

Contents

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|----------|---|------------------|---|
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| <u> </u> | V | <u>_</u> | |

<u>Title Page</u>

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Preface

Roots and Their Soil Interactions: What We Can Learn from Genomics

Chapter 1: Genomics of Root Development

Introduction

Genomics of LRI

Rise of New Technologies to Understand Lateral

Root Development

ComparativOmics, the Future

Acknowledgments

References

<u>Chapter 2: The Complex Eukaryotic</u> <u>Transcriptome: Nonprotein-Coding RNAs</u> <u>and Root Development</u> <u>Genomic Approaches Reveal Novel Aspects of the Eukaryotic Transcriptome</u>

The Role of RNA-Binding Proteins in npcRNA

Metabolism and Activity

Nonprotein-Coding RNAs in Root Development

<u>Future Perspectives</u>

Acknowledgments

References

<u>Chapter 3: Genomics of Auxin Action in Roots</u>

<u>Introduction</u>

The Basis of Auxin Biology

<u>Auxin Genomics in Root Development</u>

Auxin and Root Hair Development

Auxin in Gravitropism

Auxin in LR Initiation

Conclusion

Acknowledgments

References

<u>Chapter 4: Cell-Type Resolution Analysis of</u> <u>Root Development and Environmental</u> <u>Responses</u>

Introduction

Tools for Cell-Type Resolution Analysis

<u>Analysis of Spatiotemporal Expression Patterns in the Arabidopsis Root</u>

| Analysis of Cell-1 | <u>ype-Specific</u> | Expression | Patterns |
|---------------------------|---------------------|-------------------|-----------------|
| in the Rice Root | | | |

Cell-Type-Specific Analysis of Auxin

Cell-Type-Specific Analyses of Chromatin

Cell-Type-Specific Analyses of Responses to

Environmental Change

Future Prospects

Acknowledgments

References

<u>Chapter 5: Toward a Virtual Root:</u> <u>Interaction of Genomics and Modeling to</u> <u>Develop Predictive Biology Approaches</u>

Introduction

<u>Assembling Root Gene Regulatory Pathways</u> <u>Using Genomics</u>

<u>Modeling Well-Characterized Small Root Gene</u> <u>Regulatory Networks</u>

<u>Building New Large-Scale Root Gene Regulatory</u> <u>Network</u>

<u>Multi-Scale Modeling Approaches to Study Root</u> <u>Growth and Development</u>

<u>Conclusions and Future Challenges</u> References

Chapter 6: Genomics of Root Hairs

Genomics with Single Cells
Root Hair Development

High-Throughput Approaches for the
Characterization of Root Hairs
Functions of Root Hair-Specific Genes
The Regulatory Pathway for Root Hair-Specific
Genes
Perspective
Acknowledgments
References

<u>Chapter 7: The Effects of Moisture</u> <u>Extremes on Plant Roots and Their</u> <u>Connections with Other Abiotic Stresses</u>

Introduction

Low Water Availability—Drought

Excess Water—Soil Waterlogging, Flooding, and

<u>Submergence</u>

Common Plant Root Responses to Abiotic

Stressors

Continuing Challenges in Breeding for Plant Root

Systems Tolerant to Abiotic Stress

Acknowledgments

References

<u>Chapter 8: Legume Roots and Nitrogen-Fixing Symbiotic Interactions</u>

Genetic Dissection of the Legume Root System
Functional Genomic Analyses of Legume Nodules
and Roots

Concluding Remarks

<u>Acknowledgments</u> References

<u>Chapter 9: What the Genomics of</u> <u>Arbuscular Mycorrhizal Symbiosis Teaches</u> <u>Us about Root Development</u>

<u>Forward and Reverse Genetics for Identifying Myc</u> <u>Mutants</u>

Comparative Transcriptomics of AM Symbiosis: Toward Identification of Genes Involved in Root Development

Small RNAs in AM Symbiosis

<u>Acknowledgments</u>

References

<u>Chapter 10: How Pathogens Affect Root</u> Structure

<u>Introduction</u>

Root Infection and Feeding Cell Ontogenesis
Genome-Wide Analysis of the Plant Response to
Infection

<u>The Plant Cytoskeleton Is Targeted by Root Pathogens</u>

Root Pathogens Hijack Cell Cycle Regulators
Severe Cell Wall Remodeling Is Associated with
Feeding Site Formation

<u>Phytohormones Regulating Development and Defense May Control Feeding Site Formation</u>

| Role of miRNAs in | <u>Feeding</u> | Site | Formation | and |
|-------------------|----------------|------|------------------|-----|
| <u>Function</u> | | | | |

Nematode Effectors That Alter Root Cell

<u>Development during Parasitism</u>

Conclusion

<u>Acknowledgments</u>

References

<u>Chapter 11: Genomics of the Root-</u> <u>Actinorhizal Symbiosis</u>

Introduction

Actinorhizal Symbiosis

Development of Actinorhizal Nodules

Genomic Resources for Studying Actinorhizal

<u>Symbiosis</u>

What Did We Learn from Actinorhizal Genomics?

