

Chapter 2

EST-Based Approach for Dissecting Root Architecture in Barley Using Mutant Traits of Other Species

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2.1 Introduction

There are increasing evidences that root architecture is a fundamental aspect of plant growth. The role of root system includes acquisition of water and nutrients, anchorage of the plant in the soil, synthesis of hormones, and also storage functions. It was generally considered that root characteristics could be important for breeding, to obtain genotypes of a higher adaptability to unstable soil and climatic conditions (Gorny 1992; De Dorlodot et al. 2007) and higher productivity (Lynch 1995). Despite their importance, little is known about genetic basis of root system formation and architecture in major crop species. A great progress in understanding the molecular processes underlying root development has been achieved only in *Arabidopsis thaliana* (Scheres et al. 2002; Casimiro et al. 2003; Casson and

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Lindsey 2003; Ueda et al. 2005; Zhang et al. 2007; Busov et al. 2008). This progress was accomplished through detailed analysis of root mutants with the use of advanced molecular, genomic, and bioinformatic tools available for *Arabidopsis*. Recently, several root mutants have been reported in three cereal species, rice (Ma et al. 2001; Zimmer et al. 2003; Liu et al. 2005; Inukai et al. 2005; Jiang et al. 2005; Li et al. 2006a; Kim et al. 2007), maize (Lim et al. 2005; Woll et al. 2005; Wen et al. 2005; Hochholdinger et al. 2008), and wheat (Wang et al. 2006). Some of them have become the subject of studies similar to *Arabidopsis* that have led to the identification of homologous and novel genes controlling root system formation in monocotyledons (Morita and Kyoizuka 2007). There is, however, a lack of similar knowledge in barley. These differences in progress of knowledge between monocotyledonous and dicotyledonous species could be considered as a result of the more extensive size of adult cereal root systems and lack of such efficient screening strategies like those developed for *Arabidopsis*. Based on this, we will focus on root development in monocotyledons, especially in barley, which is the fourth most important crop in the world after maize, wheat, and rice. Recently, it is becoming a novel cereal model plant because of its true diploidy (Sreenivasulu et al. 2008).

Root system of monocotyledonous plants is generally composed of two fundamental parts: seminal root system, which develops from initials present in embryo, and nodal (often called adventitious or shoot-borne) root system, which originates from shoot (Hackett 1968). The dicotyledonous species develop a taproot system with one primary root and lateral branches, which remain active during the whole life cycle. However, dicotyledonous plants can also form roots called “adventitious” under unusual circumstances such as wounding or hormone application, etc., at uncharacteristic sites on a plant. Following Hochholdinger and coworkers (2004), we also suggest not calling monocotyledonous stem-derived crown and brace roots “adventitious” because they belong to the normal developmental program of cereals. Despite having to fulfill the same fundamental functions, the root systems of monocotyledons and dicotyledons differ both in morphology and anatomy. In monocotyledons, the secondary root growth do not occur, and root vessels are relatively uniform cylinders (in the absence of environmental stimuli) (Gorny 1992). The adult crop plant exhibits an extensive shoot-born root system, which plays a major role in the postembryonic root architecture (Hochholdinger et al. 2004; Hochholdinger and Zimmermann 2008). Nevertheless, it has been reported that maize seminal roots have relatively high water uptake capacity compared to other root types, which makes them important throughout whole plant life (Osmont et al. 2007).

2.2 Root Mutants of *Arabidopsis* Published in Pubmed

Both forward and reverse genetic approaches have been used to increase knowledge about root architecture. As there are many mutagenesis methods, the use of chemical mutagenesis mostly by EMS and insertional mutagenesis using T-DNA insertion, followed by mutant screening, apparently dominates. Using EMS, 147 gene alleles were obtained, 140 alleles by insertional mutagenesis (e.g., 19 by

transposable elements, 118 by T-DNA, 2 by promoter trap and 1 by activation tagging), whereas 22 alleles were obtained by physical approach (nine by fast neutrons, six by X-ray, seven by gamma rays). Reverse approach (e.g., RNAi, overexpression) were also commonly used to study influence of a gene of interest on root traits.

Using these strategies, it was possible to build the model pattern of root development in dicotyledons, based on data from reference *Arabidopsis*. Up to now, many genes have been shown to be involved in various aspects of *Arabidopsis* root development (Tables 2.1 and 2.2). Many of them have a pleiotropic effect not only on various stages of root development but also on whole plant per se. Nevertheless, we divided *Arabidopsis* genes controlling root system into formation of radial and longitudinal pattern, keeping in mind that assigning genes to only one chosen category could be misleading. The *Arabidopsis* radial pattern consists of a number of defined cell types organized in concentric layers, with the epidermis, ground tissue composed of cortex and endodermis, and the last main part called stele, which includes pericycle surrounding the central vascular cylinder (Scheres et al. 2002; Casson and Lindsey 2003). Based on this, we secondly divided genes responsible for root radial pattern into three groups, which assemble genes involved in epidermis, ground tissue, and stele development.

The first one (Table 2.1) includes genes involved in root hair development as a specific product of root epidermis. Both monocotyledonous and dicotyledonous root systems increase absorptive surface through the formation of root hairs. In *Arabidopsis*, root hairs always form on epidermal cells positioned over the radial cell wall between cortical cells (Dolan and Costa 2001). However, it is difficult to predict root hair-forming epidermal cells in cereals (Hochholdinger et al. 2004). In *Arabidopsis*, epidermis is composed of trichoblasts, which develop into root hair cells, and atrichoblasts, which remain hairless. The identity of these cells is regulated by positional information – hair-forming cells are located above two underlying cortical cells. The genetic analysis of root hair development has identified at least 39 genes that are required for the initiation and growth of the root hair. Some of them, such as *TRANSPARENT TESTA GLABRA1* (*TTG1*), *GLABRA3* (*GL3*), *ENHANCER OF GLABRA3* (*EGL3*), and *GLABRA2* (*GL2*), have been well described (Galway et al. 1994; Walker et al. 1999; Bernhardt et al. 2003). Both *TTG1* and *GL2* mutants have root hairs at nearly all root epidermal cells (Walker et al. 1999; Ohashi et al. 2003), whereas *GL3* and *EGL3* mutants have reduced numbers of atrichoblasts (Bernhardt et al. 2003). *TTG1* encodes a protein with WD40 repeats (Mendoza and Alvarez-Buylla 2000), which is localized in the nuclei of trichomes at all developmental stages (Zhao et al. 2008). It seems that *GL2* is a direct target of *GL3* and *EGL3*, whereas *TTG1* is directly regulated by *GL1* (Zhao et al. 2008).

The second group includes genes responsible for ground tissue patterning, composed of one cortex and one endodermis layer (Table 2.1), which originate from the common initial cell adjacent to the quiescent center (QC) (Scheres et al. 2002). Outside the endodermis, there are 4–6 layers in barley (Jackson 1922) and 8–15 in rice and corn (Hochholdinger et al. 2004) of bigger and thin-walled loosely packed

Table 2.1 Mutated genes responsible for *Arabidopsis* root radial pattern

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|---|------------------|---|---|---|
| Root hairs | | | | |
| <i>TRANSPARENT TESTA GLABRA1 (TTG1)</i> | AT5G24520 | <i>ttg-1</i> /EMS | All cells with root hairs | Galway et al. (1994), Walker et al. (1999) |
| <i>GLABRA2 (GL2)</i> | AT1G79840 | <i>p777T</i> -DNA insertion | All cells with root hairs | Ohashi et al. (2003) |
| <i>WEREWOLF (WER)</i> | AT5G14750 | <i>wer-1</i> /EMS | All cells with root hairs | Lee and Schiefelbein (1999) |
| <i>CAPRICE (CPC)</i> | AT2G46410 | <i>cpc-1/T</i> -DNA insertion | All cells without root hairs | Wada et al. (1997) |
| <i>GLABRA3 (GL3)</i> | AT5G41315 | <i>gl3-1</i> /EMS | Reduced number of atrichoblasts (much more root hairs) | Bernhardt et al. (2003) |
| <i>ENHANCER OF GLABRA3 (EGL3)</i> | AT1G63650 | <i>egl3-77439/T</i> -DNA insertion | Reduced number of atrichoblasts (much more root hairs) | Bernhardt et al. (2003) |
| <i>ENHANCER OF TRIPTICHOH AND CAPRICE1 (ETC1)</i> | AT1G01380 | EMS | All cells without root hairs or root hairs are very sporadic | Kirk et al. (2004) |
| <i>ETROPIC ROOT HAIR 1 (ERH1)</i> | ? | <i>erh1</i> /fast neutrons | Reduced number of atrichoblasts (much more root hairs) | Hauser et al. (1995), Schneider et al. (1997) |
| <i>ETROPIC ROOT HAIR3 (ERH3)</i> | AT1G80350 | Gamma rays | Reduced number of atrichoblasts (much more root hairs) | Hauser et al. (1995), Schneider et al. (1997) |
| <i>TORNADO1 (TRN1)</i> | AT5G55540 | <i>trn1-1/T</i> -DNA insertion | Radial pattern is unsettled, pattern of root hairs is twisted like DNA helix | Dolan (2000) |
| <i>TORNADO2 (TRN2)</i> | AT5G46700 | <i>trn2-2</i> /EMS | Radial pattern is unsettled, pattern of root hairs is twisted like DNA helix | Dolan (2000) |
| <i>ROOT HAIRLESS 1 (RHL1)</i> | AT1G48380 | <i>rhl1-1/T</i> -DNA insertion | Root hairs very sporadic, pattern of trichoblasts and atrichoblasts unsettled | Schneider et al. (1997, 1998) |
| <i>ROOT HAIRLESS 2 (RHL2)</i> | AT5G02820 | <i>rhl1-2</i> /unknown T-DNA insertion | Root hairs very sporadic, pattern of trichoblasts and atrichoblasts unsettled | Schneider et al. (1997) |
| <i>ROOT HAIRLESS 3 (RHL3)</i> | AT3G20780 | <i>rhl3-1</i> /EMS | Root hairs very sporadic, pattern of trichoblasts and atrichoblasts unsettled | Schneider et al. (1998) |
| <i>CONSTITUTIVE TRIPLE RESPONSE (CTR1)</i> | AT1G01380 | <i>ctrl-6/T</i> -DNA insertion | Root hairs are formed on other place than usually | Kieber et al. (1993), Dolan et al. (1994) |
| | AT1G66340 | <i>etr1-1</i> /EMS | | Masucci and Schiefelbein (1996) |

| | | | | | |
|---------------------------------------|-----------|--|--|---|--|
| <i>ETHYLENE RECEPTOR 1 (ETR1)</i> | | | | Root hairs are formed near to the basal part of cell | |
| <i>ETHYLENE OVERPRODUCER 1 (ETO1)</i> | AT3G51770 | <i>eto1-1/EMS</i> | | Root hairs are formed near to the apical part of cell | Masucci and Schiefelbein (1996), Yoshida et al. (2006) |
| <i>ROOT HAIR DEFECTIVE 6 (RHD6)</i> | ? | EMS | | Root hairs are very sporadic and formed near to the basal part of cell, more than one root hair on one cell | Masucci and Schiefelbein (1994), Dolan (2001) |
| <i>SALT OVERLY SENSITIVE 4 (SOS4)</i> | AT5G37850 | <i>sos4-1/EMS</i> | | Root hairs are very, very sporadic | Shi and Zhu (2002) |
| <i>ROOT HAIR DEFECTIVE 1 (RHD1)</i> | AT1G64440 | <i>rhd1-2/EMS</i> <i>rhd1-1/EMS</i> | | Primordium is very big, root hairs with normal length | Schiefelbein and Somerville (1990) |
| <i>TIP GROWTH DEFECTIVE 1 (TIP1)</i> | AT5G20350 | <i>tip1-1/EMS</i> | | Primordium is bigger, root hairs are shorter and often branched, sometimes there are 2–4 root hairs on one cell | Ryan et al. (1998) |
| <i>SUPERCENTIPEDE 1 (SCN1)</i> | ? | EMS | | 1–5 primordia on one cell | Grierson et al. (2001) |
| <i>TINY ROOT HAIR 1 (TRH1)</i> | AT4G23640 | <i>trh1/EMS</i> | | Root hair growth stopped at primordium stage | Rigas et al. (2001), Vicente-Agullo et al. (2004) |
| <i>HAIR DEFECTIVE 2 (RHD2)</i> | AT5G51060 | <i>rhd2-1/EMS</i> | | Root hair growth stopped at primordium stage | Schiefelbein and Somerville (1990) |
| <i>SHAVEN1.2.3 (SHV1.2.3)</i> | ? | EMS | | Root hairs are shorter | Parker et al. (2000) |
| <i>KOJAK (KJK)</i> | AT3G03050 | <i>csld3-1/T-DNA insertion</i> | | Root hairs rupture at their tip soon after initiation | Favery et al. (2001) |
| <i>MRH2</i> | AT3G54870 | <i>mrh2-1/T-DNA insertion</i> | | Mutant exhibits wavy and branching root hair phenotype | Yang et al. (2007) |
| <i>LRR/EXTENSIN 1 (LRX1)</i> | AT1G12040 | <i>lrx1/En-1 transposition</i> | | Root hairs are shorter, often branched | Baumberger et al. (2001) |
| <i>DEFORMED ROOT HAIRS 1 (DER1)</i> | ? | EMS | | Root hairs are shorter, primordium is bigger, and sometimes there are 2 root hairs on one cell | Ringli et al. (2002) |
| | AT2G35630 | EMS | | Root hairs are wavy and branched | Whittington et al. (2001) |

(continued)

Table 2.1 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/ reverse approach | Mutant phenotype | References |
|--|------------------|---|---|---|
| MICROTUBULE ORGANIZATION 1 | | | | |
| <i>(MOR1)</i> | | | | |
| INCOMPLETE ROOT HAIR ELONGATION | | | | |
| <i>(IRE)</i> | | | | |
| ROOT HAIR DEFECTIVE 3 | | | | |
| <i>(RHD3)</i> | AT5G62310 | T-DNA insertion | Root hairs are shorter | Oyama et al. (2002) |
| ROOT HAIR DEFECTIVE 4 | | | | |
| <i>(RHD4)</i> | AT3G13870 | <i>rhd3-1</i> /EMS | Root hairs are shorter and wavy | Schiefelbein and Somerville (1990), Galway et al. (1997), Zheng et al. (2004) |
| CAN OF WORMS 1 | | | | |
| <i>(COW1)</i> | ? | EMS | Root hairs are shorter and wavy | Schiefelbein and Somerville (1990) |
| BRISTLED1 (BST1) | | | | |
| <i>CENTPEDE 1,2,3</i> | AT4G34580 | T-DNA insertion | Root hairs are shorter, wavy, and 1–3 on one cell | Grierson et al. (1997), Böhme et al. (2004) |
| <i>(CEN1,2,3)</i> | AT5G65090 | Fast neutrons | Root hairs are shorter, wavy and branched | Parker et al. (2000) |
| ACTIN 2 (ACT2) | ? | EMS | Root hairs are shorter, wavy and branched | Parker et al. (2000) |
| SUPRESOR OF AUXIN RESISTANCE | | | | |
| <i>(SAR1)</i> | AT3G18780 | <i>act2-3</i> /T-DNA insertion | Root hairs are shorter and branched | Kellaar et al. (2003) |
| ROOT AND POLLEN ARFGAP (RPA) | AT2G33120 | EMS | Root hairs are longer and on almost all cells | Cernac et al. (1997) |
| | AT2G35210 | T-DNA insertion | Aberrant root hair phenotype, including bulged, branched and shorter root hairs | Song et al. (2006) |
| Ground tissue pattern (cortex + endodermis) | | | | |
| POM-POM1 (POM1) | | | | |
| | AT1G05850 | <i>pom 1-1</i> /T-DNA insertion | Shorter root and significantly greater cell volume | Hauser et al. (1995), Scheres et al. (2002) |
| POM-POM2 (POM2) | | | | |
| | ? | <i>pom2-1</i> , 2-2/fast neutron | Shorter root and significantly greater cell volume | Hauser et al. (1995), Scheres et al. (2002) |
| | ? | <i>qui-1</i> /X-ray | Shorter root and significantly greater cell volume, decreased cell elongation, | Hauser et al. (1995), Scheres et al. (2002) |
| | | <i>qui-2</i> /T-DNA insertion | | |

