Chapter 1
Introduction to Root Genomics

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1.1 Introduction

The twenty first century has been marked by climate awareness and an overall increase in conscience towards environmentally friendly agriculture. Despite the natural phenomena playing hard against most crops, we need to gather all the possible information on the plant–soil–water interactions in order to breed for this century. Abiotic and biotic stresses will be targeted as most of the frontiers for agriculture lie in nonoptimal areas, and genetic improvements through science will play a major role in this conquer.

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Root development, one of the major processes essential to the development of flowering plants, remains poorly understood. Roots are a hidden part of plants for many aspects and have not been the main subject of interest of researchers. Nevertheless, roots play a major role in the plant–soil interactions, regarding biological and physical aspects. The understanding of the physiological, molecular, and developmental processes that roots undergo may represent a giant step on the achievement of a more sustainable and energy-efficient agriculture. This book may serve as a reference book in this context. Some concepts about root genomics together with an overview on different chapters presented in this volume are given in this article.

1.2 Root Genomics: An Overview

Root genomics research can be divided in the following four areas of research: (1) root growth and development; (2) functional analyses of abiotic stress responses; (3) functional analyses of biotic stress responses; and (4) quantitative trait loci (QTL) analysis and molecular breeding. The understanding of basic mechanisms involving root development and the interactions of roots and soils under various abiotic and biotic stresses will pave the way for the next decades. Also, mutations obtained in model species through the use of high throughput techniques such as TILLING (targeted induced local lesions in genome) are turning root genomics an exciting subject in plant molecular biology. An attempt has been made to cover all the above-mentioned four areas of root genomics research.

1.2.1 Root Growth and Development

The breakthrough depiction of root development has started with *Arabidopsis* roots (Dolan et al. 1993, 1994; Scheres et al. 1996). The events of division, enlargement, and differentiation of cells in the roots are spatially separated. At the root tip, there is a region of continuous cell division, the RAM (root apical meristem). The new cells formed enlarge by a factor of 100-fold through a process of cell elongation. After the cells reach a mature size, they differentiate into the various cell types of the root. Root growth is accompanied by the formation of a series of lateral roots, resulting in a branching pattern that covers higher volumes of soil space in every step of branching. A range of root systems can be found in different plants including from shallow patterns to very deep roots. Therefore, the identification of factors affecting the patterns of root development is the major point in decoding the genetic control of this organ.

In a paleontological context, the role of auxin in morphogenesis has allowed the identification of vascular patterns preserved in fossils as records of auxin gradients and growth dynamics (Boyce 2010). Roots evolved independently at least in lycophytes and euphyllophytes (Gensel et al. 2001). Root traces have been found in early Devonian soil horizons, contemporaneous with attached roots in lycophyte related fossils. The presence of root hairs, root cap, and endogenous initiation shared by roots has been proposed to have highly divergent origins (Boyce 2010). Shared regulation by similar helix-loop-helix transcription factors (Menand et al. 2007) suggests a homology between rhizoids and root hairs. The origin of root caps, on the other hand, is suggested to be a response to the need of having a protective tissue to the root apical meristem, a fast-growing region constantly in contact with a solid surface, i.e., the soil. The appearance of adventitious roots may date the evolution of endogenous initiation combined with reversed auxin transport, since the first appears to have occurred repeatedly through times and is suggested to have been required for the establishment of vascular continuity (Boyce 2005). Anatomical homogeneity/heterogeneity is suggested as a reflection of stable/unstable environments faced by land plants and epiphytes/swamp plants, respectively. Despite the environmental differences, auxin transport mechanisms are thought to limit the anatomical variations in roots (Boyce 2005; Raven and Edwards 2001).