Conclusion and Future Directions

<u>Acknowledgments</u>

References

Chapter 12: Plant Growth Promoting Rhizobacteria and Root Architecture

Introduction

Different Root Niches for PGPR Colonization

PGPR Recognition by Plants

Modulation of Root Growth and Architecture by PGPRs

Mechanisms of Plant Growth Promotion by PGPRs

<u>Plant Genetic Programs Controlling Modulation of</u> <u>Root Growth and Architecture by PGPRs</u>

Conclusions

<u>Acknowledgments</u>

<u>References</u>

<u>Chapter 13: Translational Root Genomics</u> <u>for Crop Improvement</u>

Introduction

Root Research for Crop Improvement

Genetic Dissection of Root Traits

Molecular Dissection of Root Traits

Molecular Breeding for Root Traits

Summary and Outlook

Acknowledgments

References

Index

Advertisements

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Preface

Roots and Their Soil Interactions: What We Can Learn from Genomics

Developmental plasticity allows higher organisms to adapt to their environment. In contrast to animals, plants exhibit a remarkable flexibility in their architecture and growth pattern in response to external conditions, due to the continuously active shoot and root meristems and their capability to generate new organs after embryogenesis. External cues influence plant growth by modulating hormone levels and signaling. The root architecture of the plant constitutes an important model to study how developmental plasticity is translated into growth responses under different soil conditions and plays an important role in water and nutrient acquisition. Indeed, primary development and the formation of de novo meristems to lateral roots are conditioned bv the generate environment. Lateral root growth and development is the main determinant of the shape of the root system, a trait controlled by internal cues and external factors. In addition to Arabidopsis, there are other relevant models where genomic information is becoming available, notably cereals and legumes. Both plants are able to develop symbiotic interactions with soil organisms, namely, mycorrhizal fungi and, for legumes, soil rhizobia. These interactions lead to further adaptation of root growth, the so-called mycorrhizal roots, and even to the formation of new organs, distinct from lateral roots, the nitrogen-fixing root nodules.

The diversity of root responses to biotic and abiotic stresses as well as symbiotic interaction can be analyzed at a genome-wide scale using transcriptomic and proteomic approaches. The advent of genomic technologies will open new perspectives for the analysis of how roots adapt to the soil environment. This work, mainly done in model systems such as Arabidopsis, uncover diverse regulatory genes (e.g., environmental sensors, protein kinases, transcription factors, and more recently, small regulatory RNAs) that participate in genetic programs, regulating root growth and architecture. Integration of these data with genomic approaches on different genetic backgrounds has already revealed, and will continue to reveal, critical regulatory networks and molecular hubs, whose orthologs could then be analyzed in crop plants to establish the generality of these mechanisms and impact agricultural practices.

This book contains 13 chapters from recognized experts in the field, which provide a comprehensive and integrated view of how root genomics can open new perspectives for root physiology and agriculture. The first six chapters deal with various novel areas where genomics, in combination modeling, physiology, in-depth analysis with transcriptome, and epigenetics, have revealed several regulatory networks controlling diverse aspects of root growth and development. Then, the remaining chapters describe genomic approaches being applied for the analysis of root responses to the soil environment, such as abiotic stresses, symbiotic interactions, or pathogenic nematode The final chapter focuses on translational infections. genomics and how genomics can guide crop improvement. I hope that this book will serve many, from plant researchers physiologists, breeders, plant and crop graduate and their professors who want to have an overview of the highlights in root genomics and how this information could be screened and integrated without having considerable expertise in bio-statistics. While reading this book, the reader will realize how fascinating the actual global view of the genome is and how many complex mechanisms remain to be discovered to understand root growth and development. There are exciting agricultural challenges, such as the modulation of root architecture or drought adaptation, which may derive from the application of this new fundamental understanding of life principles to the control of major root traits.

Martin Crespi

1 Genomics of Root Development

Boris Parizot and Tom Beeckman

Introduction

Roots: Rising from the Underground

Because of the different roles the root system plays in overall plant growth, root architecture is a fundamental aspect of plant growth and development. The root system especially acquires water and nutrients from the soil, anchors the plant in the substrate, synthesizes hormones and metabolites, interacts with symbiotic microorganisms, storage functions. In liaht insures characteristics, more and more breeders turn their attention to this underground organ in order to increase yield. This requires a better understanding of the relation of this part of the plant with the environment and of its highly adaptive behavior (Lynch 2007; Gewin 2010; Den Herder et al. 2010).

angiosperms, major Within differences architecture between dicotyledonous and monocotyledonous plants exist. Dicots develop a tap root system composed of a main primary root, already formed during embryogenesis, which grows vertically into the soil and gives rise to the emergence of numerous lateral roots extending the surface area. Monocots have a fibrous root system in which the embryonic primary root is only important for the early development of the plant (Feix et al. 2002) and in which an extensive postembryonic shoot-born root system is formed later on. Very little is known about the genetic and molecular mechanisms involved in the development and architecture of system major crop species, generally the root in

monocotyledonous plants. Lack of insight is certainly a consequence of the difficulty to access and observe this organ in its natural habitat, namely the soil. Moreover, and probably because of this hidden character, the root has been neglected for a long time in crop improvement and in agricultural approaches aiming at increasing shoot biomass. Nevertheless, while most of the work has been done on Arabidopsis thaliana, the awareness of the importance of the root system in modulating plant growth, together with progress in sequencing and new molecular techniques, has understanding caused renewed interest in species (Hochholdinger mechanisms in crop Zimmermann 2009; Coudert et al. 2010).