| | | | | |
|---|-----------|---|--|--|
| <i>PROCUSTE1/QUILL/</i> <i>ATCESA6 (PRCI/</i> <i>QUI)</i> | | <i>qui-3/EMS</i> | specifically in roots and dark-grown hypocotyls | |
| <i>COBRA (COB)</i> | AT5G60920 | <i>cob1-4/EMS</i> <i>cob-2/X-ray</i> <i>cob-2/T-DNA</i> insertion <i>shr-1/T-DNA</i> insertion | Abnormal root cell expansion, greatest in the epidermal cells | Benfey et al. (1993), Scheres et al. (2002), Roudiera et al. (2005) |
| <i>SHORT ROOT (SHR)</i> | AT4G37650 | | Determinate root growth, very short root missing an internal cell layer, mutant layer has attributes of cortex only | Benfey et al. (1993), Scheres et al. (2002), Franco-Zorrilla et al. (2005) |
| <i>SCARECROW (SCR)</i> | AT3G54220 | <i>scr-4, scr-1/T-DNA</i> insertion | Defects in the division and/or specification of endodermis and cortex | Benfey et al. (1993), Scheres et al. (2002) |
| <i>KORRIGAN (KOR)</i> | AT5G49720 | <i>kor1-1/EMS</i> <i>kor1-2/Agrobacterium</i> transformation | Radially expanded hypocotyl cells, impaired root expansive growth, formation of aberrant cell plates, incomplete cell walls, and multinucleated cells, leading to severely abnormal root morphology (cells divided randomly and often contained incomplete cell walls) | Zuo et al. (2000), Scheres et al. (2002) |
| <i>LION'S TAIL</i> | ? | T-DNA insertion | Abnormal root cell expansion, greatest in the stele cells | Benfey et al. (1993), Hauser et al. (1995), Scheres et al. (2002) |
| <i>SABRE (SAB)</i> | AT1G58250 | EMS | Abnormal root-cell expansion, primarily in radial orientation. Expansion greatest in cortex cells | Benfey et al. (1993) |
| <i>FAKEL (FK)</i> | AT3G52940 | T-DNA insertion | Short roots and hypocotyl, defective cell shape, supernumerary cell layers and aberrant vascular patterning | Souter et al. (2002) |
| <i>HYDRA 1 (HYD1)</i> | AT1G20050 | <i>hyd1-2/ T-DNA</i> insertion | Short roots and hypocotyls, defective cell shape, supernumerary cell layers and aberrant vascular patterning. Root may cease cell division within 2 weeks after germination, or may continue to grow very slowly until the seedling dies | Souter et al. (2002) |

(continued)

Table 2.1 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|---------------------------------|------------------|---|--|---|
| <i>CUDGEL-1</i> | ? | <i>cul-1/X-ray</i> | Shorter root and significantly greater cell volume | Hauser et al. (1995), Scheres et al. (2002) |
| <i>SCHIZORIZA (SCZ)</i> | ? | Ac/Ds | Subepidermal layer (ground tissue) develops root hairs – supernumerary layers in the ground tissue | Mylona et al. (2002) |
| <i>KNOPF (KNF)</i> | AT1G67490 | <i>knp-14/EMS</i> | Radially swollen root phenotype due to cellulose deficiency and isotropic embryo growth | Gillmor et al. (2002) |
| <i>RADIAL SWELLING 1 (RSW1)</i> | AT4G32410 | <i>rsw1-1, 1-2/EMS</i> | Radially swollen root phenotype due to cellulose deficiency and isotropic embryo growth | Gillmor et al. (2002) |
| <i>RADIAL SWELLING 3 (RSW3)</i> | AT5G63840 | <i>rsw3-1/EMS</i> | Temperature-sensitive, cellulose-deficient mutant with radially swollen roots | Burn et al. (2002) |
| <i>RADIAL SWELLING 4 (RSW4)</i> | ? | EMS | Radially swelling roots and temperature sensitive phenotype. Cortical microtubules and cellulose microfibrils are neither depleted nor disoriented | Wiedemeier et al. (2002) |
| <i>RADIAL SWELLING 7 (RSW7)</i> | ? | EMS | Radially swollen roots and temperature sensitive phenotype. Cortical microtubules and cellulose microfibrils are neither depleted nor disoriented | Wiedemeier et al. (2002) |
| <i>PLEYADE (PLE)</i> | AT5G51600 | <i>ple-1, -2/EMS, ple-3/T-DNA</i> | Shorter roots exhibit a wavy growth pattern and develop more lateral roots. Irregular cell expansion, multinucleated cells, cell wall stubs, epidermis, cortex and endodermis are radially enlarged; symmetry of the vascular tissues is disrupted and synchronized cell divisions in incompletely separated cells that are all characteristics of defective cytokinesis | Müller et al. (2002) |

| | | | | |
|----------------------|-----------|---|---|-----------------------|
| <i>HYADE1 (HYA1)</i> | ? | <i>hya-1, -2, -3/EMS</i> | Shorter roots exhibit a wavy growth pattern and develop more lateral roots. Irregular cell expansion, multinucleate cells, cell wall stubs, epidermis, cortex and endodermis are radially enlarged; symmetry of the vascular tissues is disrupted and synchronized cell divisions in incompletely separated cells that are all characteristics of defective cytokinesis | Müller et al. (2002) |
| <i>BOTERO1 (BOT)</i> | ? | <i>bot1-1, 1-3, 1-4, 1-5/EMS</i> <i>bot1-2/retrotransposon Tnt1</i> <i>bot1-7, 1-8/T-DNA</i> insertion | Shorter and thicker root and hypocotyl. Affected in anisotropic growth, loosely organized microtubules | Bichet et al. (2001) |
| <i>CLUB</i> | ? | EMS | Lack of primary root. Cell wall stubs, gapped walls and multinucleate cells. Incapable of growing long root hairs, likely to represent a tip growth defect. | Söllner et al. (2002) |
| <i>BUBLINA</i> | ? | EMS | Lack of primary root. Cell wall stubs, gapped walls and multinucleate cells. Long root hairs. | Söllner et al. (2002) |
| <i>BIMS</i> | ? | EMS | Lack of primary root. Cell wall stubs, gapped walls and multinucleate cells. Long root hairs. | Söllner et al. (2002) |
| <i>MASSUE</i> | ? | EMS | Stunted root, cell wall stubs, gapped walls and multinucleate cells | Söllner et al. (2002) |
| <i>BLOATED</i> | ? | EMS | Stunted root, cell wall stubs, gapped walls and multinucleate cells. Long root hairs | Söllner et al. (2002) |
| <i>ROD</i> | ? | EMS | Stunted root, cell wall stubs, gapped walls and multinucleate cells | Söllner et al. (2002) |
| <i>KEULE</i> | AT1G12360 | EMS | Lack of primary root. Cell wall stubs, gapped walls and multinucleate cells. Incapable | Söllner et al. (2002) |

(continued)

Table 2.1 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|--|------------------|---|---|--|
| <i>KNOLLE</i> | AT1G08560 | X-ray | of growing long root hairs, likely to represent a tip growth defect. Lack of primary root. Cell wall stubs, gapped walls and multinucleate cells. Cytokinesis defects are more severe than in <i>keule</i> mutants: severely perturbed epidermis and long root hairs | Söllner et al. (2002) |
| <i>HINKEL (HIK)</i> | AT1G18370 | EMS | Long root hairs, cell wall stubs, gapped walls and multinucleate cells | Söllner et al. (2002) |
| <i>SHORT BLUE ROOT (SBR)</i> | ? | EMS | Deformation of epidermal cells, larger meristematic cells, disorganized root vascular tissue. Reduced lateral root initiation, adventitious roots often form on hypocotyl | Subramanian et al. (2002) |
| Stele pattern (pericycle + vasculature) | | | | |
| <i>ALTERED PHLOEM DEVELOPMENT (APL)</i> | AT1G79430 | En-1 transposition | Defects in vascular tissue | Bonke et al. (2003) |
| <i>LONESOME HIGHWAY (LHW)</i> | ? | EMS | Lack of root bilateral symmetry: reduced the number of cells in the center of the root, single xylem and phloem poles | Ohashi-Ito and Bergmann (2007) |
| <i>WOODEN-LEG (WOL)</i> | AT2G01830 | <i>ahk4-1</i> /T-DNA insertion <i>wol-1</i> /EMS | Protoxylem is the only tissue in the vascular cylinder | Scheres et al. (2002), Sieberer et al. (2003), Franco-Zorrilla et al. (2005) |
| <i>KOBITO 1 (KOB1)</i> | AT3G08550 | <i>eldl-1</i> /gamma rays | Cellulose-deficient dwarf mutant. Randomized microfibrils occluded by a layer of pectic material | Pagant et al. (2002) |

| | | | | |
|--|-----------|---|--|----------------------------|
| <i>IRREGULAR XYLEM 1</i> (<i>IRX1</i>) | AT4G18780 | <i>irx1-1</i> /EMS | Severe deficiency in the deposition of cellulose in secondary cell walls, which results in collapsed xylem cells | Taylor et al. (2000) |
| <i>IRREGULAR XYLEM 3</i> (<i>IRX3</i>) | AT5G17420 | <i>irx1-5</i> / T-DNA insertion <i>irx3-1</i> /EMS | Severe deficiency in the deposition of cellulose in secondary cell walls, which results in collapsed xylem cells | Taylor et al. (2000) |
| <i>ECTOPIC LIGNIFICATION 1</i> (<i>ELI-1</i>) | ? | EMS | Mutant exhibits altered patterns of lignification (ectopic lignification), stunted phenotype and disorganized xylem tissue | Caño-Delgado et al. (2000) |

cortical cells (Briggs 1978), whereas in *Arabidopsis*, root comprises only one endodermis and one cortical layer (Scheres et al. 2002). The one layer of endodermis is exceptionally thick-walled, just like that reported earlier in rice, maize, and onion (Jackson 1922) with a “Caspian strip” in the walls (Karas and McCully 1973). Many mutations that disrupt patterning of the ground tissue have been identified. For example, both the *SCARECROW* (*SCR*) and *SHORT ROOT* (*SHR*) mutants have a single layer instead of cortex and endodermis. These genes encode putative transcription factors of the GRAS family responsible for specifying QC and for controlling the periclinal cell division of the daughter cell of their common initial cell, which leads to two adjacent layers (Ueda et al. 2005). However, *SCR* mutant layer has differentiated attributes of both cortex and endodermis, whereas *SHR* layer attribute only to cortex (Scheres et al. 2002). *SCR* was previously shown to act downstream of *SHR* (Ueda et al. 2005), whereas Levesque and coworkers (2006) suggested that *SHR* not only directly regulates the transcription of *SCR* through binding to the chromatin upstream of the gene but also functions in development of the vascular tissue.

In the middle of the young barley root is a duct bordered by thin-walled cells, which becomes thickened during aging. The continuity of one layer of pericycle cells is broken by the xylem groups, which contain large vessels. The number of xylem groups in barley root is from 6 to 8 alternating with groups of phloem (Jackson 1922). Protoxylem elements abut directly to the single layer of endodermis, the walls of which thicken with age (Briggs 1978). Fully developed monocotyledonous root consists of much more thickened cell walls in stele, and sclerenchyma develops in the outer cortex (Briggs 1978). In contrast to monocotyledonous root radial pattern, the primary vascular pattern in *Arabidopsis* roots involves a xylem axis and two phloem poles, surrounded by one pericycle layer (Scheres et al. 2002). Only few *Arabidopsis* genes, which are responsible for stele pattern, have been described (Table 2.1). In the *WOODEN-LEG* (*WOL*) mutant, protoxylem is the only tissue in the vascular cylinder (Sieberer et al. 2003). It has been shown that this gene encodes a cytokinin receptor (Franco-Zorrilla et al. 2005), which is required for asymmetric cell divisions of phloem and procambium initial cells (Scheres et al. 2002). Defects in vascular tissue could be also observed in *ALTERED PHLOEM DEVELOPMENT* (*APL*) mutant. This gene, which encodes a MYB transcription factor, has a dual role both in promoting phloem differentiation and in repressing xylem differentiation during vascular development (Bonke et al. 2003).

Root meristem tissues are organized in longitudinal cell files. From the root tip to the plant base, three main regions could be distinguished: the division, elongation, and the differentiation zone (Table 2.2). During both monocotyledons and dicotyledons embryogenesis, first the primary or embryonic radicle and few seminal roots are formed, respectively, whereas lateral roots (LRs) originate from existing roots postembryonically. LRs originate from the group of pericycle cells in *Arabidopsis* (Malamy and Benfey 1997; Scheres et al. 2002), whereas in monocotyledons, endodermis is also involved (Hochholdinger et al. 2004; Karas and McCully 1975). In *Arabidopsis*, lateral roots emerge from the pericycle cells adjacent to

Table 2.2 Mutated genes responsible for *Arabidopsis* root longitudinal pattern

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|---|------------------|--|---|--|
| Meristematic zone | | | | |
| <i>ROOT PRIMORDIUM DEFECTIVE 1 (RPD1)</i> | AT4G33495 | <i>rpdl-1</i> /EMS | Temperature-sensitive mutant with defects at the initial stage of root primordium development. Embryogenesis arrested at the globular stage | Konishi and Sugiyama (2006) |
| <i>HALTED ROOT (HLR)</i> | AT4G29040 | <i>hlr-1, hlr-2</i> /T-DNA insertion | In postembryonic meristems the cellular organization is disrupted, the activity of proteasomes is reduced | Ueda et al. (2004) |
| <i>RUB1 CONJUGATING ENZYME 1 (RCE1)</i> | AT4G36800 | T-DNA insertion | Dwarf phenotype. Reduced response to the change in the gravity vector deficient in auxin and jasmonate response, fewer lateral roots in response to auxin | Dharmasiri et al. (2003) |
| <i>PLETHORA 1 (PLT1)</i> | AT3G20840 | <i>plt1-1, 1-2, 1-3, 1-4, 1-5</i> /T-DNA insertion | Mutant shows an abnormal cellular organization of the hypophyseal derivatives | Aida et al. (2004) |
| <i>PLETHORA 2 (PLT2)</i> | AT1G51190 | <i>plt2-2</i> /T-DNA insertion | Mutant shows an abnormal cellular organization of the hypophyseal derivatives | Aida et al. (2004) |
| <i>GNOMI/EMB30 (GN)</i> | AT1G13980 | <i>emb30-1, emb30-2, gn</i> /EMS | Failure in maintenance of primary root meristem activity; reduced LR number | Shevell et al. (2000), Geldner et al. (2003) |
| <i>STEROL METHYLTRANSFERASE 1 (SMT1)</i> | AT5G13710 | EMS | Mutants displays several conspicuous cell polarity defects, primary and lateral roots are shorter | Willemssen et al. (2003) |
| <i>FASS (FS)</i> | AT5G18580 | EMS | Drastically changed the shape of the seedling without altering body pattern and affected cell elongation and orientation of cell walls | Torres-Ruiz and Jürgens (1994) |
| <i>HOBBIT (HBT)</i> | AT2G20000 | EMS | Postembryonic meristem activity is absent and the distal cell types (QC, columella- and lateral root cap) do not differentiate. The earliest defect found in mutants is disturbance of cell division planes in the hypophysis, the progenitor cell for the QC and columella | Billou et al. (2002), Scheres et al. (2002) |

(continued)

