13 Translational Root Genomics for Crop Improvement

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Introduction

Breeding of crop plants in the 21st century needs consciousness and awareness of climate change. For instance, both biotic and abiotic stresses need attention of breeders in order to breed crops showing resistance/tolerance to these stresses in a changing climate scenario. In developing countries, drought is the major abiotic stress and is already limiting crop productivity in several species. This tendency is going to worsen the situation in the years to come (Varshney et al. 2011a). Enhancing crop productivity in resource-poor dry land conditions is a formidable challenge. Conserving resources through management practices and engineering plants for superior extraction of these resources coupled with an increased efficiency of resource utilization deserve emphasis. Though resource conservation through management practices are equally important, development of superior resource use efficiency as a seed-based technology always has greater acceptance and adaptability.

Roots, which are underground hidden parts of plants, are considered as first plant organs to be exposed, as well as to respond in stresses. However, among several parts of the plant, roots have received little attention of researchers so far despite their major role in plant–soil interactions (Sheshshayee et al. 2011). Thus, they seem to hold the key for the next plant breeding revolution, leading to improved crop productivity in environmentally challenged situations. Recent advancements in plant genomics are certainly of help in crop improvement efforts (Varshney et al. 2005) and genomics-assisted breeding applications such as marker-assisted selection (MAS) have been already used in developing superior cultivars in several crop species (Varshney et al. 2006, 2010; Gupta et al. 2010). The field of root genomics is an exciting and promising field of research and some technical advancements in plant-omics are believed to generate some useful data for pursuing translational research. Whole genome approaches such as microarrays or next-generation sequencing (NGS)-based transcript profiling or functional genomics approaches may provide some useful information about the type and nature of structural and functional genes involved in various aspects of root growth, development, and water and nutrient uptake. In addition, on the basis of whole genome sequence available for several crop species (for references, see Jackson et al. 2011; Morrell et al. 2012) or gene information available in model plant species, use of comparative genomics or bioinformatics approaches may provide interesting candidate genes. Once the details of these genes are known, some other approaches like overexpression, TILLLING (Targeting-Induced Local Lesions IN Genomes; Varshney et al. 2011b), qRT-PCR, gene-knockout mutant analysis may be used to further validate their utility in root trait improvement.

In this article, we highlight the importance of root genomics research in the context of drought stress and discuss recent developments in genetic and molecular dissection of root traits. A special emphasis has been given on translational root genomics for developing superior varieties through molecular breeding for root traits.

Root Research for Crop Improvement

Studying roots in higher plants assumes importance because they provide firm anchorage of the plant in their soil substratum and helps in absorption and effective supply of water and nutrients to the shoot. These are the most important roles of the root system (Varshney et al. 2011b). In addition, roots assume importance for plants by producing a number of growth hormones, including cytokinins and ABA. From an ecological point of view, roots play some role in weathering of rocks, thus leading to the formation of soil. Sometimes, tiny roots spread out by growing horizontally and form a thick mat-like network; they may prevent soil erosion and through their symbiotic association, roots with rhizobia, mycorrhiza, and other organisms can fix atmospheric nitrogen or enrich mineral soil content. However, keeping in view the current scenario of importance of drought in view of changing climate, the water mining capacity of roots from deeper soil profiles is considered as one of the important adaptive strategies evolved by plants to survive water-scarce conditions. With an objective of paying more attention on root research at genetic, physiological, and molecular level, a *Plant Root Genomics Consortium* was developed by University of Missouri in collaboration of other partners from USA (http://rootgenomics.rnet.missouri.edu/prgc/index.html). The primary goal of this consortium is to develop understanding of molecular mechanisms used by plant roots to get water and nutrition from soil and to find out the possible role of roots in adaptation to drought conditions and further transfer this knowledge for crop improvement through various breeding and biotechnological approaches. Discussions are currently underway to extend this consortium into an International Root Genomics Consortium.

