



From weeds to crops: genetic analysis of root development in cereals

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Root development of *Arabidopsis*, *Zea mays* (maize) and *Oryza sativa* (rice) differs in both overall architecture and the anatomy of individual roots. In maize and rice, the post-embryonic shoot-borne root system becomes the major backbone of the root stock; in *Arabidopsis*, the embryonic root system formed by a simple primary root and its lateral roots remains dominant. Recently, several specific root mutants and root-specific genes have been identified and characterized in maize and rice. Interestingly, some of these mutants indicate that the formation of primary-, seminal-, crown- and lateral roots is regulated by alternative root-type-specific pathways. Further analyses of these unique pathways will contribute to the understanding of the complex molecular networks involved in cereal root formation.

Plant roots have two major functions: the acquisition of water and nutrients from the soil, and anchorage. The proper establishment of the basic architecture of the whole root system is an important prerequisite to the fulfilment of these functional requirements, particularly in agronomically important crops such as cereals, which account for 70% of food production worldwide [1]. The structure of the root system is shaped by an endogenous genetic program as well as by external factors perceived from the biotic and abiotic environment [2,3]. Variability of root formation in response to environmental conditions complicates the identification of genetic components involved in root formation. The identification of specific root MUTANTS (see Glossary) is also hampered by the inheritance of many root characters in a complex manner. This is documented by the many genotypic variations of the root system in cultivars or inbred lines of various cereals that could not be attributed to a defect in a single gene [4]. Root traits of *Zea mays* (maize) that are controlled by various interacting loci include, for example, primary root weight and primary root diameter [5]. Several of these traits have been mapped using quantitative trait locus (QTL) analyses [5,6]. Recently, several MONOGENIC MUTANTS have been identified that affect root formation in cereals. Only a few of these mutants have been isolated in cereals other than maize and *Oryza sativa* (rice) [7]. This article highlights the current state of genetic analysis of root development in the monocot cereals maize and rice, and

compares some aspects of the cereal root system with that of *Arabidopsis*, which is organized in a different way morphologically and anatomically.

Morphology of cereal and *Arabidopsis* root systems

The monocot cereals, including maize (Figure 1) and rice, display a complex root structure comprising several root types. The overall root structures of the maize and rice root systems are similar in organization [8,9]. Both maize and rice form an embryonic primary root that becomes visible only two or three days after germination. Characteristically, maize forms a variable number of seminal roots that emerge from the SCUTELLAR NODE about a week after germination and are also embryonic [10]; this second root type does not develop in rice. Shoot-borne roots are initiated from consecutive underground and aboveground nodes of the stem and are called crown and brace roots, respectively. Crown root formation in maize starts ~10 days after germination, whereas brace roots are formed late in development, ~6 weeks after germination [10]. Margaret McCully and co-workers have extensively studied the anatomy and physiology of shoot-borne roots of maize and their development under natural conditions [2,3,11]. All root types in maize and rice share the common feature of forming lateral roots and root hairs [10], although the aboveground brace roots form lateral roots

Glossary

Adventitious root: roots that are formed at unusual sites or under unusual circumstances such as wounding or hormone application. In cereals, some researchers also use this term for shoot-borne roots that are formed during the normal developmental program. We suggest designating these shoot-borne roots as crown- and brace roots.

Bacterial artificial chromosome: vector used to clone DNA fragments of an average size of 150 kb based on the F-factor plasmid found in *E. coli*.

Coleoptilar node: the first node between the mesocotyl and the first internode in cereal seedlings, from which shoot-borne roots emerge.

Cortical cells: root cell type that comprises the cortex. Extends between epidermis and endodermis.

Endodermal cell: innermost cell type of the root ground tissue, which surrounds the vascular tissue.

Monogenic mutants: plants that carry defects in single genes.

Mesocotyl: the internode that is located between the scutellar node and the coleoptilar node in cereals.

Mutants: plants that carry a defect (mutation) in at least one gene compared with the normal (wild-type) situation.

Pericycle: outermost cell layer of the central cylinder, between endodermis and vasculature. Cell layer in which post-embryonic roots are initiated.

Pleiotropic: mutant that is affected in more than one morphological character.