Studying root development requires model species with simple root architecture. *Arabidopsis* and rice are model species that have been fully sequenced and therefore can provide good models for monocot and dicotyledoneous root development. *Arabidopsis* root is composed of 15 distinct cell types arranged as concentric cylinders around the radial axis (Iyer-Pascuzzi et al. 2009). MicroRNA-mediated signaling has been reported to be involved in plant root development (Meng et al. 2010). Several of these miRNAs are interestingly shared by *Arabidopsis* and rice despite their differences in root patterns and architecture. However, only a few genes governing root development have been described in cereals, and differences between monocots and dicots are quite remarkable when one regards at the root system. Therefore, both models are necessary for the better understanding of the branching patterns and functional specificities of roots. Two crown rootless mutants, *crown-rootless4* (*crl4*) and *OsGnom1*, affect the gene orthologous to *GNOM1* in *Arabidopsis* (Kitomi et al. 2008; Liu et al. 2009). *GNOM1* is a membrane-associated guanine-nucleotide exchange factor of the ADP-ribosylation factor G protein (ARF_GEF) that regulates the traffic of PIN1 (PINFORMED 1) auxin efflux carrier proteins that regulates auxin transport. *GNOM1* is thought to be required for the formation of the lateral primordium in Arabidopsis, by acting on the asymmetrical division of pericycle cells (Coudert et al. 2010). Recently, a new notion on root system architecture (RSA) has been described (Dorlodot et al. 2007). Root architecture importance for plants lies in the fact that soil nutrients are not evenly distributed and the ability to spatially deploy roots can constitute an advantage.

Developmental models could be an alternative to improve phenotyping in this very plastic organ. Mapping the dynamics of roots per se or after inducing root development under different stresses could bring better understanding and establish genotype differences. Shoot-borne-root formation characterizes the difference between cereals and the dicot model plant Arabidopsis. Several mutants that are impaired in shoot-borne-root formation (4), lateral roots (4), primary root (6), and root hairs (4) have been described in maize and rice (Hochholdinger et al. 2004).

Some of these genes controlling root development have been recently cloned and will shed light on the influence of distinct root functions and architecture on grain yield and performance in water-limited conditions (Hochholdinger and Tuberosa 2009). However, the overall trend is that single mutant standard analysis is shifting to genome-wide approaches, leading to a speeding up of the process of generating information. Proteomics- and metabolomics-generated datasets will need integration with bioinformatics tools in order to translate the overwhelming amount of data into biological meaningful phenomena.

1.2.2 Biotic Stress Tolerance

Biotic stress is caused by organism attacks to plants and can be caused by different pathogens (virus, bacteria, or fungi) or pests (insects). Pathogen infections trigger plant response mechanisms that are not restricted to the infection organ. The plant senses the pest attack and responds with a range of different expressions of genes regulating metabolites such as proteinase inhibitors, toxins, or volatiles that repel pests or attract natural enemies. Herbivores or pathogens can elicit different types of defense reaction. When vacuoles and trichomes are bursted as a consequence of a chewing herbivore attack, compounds such as organic isothiocyanates can be released (Bruce and Pickett 2007).

An interesting point of view is brought by on the cross-talk between shoot and root (Van Dam et al. 2004; Bezemer and van Dam 2005). Induced responses are complicated. The fact that hormone signaling pathways govern biotic and abiotic stress responses is characterized by the fact that ABA is involved in many abiotic responses and acts as a negative regulator of disease resistance (Fujita et al. 2006). Other phytohormones, such as Salycilic acid (SA), Jasmonic Acid (JA), and Ethylene (ET), play critical roles in biotic responses. Other responses are mediated by MAP-kinase cascades, which control many biotic and abiotic responses. Other evidence of this cross-talk is the presence of Reactive Oxygen Species (ROS) at converging points between biotic and abiotic response pathways. The integration of this network of responses is essential for the understanding of how roots participate in this process and the intricate process of cross-signaling that this may need.

1.2.3 Abiotic Stress Tolerance

Roots are subjected to a wide range of stresses such as drought, flooding, salinity, as well as nutrient starvation and metal toxicity such as Al, Cd, Fe, As, and Hg. Cadmiun is a nonessential element for plants, its toxicity resulting in chlorosis and stunting. Chlorosis seems to be an indirect effect on the uptake, transport, and use of other elements such as Ca, Mg, Fe, Mn, Cu, Zn, P, and K. Cd also interferes with hormones and disturbs plant water status, causing reduction of root hydraulic conductivity, decrease of transpiration, and increase of stomatal resistance (Prasad 1995; Das et al. 1997; Aina et al. 2007). A proteomics approach revealed the importance of two metabolic enzymes induced by 10 uM Cd that seems to play a key role in the response to several abiotic stresses: alanine aminotransferase (ALT) and Hexoquinase (HXK) suggest that these could be potential biomarkers for the study of Cd toxicity (Aina et al. 2007). The accumulation of NaCl at root peripheral regions limits growth by exerting osmotic and ionic stresses. Ionic stress is a consequence of Na^+ and Cl^- accumulation, disturbing the K^+/Na^+ ratio in the plant cell (Hasegawa et al. 2000). Time-dependent effect of NaCl on the activities of tonoplast proton pumps, showing distinct profiles for vacuolar proton transporting ATPase and vacuolar proton transporting pyrophosphatase were reported. Activity alterations were found to be due to posttranslational changes (Kabata and Ktobus 2008). The effects of salinity on *Arabidopsis* cells have been recently investigated (Dinnenny et al. 2008). Transcriptional changes in response to salinity seem to be highly constrained by developmental parameters. Iron deprivation and salt stress data sets were compared. The largest set of coregulated genes displayed concerted down-regulation in the epidermis and encoded genes important for protein biosynthesis. Epidermis cells seem to present the least conserved patterns when different stresses are applied (13–15%). A range of 244 genes are cell-type-specific and whose expression pattern does not substantially change with stress. Chloroplast accumulation was found to be a novel feature of the cortex in light-grown roots. Interestingly, rice roots under excess iron stress seem to accumulate Rubisco peptides, as revealed by proteomic studies (Costa de Oliveira, unpublished).