Table 2.2 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|--|------------------|--|--|---|
| <i>BODENLOS (BDL)</i> | AT1G04550 | EMS | Mutant failure to establish the hypophysis which caused severe primary root defects | Hamann et al. (1999, 2002), Scheres et al. (2002) |
| <i>MONOPTEROS (MP)</i> | AT1G19850 | EMS | Mutant failure to establish the hypophysis which caused severe primary root defects (loss-of-function) | Hamann et al. (2002) |
| <i>ACID-INDUCED PROTEIN 13 (IAA13)</i> | AT2G33310 | EMS | Lack of root caused by failure in the specification of the hypophysis and subsequent abnormal cell division patterns | Weijers et al. (2005) |
| <i>ROOT MERISTEMLESS 1 (RML1)</i> | AT4G23100 | EMS | Extremely short mature root (1–2 mm) composed of the same number of cells and cell files as the embryonic root, unable to establish and maintain an active, undifferentiated meristematic zone (mutation does not affect axial and radial patterns of root cell organization). Mutant produces lateral roots readily | Vernoux et al. (2000) |
| <i>ROOT MERISTEMLESS 2 (RML2)</i> | ? | EMS | Extremely short mature root (1–2 mm). Mutant produces nodule-like structures but not lateral roots. Limited number of cell divisions | Cheng et al. (1995) |
| <i>HISTIDINOL-PHOSPHATE AMINOTRANSFERASE (HPA)</i> | AT1G71920 | <i>emb-2196</i> T-DNA insertion <i>hpa11</i> EMS | Very short root system, unable to sustain primary root growth 2 days after germination | Mo et al. (2006) |
| <i>INCURVATA 4 (ICU4)</i> | AT1G52150 | <i>icu4-1</i> , <i>icu4-2</i> /En-2 transposition <i>icu4-3</i> , <i>icu4-4</i> /T-DNA insertion | Longer root hairs, higher number of secondary roots, reduced root length and an aberrant cell pattern in the root apical meristem | Ochando et al. (2006) |
| <i>TEB/CHI (TEB)</i> | AB192295 | <i>teb-1</i> /T-DNA insertion | Short root, split root tip and an aberrant pattern of cell division in postembryonic development | Inagaki et al. (2006) |
| <i>TONSOKU (TSK)</i> | AT3G18730 | T-DNA insertion | Short roots and altered responses to DNA damage | Inagaki et al. (2006) |

| | | | | |
|--|-----------|---|--|--------------------------|
| <i>RETINOBLASTOMA-RELATED (RBR)</i> | AT3G12280 | <i>rbt1-3/</i> T-DNA insertion | Supernumerary stem cells | Wildwater et al. (2005) |
| <i>AUXIN INFLUX 1 (AUX1)</i> | AT2G38120 | <i>aux1110, aux12, aux1106, aux17, aux122/EMS, aux121/X-ray</i> | 50% reduction in number of LR primordia, reduced auxin-sensitive root elongation, perturbed in gravitropism | Casimiro et al. (2003) |
| <i>PIN-FORMED 1 (PIN1)</i> | AT1G73590 | En-1 transposition | Defects in auxin transport. Reduction of root length, meristem size and root elongation zone size | Friml et al. (2003) |
| <i>PIN-FORMED 2 (PIN2)</i> | AT5G57090 | En-1 transposition | Defects in auxin transport. Reduction of root length, meristem size and root elongation zone size | Muller et al. (1998) |
| <i>PIN-FORMED 3 (PIN3)</i> | AT1G70940 | <i>pin3-5/</i> T-DNA insertion | Defects in auxin transport. Reduction of root length, meristem size and root elongation zone size. Subtle cell division defects in the QC and columella root cap | Friml et al. (2003) |
| <i>PIN-FORMED 4 (PIN4)</i> | AT2G01420 | <i>pin4-3/</i> transposon insertion | Defects in auxin transport. Reduction of root length, meristem size and root elongation zone size. Subtle cell division defects in the QC and columella root cap | Friml et al. (2003) |
| <i>PIN-FORMED 7 (PIN7)</i> | AT1G23080 | <i>pin7-1, pin7-3/</i> transposon insertion <i>pin7-2/</i> T-DNA insertion | Defects in auxin transport. Reduction of root length, meristem size and root elongation zone size. Subtle cell division defects in the QC and columella root cap | Friml et al. (2003) |
| <i>PINOID (PID)</i> | AT2G34650 | <i>pid-1, pid-2/EMS</i> insertion | Mutants do not display a root phenotype. Constitutive overexpression results in a consumption of the primary root meristem within a few days after germination: all cells at the root tip become elongated and root hairs cover the primary root tip | Shishkova et al. (2008) |
| <i>ISOPENTENYLTRANSFERASE 3 (IPT3)</i> | AT3G63110 | <i>atipt 3/</i> T-DNA insertion | Triple cytokinin biosynthetic mutant with severely reduced cytokinin level. Enlarged RAM shows an increased number of meristematic cells | Dello-Ioio et al. (2007) |

(continued)

Table 2.2 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|---------------------------------------|------------------|---|---|--------------------------|
| <i>ISOPENTENYLTRANSFERASE (IPT5)</i> | AT5G19040 | <i>atipt 5/T-DNA</i> insertion | Triple cytokinin biosynthetic mutant with severely reduced cytokinin level. Enlarged RAM shows an increased number of meristematic cells | Dello-Ioio et al. (2007) |
| <i>ISOPENTENYLTRANSFERASE (IPT7)</i> | AT3G23630 | <i>atipt 7/T-DNA</i> insertion | Triple cytokinin biosynthetic mutant with severely reduced cytokinin level. Enlarged RAM shows an increased number of meristematic cells | Dello-Ioio et al. (2007) |
| <i>ENDO-BETA-1,4-GLUCANASE (CEL5)</i> | ? | T-DNA insertion | Mutant forms the root cap and sheds root cap cells but sloughing is less efficient compared to wild type | Campillo et al. (2004) |
| <i>NO HYDROTROPIC RESPONSE (NHR)</i> | ? | EMS | No positive hydrotropic response. Abnormal root cap morphogenesis and reduced root growth sensitivity to abscisic acid (ABA) and the polar auxin transport inhibitor N-(1-naphthyl) phthalamic acid (NPA). Homozygous condition results in a lethal phenotype | Eapen et al. (2003) |
| <i>MIZU-KUSSEI 1 (MIZ1)</i> | ? | EMS | Mutant impaired in hydrotropism but shows normal gravitropism and elongation growth | Kobayashi et al. (2007) |
| <i>SKU 5</i> | AT4G12420 | T-DNA insertion | Roots skewed and looped away from the normal downward direction of growth | Sedbrook et al. (2002) |
| <i>SPIRAL 1 (SPR1)</i> | AT2G03680 | <i>spr1-1/EMS spr1-5/T-DNA</i> insertion | Right-handed helical root growth | Nakajima et al. (2004) |
| <i>LEFTY 1</i> | ? | EMS | Left-handed helical growth; epidermal cell files of lefty roots begin to skew at the region where first root hair is emerging | Thitamadee et al. (2002) |
| <i>LEFTY 2</i> | ? | EMS | Left-handed helical growth; epidermal cell files of lefty roots begin to skew at the region where first root hair is emerging | Thitamadee et al. (2002) |

| | | | | |
|----------------------------------|-----------|---|---|--|
| WAVY GROWTH 2 (WAV2) | AT5G20520 | <i>wav2-1, wav2-2/</i> T-DNA insertion | Enhanced wavy root growth | Mochizuki et al. (2005) |
| WAG1 | AT1G53700 | <i>wag1-1, wag1-2/</i> T-DNA insertion | Wavy root phenotype | Santner and Watson (2006) |
| WAG2 | AT3G14370 | <i>wag2-1/</i> T-DNA insertion | Wavy root phenotype | Santner and Watson (2006) |
| AUXIN RESPONSE FACTOR 10 (ARF10) | AT2G28350 | <i>arf10-2/</i> T-DNA insertion | <i>arf10 arf16</i> double mutant displays uncontrolled cell division and blocked cell differentiation in the root distal region and shows a tumor-like root apex and loss of gravity-sensing | Wang et al. (2006) |
| AUXIN RESPONSE FACTOR 16 (ARF16) | AT4G30080 | <i>arf16-2/</i> T-DNA insertion | Uncontrolled cell division and blocked cell differentiation in the root distal region. Mutant shows a tumor-like root apex and loss of gravity-sensing | Wang et al. (2006) |
| ADENYLATE KINASE 2 (AK2) | ? | T-DNA insertion | Mutant exhibits significantly elevated root growth, cap morphogenesis defects, along with alterations in root sensitivity to gravistimulation and slower kinetics of root gravitropic curvature | Carrari et al. (2005), Young et al. (2006) |
| ADENYLATE KINASE 3 (AK3) | ? | T-DNA insertion | Mutant exhibits significantly elevated root growth, cap morphogenesis defects, along with alterations in root sensitivity to gravistimulation and slower kinetics of root gravitropic curvature | Carrari et al. (2005), Young et al. (2006) |
| Elongation zone | | | | |
| QUASIMODO 1 (QUA) | AT3G25140 | <i>qual-1, qual-2/</i> T-DNA insertion | Reduced cell adhesion. Dwarf phenotype and rough aspect resulting from numerous cells protruding from their cotyledons, leaves, and hypocotyls | Bouton et al. (2002) |
| PROPORZ 1 (PRZ1) | AT4G16420 | <i>prz1-1/</i> T-DNA insertion | Mutant exhibits defects in cell and organ differentiation | Sieberer et al. (2003) |

(continued)

Table 2.2 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|---|------------------|--|---|----------------------------|
| <i>DAWDLE (DDL)</i> | AT3G20550 | T-DNA insertion | Mutant plants exhibit shortened roots caused by lower number of cell divisions | Morris et al. (2006) |
| <i>CYTOKININ ROOT SYNDROME (CKR1)</i> | ? | <i>ckr1-7,-8,-12,-50,-09/EMS</i> | Mutant exhibits significantly elevated root growth with shorter root hairs and altered response to cytokinin | Su and Howell (1992) |
| <i>POLARIS (PLS)</i> | AT4G39403 | Promoter trap | Short-root phenotype, relatively short and radially expanded cells, altered response to exogenous auxins and cytokinins, enhanced ethylene-response phenotype, defective auxin transport and homeostasis, and altered microtubule sensitivity to inhibitors | Chilley et al. (2006) |
| <i>YADOKARI 1-D (YADK 1-D)</i> | ? | T-DNA insertion | Dwarf mutant: short hypocotyl and primary root, reduced apical dominance and reduced number of lateral roots | Takase et al. (2004) |
| <i>MURUS 1 (MUR1)</i> | AT3G51160 | <i>mur1-1, 1-2/EMS</i> | Root growth defects, altered cell walls which are more brittle | Freshour et al. (2003) |
| <i>BREVIS RADIX (BRX)</i> | AT1G31880 | T-DNA insertion | Roots composed of shorter as well as fewer cells. Reduction in mature cell size as well as cell proliferation causes slow primary root growth | Mouchel et al. (2004) |
| <i>PETIT 1 (PT1)</i> | ? | <i>pet1-1/fast neutrons</i> | Defective in aspects of root and hypocotyl elongation and presence of gaps in internal cortical and epidermal cell walls | Kurata and Yamamoto (1998) |
| <i>PROCUSTE 1 (PRC1)</i> | ? | <i>prc1-8, 1-10, 1-12, 1-19/ T-DNA insertion</i> | Decreased cell elongation in roots and dark-grown hypocotyls | Fagard et al. (2000) |
| <i>CONSTITUTIVE EXPRESSION OF VSP1 1 (CEV1)</i> | AT5G05170 | <i>ixr1-1, 1-2/EMS</i> | Stunted phenotype. Short hypocotyls in dark-grown seedlings. Roots have reduced cellulose content, increased production of jasmonate and ethylene | Ellis et al. (2002) |

| | | | | |
|---|-----------|---|--|---|
| ARABIDOPSIS THALIANA ACT7 (ACT7) | AT5G09810 | <i>act7-2, 7-3, 7-4/</i> T-DNA insertion | Increased root twisting and waving, and retarded root growth. Root apical cells are not in straight files and contain oblique junctions between cells | Gilliland et al. (2003) |
| WAVE-DAMPENED 2 (WVD2) | AT5G28646 | <i>Overexpression wvd2-1/Ac/Ds</i> | Constitutive right-handed helical growth in both roots and etiolated hypocotyls and impaired anisotropic expansion. | Yuen et al. (2003) |
| WVD2-LIKE 1 (WDL1) | AT3G04630 | <i>Overexpression/Ac/Ds</i> | Constitutive right-handed helical growth in both roots and etiolated hypocotyls and impaired anisotropic expansion | Yuen et al. (2003) |
| PICKLE, SUPPRESSOR OF SLR 2 (PCL) | AT2G25170 | EMS | Primary root differentiates improperly and expresses embryonic characteristics after germination | Li et al. (2005) |
| STUNTED PLANT 1 (STP1) | ? | EMS | Roots elongate more slowly than in the WT | Baskin et al. (1995), Beemster and Baskin (2000) |
| XYLOGLUCAN ENDOTRANGLUCOSYLASE/HYDROLASE 21 (XTH21) | AT2G18800 | T-DNA insertion | Stunted phenotype with shorter root hairs and perturbation in epidermis cell formation | Liu et al. (2007) |
| ZINC FINGER OF ARABIDOPSIS THALIANA 6 (ZAT6) | ? | RNAi/ overexpression | RNAi mediated silencing results in lethality. Overexpression affects root development and retards seedling growth as a result of decreased Pi acquisition | Devaiah et al. (2007) |
| MULTIDRUG RESISTANCE P -GLYCOPROTEIN (PGP4) | AT2G47000 | <i>pgp4-1, 4-3, 4-4/</i> T-DNA insertion | Reduced root gravitropic bending and elongation as well as lateral root formation | Terasaka et al. (2005) |
| RESISTANT TO IBA (RIB1) | ? | <i>Ac/Ds</i> | Shorter primary root, increased number of lateral roots and elongation defects in root gravitropism. Less sensitive to growth inhibition by IBA and less sensitive to IBA in stimulation of lateral root formation | Poupart and Waddell (2000), Poupart et al. (2005) |
| XIPOTL 1 | ? | T-DNA insertion | Short primary root, a high number of lateral roots and short epidermal cells with aberrant morphology and few root hairs | Cruz-Ramírez et al. (2004) |

(continued)

Table 2.2 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|---|------------------|--|---|-------------------------|
| <i>PHOSPHOLIPASE DS 1 (PLDζ1)</i> | ? | T-DNA insertion | Slower elongation of primary root and longer lateral roots in low phosphate conditions | Li et al. (2006a, b) |
| <i>PHOSPHOLIPASE DS 2 (PLDζ2)</i> | ? | T-DNA insertion | Slower elongation of primary root and longer lateral roots in low phosphate conditions | Li et al. (2006a, b) |
| <i>WEAK ETHYLENE INSENSITIVE 2 (WEI2)</i> | AT5G05730 | <i>wei2-1</i> , 2-3/EMS | Root-specific ethylene insensitivity. Upregulation of <i>WEI2/ASA1</i> and <i>WEI7/ASB1</i> by ethylene results in the accumulation of auxin in the tip of primary root, whereas loss-of-function mutations in these genes prevent the ethylene-mediated auxin increase | Stepanova et al. (2005) |
| <i>WEAK ETHYLENE INSENSITIVE 7 (WEI7)</i> | AT1G25220 | <i>wei7-1</i> , 7-2/Ac/Ds | Root-specific ethylene insensitivity. Upregulation of <i>WEI2/ASA1</i> and <i>WEI7/ASB1</i> by ethylene results in the accumulation of auxin in the tip of primary root, whereas loss-of-function mutations in these genes prevent the ethylene-mediated auxin increase | Stepanova et al. (2005) |
| <i>HISTONE MONOUBIQUITINATION 1 (HUB1)</i> | AT2G44950 | <i>hub1-1</i> /EMS <i>hub1-2</i> , <i>hub1-3</i> /T-DNA insertion | Slow primary root growth | Fleury et al. (2007) |
| <i>SCARFACE (SFC)</i> | AT5G13300 | <i>sfc-9</i> /T-DNA insertion | Shorter roots | Sieburth et al. (2006) |
| Differentiation zone: lateral roots (LR) | | | | |
| <i>ARABIDILLO-1</i> | AT2G44900 | T-DNA insertion | Fewer lateral roots | Coates et al. (2006) |
| <i>ARABIDILLO-2</i> | AT3G60350 | T-DNA insertion | Fewer lateral roots | Coates et al. (2006) |
| <i>SUPERROOT 1 (SUR1)</i> | AT2G20610 | <i>sur1-2</i> , <i>1-3</i> , <i>1-4</i> , <i>1-5</i> , <i>1-6</i> /EMS | Increased LR number and formation of additional adventitious root | Celenza et al. (1995) |

| | | | | |
|---|-----------|----------------------------------|---|---|
| <i>SUPERRROOT 2 (SUR2)</i> | AT4G31500 | En-1 transposition | Numerous adventitious roots begin to grow from the hypocotyl, lateral root primordium develop at high frequency, root hairs appear at higher density and root elongation is reduced | Casimiro et al. (2003), Casson and Lindsey (2003) |
| <i>ABERRANT LATERAL ROOT FORMATION 4 (ALF4)</i> | AT5G11030 | <i>alf4-1</i> /gamma rays | Unable to produce lateral roots and does not respond to exogenous auxins | Celenza et al. (1995), Casimiro et al. |
| <i>CEGENDUO (CEG)</i> | ? | T-DNA insertion | Increased lateral root production | Dong et al. (2006) |
| <i>KIP-RELATED PROTEIN 2 (KRP2)</i> | AT3G50630 | Overexpression | Mutations do not give any remarkable morphological phenotypes what indicates the presence of redundant functions. The number of lateral roots in overexpression line was reduced by 60% compared with that in the wild type | Himanen et al. (2002) |
| <i>KANADI (KAN)</i> | AT5G16560 | <i>kan1-2</i> /EMS | Reduced primary root length and reduced lateral root (LR) number | Hawker and Bowman (2004) |
| <i>KANADI 2 (KAN2)</i> | AT1G32240 | <i>kan2-1</i> /EMS | Reduced primary root length and LR number | Hawker and Bowman (2004) |
| <i>KANADI 3 (KAN3)</i> | AT4G17695 | <i>kan3-1</i> /EMS | Reduced primary root length and fewer lateral roots | Hawker and Bowman (2004) |
| <i>PHABULOSA 6 (PHB6)</i> | AT2G34710 | EMS | Reduced LR number | Hawker and Bowman (2004) |
| <i>PHAVOLUTA 5 (PHV5)</i> | AT1G30490 | T-DNA insertion | Reduced LR number | Hawker and Bowman (2004) |
| <i>REVOLUTA 10 (REV10)</i> | AT5G60690 | T-DNA insertion | Reduced LR number | Hawker and Bowman (2004) |
| <i>AUXIN RESPONSE FACTOR 8 (ARF8)</i> | AT5G37020 | <i>arf8-1</i> / T-DNA insertion | Long-hypocotyl phenotype in light conditions and increased formation of LR | Tian et al. (2004) |
| <i>AUXIN RESPONSE FACTOR 10 (ARF19)</i> | AT1G19220 | <i>arf19-1</i> / T-DNA insertion | Mutant with reduced LR development | Okushima et al. (2007) |
| <i>TRANSPORT INHIBITOR RESPONSE 1 (TIR1)</i> | AT3G62980 | <i>tir1-9</i> /T-DNA insertion | Reduced LR number. Reduced auxin-transport-inhibitor-sensitive root elongation | Xie et al. (2000), Casimiro et al. (2003) |