The role of roots is very significant to enhance drought tolerance. In simpler terms, drought tolerance is the ability of a plant to avoid or tolerate stress at organism level (Levitt 1972; Blum 2005). Drought is often regarded as a major threat to ecosystems, as water stress limits crop yield more than all other biotic and abiotic factors combined (Lambers et al. 2008). In these situations, the ability of the plants to explore water resource by reaching roots deep in the soil and extracting water has great relevance in maintaining water relation as well as carbon assimilation. Therefore, genotypes with long deep-roots have been found more tolerant to drought (Li et al. 2005a; Kashiwagi et al. 2005, 2006; Reynolds and Tuberosa 2008). In addition, some other related traits have been suggested to help plants to perform better in water-limited conditions. For instance, low leaf conductance under nonlimited water conditions during the vegetative stage, higher fraction of transpirable soil water (FTSW) thresholds that reduce transpiration, thus avoiding rapid soil water depletion, and low leaf expansion rate when soil moisture is still nonlimiting for plant growth have been suggested in chickpea (Zaman-Allah et al. 2011).

Genetic Dissection of Root Traits

### Quantitative Trait Locus (QTL) Discovery for Root Traits

In simple terms, a QTL is a segment of DNA that affects a quantitative trait or the region within genome that contains genes associated with a particular quantitative trait. The plant root system is

considered highly dynamic and responds to changes in environmental parameters, including stresses such as drought, nutrient deficiencies, water logging, and salinity. However, despite their essential role in plant growth, adaptation, and mineral nutrient acquisition, the root system has remained unexplored, owing to the difficulty in screening techniques until recently. Once the considerable understanding of root growth and development, both at the whole plant level and at the molecular level, is achieved, the next step is to devise strategies for identification of important genes/QTLs associated with various root traits followed by their validation and subsequently introgression into crops through molecular breeding approaches (Varshney et al. 2011b). In terms of genetic control, root traits are believed to be complex controlled by a number of genes/QTLs. Therefore, understanding the genetic control of root development and functions of component root traits is considered inherently important for breeding improved cultivars for root traits that are well adapted to variable climates. For QTL mapping studies, generating large-scale and precise phenotyping data on mapping populations is very critical. In recent years, significant progress has been made toward improving phenotyping capabilities (Manschadi et al. 2008; Gregory et al. 2009; Hund et al 2009; Nagel et al. 2009; Yazdanbakhsh and Fisahn 2009; Chen et al. 2011) as well as marker genotyping capacities (see Mir et al., in press). As a result, marker-trait association (MTA) studies are gaining importance to gain new insights into the genetic control of root system architecture (see de Dorlodot et al. 2007; Courtois et al. 2009; Hochholdinger and Tuberosa 2009; Coudert et al. 2010; Kell 2011; Gowda et al. 2011; Tuberosa et al. 2011).

In general, there are two important approaches for the study of MTA: (i) QTL interval mapping commonly called linkage mapping/linkage analysis-based QTL mapping and (ii) linkage disequilibrium-based association mapping (Figure 13.1). Both approaches have their own advantages and disadvantages and have been already used for discovering QTLs/genes for a variety of traits in all important crop plants (see Myles et al. 2009; Rafalski 2010). The various steps involved in both approaches have been discussed elsewhere (see Varshney et al. 2011b; Chamarthi et al. 2011; Figure 13.1). By using one of these two approaches, QTLs for root traits have been identified in about 15 plant species (Kalliokoski et al. 2008). However, rice, maize, and wheat among cereal crops and soybean, common bean and chickpea among legumes have dominated root trait QTL studies. Some of these important QTL studies have been summarized in Table 13.1.

Rice is probably the crop species in which a maximum number of QTL studies for root traits have been targeted (see Courtois et al. 2009; Priya et al. 2009). More than 900 QTLs related to root traits such as maximum length, number, thickness, volume, and their effects on yield under varying moisture regimes have been studied in rice (Kamoshita et al. 2002a; MacMillan et al. 2006; Steele et al. 2006, 2007; Yue et al. 2006). Since precise phenotyping is considered crucial in the study of MTA for root traits, a range of phenotyping platforms and methods including green house (Komoshita et al. 2002b), hydroponic cultures (Obara et al. 2010), basket method (Uga et al. 2011), poly vinyl chloride (PVC) cylinders (Qu et al. 2008), and field conditions (Ikeda et al. 2007; Yue et al. 2008) have been used. In terms of genetic localization, QTLs for maximum root length have been identified almost on all 12 chromosomes (Hemamalini et al. 2000; Zhang et al. 2001; Kamoshita et al. 2002a, 2002b; Courtois et al. 2003; Horii et al. 2006; MacMillan et al. 2006; Yue et al. 2006). A major QTL for root length (*qRL6.1*) based on phenotyping of seedlings grown under hydroponic conditions has been identified on chromosome 6 (Obara et al. 2010) and delimited to a 337 kb region of the Nipponbare genome. Another major QTL controlling RDR (for ratio of deep rooting), which explains 66.6% total phenotypic variation (PV) was detected on chromosome 9 by using RIL populations derived from a cross IR64 × Kinandang Patong (Uga et al. 2011).