Scutellar node: morphological structure of the cereal seedling that separates primary root and mesocotyl, and from which the seminal roots emerge.

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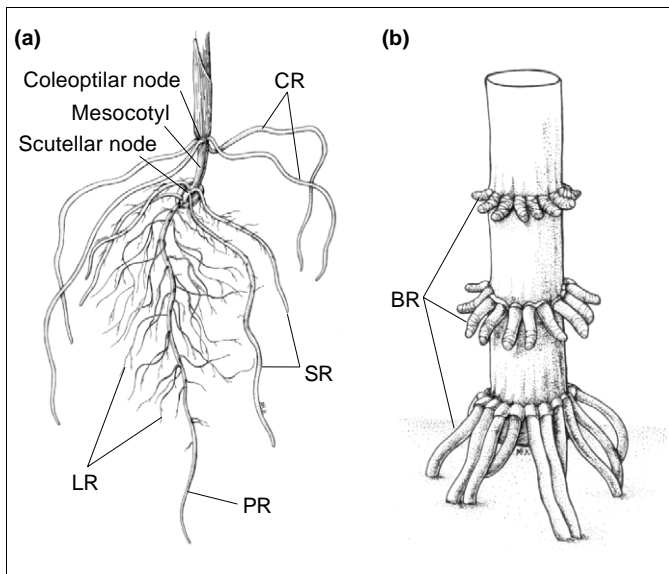


Figure 1. Maize root system at different developmental stages. (a) 14-day-old maize seedling displaying primary (PR), seminal (SR), shoot-borne crown (CR) and lateral (LR) roots. Morphological seedling structures of cereals described in the text are labelled. (a) Reproduced, with permission, from Ref. [9]. (b) Aboveground root stock of an adult maize plant composed of shoot-borne brace roots (BR). Drawings by Miwa Kojima (Iowa State University).

only after penetrating the soil [10]. In cereals, communication at the root–soil interface (i.e. water and nutrient uptake) is facilitated by a structure called rhizosheath, which contains tightly bound soil particles associated with root-hair-bearing roots and rhizobacteria [2]. Plants with this structure have an increased root surface in intimate contact with a considerable volume of soil. Rhizosheaths are only rarely seen in dicots such as *Arabidopsis* [2].

The morphological and anatomical simplicity of the *Arabidopsis* root system is exceptional even compared with other dicots. This quality has made *Arabidopsis* an ideal model organism for genetic analyses of root formation in higher plants [12–14]. The morphology of the *Arabidopsis* root system is characterized by the formation of only one major root type, the primary root, which is already established during embryogenesis [15]. Post-embryonic lateral roots emerge from the primary root later in development [16,17].

The major difference between the root systems of cereals and *Arabidopsis* is that the embryonic root system in cereals is functionally important only during the early stages of plant development [10]. An extensive post-embryonic shoot-borne root system makes up the major backbone of the cereal root stock a few weeks after germination [8,9], whereas, in *Arabidopsis*, the embryonic primary root system remains dominant during the whole life cycle (Table 1).

In addition to the genetically determined roots, ADVENTITIOUS ROOTS are formed under unusual circumstances such as wounding or hormone application at uncharacteristic sites on a plant [18]. Some authors also use the term ‘adventitious roots’ to describe the shoot-borne root system in cereals. We would suggest not calling the stem-derived crown and brace roots ‘adventitious’ because they belong to the normal developmental program of cereals.