In the scope of root development and its interaction with the soil, in this chapter, we propose to focus on the mechanisms involved in root branching, which is a major determinant of root system architecture. The plasticity of the root system represents indeed an important potential for plants. beina sessile organisms, to adapt heterogeneity of their environment. The soil is a complex mixture of solid, gaseous, and liquid phases, wherein nutrients are unequally distributed. Plants have therefore developed a highly sophisticated regulatory system to control their root architecture, in response to environmental cues, by modulating intrinsic pathways to optimize their root distribution in the soil and consequently quarantee an optimal uptake of nutrients necessary for growth and development (reviewed in Croft et al. 2012).

Primary Root Structure and Development: Lessons from the Arabidopsis Model

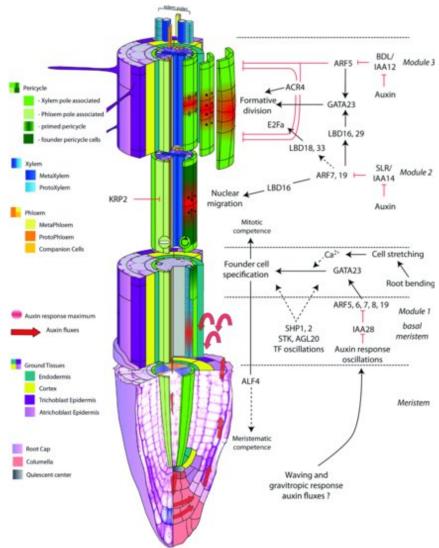
Branching of roots occurs through the development of new meristems inside the primary parent root. We therefore first discuss briefly the structure and development of the primary root in *Arabidopsis*, the model species in which major insights were obtained, thanks to its simple root architecture (Dolan et al. 1993; Malamy and Ryan 2001; Scheres et al. 2002; Casimiro et al. 2003; Casson and Lindsey 2003; Ueda et al. 2005; Iyer-Pascuzzi et al. 2009; Peret et al. 2009).

The root can be divided in three main zones. The most distal, at the tip of the root, is the meristematic zone, where the so-called initial cells give rise to the tissues constituting the root. The initial cells are kept in an undifferentiated state by the neighboring quiescent center (Van den Berg et al. 1997), a mitotically less active region, composed of few central cells in *Arabidopsis*. Higher up, in the elongation zone, cells progressively stop dividing and start to expand longitudinally. Finally, cells differentiate and acquire their final cell fate in the maturation zone (Truernit et al. 2006), which can be recognized by the appearance of the anatomical structures of the vascular tissues.

Distinct cell types are then composing the mature root (Figure 1.1). The outer layers, endodermis, cortex, and epidermis are organized in concentric layers and present a radial organization toward the longitudinal axis of the primary root (Dolan et al. 1993). The epidermis, which is the outermost layer of the root, is in direct contact with the soil and is often designated as rhizodermis. It is composed of two populations of cells: one producing root hairs and the other nonhair cells (Schneider et al. 1997). The root hairs are responsible for the major part of the nutrient uptake from the soil (Muller and Schmidt 2004) and also play other important roles such as the initial contact with certain symbiotic partners (Gilroy and Jones 2000; Perrine-Walker et al. 2011). Cortex and endodermis constitute the ground tissue and are derived from one single initial cell in Arabidopsis (Dolan et al. 1993; Scheres et al. 1994). The stele is situated internal to these layers and comprises the vascular cylinder, consisting of two bilateral poles of xylem alternating with two bilateral poles of phloem separated by procambium cells (Dolan et al. 1993). The stele also contains a heterogeneous layer, the

pericycle, interfacing the vascular cylinder and the outer layers, playing a predominant role in root architecture and root branching (Parizot et al. 2008).

FIGURE 1.1 Structure of the primary root and different steps of lateral root initiation. See the text for detailed description.



Root Branching

In dicotyledonous plants, such as *Arabidopsis*, elaboration of the root system occurs postembryonically by the formation of numerous secondary roots from the primary root that was formed during embryogenesis. These new roots are comparable to the primary root in structure and will be able

to reiterate the branching process by in turn initiating tertiary roots. Roots of second, third, and higher order are defined as lateral roots. The plant can also produce adventitious roots, which initiate mostly at the base of the hypocotyl. Different markers related with cell identity show a similar pattern in the primary and lateral roots (Malamy and Benfey 1997b; Laplaze et al. 2005), indicating the possibility of a common developmental pathway. This hypothesis is supported by a high number of mutants affected in genes root patterning, such SHORTROOT. involved in as SCARECROW, and LONESOME HIGHWAY, showing similar defects in the primary and lateral roots (Helariutta et al. 2000; Wysocka-Diller et al. 2000; Parizot et al. 2008; Lucas et al. 2011). However, some differences can be observed in the behavior of the primary and the lateral roots toward external cues such as gravity and substrate nutrient 1998: concentrations (Zhang and Forde Mullen Hangarter 2003; Bai and Wolverton 2011). A mutation in the MONOPTEROS impairs the apical-basal formation of the embryo and leads to plants lacking a primary root, but that are still able to generate adventitious roots (Berleth and Jurgens 1993; Przemeck et al. 1996), indicating that early pathway(s) required for the embryonic formation of root meristem are not а required postembryonically. Also, a mutation in the gene WOODEN LEG has a major effect on the primary root development, with the suppression of the phloem elements and a drastic reduction in lateral root initiation (LRI), but does not affect the formation and branching of adventitious roots (Kuroha et al. 2006).