In the case of maize, QTLs for various root traits have been identified based on phenotyping using a range of soil moisture regimes (Tuberosa et al. 2002a, 2003; Landi et al. 2007). QTLs of root pulling resistance at flowering time were identified based on phenotyping in field conditions (Giuliani et al.
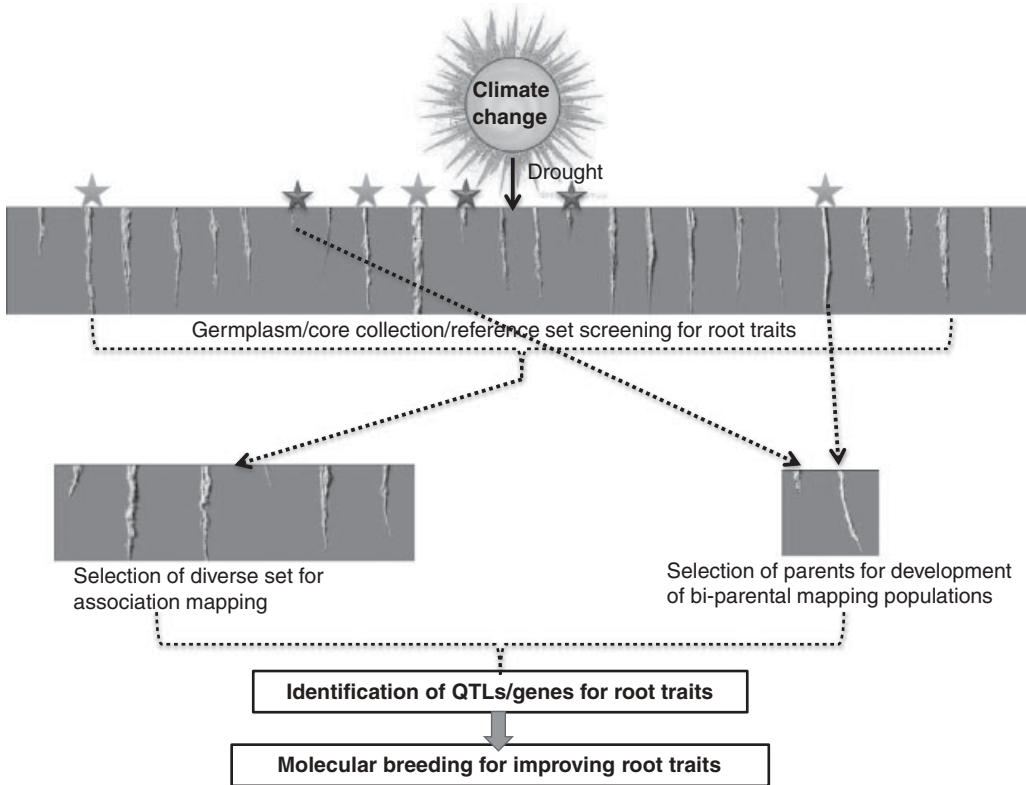
Figure 13.1 A schematic figure showing discovery and translation of root trait QTLs for crop improvement. The figure shows screening of germplasm under natural conditions for root traits. While a diverse set of germplasm showing a variation of root traits is selected and used for association mapping, contrasting lines comprising of higher root, and lower root biomass are selected for developing biparental mapping populations and linkage mapping-based QTL analysis. Once major QTLs are identified, molecular breeding for these QTLs can lead to development of superior lines for improved root traits. Red stars indicated lines with short roots (mostly drought susceptible), while green lines indicated lines with long roots (mostly drought tolerant). (For a color version of this figure, see the color plate section.)

