Root herbivory
 - future trends 249-250
 - plant growth and physiology changes and 234-236
 - research path and 233-234
 - root defence via fungal partners 240-249
 - significance of 231-233
- Root growth angle (RGA) 415
 - of branch and adventitious roots 5
- Root hair defective-six like (RSL) 411
- Root *Hairless1* (*OsRHL1*) gene 411
- Root hairs 8
 - function, in structured soil 139-141
 - interactions with environment 138-147
 - phylogenetic and genetic variation in 132-138
 - physiology and development 128-131
 - prospects for utilising 149-150
 - root water uptake and 382-383
 - significance of 127-128
 - trade-offs and interactions 147-149
- Root herbivory 232-235, 245-246
 - direct resistance to 237-239
 - indirect resistance via natural enemy recruitment 239-240
 - life history traits and ecology 232
 - root defences against 236-240
 - tolerance of 236-237
- Root hydraulics 374
- Root-knot nematodes 272, 277-278
 - resistance against 284-285
- Root length density (RLD) 537, 538, 540-541
- RootScan program 122
- Rootstocks 561-563
 - future trends 578-579
 - nutrient relations 563
 - rooting volume increase 563-566
 - nutrient uptake efficiency increase 566-568
 - beneficial soil microbes recruiting 568
 - nutrient utilisation efficiency increase 569-570
 - phytohormones 573-576
 - tomato rootstock case study, as strategy to overcome abiotic stress in Ghana 576-578
 - water relations 570
 - root vigour and morphology 571
 - leaf gas exchange 572-573
 - canopy vigour 573
- Root system architectural (RSA) models 3-4, 396, 436-437
 - adaptation to environmental conditions 49-53
 - application of 4
 - root traits 4-8
 - root processes 8-10
 - trait synergies and integrated phenotypes 10-11
 - soil environment simulation 11-12
 - rhizosphere processes and soil biota simulation 12-13
 - application in breeding 13
 - application in agronomy and ecology 13-15
 - application to refine experimental measurements 15-16
 - challenges and future directions 23
 - development, advances in 16
 - continued model coupling 16-17
 - platforms modeling 17-20
 - model simplification 21-22
 - input and output handling 22-23
- Root water uptake 382-386
 - agronomic context, and drought tolerance 373-375
 - future trends 386-387
 - root-induced changes in pore size distribution 385

- soil drying and 378-379
and water flow principles in soil and plants 375-382
- Root-yield-1.06* 417
- RSA. *see* Root system architectural (RSA) models
- RSL4 transcription factor 137
- RST-106* rootstock 564, 565
- Rytidosperma richardsonii* 324
- SA. *see* Salicylic acid (SA)
- Salicylic acid (SA) 44, 45, 242
- Schizogeny 111
- S-deprivation 119, 120
- Sedentary endoparasites 270
- Seminal root number (SRN) 419
- Sensitivity analysis 21
- Serratia liquefaciens* KM4 474
- Shintoza* rootstock 569
- Shoot herbivores, life history traits and ecology of 232
- Shoot root number (SRN) 425
- Sieve elements 281
- SimRoot model 13, 15
- Single nucleotide polymorphism (SNP) 414, 421, 423-424, 433, 435, 436
- SNP. *see* Single nucleotide polymorphism (SNP)
- Software platforms for simulation (SPFS) 19-20
- Soil hardness and root growth, interactions between 11
- Soil nitrate 71
- Soil nitrification 198-199
- Soil nutrient mineralisation 198
- Soil salinity 473-476
- Soil test P (STP) 603-605, 611
concentrations, understanding and managing variability in 614-616
- SoilWater App 552
- Soil zymography 336, 354
- Solanum* spp.