The monocots, such as maize, form different types of roots: primary, seminal, and adventitious roots, which can all form lateral roots. These root types also present similarities in their structures. However, mutants missing only a subset of these root types have been isolated, indicating that at least a part of the genetic program necessary for their formation is

root-type specific (Woll et al. 2005; Hochholdinger and Tuberosa 2009).

Lateral Root Initiation

In Arabidopsis and most other dicotyledonous plants, lateral roots are formed from a restricted number of pericycle cells located in front of the xylem poles (Figure 1.1). The pericycle is a heterogeneous tissue composed of quiescent cells adjacent to the phloem poles and cells competent for LRI in front of the xylem poles (Beeckman et al. 2001; Parizot et al. 2008). Therefore, this layer presents a radial bilateral symmetry along the primary root, which reflects the diarch symmetry of the more internal vascular bundle as compared to the surrounding concentric radial layers of the outer tissues. The subpopulation of pericycle cells adjacent to the xylem poles can be considered as an extended meristem, as they conserve the ability to divide after leaving the root apical meristem (in contrast to the cells in front of the phloem poles), and give rise to the formation of a new organ (Beeckman et al. 2001; Casimiro et al. 2003). Although up to three adjacent pericycle cell files associated with each xylem pole are dividing during lateral root formation, cell lineage experiments have shown that only the central cell file will contribute significantly to the formation of the lateral root primordium (Kurup et al. 2005).

The first pericycle cell divisions that will give rise to a lateral root (i.e., formative divisions) can only be detected several millimeters above the primary root meristem, whereas in the lower part of a region named developmental window (Dubrovsky et al. 2006), it has been demonstrated that a subset of pericycle cells is already specified for LRI in a zone situated immediately above the primary root apical meristem, the basal meristem (De Smet et al. 2007; De Rybel et al. 2010b). The phytohormone auxin is most likely the signal triggering this priming, as auxin response

recorded using the auxin response marker DR5 shows pulsations in the protoxylem cells of the basal meristem with a periodicity that can be correlated with the initiation of new lateral roots (Ulmasov et al. 1997; De Smet et al. 2007; De Rybel et al. 2010b; Moreno-Risueno et al. 2010). Up to now, different hypotheses have been proposed to explain the origin of these oscillating auxin response maxima in the protoxylem cells, and no consensus has been reached yet. Also the mechanism by which this auxin signal in the protoxylem cells is translated into the specification of founder cell identity in the neighboring pericycle cells is still unknown. Nevertheless, this intrinsic mechanism can be overruled, as the application of auxin on mature parts of the root above the basal meristem is still able to trigger LRI (Himanen et al. 2002), further reflecting the high plasticity of the root system.

The first morphological event preceding the division of two pericycle founder cells is the simultaneous migration of their nuclei to their common cell wall (De Smet et al. 2007). This migration is followed by an asymmetric anticlinal division of the pericycle cells, resulting in the formation of a core of small daughter cells flanked by larger cells (Dubrovsky et al. 2000). Successive anticlinal and periclinal divisions give rise to a lateral root primordium. Further divisions and elongation of the primordium cells result in the formation of a fully autonomous root, with a meristem similar to that of the primary root (Malamy and Benfey 1997b; Dubrovsky et al. 2001). Although the place of LRI differs between plant species, early patterning of the primordium is guite conserved (Casero et al. 1995; Malamy and Benfey 1997bb). The frequency of LRI in the Arabidopsis primary root can fluctuate in response to tropic and/or mechanical stimuli (De Smet et al. 2007; Ditengou et al. 2008; Laskowski et al. 2008; Lucas et al. 2008a). For example, a gravitropic stimulus applied to seedlings induces a lateral root at the place where the root bends to recover its normal growth angle (Lucas et al. 2008a).

Genomics of LRI

Most of the work on root development focused on the analysis of single mutants and allowed the discovery of many processes involved in the patterning of the different cell types within the primary root and in LRI. These studies show that root growth and development are complex processes with intricate pathways dealing with hormone biosynthesis, transport and signaling, tissue differentiation and dedifferentiation, nutrient sensing, cell divisions, and others (lyer-Pascuzzi and Benfey 2009; Orman et al. 2011).