2000). Recently, Ruta et al. (2010) identified 13 QTLs for six seedling traits: elongation rates of axile roots, the rate constant of lateral root elongation (kLat), the final respective lengths LAx and LLat, and the ratios kLat/ERAx and LLat/LAx. In this study, QTLs for the elongation rates of axile roots responded more clearly to water stress compared to root length. In addition, many QTLs for root traits and their responses to drought and phosphorus deficiency have been reported in maize (Lebreton et al. 1995; Guingo et al. 1998; Landi et al. 2002; Tuberosa et al. 2002b; Hund et al. 2004; Mano et al. 2005; Zhu et al. 2005a, 2005b, 2006). However, QTL analysis for root traits in response to low N stress is not well studied.

In the case of wheat, Ma et al. (2005) found a QTL for root-growth rate under Al treatment. QTLs of root traits (primary/lateral root length and number, root dry matter) under control conditions and during nitrogen deficiency were also identified (Laperche et al. 2006). Several studies identified QTLs for early root growth in wheat (An et al. 2006; Laperche et al. 2006; Li et al. 2007; Sanguineti et al. 2007; Sharma et al. 2011). In a recent study, a total of 15 QTLs, including 6 additive and 9

Table 13.1 Root trait QTLs identified in some important cereals and legume crop plants.

Crop	Mapping Population	Traits	Environment	QTLs	Phenotypic Variation Explained (PVE; %)	Reference
Rice	IR64 × INRC10192 (RIL)	Shoot length, maximum root length, shoot dry weight, root dry weight, and root to shoot dry weight ratio	PEG-induced stress conditions	19	7.9–29.8	Srividhya et al. 2010
	IR64 × Kinandang Patong (RIL)	Ratio of deep rooting	Basket method	1	66.6	Uga et al. 2011
	Koshihikari × Kasalath (CSSL)	Root length	Hydroponic culture	1	21.1	Obara et al. 2010
	IR64 × Kinandang Patong (RIL)	Stele transverse area, total area, and number of late metaxylem vessels	Upland field; well watered	10	18.7–23.9	Uga et al. 2008
	IRAT109 × Yuefu (RIL)	Basal root thickness, root number, maximum root length, root fresh weight, root dry weight, and root volume	PVC pipes at seedling, tillering, heading, grain filling, and mature stages	84 additive and 86 epistatic	19 and 10	Qu et al. 2008
	Otomemochi × Yumenohatamochi	Number of new roots, maximum new root length, root, and shoot ratio	Low land field, well-watered and drought stress	20	7.0–31.2	Ikeda et al. 2007
	Akihikari × IRAT109 (BIL)		Solution culture	5	8–24	Horii et al. 2006
	Bala × Azucena (RIL)	Maximum root length, maximum root thickness, root mass below 50 cm, total plant dry mass, % root mass, and shoot length	Soil box method	28	5.4–13.5	MacMillan et al. 2006
	IRAT 109 × Yuefu (DH)	Basal root thickness, total root number, maximum root length, root fresh weight, root dry weight, ratio of root fresh weight to shoot fresh weight, ratio of root dry weight to shoot dry weight	PVC cylinders, low land field, well watered, and drought	51	1.1–25.6	Li et al. 2005a
	IR1552 × Azucena (RIL)	Seminal root length, adventitious root number, lateral root length, and lateral root number	Pot culture, well watered, and drought stress	23	11.4–20.0	Zheng et al. 2003
	IAC165 × Co39 (RIL)	Root length, root thickness, and root dry weight	PVC cylinders, aerobic	29	6.3–24.4	Courtois et al. 2003
	IR64 × Azucena (DH)		PVC cylinders, well watered, and drought stress	3	12.9–30.7	Venuprasad et al. 2002
	CT9993-5-10-1-M × IR62266-42-6-2	Root thickness	Green house	8	6.8–51.8	Kamoshita et al. 2002a

(*Continued*)