S. cheesmaniae 575
S. lycopersicum 564, 566, 567, 568, 573, 575
S. melongena 569
S. pimpinellifolium 566-568, 572, 573
- Soluble phosphorus fertilisers 608
- Sorghum bicolor* 348, 595
- Source-sink models, significance of 9
- Soybean 432-433
and nitrogen fixation 173-176
- Space-time model 177
- SPACSYS model 12, 13
- Spatial and temporal redistribution, of nutrients in soil 199
- SPFS. *see* Software platforms for simulation (SPFS)
- SRN. *see* Seminal root number (SRN)
- SRN. *see* Shoot root number (SRN)
- 'Stay-green' phenotype 416
- Stipa grandis* 334
- Stomatal conductance 375-376
- STP. *see* Soil test P (STP)
- Striga* spp. 221
S. asiatica 215
S. gesnerioides 215, 219, 223
S. hermonthica 215, 219, 220
- Strigolactones
biosynthesis, transport, and signalling 79-80
interaction with hormones in nutrient deficient conditions 81, 83-84
response to nitrogen and phosphorus 80-81, 82
rice root development and 44
- Stubble-borne foliar diseases 544
- Stylet 274
- Sub1* gene 428
- Suberin 103
- Suberization
endodermal 107, 117
and lignification 103-104
- Symplastic pathway 101
- Synchrotron X-ray CT
of maize root 381, 383
scanning 129, 130
- Syncytia 271
cytoskeleton changes in giant cells and 278-280
metabolism and nutrient delivery in giant cells and 280-281
- Synthetic microbial communities 483
- Systems agronomy, for deep roots in crops 531-532
crop sequence 544-545
earlier sowing systems 542-543
varietal selection and agronomy for 546-547
grazing wheat 547
future 552-553
genetic improvements 548-549
legacy effects accounting 549-550
long-term soil management 543-544

- root depth increment 539
 wheat with longer vegetative stage 539-540
 higher seedling density 540-541
 ear removal impact on root growth in post-anthesis period 541-542
 deep ripping to reduce soil density and strength 542
 subsoil water
 unused 535-537
 root systems improvement to capture 537-538
 summer fallow management 545-546
 wheat-based farming systems in south-eastern Australia 532-535
 whole farm benefits scaling 550-551
- TaALMT1* gene 431
TaBW280K 435
 Targeting induced local lesions in genomes (TILLING) 397, 400, 402
 Tillage and AMF 505
 TILLING. see Targeting induced local lesions in genomes (TILLING)
 Trans-cellular pathway 101
 Transcriptome profiling 422
 Transpiration 375-376
Tribute 565
 Trichoblasts 131
Trifolium spp. 620, 628
 T. pratense 499
 T. repens 501, 606
T. subterraneum 606, 607, 616, 617, 618, 620-622, 625-628
Triticum aestivum 423
Trophotylenchus spp. 271
TTD1. see *OsTryptophan Deficient Dwarf1* (*TTD1*)
- Uruguay 246
- Vacuolar cell death 112
VERNALIZATION1 (*VRN1*) gene 423, 424
VisHKT1 gene 567
Vitis spp.
 V. champinii 567
 V. rupestris 567
 VOCs. see Volatile organic compounds (VOCs)
 Volatile organic compounds (VOCs) 239, 245
 root exudation of 240
VRN-H1 gene 424
Vulpia spp. 617
- Water availability 52-53
 Water uptake 9-10
 WCR. see Western corn rootworm (WCR)
 Weedy root parasites, plant root response to 215-216
 future trends in research 222-224
 host plant defence and 218, 220
 pre-penetration defence mechanisms 220-222
 post-penetration defence mechanisms 222
 host-parasitic weed interaction and 216-217
 seed dispersal and germination 217-218
 host infection 218
 Western corn rootworm (WCR) 232, 238
 Wheat 660K SNP array 423
 Wireworms 232
 WUEi. see Intrinsic water-use efficiency (WUEi)
- Xiphinema* spp. 269
 X. index 269, 273
 Xylem 220, 377
- Zea mays* 595, 596