LRI has been increasingly studied over the last decade in the light of transcriptomics and proteomics. extraction for these analyses evolved from simple global root harvesting to more elaborated sampling techniques allowing a specific access to the tissues involved, such as laser capture microscopy (LCM; Woll et al. 2005) or cell sorting (De Smet et al. 2008). Also, the possibility to synchronize LRI circumvented the problems due to the discreteness of this event in plants grown in natural conditions (Himanen et al. al. 2004). Different Himanen et large-scale transcriptome and proteome studies have therefore been realized in different species, mainly Arabidopsis and maize, yielding information on various aspects of this de novo organogenesis: auxin response, asymmetric cell division, and pericycle tissue involvement. While these studies focused initially on the onset of lateral root development, a new era initiates now with the study of the formation and the patterning of the primordium after LRI and the emergence of the primordia from the parent root. Moreover, many other experiments are dealing with mechanisms related to LRI, such as meristem function, pericycle identity, and hormone

treatment, and bring useful novel information, shedding light on this process. A list of omics experiments, directly or indirectly related to LRI is displayed in <u>Table 1.1</u>. A challenging task for the community will be to handle this wealth of data and search for appropriate system biology strategies to better understand the LRI process at the molecular level. To address this, a common effort of the biologists and the bioinformaticians is needed to design better experiments, rationalize and interpret the data, and make it accessible and understandable for the community. The most often characterized process in relation to LRI is the response to the hormone auxin.

<u>Table 1.1</u> Omics Experiments dealing directly or indirectly with lateral root initiation. Publication year and reference, species, technique and experimental design, platform, tissues and preparation, pathways, treatments, and the biological process questioned by the experiment.

| Reference | Species | Omics technique & Experimental design | Platform / Technique |
|-----------|---------|---------------------------------------|----------------------|

Year

| 003 | Nimbour of al | 445 | | Transcriptome atlas using FACS and GFP-reporter lines | Affymetrix ATH1 |
|------|----------------------|-----|--|--|--|
| 20 | Birnbaum et al. | Ath | Ts | | |
| | lmin et al. | Mtr | Pr | Protein expression at the globular stages of somatic embryogenesis | Two-dimensional electrophoresis + MALDI-TOF-MS and MS/MS |
| | Menges et al. | Ath | Ts | Gene expression profiles during normal culture growth, synchronous cell cycle re-entry and synchronous cell cycle progression | Affymetrix ATH1 |
| 2004 | Brinker et al. | Pta | Ts | Gene expression during adventitious root development by treating hypocotyls with auxin | Custom Pinus taeda microarray (2,178 cDNAs) |
| | Himanem et al. | Ath | Ts | Gene expression during lateral root inducible system (LRIS) | Spotted cDNA microarray (4k, Incyte Microarray Systems, Fremont, CA) |
| | Hochholdinger et al. | Zma | Pr | Comparison of protein accumulation between Irt1 mutant and wild type | Two-dimensional separation of proteins and MALDI TOF mass spectrometry |
| | Nemhauser et al. | Ath | Ts | Gene expression upon treatment with Auxin or Brassinolide | Affymetrix ATH1 |
| 2005 | Casson et al. | Ath | Ts | Gene expression in the apical and basal domains of the embryo at globular and heart stage | Affymetrix ATH1 |
| | Nawy et al. | Ath | Ts | Tissue layer specific gene expression using FACS and GFP-reporter lines of the quiescent center and columella root cap | Affymetrix ATH1 |
| | Okushima et al. | Ath | Ts | Comparison of gene expression upon auxin treatment between arf7, orf19, and ar7 arf19 mutants and wild type | Affymetrix ATH1 |
| | Vanneste et al. | Ath | Ts | Comparison of gene expression upon lateral root inducible system (LRIS) between sir mutant and wild type | Affymetrix ATH1 |
| | Woll et al. | Zma | Ts | Comparison of gene expression between rum1 mutant and wild type pericycle cells | Spotted cDNA microarray (12k , Generation II, Version A lowa State MicroArray Facility) |
| 2006 | Che et al. | Ath | Ts | Gene expression during shoot, root and callus development in Arabidopsis tissue culture | Affymetrix ATH1 |
| | Druka et al. | Hvu | Ts | Transcriptome atlas | Affymetrix Barley1 GeneChip |
| | Jiang et al. | Zma | Ts | Gene expression in the root cap, compared to the primary meristem and the quiescent center | Affymetrix Heterologous rice GeneChips |
| | Laskowski et al. | Ath | Ts | Gene expression during auxin treatment of seedlings roots | Custom Arabidopsis microarrays |
| | Lee et al. | Ath | Ts | Tissue layer specific gene expression using FACS and GFP-reporter lines of the phloem, xylem, and cortex | Affymetrix ATH1 |
| | Levesque et al. | Ath | Ts | Comparison of tissue layer specific gene expression in shr mutant in comparison with wild type | Affymetrix ATH1 |
| | Liu et al. | Zma | Pr | Comparison of protein accumulation between the mutant rum1 and wild type | Two-dimensional electrophoresis + nanoHPLC-ESI- MS/MS massspectrometry |
| | Mouchel et al. | Ath | Ts | Comparison of gene expression in a natural allele variant of BRX gene with wild type, upon treatment with Auxin or Brassinolide | Affymetrix ATH1 |
| 2002 | Brady et al. | Ath | Ts | Transcriptome atlas using FACS and GFP-reporter lines | Affymetrix ATH1 |
| | Dembinsky et al. | Zma | Comparison of gene expression and protein accumulation between the stele, the pericycle and the ground tissues | Custom 12K microarray (GenII vA: GPL 4876) and 2D electrophoresis + nanoHPLC-ESI-MS/MS | |
| | van Noorden et al. | Mtr | Pr | Comparison of protein accumulation between nodule initiation and auxin treatment in Medicago truncatula | Two-dimensional DIGE electrophoresis + MALDI- TOF/TOF MS |