Table 13.1 *(Continued)*

Crop	Mapping Population	Traits	Environment	QTLs	Phenotypic Variation Explained (PVE; %)	Reference
	CT9993 × IR62266 (DH)	–	Wax-petrolatum layer system and field	36	8.0–37.0	Zhang et al. 2001
	ZYQ8 × JX17	Maximum root length, dry root weight, root/shoot ratio of dry weight	Solution culture	5	10.4–19.9	Xu et al. 2001
	IR64 × Azucena (DH)	PVC cylinders	PVC cylinders; drought stress	29	11.9–26.7	Hemamalini et al. 2000
Maize	Lo964 × Lo1016 (RIL)	Elongation rates of axile roots, rate constant of lateral root elongation	Roots were grown in pouches under well-watered conditions or at low water potential induced by the osmolyte (PEG 8000)	13	2.3–21.9	Ruta et al. 2010
	Z3 × 87-1	Number of axial roots, average axial root length, length of lateral root, root length	Hydroponics	17	11–43.7	Liu et al. 2008
	B73 × *Zea luxurians* (F₂)	Root angle	Greenhouse	4	0.123–0.396	Omori and Mano 2007
	B73 × Mo17 (RIL)	Fractal dimension (FD)1, FD2, FD change over time	–	47	24.6–46.8	Bohn et al. 2006
	B73 and Mo17 (RIL)	Seminal root length and seminal root number		5	11–25.4	Zhu et al. 2006
	B73 and Mo17 (RIL)	Root hair length, RHL under high fertility, root hair length under low phosphorus	Cigar roll culture system	5	9.6–31.9	Zhu et al. 2005a
	B73 × Mo17 (RIL)	Lateral root length, lateral root number under high fertility, lateral root number under low fertility	Cigar roll culture system	8	3.5–18.9	Zhu et al. 2005b
	B64 × Na4 (F₂)	Adventurous root formation	Flooding condition	40	–	Mano et al. 2005
	Lo964 × Lo1016 (F₂:₄)	Root weight, root length, diameter of primary and seminal roots		40	–	Hund et al. 2004
	Lo964 × Lo1016 (F₃ families)	Root length, primary root diameter, primary root weight, weight of adventitious seminal roots	Hydroponics	37	6.8–36.2	Tuberosa et al. 2002a
	Lo964 × Lo1016 (F₃ families)	Vertical root pulling resistance	Hydroponics	19	–	Landi et al. 2002

Crop	Population	Traits	Growth condition			Reference
Wheat	Xiaoyan 54 × Jing 411 (RIL)	Maximum root length, primary root length, lateral root length, total root length, and root tip, and number of seminal roots	Hydroponics	22	4.2–68	Ren et al. 2011
	Pavon 76 × Pavon 1RS.1BL	Root length and root weight	Green house, natural photoperiod	15	–	Sharma et al. 2011
	Huapei 3 × Yumai 57, (immortalized F₂)	Root total length, root surface area, root average diameter, root volume, root tips, maximum root length, shoot dry weight, root dry weight, and ratio of root dry weight to shoot dry weight per plant	Hydroponics	19	0.01–11.91	Li et al. 2010
	Creso × Pedroso (RIL)	Length, ProjArea, SurfArea, average diameter, LenPerVol, volume	Hydroponics	–	60	Petrarulo et al. 2009
	Hanxuan 10 × Lumai 14	Root length, root number, and root dry matter	Hydroponics	30	10	Li et al. 2007
		Shoot dry weight (SDW), root dry weight (RDW), tiller number (TN), and NUP (total plant N uptake) per plant	Hydroponics, field	17, 17	4.3–9.6, 6–21.9	An et al. 2006
Soybean	Essex × Forrest	Basal root thickness, maximum root length, lateral root number, root dry weight, root fresh weight, shoot fresh weight, shoot dry weight (SDW), RDW/SDW, and RFW/SFW	–	19	12–34	Williams et al. 2012
	PI416937 × Benning	Fibrous roots	Field	5	51	Abdel-Haleem et al. 2011
	Hartwig × Flyer (RIL)	Basal root thickness, maximum root length, lateral root number, root dry weight, root fresh weight, shoot dry weight (SDW), RDW/SDW, and RFW/SFW	Greenhouse	43	–	Ouertani et al. 2010
	BD 2 × BX10 (RIL)	Total root length, total root surface area, root width, ratio of root/shoot, root dry weight, root P content, plant P-content, shoot P content, plant dry weight, shoot dry weight, seed number per plant, seed weight per plant	Field	31	10.9–18.7	Liang et al. 2010
	Essex × Forrest	Basal root thickness, lateral root number, maximum root length, root fresh weight, root dry weight, shoot fresh weight, shoot dry weight	Green house and field	89	–	Washington et al. 2009
	Kefeng 1 × Nannong 1138-2	Dry root weight, total root length and root volume	Green house	13	3.6–24.7	Gai et al. 2007

(Continued)