(continued)

Table 2.2. (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|--|------------------|---|--|---|
| <i>ENHANCER OF TIR1-1 AUXIN RESISTANCE (ETA3)</i> | AT1G19220 | EMS | Auxin-resistant root growth in seedlings and reduced LR development | Gray et al. (2003) |
| <i>ARABIDOPSIS SERINE/THREONINE KINASE 1 (ASK1)</i> | AT1G10940 | <i>ask1-1</i> /Ac/Ds | Decreased number of LR | Fukaki et al. (2005) |
| <i>ASK2</i> | AT3G61160 | <i>ask2-1</i> /T-DNA insertion | Decreased number of LR | Fukaki et al. (2005) |
| <i>CULLIN-ASSOCIATED AND NEDDYLATION DISSOCIATED, HEMIVENATA (CAND1)</i> | AT2G02560 | EMS | Decreased number of LR | Fukaki et al. (2005) |
| <i>TRANSPORT INHIBITOR RESPONSE 3 (TIR3)</i> | AT3G02260 | <i>tir3-1</i> //EMS and gamma rays | Reduced LR number. Reduced auxin-transport-inhibitor-sensitive root elongation | Ruegger et al. (1997), Lopez-Bucio et al. (2005) |
| <i>ANR1</i> | AT2G14210 | <i>ANR1-KO</i> /dSpm transposon insertion | Does not show the nitrate-induced stimulatory effect (down-regulated expression) | Montiel et al. (2004) |
| <i>ARABIDOPSIS DUAL-AFFINITY NITRATE TRANSPORTER GENE ANRT1.1 (NRT1.1)</i> | ? | T-DNA insertion | Does not show the nitrate-induced stimulatory effect | Zhang et al. (2007) |
| <i>LATERAL ROOT INITIATION (LIN1)</i> | AT1G08090 | EMS | LR development insensitive to high-sucrose, low-nitrogen medium | Cerezo et al. (2001), Casimiro et al. (2003), Zhang et al. (2007) |
| <i>IAA-ALANINE RESISTANT 2 (IAA28/IAR2)</i> | AT5G25890 | <i>iaa28-1</i> /EMS | Defective in LR formation, reduced LR number. Defects in root hair development, resistance to the stimulatory effects of low P on root hair and LR formation | Lopez-Bucio et al. (2002) |
| <i>MULTIDRUG RESISTANCE-ASSOCIATED PROTEIN 5 (MRP5)</i> | AT1G04120 | <i>mrp5-1</i> /T-DNA insertion | Increased LR number, decreased root length | Gaedeke et al. (2001), Casimiro et al. (2003) |

| | | | | |
|---|-----------|---------------------------------|---|---|
| <i>DWARF IN LIGHT 1 (DFL1)</i> | AT5G54510 | Activation-tagging plasmid | Altered hypocotyl length in light and reduced LR number but the primary root length is almost the same as in the WT. Auxin insensitive | Nakazawa et al. (2001), Casimiro et al. (2003) |
| <i>AUXIN RESISTANT 1 (AXR1)</i> | AT1G05180 | <i>axr1-3/EMS</i> | Agravitropic root, reduced LR number. Reduced auxin-sensitive root elongation | Lopez-Bucio et al. (2002), Casimiro et al. (2003) |
| <i>AUXIN RESISTANT 2 (AXR2)</i> | AT3G23050 | <i>axr2-5/T-DNA insertion</i> | Agravitropic root, reduced LR number. Short hypocotyls in dark conditions. | Lopez-Bucio et al. (2002) |
| <i>AUXIN RESISTANT 3 (AXR3)</i> | AT1G04250 | <i>axr3-3/EMS</i> | Reduced root elongation and increased lateral root number | Lopez-Bucio et al. (2002) |
| <i>AUXIN RESISTANT 4 (AXR4)</i> | AT1G54990 | <i>axr4-2/gamma rays</i> | Reduced LR number. Reduced auxin-sensitive root elongation | Lopez-Bucio et al. (2002), Casimiro et al. (2003) |
| <i>AUXIN RESISTANT 5 (AXR5)</i> | AT4G14560 | <i>axr5-1/unknown</i> | Gain-of-function mutation; mutants are resistant to auxin and display a variety of auxin-related growth defects including defects in root and shoot tropisms and reduced LR number on auxin | Yang et al. (2004), De Smet et al. (2006) |
| <i>AUXIN RESISTANT 6 (AXR6)</i> | ? | <i>atcul1-5/T-DNA insertion</i> | Reduced lateral root number. Reduced auxin-sensitive root elongation | Lopez-Bucio et al. (2002), Casimiro et al. (2003) |
| <i>NO APICAL MERISTEM CUP-SHAPED COTYLEDON (NAC1)</i> | AT1G56010 | RNAi/ overexpression | RNAi lines have reduced LR number; overexpressing lines have increased LR number. | Montiel et al. (2004), Scheres et al. (2002), Xie et al. (2000) |
| <i>PEROXISOMAL ABC TRANSPORTER 1 (PXA1)</i> | AT4G39850 | EMS | Reduced IBA-sensitive root elongation. Reduced LR number | Zolman et al. (2001), Casimiro et al. (2003) |
| <i>SEVEN IN ABSENTIA HOMOLOG 5 (SINAT5)</i> | AT5G53360 | Overexpression | Overexpression leads to reduced LR formation | Casimiro et al. (2003) |
| <i>PASTICCINO 1 (PAS1)</i> | AT3G54010 | <i>pas1-1/T-DNA insertion</i> | Reduced LR number and short primary root | Faure et al. (1998), Casimiro et al. (2003) |
| <i>PASTICCINO 2 (PAS2)</i> | AT5G10480 | EMS | Increased LR number and short primary root | Faure et al. (1998) |
| <i>PASTICCINO 3 (PAS3)</i> | ? | | Reduced LR number and short primary root | Faure et al. (1998) |

(continued)

Table 2.2 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|---|------------------|---|--|--|
| | | <i>pas3-1, 3-2, 3-3, 3-4/</i> EMS | | |
| <i>SOLITARY ROOT1/ IAA14 (SLR1/ IAA14)</i> | AT4G14550 | <i>iaa14-1/</i> T-DNA insertion | Absence of LR development, reduced number of root hairs | Scheres et al. (2002), Casimiro et al. (2003), Montiel et al. (2004), Fukaki et al. (2006) |
| <i>LATERAL ROOT PRIMORDIUM 1 (LRP1)</i> | AT5G12330 | Gene trap transposon | Delayed lateral root initiation | Smith and Fedoroff (1995) |
| <i>NON-PHOTOTROPIC HYPOCOTYL (NPH4)</i> | AT5G20730 | <i>nph4-1, 4-2, 4-3, 4-4/</i> fast neutrons | Decrease in lateral and adventitious root formation | Stowe-Evans et al. (1998), Casimiro et al. (2003) |
| <i>SHORT HYPOCOTYL (SHY2)</i> | AT1G04240 | <i>shy2-2/</i> EMS | Significantly shorter roots of <i>shy2-2</i> mutants with very few lateral roots, whereas the <i>shy2-22</i> and <i>shy2-24</i> mutants form more and much longer LR than the WT | Tian and Reed (1999) |
| <i>KNOTTED-LIKE (KNAT6)</i> | AT1G23380 | T-DNA insertion | Down-regulation of <i>KNAT6</i> expression by RNA interference was associated with an increased total number of lateral roots | Dean et al. (2004), Montiel et al. (2004) |
| <i>MASSUGU2/IAA19 (MSG/IAA19)</i> | AT3G15540 | EMS | Defective in lateral root formation and root gravitropism | Tatematsu et al. (2004) |
| <i>PUCHI</i> | ? | <i>puchi-1/</i> T-DNA insertion | Disturbed cell division patterns in the lateral root primordium, resulting in swelling of the proximal region of lateral roots | Hirota et al. (2007) |
| <i>CYTOPLASMIC-INVERTASE 1 (AtCYT-INV1)</i> | ? | EMS | Insensitivity to osmotic stress-induced inhibition of lateral root growth. Short primary root, smaller size of leaves and siliques | Qi et al. (2006) |

| | | | | |
|---|-----------|--------------------------------|---|------------------------------|
| <i>LATERAL ORGAN BOUNDARIES- DOMAIN16 (LBD16)</i> | AT2G42430 | Overexpression | Overexpression induces lateral root formation | Okushima et al. (2007) |
| <i>LATERAL ORGAN BOUNDARIES- DOMAIN29 (LBD29)</i> | AT3G58190 | Overexpression | Overexpression induces lateral root formation | Okushima et al. (2007) |
| <i>XB3 ORTHOLOG 2 IN ARABIDOPSIS THALIANA 32 (XBAT32)</i> | AT5G57740 | T-DNA insertion | Poor root system and severe defects in lateral root production. Defective in cell divisions that are required for lateral root initiation | Nodzon et al. (2004) |
| <i>IAA-LEUCINE RESISTANT 2 (ILR2)</i> | AT3G18485 | <i>ilr2-1</i> /T-DNA insertion | Defective in lateral root formation and primary root elongation | Magidin et al. (2003) |
| <i>IAA-LEUCINE RESISTANT 1 (ILR1)</i> | AT3G02875 | <i>ilr1-1</i> /EMS | Shorter hypocotyl and fewer lateral roots on unsupplemented medium | Rampey et al. (2004) |
| <i>IAA-LEUCINE-RESISTANT (ILR)- LIKE GENE 2 (ILL2)</i> | AT5G56660 | <i>ilr2-1</i> /T-DNA insertion | Shorter hypocotyl and fewer lateral roots on unsupplemented medium | Rampey et al. (2004) |
| <i>IAA-ALANINE RESISTANT 3 (IAR3)</i> | AT1G51760 | <i>iar3-1</i> /EMS | Shorter hypocotyl and fewer lateral roots on unsupplemented medium | Rampey et al. (2004) |
| <i>HOMEOBOX-LEUCINE ZIPPER PROTEIN HAT4 (ATHB-2/HAT4)</i> | AT4G16780 | Overexpression | Elevated <i>ATHB-2</i> levels inhibit specific cell proliferation such as secondary growth of the vascular system and lateral root formation. Reduced LR number. | Steindler et al. (1999) |
| <i>ROOTS CURL IN NP (RCN1)</i> | AT1G25490 | T-DNA insertion | Lateral roots exhibit reduced NPA sensitivity, gravitropic response and increased auxin transport. | |
| <i>RHO-RELATED PROTEIN FROM PLANTS 2 (ROP2)</i> | AT1G20090 | Overexpression | Constitutively active GTP-bound rop2 (CA-rop2): increased LR number; and dominant negative GDP-bound rop2 (DN-rop2) reduced LR number | Li et al. (2001) |
| <i>SEUSS (SEU)</i> | AT1G43850 | <i>seu-3</i> /EMS | Pleiotropic phenotype that includes reductions in several classic auxin responses such as apical dominance, lateral root initiation, sensitivity to exogenous auxin | Pfluger and Zambryski (2004) |
| <i>ARABIDOPSIS RESPONSE REGULATOR 3 (ARR3)</i> | AT1G59940 | T-DNA insertion | Lateral root formation is more sensitive to cytokinin inhibition | To et al. (2004) |

(continued)

Table 2.2. (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|---|------------------|---|---|--|
| <i>ARABIDOPSIS RESPONSE REGULATOR 4 (ARR4)</i> | AT1G10470 | T-DNA insertion | Lateral root formation is more sensitive to cytokinin inhibition | To et al. (2004) |
| <i>ARABIDOPSIS RESPONSE REGULATOR 5 (ARR5)</i> | AT3G48100 | T-DNA insertion | Lateral root formation is more sensitive to cytokinin inhibition | To et al. (2004) |
| <i>ARABIDOPSIS RESPONSE REGULATOR 6 (ARR6)</i> | AT5G62920 | T-DNA insertion | Lateral root formation is more sensitive to cytokinin inhibition | To et al. (2004) |
| <i>ARABIDOPSIS RESPONSE REGULATOR 8 (ARR8)</i> | ? | T-DNA insertion | Lateral root formation is more sensitive to cytokinin inhibition | To et al. (2004) |
| <i>ARABIDOPSIS RESPONSE REGULATOR 9 (ARR9)</i> | AT3G57040 | T-DNA insertion | Lateral root formation is more sensitive to cytokinin inhibition | To et al. (2004) |
| <i>CYTOKININ OXIDASE/DEHYDROGENASE 1 (CKX1)</i> | AT2G41510 | Overexpression | Increased growth of the primary root and increased number of lateral roots | Werner et al. (2003) |
| <i>CYTOKININ OXIDASE/DEHYDROGENASE 3 (CKX3)</i> | AT5G56970 | Overexpression | Increased growth of the primary root and increased number of lateral roots | Werner et al. (2003) |
| <i>E1-CONJUGATING ENZYME-RELATED1-1 (ECR1)</i> | AT5G19180 | <i>ecr1-1</i> /EMS | Resistant to the auxin-like compound indole-3-propionic acid, produces fewer lateral roots than wild type, displays reduced adult height | Woodward et al. (2007) |
| <i>RING-BOX 1 (RBX1)</i> | AT5G20570 | Overexpression | Transgenic plants (35S::RBX1) had smaller cotyledons and produced fewer lateral roots than WT plants | Gray et al. (2002) |
| <i>BUSHY AND DWARF (BUD1)</i> | AT1G18350 | Sense/antisense RNA expression system | Significantly fewer lateral roots, loss of apical dominance, shorter hypocotyl at high temperature (29°C) under light. Deficiency in polar auxin transport | Dai et al. (2006) |
| <i>LONG HYPOCOTYL 5 (HY5)</i> | ? | T-DNA insertion | Altered hypocotyl length in light and increased LR number. Emergence of LR occurs earlier than in WT, resulting in overall enhanced root system growth. The gravitropism of <i>hy5</i> roots is reduced | Casimiro et al. (2003), Sibout et al. (2006) |