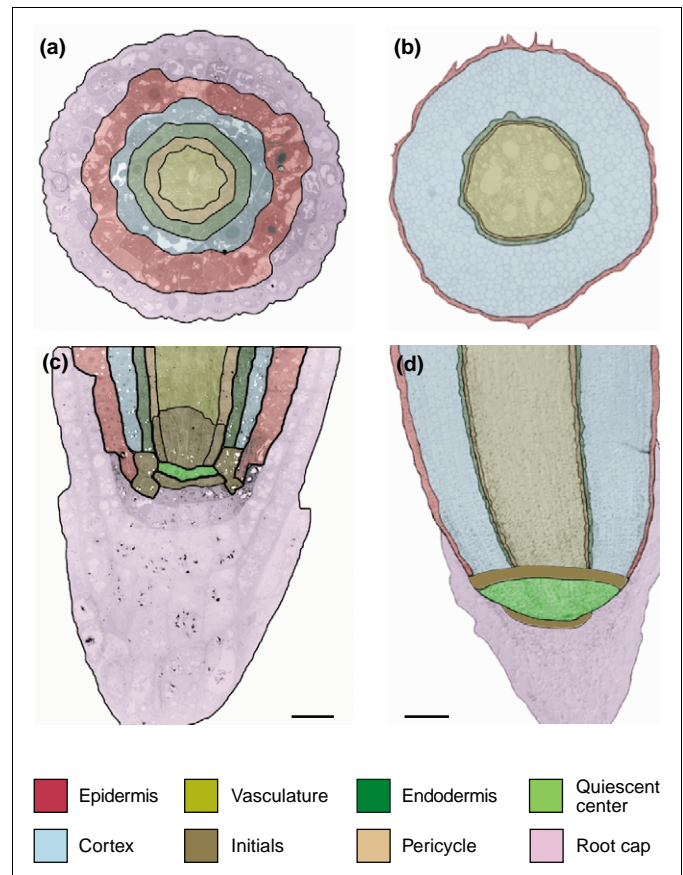


Figure 2. Anatomical organization of the *Arabidopsis* (a,c) and maize (b,d) primary root in median longitudinal (c,d) and transverse (a,b) sections, showing the different cell types and their relative positions. The major anatomical differences between *Arabidopsis* and maize are summarized in Table 1. Notice that the upper margins of (c) and (d) represent the longitudinal positions of the root from where the transverse sections were obtained. The images are light microscopic (b,d) and electron microscopic (a,c) photographs that have been coloured. Scale bars: (a,c) = 10 μm ; (b,d) = 200 μm . Electron microscopic photographs of *Arabidopsis* were provided by York-Dieter Stierhof (University of Tübingen).

Functional anatomy of cereal and *Arabidopsis* roots

Cereal and *Arabidopsis* roots show distinctly different anatomies [8,10,13] (Figure 2, Table 1). First, different tissue organization is observed in radial patterning (Figure 2). The ground tissue of maize and rice roots consists of eight to 15 layers of CORTICAL CELLS and one ENDODERMAL CELL layer [8,10], whereas the *Arabidopsis* root is composed of only one endodermal and one cortical cell layer. The radial number of cortical cells in maize and rice is variable, whereas the single *Arabidopsis* cortex cell layer circumferentially contains a fixed number of eight cells. Furthermore, cereal roots show some differences in longitudinal organization from *Arabidopsis* roots beyond the common organization into root cap, meristematic, elongation and differentiation zones [19,20]. In maize and rice, the quiescent centre (QC), a central region of the root tip with reduced mitotic activity, consists of 800–1200 cells [21] and is surrounded by the proximal and distal meristems, which consist of several hundred cells [10]. These meristematic cells initiate the emerging root and the root cap. *Arabidopsis* forms a small QC that always contains four cells surrounded by a limited number of initial cells that give rise to the surrounding root tissues [15]. The functional analysis of the *Arabidopsis* QC using

Table 1. Major differences between the root systems of cereals and *Arabidopsis*

	Cereals	<i>Arabidopsis</i>
Morphology		
Embryonic root system	Primary root and seminal roots (in maize)	Primary root
Shoot-borne root system	Extensive	Missing
Root hair pattern	Irregular	Regular
Anatomy		
Cell types forming lateral roots	Pericycle and endodermis	Pericycle
Number of cortical cell layers	8–15	1
Number of cortical cells (transverse)	Variable	8
Number of quiescent centre cells	800–1200	4
Number of root initial cells	Few	Several hundred

laser ablation of individual QC cells have implied that the major function of the QC is the maintenance of stem cells by suppressing the differentiation of initial cells [22]. The functional dissection of the maize and rice QCs via laser ablation experiments is difficult owing to their large size. However, it has been demonstrated that the cells in and around the QC contain patterning information by experiments showing that maize root apices can be regenerated after the complete removal of the root cap and the QC [23, 24]. Recent studies on maize have shown that the inactivity of these QC cells, and therefore the establishment and elaboration of the QC, is mainly due to the maintenance of a highly oxidizing environment and the position of the auxin concentration maximum in the root cap, which prevents cell division [21].