Table 13.1 *(Continued)*

Crop	Mapping Population	Traits	Environment	QTLs	Phenotypic Variation Explained Explained (PVE; %)	Reference
Common bean	DOR364 × G19833 and G2333 × G198339 (RILs)	Number of basal root whorls	Growth pouch	2	25–58	Miguel et al. 2009
	G19833 × AND696	Root growth, seed yield, seed P content, and P use efficiency	Field	29	18–33	Cichy et al. 2009b
	DOR 364 × G19833	Root length, specific root length, P-accumulation, tap root length, tap root diameter	Field and green house	26	0.08–0.51	Beebe et al. 2006
	G2333 × G19839	Number of adventitious, adventitious dry weight, adventitious length, adventitious specific root length, shoot dry weight.	Green house and field	19	19–61 field condition and 18–39 green house	Ochoa et al. 2006
	DOR364 × G19833 (RIL)	Total root hair length for basal roots, hair length for tap roots	Solution culture	19	0.33–0.5	Yan et al. 2004
	DOR364 × G19833 (RIL)	Basal root angle, shallow basal root length, phosphorous root acquisition	Growth pouch and field	16	9.3–20.3	Liao et al. 2004
Chickpea	ICC 4958 × ICC 1882	Root length, root volume, root length density, root surface area, root dry weight, shoot length, shoot dry weight	Field	52	35	Varshney et al. (unpublished)
	ICC 283 × ICC 8261	Root length, root volume, root length density, root surface area, root dry weight, shoot length, shoot dry weight	Field	45	35	Varshney et al. (unpublished)

epistatic QTLs have been detected for different traits of root length and root weight on 1RS segment using a high-resolution chromosome arm-specific mapping population (Sharma et al. 2011). In the case of sorghum, nodal root angle (qRA) that influences vertical and horizontal root distribution in the soil profile is considered one of the most important traits that may provide new opportunities for improving drought adaptation mechanisms. Mace et al. (2012) have reported four QTLs for qRA in addition to three QTLs for root dry weight: two for shoot dry weight and three for plant leaf area. Further, qRA QTL explained 58.2% of the phenotypic variance was also validated across a range of diverse inbred lines.

Among legumes, QTLs for root fresh weight, maximum root length, basal root thickness, lateral root number, root dry weight, total root surface area, root width, ratio of root/shoot, root dry weight, root P content, plant P content, and shoot P content have been identified in soybean under field conditions (Liang et al. 2010; Abdel-Haleem et al. 2011) as well as under greenhouse conditions (Gai et al. 2007; Washington et al. 2009). On the other hand, a large number of QTLs for P efficiency have been identified in soybean (Li et al. 2005b; Zhang et al. 2009). In the case of common bean, a large number of QTLs for root morphology and physiology as related to P nutrition have been reported (Beebe et al. 2006; Li et al. 2007; Chen et al. 2009; Cichy et al. 2009a; Li et al. 2009). More interestingly, QTLs for basal root growth and development were shown tightly linked with the QTLs for P uptake efficiency under field conditions (Beebe et al. 2006). In the case of chickpea, based on phenotyping of root traits under PVC cylinder and SSR genotyping on two mapping populations (ICC 4958 × ICC 1882 and ICC 283 × ICC 8261), a genomic region, harboring QTLs for various drought tolerance related root traits, has been identified on linkage group 4, which explained more than 35% phenotypic variation (unpublished data).

Meta-QTL Analysis for Root Traits

As different QTL studies employ different mapping populations like recombinant inbred lines (RILs), doubled haploids (DHs), backcross introgression lines, and near isogenic lines (NILs) that segregate for different root traits, it is difficult to exploit the varietal difference for improved root traits by MAS and for identification of concerned alleles. In this context, meta-analysis of QTLs is considered one of the best approaches that is conducted when hundreds of QTLs based on large number of studies involving a number of mapping populations are available in the published literature. This approach is a useful reductionist approach to bring down the number of genuine and real QTLs for their efficient use in MAS. Meta-analysis of QTLs provides narrow confidence intervals for meta-QTLs (MQTLs), permitting easier positional candidate gene identification. Meta-analysis of QTLs is usually applied to multiple mapping populations, but can be applied to one also (Khowaja et al. 2009).