| | | | | |
|--|-----------|--|--|-----------------------|
| WALL-ASSOCIATED SER/THR KINASE (WAK4) LIKE AUX1 (LAX3) | AT1G21210 | Antisense gene | Impaired cell elongation and blocked LR formation | Lally et al. (2001) |
| | AT1G77690 | T-DNA insertion | Nearly 40% reduction in numbers of emerged lateral roots | Swarup et al. (2008) |
| ABA DEFICIENT 1 (ABA1) | AT5G67030 | aba1-1/EMS | ABA sensitive, reduced ABA inhibitory effect on LR length. Shorter primary root | Signora et al. (2001) |
| ABA DEFICIENT 2 (ABA2) | AT1G52340 | aba2-1, 2-3, 2-4/EMS | ABA sensitive, reduced ABA inhibitory effect on LR length. Shorter primary root | Signora et al. (2001) |
| ABA DEFICIENT 3 (ABA3) | AT1G16540 | aba3-1/EMS | ABA sensitive, reduced ABA inhibitory effect on LR length | Signora et al. (2001) |
| ABA DEFICIENT 4 (ABA4) | ? | 3-2/gamma rays aba4-1/T-DNA insertion | ABA insensitive, reduced ABA inhibitory effect on LR length | Signora et al. (2001) |
| ABA DEFICIENT 5 (ABA5) | ? | unknown | ABA insensitive, reduced ABA inhibitory effect on LR length | Signora et al. (2001) |
| ABSCISIC ACID INTENSIVE 1 (ABI1) | AT5G57050 | EMS | Reduced ABA inhibitory effect on LR length | De Smet et al. (2003) |
| ABSCISIC ACID INTENSIVE 1 (ABI2) | AT3G24650 | EMS | Reduced ABA inhibition on LR length | De Smet et al. (2003) |
| ABSCISIC ACID INTENSIVE 1 (ABI3) | AT3G24650 | EMS | Reduced ABA inhibitory effect on LR length | De Smet et al. (2003) |
| ABSCISIC ACID INTENSIVE 1 (ABI4) | AT2G40220 | Gamma rays | Reduced ABA inhibitory effect on LR length | De Smet et al. (2003) |
| ABSCISIC ACID INTENSIVE 1 (ABI5) | AT2G36270 | abi5-1/T-DNA insertion | Reduced ABA inhibitory effect on LR length | De Smet et al. (2003) |
| ENHANCED RESPONSE TO ABA 1 (ERA1) | AT5G40280 | unknown | Increased number of lateral roots | Brady et al. (2003) |
| LATERAL ROOT ABA-INSENSITIVE (LABI) | ? | EMS | Shorter primary root phenotype and ability to produce visible LRs in the presence of ABA. Mutants are less sensitive to the high-nitrate induced inhibition on LRs | Zhang et al. (2007) |
| FLOWERING TIME CONTROL PROTEIN ALPHA (FCA) | AT4G16280 | EMS | Reduced sensitivity to the inhibitory effect of ABA on LRs | Zhang et al. (2007) |

(continued)

Table 2.2 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|---|------------------------|---|--|---|
| <i>HOMEODOMAIN-LEUCINE ZIPPER</i> <i>PROTEIN HAT2 (HAT2)</i> | AT5G47370 | Overexpression | Mutations of the <i>HAT2</i> gene did not produce any remarkable morphological phenotypes (mutants responded to gravity, exogenous auxin, and auxin transport inhibitor in similar ways to wild-type plants) indicating the presence of redundant functions among the HD-Zip II subfamily genes. 35S::HAT2 plants showed reduced lateral root elongation, and reduced auxin sensitivity compared to wild-type plants | Sawa et al. (2002) |
| <i>PI DEFICIENCY RESPONSE</i> <i>2 (PDR2)</i> | ? | EMS | Disrupted Pi sensing | Ticconi et al. (2004) |
| <i>UBIQUITIN-LIKE MODIFIER</i> (SUMO) <i>E3 LIGASE (AtSIZ1)</i> <i>WRKY75</i> | AT5G60410 | <i>siz1-1, 1-2, 1-3/</i> T-DNA insertion | Cessation of primary root growth, extensive lateral root and root hair development | Miura et al. (2005) |
| | AT5G13080 | RNAi | Suppression of <i>WRKY75</i> expression through RNAi silencing results in significantly increased LR length and number, as well as root hair number | Devaiah et al. (2007) |
| <i>ABERRANT LATERAL ROOT</i> <i>FORMATION 3 (ALF3)</i> | ? | <i>alf3-1/EMS</i> | Mutant is able to initiate lateral root primordium formation but then arrests at the emergence stage | Celenza et al. (1995), Casimiro et al. (2003) |
| <i>RELATED TO ABI3/VPI 1 (RAV1)</i> <i>INDOLE-3-BUTYRIC</i> <i>ACID-RESPONSE (IBR5)</i> | AT1G13260 AT2G04550 | Overexpression <i>ibr5-1/EMS</i> | Overexpression causes retarded LR development Light-grown seedlings have longer primary roots with slightly fewer lateral roots. Lateral roots in <i>ibr5-1</i> elongate less than in the WT; hypocotyl and roots elongate normally in the dark | Hu et al. (2004) Monroe-Augustus et al. (2003) |
| <i>LRD2</i> | ? | EMS | Mutant has an altered response to exogenous ABA | Deak and Malamy (2005) |

Adventitious roots

| | | | | | |
|---|-----------|----------------------------|--|--|-----------------------------|
| <i>ARGONAUTE 1 (AGO1)</i> | AT1G48410 | EMS | | Reduced formation of adventitious roots in response to auxin. Defect of hypocotyl elongation in response to auxin | Sorin et al. (2005) |
| <i>AUXIN RESPONSE FACTOR 17 (ARF17)</i> | AT1G77850 | T-DNA/overexpression | | Overexpression line produces fewer adventitious roots than the WT | Sorin et al. (2005) |
| <i>HASTY (HST)</i> | AT3G05040 | <i>hst-6</i> /EMS | | Mutants have reduced size of roots and form adventitious roots from the base of the hypocotyl | Bollman et al. (2003) |
| <i>ROOT INITIATION DEFECTIVE 1 (RID1)</i> | ? | <i>hst-7</i> /X-ray EMS | | Temperature-sensitive, defective in the initial or the pre-morphogenic stage of adventitious root formation | Konishi and Sugiyama (2003) |
| <i>ROOT INITIATION DEFECTIVE 2 (RID2)</i> | ? | EMS | | Temperature-sensitive, defective in the initial or the pre-morphogenic stage of adventitious root formation | Konishi and Sugiyama (2003) |
| <i>ROOT INITIATION DEFECTIVE 3 (RID3)</i> | ? | EMS | | Temperature-sensitive, defective in the initial or the pre-morphogenic stage of adventitious root formation | Konishi and Sugiyama (2003) |
| <i>ROOT INITIATION DEFECTIVE 4 (RID4)</i> | ? | EMS | | Temperature-sensitive, defective in the initial or the pre-morphogenic stage of adventitious root formation | Konishi and Sugiyama (2003) |
| <i>ROOT INITIATION DEFECTIVE 5 (RID5)</i> | ? | EMS | | Temperature-sensitive, reduced frequency of root initiation at 28°C without affecting the later stages of root formation. The rate of adventitious rooting generally depends on the concentration of exogenous auxin | Konishi and Sugiyama (2003) |
| <i>ROOT PRIMORDIUM DEFECTIVE 1 (RRD1)</i> | ? | EMS | | Temperature-sensitive, mutant can establish adventitious roots but fails to maintain their growth. Strongly inhibited subsequent growth of adventitious roots at 28°C | Konishi and Sugiyama (2003) |

(continued)

Table 2.2 (continued)

| Gene name (alias) | Accession number | Allele/mutation strategy/reverse approach | Mutant phenotype | References |
|--|------------------|---|---|-----------------------------|
| <i>ROOT PRIMORDIUM DEFECTIVE 2 (RRD2)</i> | ? | EMS | Temperature-sensitive, mutant can establish adventitious roots but fails to maintain their growth. Strongly inhibited subsequent growth of adventitious roots at 28°C | Konishi and Sugiyama (2003) |
| <i>ROOT PRIMORDIUM DEFECTIVE 4 (RRD4)</i> | ? | EMS | Temperature-sensitive, mutant can establish adventitious roots but fails to maintain their growth. Strongly inhibited subsequent growth of adventitious roots at 28°C | Konishi and Sugiyama (2003) |
| <i>LR</i> lateral root, <i>RAM</i> root apical meristem, <i>QC</i> quiescent centre, <i>WT</i> wild type | | | | |

the xylem poles (Benjamins and Scheres 2008), whereas in barley from pericycle and endodermis adjacent to phloem (Briggs 1978) just like in rice and corn (Hochholdinger and Zimmermann 2008). The general structure of barley lateral roots seems to be the same as the seminal and nodal roots, despite their different origins. The transverse section exhibit typical thick-walled endodermis and single large axile duct surrounded by much more thicker tissue (Gorny 1992). For LR initiation, auxin plays a crucial role in both monocotyledonous (Chhun et al. 2007) and dicotyledonous (Tian and Reed 1999; Casimiro et al. 2003) species.

More than 170 genes have been described as important for longitudinal pattern in *Arabidopsis*. Alterations in these genes cause often severe phenotype, such as in the case of *GNOM* (*GN*). Mutants of this gene display a range of phenotypes, but all of them lack a root (Shevell et al. 2000). This gene encodes an ARF GDP/GTP exchange factor involved in embryonic axis formation and polar localization of PIN1 (Geldner et al. 2004). It was shown that mutations in this gene disrupt the polarity of auxin transport and thereby cause defects not only in gravitropism (Geldner et al. 2003) but also hydrotropism (Miyazawa et al. 2009). Lack of a primary root is characteristic for *BODENLOS* (*BDL*) and *MONOPTEROS* (*MP*) mutants. The *MP* gene encodes a transcription factor ARF5 (AUXIN RESPONSE FACTOR 5) that activates auxin-responsive target genes, whereas *BDL* encodes INDOLACETIC ACID-INDUCED PROTEIN 12 (IAA12) (Shevell et al. 2000). Hamann and coworkers (2002) suggested inhibitory effect *BDL* on *MP*, but exact mechanism of their action is unknown (Weijers et al. 2006). Alterations in root length could be an output of decreased number of cell divisions such as in the case of *DAWDLE* (*DDL*), cell elongation – *PHOSPHOLIPASE DS 1,2* (*PLD ζ 1*) or cell-wall formation – *MURUS 1* (*MUR1*). *DDL* mutant plants exhibit shortened roots. This gene seems to influence transcription activation by recruiting proteins to transcription complexes; however, its precise function is still unknown (Morris et al. 2006). Slower elongation of primary roots and faster of lateral roots in low phosphate conditions are characteristic for *PLD ζ 1* and *PLD ζ 2* mutants. These genes are involved in root elongation during phosphate limitation – they promote primary root growth but inhibit lateral root elongation (Li et al. 2006b). *MUR1* mutants exhibit root growth defects, where more brittle altered cell walls are observed. This gene is necessary to form essential pectin cross-links within the cell wall and proper composition of cell wall polysaccharides (Freshour et al. 2003).

Up to now, many genes have been described as involved in lateral root formation in the differentiation zone. Lateral roots are formed from the pericycle “founder cells,” which undergo a series of periclinal and anticlinal divisions to generate a new meristem (Casson and Lindsey 2003). One of the earliest genes involved in lateral root formation is *ALF4* (*ABERRANT LATERAL ROOT FORMATION 4*). The *ALF4* mutant is unable to produce lateral roots or adventitious roots and does not respond to exogenous auxins (Casimiro et al. 2003). It was suggested by DiDonato and coworkers (2004) that *ALF4* functions in maintaining the pericycle in the mitotically competent state needed for lateral root formation. There are only few mutants described as involved in lateral root emergence. *LAX3*, which has been described recently by Swarup et al. (2008), encodes an auxin influx carrier that

facilitates emergence of new primordia. Mutants exhibit nearly 40% reduction in numbers of emerged lateral roots. Many genes involved in lateral meristem activation are related to ABA, such as *ABA DEFICIENT 1 (ABAI)*. This mutant has shorter primary root, is ABA-sensitive, and exhibit reduced ABA inhibition of LRs length (Signora et al. 2001). As auxin is involved in all steps of lateral root formation, genes involved in ABA metabolism determine auxin-independent checkpoint for lateral root development. The product of the *ABAI* gene – zeaxanthin epoxidase – generates the epoxycarotenoid precursor of the ABA biosynthetic pathway (Barrero et al. 2005).

Little is known about adventitious root formation in *Arabidopsis*. Among those genes, *ARGONAUTE 1 (AGO1)* has been well described. Mutants are barely able to form adventitious roots in response to auxin and exhibit defect of hypocotyl elongation in response to auxin. Sorin et al. (2005) suggested that *AGO1* regulates genes required for adventitious root development through its action on the regulation of *ARF17* expression. Mutation in *AGO1* results in the higher levels of *ARF17* expression in hypocotyl, which in turn leads to fewer adventitious roots. *ARF17*-overexpressing line also forms fewer adventitious roots than the wild type (Sorin et al. 2005).

2.3 Root Mutants in Monocotyledonous Species Published in Pubmed

The deepest monocotyledonous root system is usually of seminal origin, whereas the upper layers of the soil are penetrated by the nodal roots (Gorny 1992). In addition to their white color, nodal roots are much thicker and less branched than seminals and maintain larger number of root hairs. The anatomy of nodal roots differs from seminal roots. Young ones have all thin-walled stele cells. There are several (four to six) large ducts in the center surrounded by parenchymatous cells. Moreover, the xylem and phloem are undetectable. Eight to nine layers of parenchymatous cells form the cortex separated from the stele by the endodermis. The fully developed roots exhibit four large ducts separated by the more thick-wall cells. Each of twelve to sixteen xylem groups contains one large vessel. The groups are separated from each other by parenchyma cells and phloem poles hard to distinguish. Outside the endodermis, there are six to eight layers of large parenchymatous cortical cells (Jackson 1922).