The responses of roots to abiotic stresses are though amenable to environmental influences as well as cell-type. The high plasticity observed in the developmental patterns plus the range of abiotic factors affecting root growth through the development of plants picture a complex scenario composed of many players as well as interactions among them.

1.2.4 QTL Analysis and Molecular Breeding

Root morphology is in most cases regulated by many genes with small effects and highly influenced by the environment. Therefore, the study of root system related genes will very often rely on QTLs analyses. A few examples on mapping and identification of QTLs explaining the variation for root traits have become available in some crop species (Price and Tomos 1997; Price et al. 2002; Giuliani et al. 2005). Adventitious rooting has been considered to improve phosphorus uptake and deep root growth to increase the ability to cope with drought (Ochoa et al. 2006; Macmillan et al. 2006; Steele et al. 2006). In some cases, QTLs associated with root traits have been cloned, e.g., root elongation in *Arabidopsis* (Sergeeva et al. 2006).

Although QTL analysis was developed to deal with environmental influence on target characters, the high degree of plasticity presented by roots can mislead studies and make it difficult to do a reliable phenotyping. However, at least in rice and maize, QTL by environment interactions have been found to be weak, and marker-assisted selection studies have been successful (Macmillan et al. 2006; Kamoshita et al. 2002; Steele et al. 2006, 2007; Giuliani et al. 2005; Landi et al. 2005).

1.3 About the Book

This book covers all the four areas of research mentioned above. Some highlights of the chapters included in this book are given below.

During the past decades, a considerable number of genes and gene networks have been well described in the model species *Arabidopsis thaliana*. This knowledge can be adapted for more complex plant systems as barley, rice, or maize. Despite their agronomic importance, only a little is known about molecular basis of root formation in crop species, and only few mutants together with corresponding genes have been well characterized. In this context, Orman and colleagues from Silesian University, Poland, have described the EST (expressed-sequence tag)-based approach, in Chap. 2, to search for potential orthologous genes involved in root morphogenesis between Arabidopsis, rice, and barley. The comprehensive gene list, developed by authors, should provide strong platform for molecular studies and gene identification in barley and related species.

Roots are exposed to a range of microbe, and there are several studies, as mentioned above, which deal with discussions on root–microbe interactions as well as impact of biotic stresses on the root architecture. The Chap. 3, authored by Mathesius and van Noorden from Australian National University, Australia, present the updates on genomics of root–microbe interactions. Microbes influence roots by producing signals, toxins, altering nutrient cycling, and by invading roots as endosymbionts or endoparasites. Genomic tools have helped to elucidate the molecular changes induced in roots by microbes. This chapter highlights some of the recent advances gained by genomic and postgenomic studies to enhance knowledge in the area of root–microbe interactions. Similarly, Deshpande and colleagues from Purdue University (USA), University of Georgia (USA), Michigan Technological University (USA), and Instituto Nacional de Tecnología Agropecuaria (INTA, Argentina), in Chap. 4, discuss the advances in the plant genetics for study of the roles of root exudates and microbes in the soil. In order to dissect the relationships between soil microbes, plant exudates, and plant function, authors planned to use host genetics to identify exudate::microbe correlates that segregate with specific plant genes. Their studies indicated the great potential for future investigations of the plant-determined chemical and organismal diversity in the soil.