For comparing root traits across experiments and developmental stages, the International Society of Root Research (ISRR, www.rootresearch.org) proposed a general nomenclature for roots (Zobel and Weisel 2010) to compare root types in different crop species. Recently, a database "QlicRice" was developed by Smita et al. (2011), which serves as a web interface and platform for data mining of abiotic stress responsive QTLs and their corresponding sequenced gene loci, which help researchers to retrieve association among different agronomic traits. Meta-analysis of drought-related QTLs in the Bala × Azucena mapping population of rice from 13 experiments and 25 independent screens resulted in three meta-QTLs within a space of 35 cM on chromosome 9 (Khowaja et al. 2009). Swamy et al. (2011) identified that the MQTL for grain yield under drought coincided with at least one of the MQTL identified for root and leaf morphology traits under drought in earlier reports.

A rational database "Rootbrowse" has also been constructed using QTLs, markers, and genome sequence information (Priya et al. 2009).

In the case of maize, MQTL analysis based on 15 independent QTL studies of 9 mapping populations resulted in the identification of seven MQTL for root traits that are colocalized with grain yield and other drought responsive traits in the field. Furthermore, on the basis of MQTL analysis, Landi et al. (2010) inferred that one single locus, root-yield-1.06, has a major constitutive effect on root traits, plant vigor and productivity across water regimes, genetic backgrounds, and inbreeding levels.

Molecular Dissection of Root Traits

Candidate Genes Based on Genome Sequence Information

As evident from Table 13.1, the root trait QTLs have been studied extensively in rice than any other crop. It is also known that the rice root system is complex, consisting of seminal, adventitious, and lateral roots. The availability of the rice genome sequence has opened some new avenues to look at the large number of QTLs already identified to control root development and to identify candidate genes in those QTL regions. In this context, a majority of root QTLs identified in rice were integrated computationally into the *japonica* genome and it was observed that a maximum number of QTLs for root development is present on chromosome 1 and fewer QTLs on some other chromosomes (Ulaganathan et al. 2007; http://www.kulab.org/research1.htm). As expected, several QTLs reported in different studies utilizing different mapping populations have been found to possess QTLs in the same genomic regions, thus showing that many QTL regions are common across different mapping populations. Some of these genomic regions possessing several overlapping QTLs could also be resolved into multiple QTLs. More interestingly, the putative candidate genes governing root development in these QTLs regions were extracted and their putative functions were computationally analyzed. This led to identification of small number of genes (200–300 genes) in some of the QTL regions, while a large number of genes (600–800 genes) were present in larger QTLs/genomic regions. In summary, computational analysis of the genes revealed and confirmed the polygenic and complex nature of root development in rice.

These genes identified in genomic regions for root development mostly belongs to categories of (a) transcription factors, (b) auxin metabolism and transport genes, (c) auxin-responsive genes, (d) auxin-related proteasome pathway genes, (e) environmental sensors, and (f) biotic and abiotic stress tolerance genes (http://www.kulab.org/research1.htm). However, it will be essential to validate these genes using functional genomics approaches like quantitative RT-PCR or reverse genetic approaches like knockout mutant analysis and TILLING. Nevertheless, availability of the genome sequence in several crop species like maize (Schnable et al. 2009), soybean (Schmutz et al. 2010), sorghum (Paterson et al. 2009), pigeonpea (Varshney et al. 2012), and others offer the possibility to identify the candidate genes underlying the QTL regions identified in these crop species.

QTL Cloning for Root Traits

Most of the QTL mapping studies involves crossing of varieties with contrasting root characteristics, development of mapping populations, and identification of number of QTLs on different chromosomes. Since most of these experiments involve the use of different sets of markers and localization

of QTLs on long genomic regions, thus making it difficult to exploit the varietal difference for improved drought tolerance by MAS and for identification of the concerned alleles. Therefore, one would like to move close to the target QTL or even use perfect functional markers for the introgression of respective QTL/gene for a root trait through molecular breeding. Therefore, efforts may be made to clone all the major and important QTL for a root trait. The positional cloning of a major QTL requires (i) large mapping population (>2000 plants) obtained after crossing two NILs for the target QTL, (ii) identifying the genomic region covering the QTL region, and (iii) validating of effect of candidate gene(s) on phenotype (see Salvi and Tuberosa 2005; Tuberosa and Salvi 2006).