Up to now, little is known about genes involved in root architecture in monocotyledons. The main information came from three species: rice, maize, and wheat (Table 2.3). Similar to dicotyledons, also forward and reverse approaches were used to study root traits. At least six mutants were obtained through Mu transposition, four by γ -irradiation, three by NaN_3 , and one by each: MNU, Tos17, and tissue culture. Reverse approach (e.g., RNAi, overexpression) were also used to study influence of a gene of interest on root traits. Several mutants have been described, which are responsible for monocotyledonous root traits. Lim and coworkers (2005) described

Table 2.3 Mutated genes responsible for monocotyledonous plants root architecture

| Gene name (alias) | Accession number | Mutation strategy/reverse approach | Mutant phenotype | References |
|---|-------------------|------------------------------------|---|---|
| Root traits | | | | |
| <i>RAN-RELATED GTP-BINDING PROTEIN (TaRAN1)</i> | AF488730 | Overexpression | Increased primordial tissue, reduced number of lateral roots and stimulated hypersensitivity to exogenous auxin | Wang et al. (2006) |
| <i>SCARECROW (ZmSCR)</i> | AF263457 | EST-based isolation | Not reported | Lim et al. (2005) |
| <i>OsASR1</i> | ? | ? | Defective seminal roots | Ge et al. (2004) |
| <i>CROWN ROOTLESS 1 (ZmCRL1)</i> | BG873644 | ? | Not reported | Inukai et al. (2005) |
| <i>CROWN ROOTLESS 2 (ZmCRL2)</i> | BE050765 | ? | Not reported | Inukai et al. (2005) |
| <i>CROWN ROOTLESS 1 (ZmCRL1)</i> | AY736375/AB200234 | MNU | Impaired initiation of nodal root primordia | Liu et al. (2005), Inukai et al. (2005) |
| <i>CASEIN KINASE 1 (OsCKL1)</i> | AJ487966 | Antisense | Reduced primary root length and fewer lateral and nodal roots | Liu et al. (2003) |
| <i>CROWN ROOTLESS 1 (OsCRL1)</i> | AB200235 | ? | Not reported | Inukai et al. (2005) |
| <i>CROWN ROOTLESS 2 (OsCRL2)</i> | AB200236 | ? | Not reported | Inukai et al. (2005) |
| <i>CROWN ROOTLESS 3 (CRL3)</i> | AB200237 | ? | Not reported | Inukai et al. (2005) |
| <i>CROWN ROOTLESS 4 (CRL4)</i> | AB200238 | ? | Not reported | Inukai et al. (2005) |
| <i>GLUTAMATE RECEPTOR LIKE CHANNEL 3.1 (GLR3.1)</i> | DQ305408 | T-DNA insertion | Short root phenotype | Li et al. (2006a, b) |
| <i>GLUCOSAMINE-6-PHOSPHATE ACETYLTRANSFERASE (GNA1)</i> | AY772189 | T-DNA insertion | Short root phenotype | Jiang et al. (2005) |
| <i>ROOT ARCHITECTURE ASSOCIATED 1 (OsRAA1)</i> | AY659938 | Overexpression | More nodal roots, shorter primary and lateral roots compare to WT | Ge et al. (2004) |
| <i>ROOTHAIR DEFECTIVE 3 (TaRHD3)</i> | AY557340 | mRNA differential display | Not reported | Shan et al. (2005) |
| <i>OsCRL2</i> | ? | Gamma rays | Impaired initiation and growth of nodal root primordia, longer primary root than WT | Inukai et al. (2001) |

(continued)

Table 2.3 (continued)

| Gene name (alias) | Accession number | Mutation strategy/reverse approach | Mutant phenotype | References |
|---|------------------|------------------------------------|---|-----------------------------|
| <i>ROOTLESS WITH UNDETECTABLE MERISTEMS 1 (RUM1)</i> | ? | Mu insertion | Deficient in the initiation of the embryonic seminal roots and the postembryonic lateral roots on the primary root | Woll et al. (2005) |
| <i>ALTERED LATERAL ROOT FORMATION (OsALF)</i> | ? | Retrotransposon Tos17 | Significantly shorter lateral roots as compared with the wild type | Rani Debi et al. (2003) |
| <i>REDUCED ROOT LENGTH 1 (OsRRL1)</i> | ? | Gamma rays | Reduced root length | Inukai et al. (2001) |
| <i>REDUCED ROOT LENGTH 2 (OsRRL2)</i> | ? | Gamma rays | Reduced root length | Inukai et al. (2001) |
| <i>SHORT LATERAL ROOTS 1 (ZmSLR1)</i> | ? | Mu insertion | Short lateral roots as a result of impaired root cell elongation | Hochholdinger et al. (2001) |
| <i>SHORT LATERAL ROOTS 2 (ZmSLR2)</i> | ? | Mu insertion | Short lateral roots as a result of impaired root cell elongation | Hochholdinger et al. (2001) |
| <i>SHORT LATERAL ROOTS 5 (OsSRT5)</i> | ? | NaN ₃ | Reduced root length | Yao et al. (2003) |
| <i>SHORT LATERAL ROOTS 6 (OsSRT6)</i> | ? | NaN ₃ | Reduced primary root length and diameter, the mutant at the seedling stage also shows inhibited lateral root elongation and altered root hair formation | Yao et al. (2003) |
| <i>PIN-FORMED 1 (PIN1)</i> | NM_001063762 | RNAi | Significantly inhibited nodal root emergence and development | Xu et al. (2005) |
| <i>PINOID (PID)</i> | NM_001073800 | Overexpression | Delay of nodal root development, curled growth of shoots and agravitropic roots | Morita and Kyoizuka (2007) |
| <i>SLENDER (SLR1-1)</i> | XM_469478 | Gamma rays | Reduced number and root length compared with the wild-type plant | Ikeda et al. (2001) |
| <i>ADP-RIBOSYLATION FACTOR (ARF) GTPASE-ACTIVATING PROTEIN (GAP) (AGAP)</i> | NM_001062427 | Overexpression | Reduced apical dominance, shorter primary roots, increased number of longer nodal roots. | Zhuang et al. (2005) |
| <i>AUXIN EFFLUX MUTANT (AEMI)</i> | ? | ? | Short lateral roots, reduced development of root hairs, agravitropic root | Rani Debi et al. (2005) |
| <i>ADVENTITIOUS ROOTLESS 1 (OsARL1)</i> | ? | Tissue culture | Defective in nodal root formation | Liu et al. (2005) |

Root hairs

| | | | | |
|---|----------|------------------|--|---|
| CELLULOSE SYNTHASE-LIKE D1 (OsCSLD1) | BK000089 | Ds gene trap | Root hair development is initiated normally, the hairs elongate less than the wild-type hairs and they have kinks and swellings along their length | Kim et al. (2007) |
| ROOTHAIRLESS 3 (ZmRTH3) | ? | Mu insertion | Impaired in root hair elongation | Wen and Schnable (1994) |
| ROOT HAIRS (OsRH2) | ? | NaN ₃ | Defective in the formation of root hairs | Ma et al. (2001) |
| ROOTHAIRLESS 1 (ZmRTH1) | AY265854 | Mu insertion | Impaired in root hair elongation | Wen and Schnable (1994), Wen et al. (2005) |
| ROOTHAIRLESS 3 (ZmRTH3) | AY265855 | Mu insertion | Impaired in root hair elongation | Wen and Schnable (1994), Hochholdinger et al. (2008) |

NaN₃ sodium azide, WT wild type

maize *ZmSCR* gene. They suggested that this gene is *Arabidopsis SCR* ortholog based on sequence and expression pattern similarity to the members of the GRAS family. It was then confirmed due to the ability to complement the *Arabidopsis SCR* mutant phenotype, which suggests conservation of function. Although the main knowledge about lateral root development came from *Arabidopsis*, rice mutant *ALF1* (*ALTERED LATERAL ROOT FORMATION*) has been isolated by Rani Debi and coworkers (2003). This mutant displayed not only significantly shorter lateral roots as compared with wild type but also reduction in both the number and length of root hairs. In maize, *SHORT LATERAL ROOTS1* (*SLR1*) and *SLR2* mutants have been reported with defective lateral root elongation (Hochholdinger et al. 2001). The defects in both mutants act specifically during early postembryonic root development, and crown roots at all the stages produced normal lateral roots similar to the wild type. In contrast, the *ALF1* mutant displays shorter lateral roots in both embryonic seminal and postembryonic crown roots up to later growth stages (Rani Debi and coworkers, 2003). Rice mutants that lack *CELLULOSE SYNTHASE-LIKE D1* (*OsCSLD1*) function develop abnormal root hairs that elongate less. It appears that *OsCSLD1* may be the functional ortholog of *Arabidopsis KOJAK*, which is involved in root hair elongation (Kim et al. 2007). The similar phenotype is observed in maize *roothairless 3* (*ZmRTH3*), which encodes a COBRA-like protein (Hochholdinger et al. 2008).

2.4 Strategy for EST Data-Mining

The goal of this work was to find an optimal, short, and efficient procedure in a search for potential orthologs between *Arabidopsis* and barley using rice for confirmation and between already reported genes in other monocotyledons and barley. The first step was to review the literature in searching for genes that are described as involved in root development. Out of 259 *Arabidopsis* and 35 monocotyledonous genes found in this search, it was possible to analyze a total number of 192 *Arabidopsis* and 21 monocotyledonous genes, whose nucleotide and protein sequences were available in GenBank database. Potential orthologs between *Arabidopsis* and barley and between other monocotyledons and barley were analyzed separately.

2.4.1 Searching for Potential Orthologs Between *Arabidopsis* and Barley

The strategy included two pipelines (Fig. 2.1). First, a search in the GeneBank for rice potential orthologs using BLASTn and BLASTp based on *Arabidopsis* nucleotide and protein sequences, respectively, was done. To minimize false positive results, more restrictive criteria (E value 10^{-5} or less) were chosen than suggested

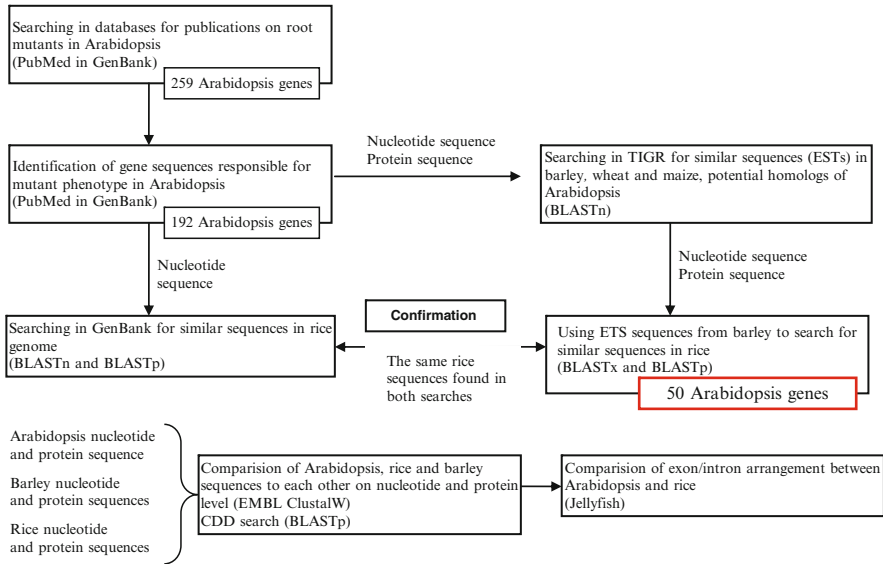


Fig. 2.1 Strategy for selection of potential barley orthologs to *Arabidopsis* genes. E value (GenBank)/Expect (TIGR) 10^{-5} or less

by Pevsner (2003). However, it should be noticed that BLAST is a heuristic version of Smith-Waterman algorithm, so it generates an output that is a list of sequences based on Score value obtained for each corresponding fragment (Koonin and Galperin 2004). In other words, the more points the alignment gets, the higher on the output list will the sequence be. Moreover, change of the parameters of BLAST searching modifies the Score value for each alignment and may automatically have an influence on the order of sequences in the result list. That is the main reason for the need to manually verify the results from BLAST searches using multiple alignment tool ClustalW.

Parallel to this, the search for barley ESTs in TIGR and GenBank databases was performed to select *Arabidopsis* genes, which have good EST coverage. To minimize false positive results, more restrictive criteria were chosen (Expect 10^{-5} or less) just like in the previous searches. The barley EST sequences were then used as a query in TIGR database in search for rice ESTs. Rice ESTs obtained through this searching were then aligned with rice nucleotide and protein sequences obtained through GenBank searching.

Using this approach, 22 genes involved in LR formation, 19 genes controlling root development, and 8 genes involved in root hair formation in *Arabidopsis* (which lead to total number of 49 genes) were identified (Table 2.4). To determine the level of similarity between *Arabidopsis*, barley, and rice, the sequences were compared on nucleotide and protein level. Nevertheless, the success of this approach depends heavily on the quality of EST sequences, which cannot be guaranteed. This is mostly due to the existence in EST artifacts during cDNA library construction and inherent errors caused by DNA sequencing procedures

Table 2.4 *Arabidopsis* genes which have potential orthologs in barley and rice genome

| Arabidopsis | | Rice | | Barley | Similarity [%] | | | | References | |
|--------------------------|---------------|--------|---------------|----------|----------------|----------|---------|------|------------|---|
| Alias | Gene acc. no. | Alias | Gene acc. no. | | EST(s) | acc. no. | At-rice | | At-barley | |
| | | | | | | | N | P | N | P |
| Lateral root development | | | | | | | | | | |
| ABAI | At5g67030 | ? | Os04g0448900 | TC159565 | | 60.6 | 57.1 | 69.6 | 59.8 | Signora et al. (2001) |
| | | | | TC189509 | | | | 70.2 | 61.5 | |
| AUX1 | AT2G38120 | LAX2 | Os01g0856500 | TC177829 | | 51.6 | 79.9 | 70.5 | 86.4 | Fukaki et al. (2005) |
| | | | Os05g0417200 | | | 32.7 | 8.84 | | | |
| AXR1 | At1g05180 | ? | Os03g0820100 | TC168107 | | 60 | 66.1 | 66.3 | 66.4 | Lopez-Bucio et al. (2002) |
| AXR2 | At3g23050 | IAA30 | Os12g0601300 | TC183661 | | 49.4 | 55.8 | 62.6 | 83.1 | Lopez-Bucio et al. (2002) |
| | | IAA13 | Os03g0742900 | TC182343 | | 59.6 | 53.1 | | | |
| CKX1 | AT2G41510 | ? | Os01g0940000 | TC153934 | | 53.6 | 55 | 63 | 64.7 | Werner et al. (2003) |
| | | | Os05g0374000 | | | 11.6 | 4.69 | | | |
| CKX3 | At5g56970 | ? | Os05g0374200 | TC153934 | | 51.6 | 40.1 | 56.5 | 46.3 | Werner et al. (2003) |
| | | | Os01g0197700 | | | 39.9 | 27.1 | | | |
| | | | Os01g0187600 | | | 28.7 | 17.7 | | | |
| | | | Os01g0775400 | | | 53.1 | 45.1 | | | |
| LIN1 | At1g08090 | ? | Os02g0112600 | TC163374 | | 60.5 | 69.9 | 68.3 | 72 | Casimiro et al. (2003), Zhang et al. (2007) |
| RCN1 | AT1G25490 | ? | Os09g0249700 | TC163839 | | 66.5 | 83.5 | 75.0 | 81.8 | Rashotte et al. (2001) |
| | | | | TC174461 | | | | 74.7 | 82.6 | |
| | | | | TC156156 | | 53.8 | 53.9 | 45 | 82.9 | Xie et al. (2002), Casimiro et al. (2003) |
| SINAT5 | AT5G53360 | SINAT5 | Os05g0238200 | | | 48.2 | 56.5 | | | |
| | | | Os02g0293400 | | | 56.7 | 53.0 | 75.5 | 79.5 | Casimiro et al. (2003) |
| SLR1 | AT4G14550 | IAA14 | Os12g0601300 | TC182343 | | 58.2 | 53.1 | | | |
| | | | Os03g0742900 | | | 48.9 | 57.7 | 64.8 | 64.0 | Casimiro et al. (2003) |
| TIR1 | AT3G62980 | TIR1 | Os05g0150500 | TC168970 | | 46.1 | 37.1 | 74.5 | 78.4 | Devaiah et al. (2007) |
| WRKY75 | AT3G01970 | WRKY75 | Os11g0490900 | TC185610 | | 62.0 | 72.8 | 69.5 | 71.4 | Hawker and Bowman (2004) |
| PHV | AT1G30490 | ATHB14 | Os03g0640800 | TC176589 | | 67.5 | 69.6 | | | |
| | | HOX33 | Os12g0612700 | | | 65.4 | 76.0 | 69.7 | 72.6 | Cheng et al. (2004) |
| CAND1 | AT2G02560 | TIP120 | Os02g0167700 | TC192976 | | 56.8 | 75.5 | 70.4 | 71.6 | Faure et al. (1998) |
| PAS2 | AT5G10480 | ? | Os01g0150200 | TC166551 | | 51.4 | 51.6 | 67.6 | 62.5 | Rampey et al. (2004) |
| ILL2 | AT5G56660 | ILL1 | Os01g0706900 | TC173699 | | | | | | |