Abiotic stresses are the major stresses for limiting crop productivity in several crop species, especially in developing countries. In majority of such cases, roots are the first plant organs to be exposed as well as to respond. Some of these abiotic stresses in the context of root genomics have been discussed in a few chapters. For instance, in Chap. 5, Gruber and colleagues from Institut des Sciences du Végétal (ISV) and Université Paris Diderot Paris 7 from France discuss the impact of abiotic stresses such as drought and salt on the action and number of root meristems to determine root architecture. In addition to Arabidopsis, authors have discussed recent results on model legumes able to interact symbiotically with soil rhizobia to form new meristems leading to the nitrogen-fixing nodule. Aluminum (Al) toxicity is another abiotic stress that limits agricultural productivity over much of the world's arable land by inhibiting root growth and development. Affected plants have difficulty in acquiring adequate water and nutrition from their soil environments and thus have stunted shoot development and diminished yield. Hoekenga from US Department of Agriculture (USDA) – Agricultural Research Station (ARS) (USA) and Magalhaes from EMBRAPA Maize and Sorghum (Brazil) discuss in Chap. 6 the Al-tolerance mechanisms. They propose and discuss the use of systems biology approaches to study the mechanisms of Al tolerance and apply this knowledge to crop improvement via marker-assisted breeding and translational genomics. Sousa and Costa de Oliveira from Eliseu Maciel School of Agronomy, Campus UFPel (Brazil) discuss, in Chap. 7, about root responses to other abiotic stresses such as soluble iron and short chain organic acids in flooded soils, especially in the context of rice. Authors review the progress on discovery of iron transporters as well as genetic variation present in rice genotypes for flooding tolerance.

A number of studies have described QTLs that provide access to valuable genetic diversity for the morphophysiological features that characterize root functionality. Although a number of major QTLs have been identified as mentioned above, none of these QTLs has been cloned so far in crop plants, mainly due to the difficulty to accurately phenotype the target traits in a sufficiently large number of plants. In this context, in Chap. 8, Tuberosa and colleagues present summary and discuss the strategies for QTL cloning, especially in the context of maize. QTL cloning should be facilitated by adoption of high-throughput phenomics platforms as well as by information made available through genome and the profiling of the transcriptome, proteome, and metabolome, all of which will contribute to the identification of plausible candidate genes. Sheshashayee and colleagues from University of Agricultural Sciences-Bangalore, India, in Chap. 9, have presented phenotyping methodology for root traits and biotechnological approaches to improve these roots traits with an objective of sustainable crop production. In Chap. 10, Varshney and colleagues from ICRISAT, India, and Hokkaido University, Japan, discuss the physiological and genomics approaches to dissect the root traits at genetic and molecular level in context of devising the strategies for breeding for root traits to enhance drought tolerance in chickpea. Authors have also discussed the use of next generation sequencing technologies towards gene discovery and marker development.

The last two chapters discuss the progress in the area of molecular breeding for root traits for crop improvement. For instance, Raman from Wagga Wagga Agricultural Institute, Australia, and Gustafson from University of Missouri, USA, in Chap. 11, review the progress made on various aspects of molecular breeding for Al resistance such as genetics, molecular mapping, comparative mapping, marker-assisted selection, candidate gene discovery and validation, and allele mining in key cereal crops including wheat, barley, rice, maize, oats, sorghum, and rye. Similarly, Ismail and

Thomson from International Rice Research Institute, Philippines, in Chap. 12, have summarized the progress made in unraveling molecular and physiological bases of tolerance of various abiotic stresses encountered in rice problem soils including salt stress and nutritional toxicities and deficiencies. Authors have also provided a brief account of the progress towards developing and using marker-assisted back crossing (MABC) for cultivar improvement in rice.

1.4 Concluding Remarks

The field of root genomics is an exciting and promising field of research. Some of these areas of research have been detailed in some chapters of the book. The technical advances in plant-*omics* are prone to generate enough data to push forward the science of root genomics. Candidate gene identification is a strategy that is getting stronger every year. The production of genomic sequences from many sequencing projects is making the availability of specific genes more frequent. Bioinformatic tools and reverse genetic approaches such as TILLING, gene knockout mutants, or RNAi are prone to increase the success in this strategy (Dorlodot et al. 2007). An ever neglected part of the plant, roots seem to hold the key for the next plant breeding revolution, leading to improved crop productivity in environmentally challenged situations.

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