Several reports are available on mapping of QTLs for different traits (see Salvi and Tuberosa 2007); however, only few reports are available where efforts have been made to clone the root trait QTLs. The major obstacle, in this context, is precise phenotyping for root traits in the thousands of plants. Nevertheless, some efforts have been made to clone the QTLs for root traits. For instance in maize two major QTLs on chromosome bins 1.06 and 2.04 (*root-ABA1*) affecting root architecture and a number of agronomic traits, including grain yield, have been targeted (Tuberosa and Salvi 2007). Similarly, efforts are underway for fine mapping/cloning of "*root-ABA1*" QTL that is responsible for root architecture and leaf ABA concentration in pearl millet (Kholova et al. 2010a, 2010b). In future, newer genomics approaches like association mapping (Rafalski 2010) and next generation sequencing (Varshney et al. 2009) are expected to facilitate cloning of QTLs for root traits.

Molecular Breeding for Root Traits

MTA studies identify important genomic regions, explaining a significant proportion of PV for root traits. Once major QTLs are identified, molecular markers associated with these QTLs need to be validated on a range of germplasm to select the candidate QTLs as well as the elite cultivars for introgression of the QTL using marker-assisted backcross (MABC) approach. This approach has been successfully used in several crops for improving different traits (Gupta et al. 2010; Varshney et al. 2010; Chamarthi et al. 2011; Kulwal et al. 2011). However, the power and efficiency of this approach has been limited, especially for root traits. For instance, Steele et al. (2006, 2007) demonstrated the power of MABC by releasing the first novel upland rice variety Birsa Vikas Dhan 111 (PY 84) through molecular breeding in the Jharkhand state of India. The variety was bred through MABC involving introgression of three genomic regions carrying root growth QTL on chromosomes 2 (root length), 9 (root thickness), and 11 (root penetration) from the donor Philippines variety Azucena into the recurrent parent Kalinga III. The target QTLs were first identified by Adam Price (now at Aberdeen University, UK) and Birgitte Courtois (CIRAD, France/IRRI, Philippines; http://www.cazs.bangor.ac.uk/ccstudio/WhatsNew/cazsWhatsNew2.php?ID=14; Cairns et al. 2009; Courtois et al. 2009; Norton and Price 2009). The variety developed in a collaborative partnership between Centre for Arid Zone Studies (CAZS) Natural Resources, Bangor University, UK; Gramin Vikas Trust, Ranchi, Jharkhand, India; and Birsa Agricultural University, Ranchi, Jharkhand, India, showed improved root growth, thus leading to improved performance under drought conditions. Similarly, Shen et al. (2001) also showed the effectiveness of QTL-based transfer of root traits, by involving the transfer of Azucena allele at four QTL alleles for deeper roots (on chromosomes 1, 2, 7, and 9) from selected DH lines into IR64. Thus, they demonstrated that NILs with an improved root system permit testing the importance of root depth for water-limited environments. In the case of chickpea also, a hotspot harboring several QTLs for drought tolerance-related traits (with >30% PV) is being introgressed into a leading chickpea variety JG11 through MABC approach

(unpublished results). Using both foreground and background selection with SSR/AFLP markers, BC_3F_4 progenies have been derived and are being evaluated for their agronomic performance under rainfed and irrigated conditions in India, Kenya, Ethiopia, and Tanzania. These are some of the nice examples of translational genomic research for crop improvement.

Summary and Outlook

Roots are considered primary targets in view of current scenario of importance of drought in changing climate. Therefore, it is important to understand genetic and molecular mechanisms involved in conferring drought tolerance through root traits. While a linkage mapping-based approach has been used extensively to identify QTLs for a range of root traits in some crop species, association mapping has also started to be used in some cases for identification of QTLs. Some efforts have also been made toward cloning of QTLs for roots traits in species like maize and pearl millet. In terms of translation, a few reports have become available on molecular breeding through MABC and superior varieties have been developed. MABC approach for translating root genomics is possible only in the case where QTLs contribute to higher PV. In the cases where root traits are controlled by many and small-effect QTLs, the MARS approach that involves intermating selected individuals in each selection cycle (Eathington et al. 2007; Ribaut and Ragot 2007; Bernardo 2008) seems to be a better approach. Genome-wide selection or genomic selection approach is the other approach that involves selection of genotypes based on genomic estimated breeding values, estimated using genome-wide marker profile data for making the crosses (Bernardo and Yu 2007). Availability of genome sequences, NGS technologies, high-throughput genotyping, as well as phenotyping facilities are expected to accelerate root genomics research, especially for translation to crop improvement.

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