| | | | | | | | | | |
|-----------------------|-----------|----------------|---------------------|----------|------|------|------|------|------------------------------------|
| <i>IAR3</i> | AT1G51760 | <i>ILL1</i> | Os01g0560000 | TC173699 | 57.1 | 63.3 | 67.0 | 68.0 | Magidin et al. (2003) |
| <i>ECR1</i> | AT5G19180 | ? | Os01g0271500 | TC158327 | 60.5 | 67.8 | 71.1 | 78.7 | Woodward et al. (2007) |
| | | | | TC165467 | 68.7 | 69.8 | | | |
| | | | | TC172176 | 59.1 | 80.1 | 77.0 | 85.0 | Gray et al. (2002) |
| <i>RBX1</i> | AT5G20570 | <i>RBX1a</i> | Os01g0106800 | TC161421 | 68.6 | 70.4 | 63.3 | 62.2 | Hawker and Bowman (2004) |
| <i>REV</i> | AT5G60690 | <i>HOX9</i> | Os10g0480200 | TC177627 | 68 | 69 | 70.6 | 70.7 | |
| | | <i>HOX10</i> | Os03g0109400 | TC176589 | | | 72.7 | 80.9 | |
| | | | | TC182801 | 65.3 | 60.1 | 56.2 | 39.4 | Zhang et al. (2007) |
| <i>AGL21</i> | AT4G37940 | <i>MAD21</i> | Os02g0579600 | TC187224 | 53.4 | 46 | 59.2 | 50.7 | Casimiro et al. (2003) |
| <i>SURI</i> | AT2G20610 | ? | Os11g0552000 | TC164962 | | | | | |
| Root hair development | | | | | | | | | |
| <i>ERH3</i> | AT1G80350 | <i>KATANIN</i> | Os01g0683100 | TC160566 | 63.3 | 81.0 | 71.3 | 76.6 | Schneider et al. (1997) |
| | | <i>p60</i> | | | | | | | |
| <i>RHL2</i> | AT5G02820 | <i>RHL2</i> | Os03g0284800 | TC174707 | 56.8 | 61.4 | 67.8 | 63.4 | Schneider et al. (1997) |
| <i>RHD1</i> | AT1G64440 | <i>GEP148</i> | Os05g0595100 | TC192755 | 60.8 | 74.2 | 61.4 | 57.4 | Schiefelbein and Somerville (1990) |
| | | <i>GEP148</i> | Os08g0374800 | | 60.6 | 62 | | | |
| <i>TIP1</i> | AT5G20350 | <i>TIP1</i> | Os02g0184000 | BU996187 | 58.7 | 63.8 | 52.1 | 57.3 | Hemsley et al. (2005) |
| | | <i>TIP1</i> | Os06g0644500 | EH091151 | 64.5 | 64.3 | 44.5 | 40.2 | |
| | | | | TC179087 | | | 42.9 | 46.1 | |
| <i>RHD2</i> | AT5G51060 | <i>RBOHD</i> | Os11g33120 | TC153922 | 42.2 | 47.7 | 56.0 | 63.8 | Schiefelbein and Somerville (1990) |
| | | | Os12g0541300 | | 55.7 | 49.5 | 58.4 | 54.7 | |
| | | | | | | | 67.5 | 66.4 | |
| <i>KJK</i> | AT3G03050 | <i>CSLD2</i> | Os06g0111800 | TC164787 | 64.4 | 79.8 | 73.7 | 85.8 | Favery et al. (2001) |
| | | <i>CSLD1</i> | Os10g0578200 | TC187976 | 59 | 75.5 | 64.9 | 64.3 | |
| | | | | | | | 65.5 | 60.7 | |
| | | | | | | | 59.2 | 54.4 | |
| <i>RHD3</i> | AT3G13870 | <i>RHD3</i> | Os01g0575000 | TC168229 | 64.0 | 62.4 | 69.0 | 70.1 | Schiefelbein and Somerville (1990) |
| | | | | TC181503 | | | 73.8 | 82.9 | |
| | | | | TC169425 | | | 66.8 | 66.5 | |
| | | | | TC177006 | | | 65.2 | 63.7 | |
| <i>ROP2</i> | AT1G20090 | <i>RAC6</i> | Os02g0120800 | TC179704 | 56.4 | 88.3 | 78.3 | 89.3 | Li et al. (2001) |

(continued)

(continued)

Table 2.4 (continued)

| Arabidopsis | | Rice | | Barley | EST(s) acc. no. | Similarity [%] | | | References | | |
|---------------------------|------------------------|-------|---------------|----------|-----------------|----------------|------|-----------|------------|--------------------------|--|
| Alias | Gene acc. no. | Alias | Gene acc. no. | | | At-rice | | At-barley | | | |
| | | | | | | N | P | N | P | | |
| Primary root architecture | | | | | | | | | | | |
| SMT1 | AT5G13710 | SMT1 | Os07g0206700 | TC155984 | | 63.4 | 77.3 | 71.5 | 77.0 | Willemssen et al. (2003) | |
| | | | Os03g59290 | | | 66.1 | 65.2 | | | | |
| | | | Os11g19140 | | | 45.7 | 32. | | | | |
| RML1// GSH1 | AT4G23100 | GSH1B | Os05g0129000 | TC162201 | | 57.6 | 65.3 | 72.4 | 78.8 | Vernoux et al. (2000) | |
| | | | Os07g0462000 | | | 62.4 | 61.2 | 74.3 | 80.2 | | |
| | | | Os02g0709200 | | | 60.7 | 68.9 | 69.2 | 76.8 | | |
| | | | Os05g0545600 | | | 36.3 | 23.7 | 70.3 | 69.7 | | |
| DDLI | AT3G20550 | SNIP1 | TC158236 | TC161796 | | 66.2 | 79.5 | 62.4 | 58.2 | Morris et al. (2006) | |
| | | | TC187976 | | | 72.7 | 69.8 | 61.9 | 50.9 | | |
| CEV1// CESA3 | AT5G05170 | CESA8 | Os07g0208500 | TC166673 | | 46.5 | 53.4 | 63.4 | 59.1 | Liu et al. (2007) | |
| | | | Os03g0808100 | | | 63.4 | 64.2 | 72.8 | 71.7 | | |
| AXTH21 PAS1 | AT2G18800 AT3G54010 | ? | Os06g0697000 | TC162239 | | | | | | Casimiro et al. (2003) | |
| | | | Os03g0367000 | | | | | | | | |
| COB | AT5G60920 | COBL3 | Os05g0386800 | TC158273 | | 48.1 | 69.9 | 70.6 | 64.0 | Scheres et al. (2002) | |
| | | | Os03g0754500 | | | 45.5 | 67.9 | 66.1 | | | |
| | | | Os10g0497700 | | | 59.9 | 44.5 | 66.7 | 37.5 | | |
| | | | Os07g0604300 | | | 54.2 | | | | | |
| KEULE | AT1G12360 | COBL2 | Os03g0416300 | TC190473 | | 62.8 | 64.5 | | | Söllner et al. (2002) | |
| | | | Os03g0416300 | | | 64.9 | 62.6 | | | | |
| | | | Os04g0252400 | | | 36.6 | 56.6 | 61.2 | 58.9 | | |
| | | | Os02g0452500 | | | 29.1 | 68.3 | 65.7 | | | |
| | | | | | | | 70.1 | 70.8 | | | |
| | | | | | | | 74.6 | 80.3 | | | |
| | | | | | | | 29.1 | 68.3 | 65.7 | | |
| | | | | | | | 70.1 | 70.8 | | | |
| | | | | | | | 74.6 | 80.3 | | | |

| | | | | | | | | | |
|---------------|-----------|-----------------|-------------------------------------|----------------------|----------------------|----------------------|----------------------|----------------------|--|
| <i>KNOLLE</i> | AT1G08560 | ? | Os03g0736500 Os12g08980 | TC179685 | 58.1 44.6 60.6 | 56.8 25.9 73.4 | 56.8 70.3 75.2 | 45.8 61.7 82.6 | Söllner et al. (2002) Taylor et al. (2000) |
| <i>IRX1</i> | AT4G18780 | <i>CESA4</i> | Os01g0750300 | TC160053 | | | 72.7 70.0 66.6 | 77.7 76.2 72.1 | Taylor et al. (2000) Taylor et al. (2000) |
| <i>IRX3</i> | AT5G17420 | <i>CESA9</i> | Os09g0422500 | TC154161 | 66.7 | 80.6 | | | |
| <i>HLR</i> | At4g29040 | ? | Os03g0298400 | TC156203 | 68.9 | 95.1 | 64.8 76.9 | 67.0 93.6 | Ueda et al. (2004) |
| <i>SKU 5</i> | AT4G12420 | ? | Os10g0508000 Os06g0104300 | TC158012 BG300903 | 57.5 64.3 | 62.4 67.5 | 65.6 61.4 | 53.5 66.4 | Sedbrook et al. (2002) |
| <i>WAV2</i> | AT5G20520 | <i>MAD18</i> | Os07g0608300 | TC166812 | 57.3 | 69.3 | 69.9 | 74.1 | Mochizuki et al. (2005) |
| <i>KORI</i> | AT5G49720 | <i>GUN9</i> | Os03g0329500 Os03g0736300 | TC154162 | 68.4 | 74.6 | 67.4 | 72.1 | Zuo et al. (2000) |
| <i>RCE1</i> | AT4G36800 | ? | Os08g0374100 Os09g0321900 | TC161238 | 56.4 43.9 41.4 | 59 30.4 28.2 | 69.3 | 48.2 | Larsen and Cancel (2004) |
| <i>FASS</i> | AT5G18580 | <i>TONNEAU2</i> | Os10g0190000 | | 43.6 | 20.1 | | | |
| <i>MUR1</i> | AT3G51160 | <i>GMD2</i> | Os05g0149800 Os06g0137700 | TC172751 TC162999 | 73.9 62.3 | 85.1 70.2 | 76.8 70 | 88.5 79.3 | Torres-Ruiz and Jürgens (1994) Freshour et al. (2003) |

Acc. no accession number, *Ar* *Arabidopsis thaliana*, *N* nucleotide, *P* protein
Bold indicates the most probable ortholog

(Liang et al. 2007), because ESTs are single pass reads. This leads to comparison of only corresponding fragments of sequences to determine similarity. Moreover, ESTs may often provide information on only a partial segment of an entire cDNA, whereas random sampling of clones leads to redundancy in EST datasets, as mention by Parkinson et al. (2002). To minimize false negative results in generation of barley consensus sequences, the CAP3 program was used, which has an ability to clip 5' and 3' low quality regions of reads (Huang and Madan 1999). To prevent “domain hits” (e.g., similarities that are caused by the conservation of fragments within families), only these *Arabidopsis*/monocotyledons sequences were chosen, which have extended barley EST coverage beyond the domain zone. Each time, the domain area on a nucleotide sequence, based on CDD search using Jellyfish, was established manually. As previously suggested by McGinnis and Madden (2004), the fastest way to compare the function of a protein is to perform a CDD search, which uses a database of motifs to characterize “conserved-domains” in a protein sequence. Following this idea, each selected sequence, which led to the confirmation of the existence of the same conserved domain in all cases (data not shown), was submitted into such analysis.

2.4.2 *Arabidopsis and Rice Genes Comparisons*

The definition of gene homology implies the existence of a common ancestor gene, which existed before speciation (in the case of orthologs) or before duplication (in relation to paralogs) (Alexeyenko et al. 2006). This implies the conservation in exon/intron arrangement between homologous genes, which led to the comparison of exon/intron organization in selected *Arabidopsis* and rice genes. In most cases, the arrangement was highly conserved between putative homologs, whereas some of them exhibited deletions or insertions (Fig. 2.2). Nevertheless, these changes have not disturbed an overall order in exon/intron arrangement.

2.4.3 *Searching for Potential Orthologs Between Other Monocotyledons and Barley*

Due to the lack of genomic sequences for most of monocotyledonous genes, it was not possible to check the level of conservation of exon/intron arrangement. Just like in the previous case, the first step was to search for barley ESTs in TIGR and GenBank databases (Fig. 2.3). This allowed selection of monocotyledonous genes, which have good EST coverage in barley genome, following the rules described above. Parallel to this, searching was done for the rice (in case of maize and wheat genes) and *Arabidopsis* sequences in GenBank. The barley ESTs were then used in a search for rice ESTs, which were compared with rice sequences from GenBank. As mentioned above, this step was performed to establish whether these sequences

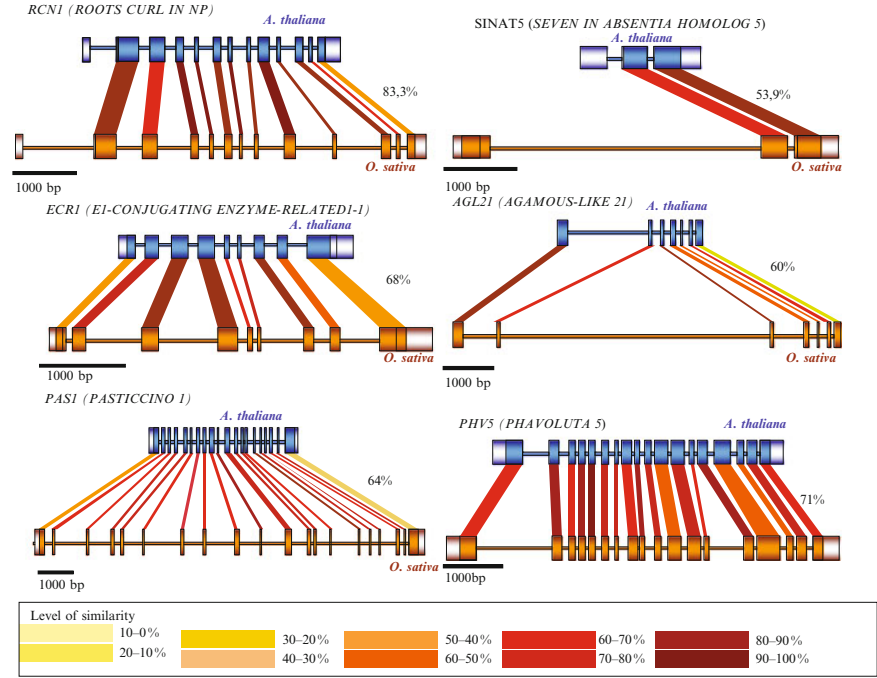


Fig. 2.2 Examples of exon/intron arrangement in orthologous *Arabidopsis* and rice genes. corresponding fragments are shaded using appropriate color in response to similarity between these fragments on protein level; *black line* = *scale bar*

are the same to confirm that the “hit” did not occur only by chance. This analysis led to the total number of ten genes, including six rice, two maize, and two wheat genes, which have potential orthologs in barley genome (Tables 2.5 and 2.6). ClustalW was also used for determining the similarity between other monocotyledons and barley sequences on nucleotide and protein level, respectively. To establish potential domains of barley proteins, CDD search was performed and confirmed in all cases the existence of the same conserved domains as in monocotyledonous proteins (data not shown).

2.4.4 Phylogenetic Analysis

Even if the pairwise approach was theoretically the most powerful one-to-one methodology to predict true orthologs, many phylogenetic methods have been well described up to now (Chiu et al. 2006; Hulsén et al. 2006; Conte et al. 2008). In order to confirm the output from manually created BLAST-based approach and to establish the relationships between each of *Arabidopsis* and rice genes, it was decided to use GreenPhyl pipeline, which has been described as the

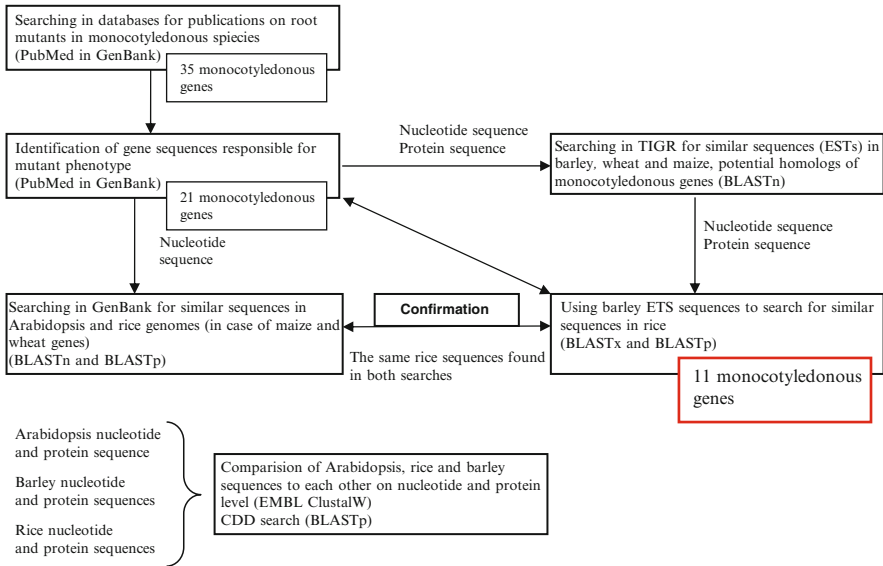


Fig. 2.3 Strategy for selection of potential barley orthologs to monocotyledonous genes. E value (GenBank)/Expect (TIGR) 10^{-5} or less

most efficient phylogenetic method (Conte et al. 2008). In many cases, a large number of proteins showing high sequence similarity to *Arabidopsis* were encoded in the rice genome (data not shown). This is likely to be the result of multiple rounds of gene and genome duplications, followed by differential gene loss (Adams and Wendel 2005; Sterck et al. 2007). Following Conte et al. (2008), only ortholog associations in which a bootstrap value was 50% and more were taken into account as statistically significant. The total number of 50 *Arabidopsis* and 11 monocotyledonous genes were analyzed using this approach. From this number, 26 *Arabidopsis* genes (13 genes involved in LR formation, 3 genes involved in root hair formation, and 13 genes involved in root development) were confirmed as potential orthologs with a bootstrap value 50% or more (Fig. 2.4). Only in case of three *Arabidopsis* and one monocotyledonous genes, the orthologs detected by GreenPhyl were different from these selected on the basis of BLAST searching. Although genes selected as potential orthologs using BLAST approach were on the phylogenetic tree, they had lower bootstrap value. For genes typed by phylogenetic approach, the GreenPhyl bootstrap values were higher than values for genes selected using BLAST and were above 50%.