Lateral roots in maize and rice are initiated via the division of PERICYCLE and endodermis cells [25], whereas *Arabidopsis* lateral roots arise completely from pericycle cells [26,27]. In maize and probably also in rice, the endodermis of the main roots gives rise to the epidermis and columella, whereas the pericycle contributes to the remaining tissues of the lateral root [25]. Whether the pericycle tissue is already differentiated and dedifferentiates upon lateral root initiation is still under debate [26,28].

Genetic dissection of root formation

Cereal root development is being characterized by a growing number of mutants specifically affected in root formation (Table 2). In maize, several root mutants have been isolated that affect not a single root type but several embryonic and post-embryonic root types, or that affect lateral root formation in a root-type-specific way [29–31] (Figure 3). This is of particular interest because, so far, most studies have considered the pathways involved in the formation of the various root types to be essentially identical. The *Arabidopsis* root system is genetically well characterized by many specific mutants. These mutants have been extensively reviewed [13,28,32] and are therefore discussed only briefly in the context of the cereal mutants.

The mutant phenotypes identified so far in cereals that influence root architecture can be grouped into four classes based on their influence on shoot-borne roots, lateral roots, root elongation and root hairs (Table 2). The following sections focus on monogenic mutants specifically affected in root formation, although one has to be aware that many PLEIOTROPIC mutants with shoot and root deficiencies are available. These include pleiotropic maize and rice

mutants with root defects during embryogenesis [33–36], seedling development [37,38] or shoot-borne root formation [39]. In *Arabidopsis*, several pleiotropic mutants have been identified that show deficiencies in lateral root formation [28].

Shoot-borne-root formation

The fundamental difference between cereals and the dicot model plant *Arabidopsis* is the presence of an extensive post-embryonic shoot-borne root system in cereals, which is missing in *Arabidopsis*. In maize and rice, several mutants have been identified that are impaired in shoot-borne-root formation. The mutant *rtcs* [29] (Figure 3) lacks all shoot-borne crown and brace roots, and the embryonic seminal roots. Histological analyses revealed that the mutation acts before the initiation of these embryonic and post-embryonic root types [29]. The only root that remains in *rtcs* is the primary root and its lateral roots, which are sufficient to generate a mature plant. Another maize mutant with generally reduced shoot-borne-root formation is *rt1*, which was identified by Jenkins in 1930 [40]. The rice mutant *cr11* [41] is also specifically affected in crown root initiation and shows a similar phenotype to *rtcs*.

Table 2. Specific maize and rice mutants affected in various aspects of root development

Gene	Species	Phenotype	Refs
Shoot-borne roots			
<i>rtcs</i>	<i>Zea mays</i>	Complete lack of shoot-borne roots	[29]
<i>rt1</i>	<i>Zea mays</i>	Fewer shoot-borne roots	[40]
<i>cr11</i>	<i>Oryza sativa</i>	Fewer crown roots	[41]
<i>cr12</i>	<i>Oryza sativa</i>	Fewer crown roots and reduced primary root length	[42]
Lateral roots			
<i>lrt1</i>	<i>Zea mays</i>	No lateral roots at embryonic roots and crown roots at first node	[30]
<i>slr1</i>	<i>Zea mays</i>	No lateral root elongation at embryonic roots	[31]
<i>slr2</i>	<i>Zea mays</i>	No lateral root elongation at embryonic roots	[31]
<i>rm109</i>	<i>Oryza sativa</i>	Lateral root initiation blocked	[43]
Primary root			
<i>rm1</i>	<i>Oryza sativa</i>	Reduced primary root elongation	[47]
<i>rm2</i>	<i>Oryza sativa</i>	Reduced primary root elongation	[47]
<i>rr11</i>	<i>Oryza sativa</i>	Reduced primary root elongation	[42]
<i>rr12</i>	<i>Oryza sativa</i>	Reduced primary root elongation	[42]
<i>srt5</i>	<i>Oryza sativa</i>	Reduced elongation of all root types	[49]
<i>srt6</i>	<i>Oryza sativa</i>	Reduced primary root elongation	[48]
Root hairs			
<i>rth1</i>	<i>Zea mays</i>	Reduced root hair elongation	[52]
<i>rth2</i>	<i>Zea mays</i>	Reduced root hair elongation	[52]
<i>rth3</i>	<i>Zea mays</i>	Reduced root hair elongation	[52]
<i>rh2</i>	<i>Oryza sativa</i>	Missing root hairs	[53]