| Tissues Tissue preparation | | Pathways Treatment | | | | | | Biological process | | | | | | | | | | | | | | | | | |
|---|-----------------|--------------------|-------------------------|--------------|-------|----------------|----------------------------|--------------------|-----|-----------|--------------|-------------|--------|--------|-------|-------------------------|----------------------------|----------------------------|-----------------------|--------------------------|-----------|--------------------------|--------------------------|-----------------|------------|
| | Organ isolation | Micro dissection | LCM micro dissection | Cell Sorting | Other | Mutants | Biotic, abiotic factors | Auxin | NPA | Cytokinin | Brassinolide | Gibberellin | Stress | Biotic | Other | Lateral Root Priming | Lateral Root Initiation | Lateral Root Patterning | Root organogenesis | Embryo & Primary root | Pericycle | Primary root meristem | Collus & Regeneration | Tissue identity | Cell Cycle |
| Primary root sections and root cell layers | | | | | | | | | | | | | | | | | | | | D | | D | | D | |
| Embryonic cultures | | | | | | | | Г | | | | | | | | | | | ī | D | | | | | |
| Cell suspension | | | | | | | | | | | | | 1 | | i | | i | | | | | | | | D |
| Hypocotyl segments | | | | | | | | i | | | | | 1 | 1 | | | i | i | D | | | | | | |
| Root section | | | | | | | | 1 | 1 | | | | T | | | | D | | | | | | | | |
| Primary roots | | | | | | irt1 | | Г | | | | | T | | | Г | D | | | | | i | | | |
| Entire seedlings | | | | | | | | D | | | D | | 7 | | | | i | | | | | | | | |
| Embryo apical and basal domains | | | | | | | | Г | | | | | T | | | | | | i | D | | i | | | |
| Quiescent center and columella root cap | | | | | | | | Г | | | | | 1 | | | | | | | | | i | | D | |
| Entire seedlings | | | | | | arf7, arf19 | | D | | | | | T | | | | i | | | | | | | | |
| Root segments | | | | | | slr | | 1 | 1 | | | | T | | | | D | | | | | | | | |
| Pericycle cells | | | | | | rum1 | | Г | | | | | T | | | | D | | | | D | | | | |
| Roat segments | | | | | | | | i | | i | | | T | | | | i | i | | | | i | D | | |
| Primary, seminal and crown roots | | | | | | | | Г | | | | | 1 | 1 | | | | | | i | | | | D | |
| Primary meristem, quiescent center, root cap | | | | | | | | Г | | | | | 1 | 1 | | Г | | | | | | D | | D | |
| Whole roots | | | | | | | | D | | | | | 1 | | | | D | | | | | | | | |
| Phicem, xylem, and cortex | | | | | | | | Г | | | | | 7 | 1 | | | 1 | | | | | | | D | |
| shr-2, pSHR:SHR:GR, shr root tips, sorted pWER:SHR:GFP | | | | | | shr | | Г | | | | | T | T | | | | | | | D | | | | |
| Primary roots | | | | | | rum1 | | | | | | | T | | | | 0 | | | | | | | | |
| Roats | | | | | | BRX variant | | D | | | D | | 1 | | | | i | | | | | | | | |
| Primary root sections and root cell layers | | | | | | | | Г | | | | | 1 | | | | i | i | | D | D | D | | D | |
| Stele, Pericycle and ground tissues | | | | | | | | | | П | | | 1 | 1 | | | i | | | | D | | | D | |
| Root segments | | | | | | suon | Nodulation | D | | | | | 1 | D | | | i | i | i | | | | | | |

| Dicotyledonous species | | | | | | | |
|--------------------------|---------------------|--|--|--|--|--|--|
| Ath Arabidopsis thaliana | | | | | | | |
| Mtr | Medicago truncatula | | | | | | |
| Gma | Glycine max | | | | | | |
| Pta | Pinus taeda | | | | | | |
| Ptr | Populus trichocarpa | | | | | | |

| _ | Monoc | otyledonous species |
|---|-------|---------------------|
| Г | Zma | Zea maize |
| | Osa | Oriza sativa |
| | Hvu | Hordeum vulgare |

| _ | | | _ | |
|---|----|------------|---|----|
| | On | nics type | | In |
| | Ts | | D | |
| | Tİ | | i | |
| | Pr | Proteome | | |
| | Mb | Metabolome | | |
| | | | - | |

| Information | | | | | | | | | |
|-------------|----------|--|--|--|--|--|--|--|--|
| D | Direct | | | | | | | | |
| i | Indirect | | | | | | | | |
| | | | | | | | | | |
| | | | | | | | | | |

| Reference | Species | Omics technique & Experimental design | Platform / Technique |
|-----------|---------|---------------------------------------|----------------------|