2.4.5 Synteny Detection in *Arabidopsis* and Rice Genomes

To establish whether gene orders remained conserved between *Arabidopsis* and rice putative orthologs, the “Cinteny” pipeline was used (Sinha and Meller 2007). From 50 *Arabidopsis* sequences selected as having potential orthologs in rice

Table 2.5 Monocotyledonous genes which have potential orthologs in barley and *Arabidopsis* genomes

| Monocotyledonous species | | Rice | | <i>Arabidopsis</i> | | Barley | Similarity [%] | | | | | | References | |
|--------------------------|---------------|---------------|---------------|--------------------|---------------|-----------------|----------------|-------|-------|------|------|------|-----------------------------|--|
| Alias | Gene acc. no. | Alias | Gene acc. no. | Alias | Gene acc. no. | EST(s) acc. no. | Mc-Os | Mc-Hv | At-Os | | | | | |
| | | | | | | | N | P | N | P | N | P | | |
| <i>Ta RANI</i> | AF488730 | <i>RANI/B</i> | Os05g0574500 | <i>RAN3</i> | AT5G55190 | TC176612 | 75.9 | 98.1 | 94.3 | 100 | 81.3 | 94.5 | Wang et al. (2006) | |
| <i>Zm RTH1</i> | AY265854* | <i>RTH1</i> | Os03g0625700 | – | AT1G47550 | TC160970 | 56.5 | 65.6 | 86.8 | 92.6 | 24.9 | 25.8 | Wen et al. (2005) | |
| | | | | | At1g47560 | TC187549 | | | | | 24.7 | 25.3 | | |
| <i>Zm RTH3</i> | AY265855 | <i>COBL7</i> | Os03g0301200 | <i>COBL7</i> | AT4G16120 | TC157935 | 61.9 | 86.7 | 82.2 | 58.5 | 57.7 | 50 | Hochholdinger et al. (2008) | |
| | | | | <i>COBL8</i> | At3g16860 | | | | | | 57.6 | 48.2 | | |
| | | | | <i>COBL9</i> | At5g49270 | | | | | | 56 | 49.2 | | |
| <i>Ta RHD3</i> | AY557340 | <i>RHD3</i> | Os01g0575000 | <i>RHD3</i> | AT3G13870 | TC168229 | 79.6 | 90.1 | 97.2 | 97.4 | 68.9 | 69.7 | Shan et al. (2005) | |
| | | | | | AT1G72960 | TC177006 | | | 95.4 | 96.8 | 64.1 | 63.8 | | |

Table 2.6 Rice genes which have potential orthologs in barley and *Arabidopsis* genomes

| Rice | | | <i>Arabidopsis</i> | | Barley | | Similarity | | | | References | |
|------------------|---------------|-----------------|--------------------|-----------------|--------|-------|------------|------|------|------|----------------------|--|
| Alias | Gene acc. no. | Alias | Gene acc. no. | EST(s) acc. no. | Os-At | Os-Hv | | | | | | |
| | | | | | N | P | N | P | N | P | | |
| <i>Os CRLI</i> | Os03g05510 | <i>JLO</i> | AT4G00220 | NP9937331 | 46.6 | 36.6 | 64 | 41.8 | 64 | 41.8 | Inukai et al. (2005) | |
| <i>Os CKLI</i> | Os02g0622100 | <i>CKII</i> | AT4G14340 | TC176778 | 49.4 | 66.8 | 86.5 | 92 | 86.5 | 92 | Liu et al. (2003) | |
| | | <i>CKLI0</i> | At3g23340 | | 67 | 66.6 | | | | | | |
| <i>Os CSLDI</i> | Os10g0578200 | <i>KJK</i> | AT3G03050 | TC164787 | 59 | 75.5 | 72.4 | 78.7 | 72.4 | 78.7 | Kim et al. (2007) | |
| | | | | TC157331 | | | 80.7 | – | 80.7 | – | | |
| <i>Os RAAI</i> | Os01g0257300 | <i>FLP1</i> | At4g31380 | BM816685 | 66.5 | 58.9 | 75.0 | 78.1 | 75.0 | 78.1 | Ge et al. (2004) | |
| | | <i>FPFI</i> | AT5G24860 | | 62.8 | 58.9 | | | | | | |
| | | | At5g10625 | | 41.5 | 39.7 | | | | | | |
| <i>Os PINI</i> | Os02g0743400 | <i>PINI</i> | At1g73590 | TC188592 | 57.1 | 68.3 | 86.5 | 53.4 | 86.5 | 53.4 | Xu et al. (2005) | |
| | | | | TC164300 | | | 82.9 | 82.1 | 82.9 | 82.1 | | |
| <i>Os SLRI-I</i> | XM_469478 | <i>GAI</i> | At1g14920 | TC156386 | 44.6 | 53.9 | 84.8 | 85.0 | 84.8 | 85.0 | Ikeda et al. (2001) | |
| | | <i>RGAI</i> | At2g01570 | | 45.7 | 53.1 | | | | | | |
| | | <i>RGLI</i> | At1g66350 | | 46.5 | 51.4 | | | | | | |
| | | <i>RGL3</i> | At5g17490 | | 48.2 | 49.4 | | | | | | |
| | | <i>RGL2</i> | At3g03450 | | 44.5 | 53.1 | | | | | | |
| <i>Os AGAP</i> | Os05g0489600 | <i>ATARFAIB</i> | AT5G14670 | TC166447 | 51.7 | 60.6 | 83.3 | 75.7 | 83.3 | 75.7 | Zhuang et al. (2005) | |
| | | | AT1G70490 | | 61.7 | 59.5 | | | | | | |
| | | | At1g10630 | | 60.6 | 59.5 | | | | | | |
| | | | AT3g62290 | | 61.6 | 29.5 | | | | | | |
| | | | At2g47170 | | 59.5 | 59.5 | | | | | | |

Acc. no.accession number, *At Arabidopsis thaliana*, *Os Oryza sativa*, *Hv Hordeum vulgare*, *N* nucleotide, *P* protein
Bold indicates the most probable ortholog

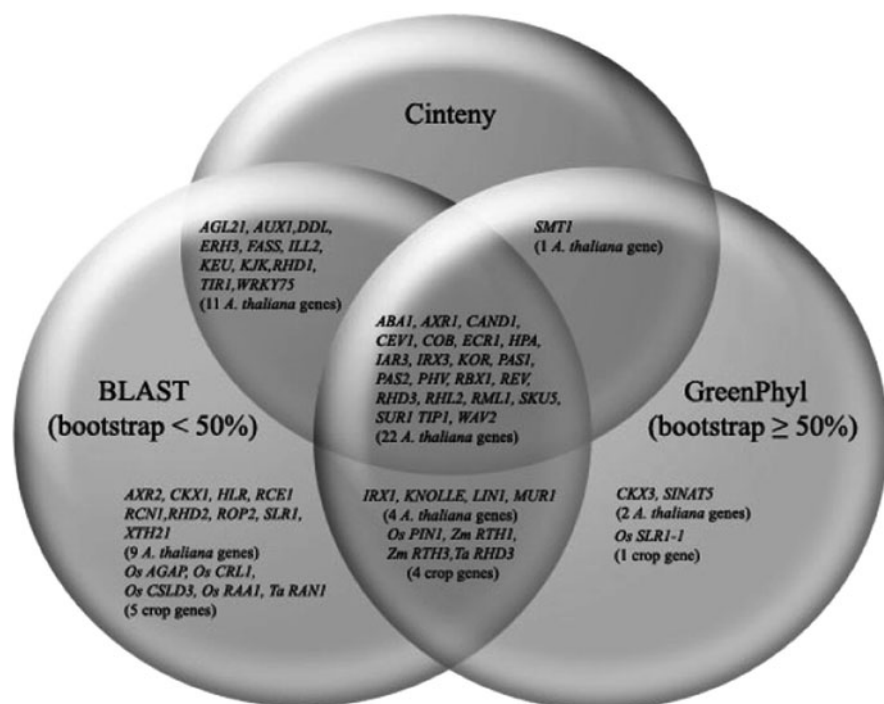


Fig. 2.4 The bird's eye on in silico analysis: best candidates for molecular cloning. Using GreenPhyl, potential ortholog associations in barley genome were considered to be significant if the supporting bootstrap value was 50% and more. Similarity searching was proceeded using E value (GenBank)/Expect (TIGR) 10^{-5} or less. Genes that are situated in the middle (belonging to all three wheels) represent genes that have been selected by smart "best hit" strategy using BLAST searching and obtained a phylogenetical confirmation using GreenPhyl (bootstrap value 50% and more), and the conservation of gene order has been confirmed by Cinteny. Genes that are listed in the BLAST wheel were selected based on "best hit" strategy and have a GreenPhyl bootstrap value lower than 50%. GreenPhyl wheel corresponds to those genes that have candidates with bootstrap value higher than 50%, while "best hit" approach selected other candidate genes that have lower bootstrap values. Those genes, which belong to Cinteny wheel, preserved conservation in gene order. Genes that belong to BLAST and GreenPhyl wheels were selected by "best hit" approach and have bootstrap value 50% and more, but Cinteny did not display synteny blocks and/or orthologs in *Arabidopsis* or rice genome. Genes that belong to both GreenPhyl and Cinteny and separately to BLAST and Cinteny exhibit conservation of gene order for genes that belong to GreenPhyl and BLAST wheels, respectively

genome, 34 exhibited conservation in gene order (15 genes involved in LR formation, 6 genes involved in root hair formation, and 12 genes involved in root development). For the rest of 16 *Arabidopsis* genes, orthologs were not detected in rice genome using synteny-based approach. Nevertheless, it has been shown previously that, where microcolinearity is broken, it is possible to find "missing" gene in nonorthologous locus (Xu et al. 2002; Ware and Stein 2003). That is the reason why the lack of synteny does not imply the absence of homology. On the

other hand, the conservation of gene order during evolution could be treated as a valuable confirmation.

2.5 In Silico vs. Laboratory Approach to Gene Identification

Information from model species could be used in gene identification in two general ways. The first one is based on laboratory approach, where designing of degenerate starters (Ma et al. 1990; Finnegan and Dennis 1993) or probes for screening libraries (Schmidt et al. 1993; Nomura et al. 2003) have been commonly used. The second one is a bioinformatic approach, which in most cases is based on sequence similarity search using BLAST, phylogenetical analysis (Conte et al. 2008), as well as on the existence of synteny, as suggested by Fritz-Laylin and coworkers (2005). In general, the combined strategy is commonly used, which is based on bioinformatic analysis followed by molecular verification, like suggested in this paper.

In spite of their obvious successes in the past, laboratory strategies alone are inappropriate for large-scale analysis. The main disadvantage is their pure sequence-based nature, which can generate false-positive results, especially in correspondence to evolutionary divergence, where the level of similarity based on sequence comparison could be very low.

The improvements in sequencing technology led to hundreds of complete genome sequences, though most come from microorganisms. Till the end of 2008, only the genomes of three dicotyledonous species (*A. thaliana*, *Populus trichocarpa* and *Vitis vinifera*), one monocotyledonous species (*O. sativa*), and a moss (*Physcometrella patens*) have been fully sequenced. Recently also, complete draft assembly of the soybean (*Glycine max*) and maize (*Zea mays*) were released. Although, new sequencing technologies are now available, the assembly of large and complex genomes is still hampered by a significant content of repetitive DNA and, in allopolyploids, by the presence of homoeologous genomes. Most of economically important crops, specifically bread (16,979 Mbp) and durum (12,030 Mbp) wheat, barley (5,100 Mbp), oat (12,961 Mbp), rye (7,933 Mbp), and maize (2,793 Mbp), have large genomes (Doležel et al. 2007). For most of them, deep collections of full-length cDNA sequences are not available. In silico methods that are based on phylogenomic analysis suffer because of the lack of universal and efficient method for generating phylogenetic trees (Fu and Jiang 2007). Even the full genomic sequence does not guarantee the propriety of such analysis. It has to be taken into account that this could straightly lead to mistakes because of wrongly generated phylogenetic tree, as suggested by Dutilh et al. (2007). However, before the start of the genome sequencing projects, large-scale EST-sequencing projects were undertaken in several cereal species, and a large number of ESTs have become available for most of them. In spite of their importance (Varshney et al. 2006; Liang et al. 2007), EST projects yielded mostly partial

cDNA sequences, which are not adequate for direct comparison and assembly of entire genes. Nevertheless, the increasing amount of ESTs unlocks the gene contents of many species and automatically creates a need to elaborate new strategies to use this knowledge. They could be analyzed using only sequence-based approach, like BLAST or FASTA, but such strategy can generate mistakes (Koonin and Galperin 2004).

Here is proposed the EST-based combined procedure for selecting potential orthologs, which is based on BLAST analysis combined with phylogenetic- and synteny-based approaches. The strategy includes a simple searching procedure used as a confirmation, which can avoid most common pitfalls during BLAST exploitation. Moreover, manual verification of the position of the evolutionary conserved fragments of proteins in domain zones using CDD search and Jellyfish program minimizes the risk of the so-called “domain hits,” especially when the protein family is large. Although it should be noticed that lack of synteny does not imply absence of homology, such searching can be very handful during selection of genes. It was demonstrated in the presented paper that bioinformatic analysis is a powerful tool, which gives the possibility to find potentially homologous sequences between two species. The procedure that combines three most commonly used in silico approaches allowed to shortlist the number of potential orthologs as good candidates for molecular cloning.

2.6 Methods

2.6.1 Rice and Arabidopsis Searches

Searches for rice and *Arabidopsis* genes were carried out in publicly available genome databases. *Arabidopsis* sequences were obtained from The *Arabidopsis* Information Resource (TAIR) database (<http://www.arabidopsis.org/>). *O. sativa* sequences being potential homologs of *A. thaliana* genes were chosen using mRNA and protein sequences of *A. thaliana* genes searched against the GenBank database using BLASTn and BLASTp with default parameters, respectively (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>). Among a large number of output sequences obtained from the search, we selected the potential orthologs based on carefully selected criteria. First, E value was very restrictive and lower than 10^{-5} (Pevsner 2003). Each of the searches has been done in both directions to avoid hits obtained just “by chance.” These sequences were also identified as potential orthologs through phylogenetic analysis using GreenPhyl (<http://greenphyl.cines.fr/cgi-bin/greenphyl.cgi>) or OrthologID; alternatively (<http://nypg.bio.nyu.edu/orthologid/>) synteny detection was proven using Cinteny (<http://cinteny.cchmc.org/>).

2.6.2 Sequence Analysis

The next stage of bioinformatic analysis was to check the degree of similarity on protein level between *A. thaliana* and *O. sativa*. The putative *O. sativa* and *A. thaliana* orthologous genomic sequences retrieved were then aligned with mRNA sequences for intron/exon junction positions, respectively, using Jellyfish program (<http://jellyfish.labvelocity.com>). This application was also used to align exon(s) of *A. thaliana* to the corresponding ones in *O. sativa* on protein level. Alignments of protein sequences were performed at The European Molecular Biology Laboratory (<http://www.ebi.ac.uk/embl/>) using the CLUSTALW program (Chenna et al. 2003) with default parameters.

2.6.3 ESTs

Searches for ESTs used in the presented publication were performed in publicly available EST libraries in The TIGR Gene Indices (Quackenbush et al. 2001) using the BLASTn and tBLASTx program with default parameters (<http://www.tigr.org/db.shtml>). This includes: barley sequences release 10.0 (June 3, 2008), wheat release 11.0 (July 13, 2008), maize release 18.0 (July 18, 2008), and rice release 17.0 (June 20, 2006). Searches for barley EST sequences corresponding to chosen monocotyledonous and *Arabidopsis* genes were also made in the GenBank EST database (<http://www.ncbi.nlm.nih.gov/dbEST/index.html>) using the tblastn program and default parameters.

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