Year

| 2008 | Benedito et al. | Mtr | Ts | Transcriptome atlas | Affymetrix Medicago GeneChip |
|--------|-----------------------|-----|----|---|---|
| | De Smet et al. | Ath | Ts | Pericycle layer specific gene expression upon lateral root inducible system (LRIS) | Affymetrix ATH1 |
| | Dineny et al. | Ath | Ts | Transcriptome atlas using FACS and GFP-reporter lines upon salt stress | Affymetrix ATH1 |
| | Holmes et al. | Mtr | Ts | Comparison of gene expression between meristematic and non- meristematic root tissues | Affymetrix Medicago GeneChip |
| | Quesada et al., | Ptr | Ts | Comparative analysis of the transcriptomes of Populus trichocarpa and Arabidopsis | 42346 K 60-mer custom made microarray |
| 2009 | Gruber et al. | Mtr | Ts | Gene expression during salt-stress in root apexes | M. truncatula 16K+ microarrays (Mt16KOLI1) |
| ı | Jiao et al. | Osa | Ts | Transcriptome atlas using laser microdissection | 70-mer custom made microarray (Qiagen/Operon) |
| ı | Mustroph et al. | Ath | ті | Translatome atlas upon salt stress | Affymetrix ATH1 |
| ı | Saleem et al. | Zma | Pr | Comparison of protein accumulation in immature embryo, cortical parenchyma and stele tissues between the mutant rum2 and wild type | Two-dimensional electrophoresis + nanoHPLC-ESI- MS/MS massspectrometry |
| ı | Sena et al. | Ath | Ts | Gene expression during recovery of cell fates after cutting the root tip, and during the regeneration process | Affymetrix ATH-121501 full genome Arabidopsis microarray |
| 2010 | Libault et al | Gma | Ts | Transcriptome atias using RNA-Seq | Illumina Solexa deep sequencing |
| | Liu et al. | Zma | Pr | Comparison of the pericycle layer specific protein accumulation between the mutant rum1 and the wild type | Two-dimensional electrophoresis + nanoHPLC-ESI- MS/MS massspectrometry |
| | Matsuda et al. | Ath | Mb | Transcriptome atlas using metabolome data | LC-ESI-MS |
| | Moreno-Risueno et al. | Ath | Ts | Gene expression oscillations in the root tip | Affymetrix ATH1 |
| | Muthreich et al. | Zma | Pr | Comparison of protein accumulation between the rtcs mutant and wild type immature embryos | Two-dimensional electrophoresis + nanoHPLC-ESI- MS/MS massspectrometry |
| | Saleem et al. | Zma | Pr | Protein accumulation in the cortical parenchyma and the stelle of primary roots | Two-dimensional electrophoresis + nanoHPLC-ESI- MS/MS massspectrometry |
| | Severin et al. | Gma | Ts | Transcriptome atias using RNA-Seq | Illumina deep sequencing |
| | Sugimoto et al. | Ath | Ts | Gene expression during in vitro callus induction | Operon Arabidopsis Genome Oligo Set Version 1.0 (Operon, Alameda, CA) |
| | Wang et al. | Osa | Ts | Transcriptome atlas on two different varieties | Affymetrix Rice GeneChip Genome Array |
| 2011 | Coudert et al. | Osa | Ts | Comparison of gene expression between crl1 mutant and wild type stem bases | Affymetrix Rice GeneChip Genome Array |
| ı | Mathesius et al. | Gma | Pr | Comparison of protein accumulation between root apexes and root segments | Two-dimensional electrophoresis + MALDI- TOF/TOF MS |
| ı | Sekhon, R. S. et al. | Zma | Ts | Transcriptome atlas | Custom made microarray |
| | Takehisa et al. | Osa | Ts | Transcriptome atias using laser microdissection | Agilent 4x44K microarray RAP-DB (G2S19F#15241) |
| lished | De Rybel et al. | Ath | Ts | Gene expression during lateral root initiation synchronization using a new chemical molecule, naxillin | Affymetrix ATH1 |
| Unpub | Ducleroq et al. | Ath | Ts | Auxin Cytokinin crosstalk and lateral root initiation | Affymetrix Tilling Microarray |
| | Middleton et al. | Ath | Ts | Gene expression during lateral root formation and emergence after synchronous induction of lateral root initiation | Affymetrix ATH1 |
| | | | | | |

| Tissues | Tissue preparation | | | | | | | Pathways Treatment | | | | | | | | Biolo | gical p | rocess | | | | | | | | |
|--|--|------------------|-------------------------|--------------|----------|------------|------------------------------|--------------------------|-----|-----------|--------------|-------------|--------|---------------------------------|-------------|--------------|--------------|----------------------------|------------|---------------|--------------------------|-----------|--------------------------|--------------------------|-----------------|------------|
| | Organ Isolation | Micro dissection | LCM micro dissection | Cell Sorting | Other | Mutants | Blottic, ablot ic factors | Ausdin | NPA | Cytokinin | Brassinolide | Gibberellin | Stress | Biotic | Other | Lateral Root | Lateral Root | Initiation Lateral Root | Patterning | organogenesis | Embryo & Primary root | Pericycle | Primary root meristem | Callus & Regeneration | Tissue identity | Cell Cycle |
| Roots, nodules and shoot tissues | ŏ | ŝ | | _ | | | Nodulation | Г | | | | | | D | | Ē | 1 | 1. | | 5 | _ | | _ | 4 | p. | |
| Xylem pole pericycle cells | | | | | Н | | | i | | | | | - | - | \dashv | | | | | | | D | | | D | , |
| Primary root sections and root | | | | | Н | - | | ŀ | | | | | | - | - | H | | ٠. | + | - | | | | | | |
| cell layers Root tips and non meristematic | | | | | Н | - | Salt stress | \vdash | | | | Ц | D | | 4 | _ | + | + | - | | i | | i | | D | |
| root segments | | | | | | | | L | | | | | | | _ | | L | 1 | | | D | | D | | | |
| Whole roots and shoot organs | | | | | | | | L | | | | | | | | | | | | | | | D | | D | |
| Roots apexes | | | | | | | Salt stress | | | | | | | | | | | | | | | | D | | | |
| Roots and shoot tissues | | | | | | | | Г | | | | | | | | | | | | | D | | D | | D | |
| Roots | | | | | П | | Нуроху | Г | | | | | | | | | Г | Т | T | | | | Г | | | |
| Embryos, cortical parenchyma and stelle | | | | | Н | rum1 | | | | | | | | | \exists | | | | + | | D | | | | D | |
| Root tips | | | | | \vdash | | | 1 | | | | | 1 | | \dashv | | | 1 | | | D | | | D | | |
| Root tip, root , root hair, nodule, | | | | | \vdash | | Nodulation | | Н | | | | - | D | - | | + | - | - | | D | | D | | D | |
| shoot tissues Pericycle cells | | | | | \vdash | | Nocuation | \vdash | H | | | | - | U . | \dashv | H | ٠ | ٠ | + | - | D. | | | | U | |
| Root, seed, shoot organs | | | | | Ш | numl | | H | | | | | _ | | 4 | L | - | Ψ. | + | | | D | _ | | _ | |
| | | | | | Ш | | | L | | | | | | | | | L | _ | 1 | | | | D | | D | L |
| Root segments corresponding to the oscillation zone | | | | | | | | L | | | | | | | | D | L | | | | | | | | | |
| Embryos | | | | | | rtes | | | | | | | | | | | | | ı | D | D | | | | | |
| Cortical parenchyma and stele | | | | | | | | Г | | | | | | | | | 1 | | Т | | | | | | D | |
| Root, nodule, seed and shoot tissues | | | | | | | Nodulation | Г | | | | | | D | | | Т | Т | | , | D | | D | | D | |
| Root, cotyledon, and petal | | | | | Н | | | i | П | i | | | 7 | | ٦ | | | | Ť | | | | ī | D | D | |
| explants Roots, callus, seed and shoot tissues | | | | | Н | | | D | Н | D | | D | | i | 1 | | | | | | D | | | D | D | |
| Stern bases | | | | | | cr/1 | | Г | | | | | | | ٦ | | † | + | ì | D | | | | | | |
| Root apexes and root segments | | | | | Н | | | \vdash | Н | | | | 1 | | \dashv | \vdash | + | + | - | | | | D | | | |
| Root, seedling and shoot tissues | | | | | \vdash | - | | \vdash | Н | H | Н | | - | - | - | \vdash | + | + | + | - | | | | | | |
| Sections, epi-exo, cortex and | | | | | \vdash | - | | H | | | | | | | - | - | - | + | ÷ | _ | | | D | | D | - |
| endo-stele tissues | | | | | | | | | | | | | | | | | ' | 1 | | | | | D | | D | |
| Root segments | | | | | | | | D | | | | | | | D | 1 | | ı | | | | | | | | |
| Xylem pole pericycle cells | | | | | Н | | | D | Н | D | | | | | ٦ | | | ı | + | | | р | | | | |
| Synchronized primordia | | | | | Н | - | | | Н | | | | 1 | | \dashv | \vdash | f | ٠. | è | D | , | | | | | |
| | | | | | | | | | | | | | | | | | | D | | 0 | | | 1 | | 1 | |
| Dicotyledon | | | | | | | | onous species a maize | | | | | | - | Omics type | | | | | - | Information | | | | | |
| | abidopsis thaliana edicago truncatula | | | | | Zma Osa | | | | | | | | Ts Transcriptome TI Translatome | | | | | | | D Direct i Indirect | | | | | |
| | | ago i e ma | | atul | d | Hvu | | | | | | | | | Pr Proteome | | | | | | | ma | irec | L | | |
| | | taed | | | | | . 10 | | | | | | | | | Metabolome | | | | | | | | | | |
| | | | ichoc | arpa | 3 | | | | | | | | | - | | | | | | _ | | | | | | |

lrt1, lateral root 1; slr, solitary root 1; arf, auxin response factor; rum1, rootless with undetectable meristems 1; shr, short root; wer, werewolf; brx, brevis radix; sunn, supernumerary nodules; rtcs, rootless concerning crown and seminal roots; crl1, crown rootless 1.