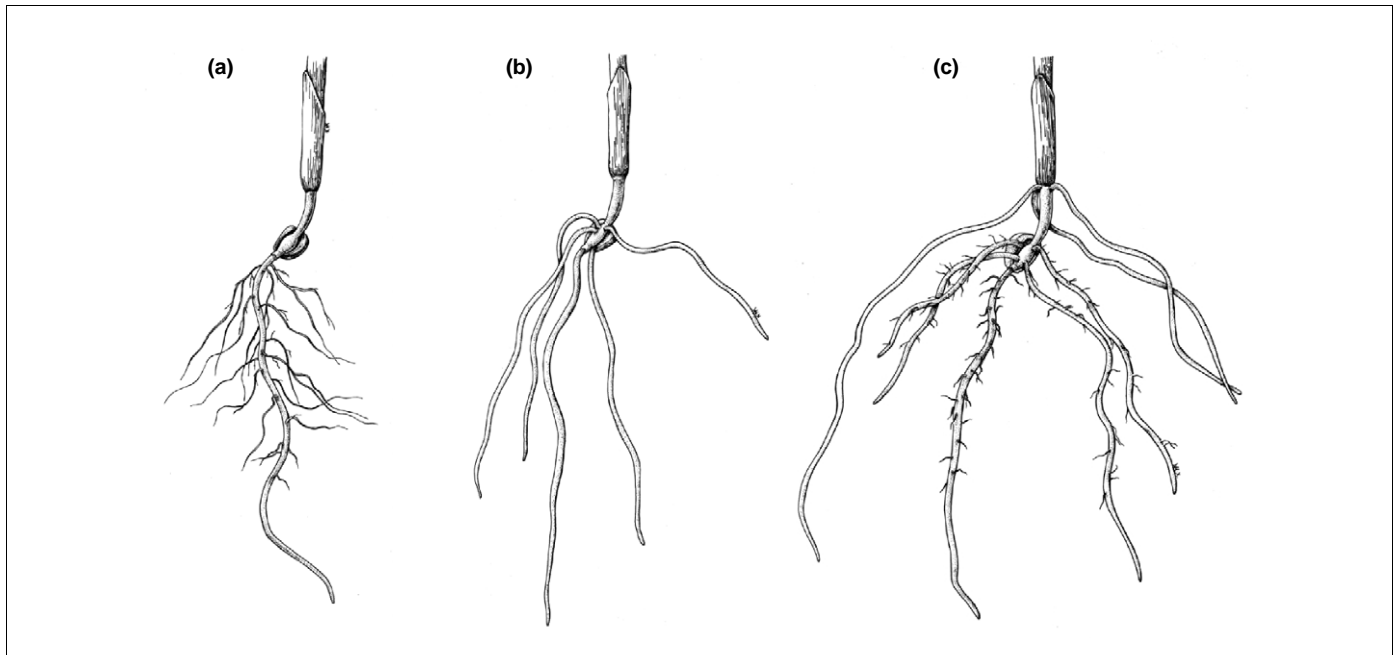


Figure 3. Monogenic recessive root mutants of maize that are affected in more than one root type or in which lateral root defects do not concern all root types. **(a)** The *rtcs* mutant. Embryonic seminal roots and post-embryonic crown and brace roots are absent. **(b)** The *lrt1* mutant. Lateral roots on primary and seminal roots are missing and crown roots at the coleoptilar node are affected. Lateral root formation on shoot-borne roots formed on higher nodes is normal. **(c)** The *slr1* and *slr2* mutants. These non-allelic mutants display a similar phenotype, with reduced root elongation of lateral roots formed on primary and seminal roots. Lateral root formation on shoot-borne roots is normal. Reproduced, with permission, from Ref. [9]. Drawings by Miwa Kojima (Iowa State University).

Because rice forms no embryonic seminal roots, *crl1* is confined to post-embryonic root development. A second rice mutant defective in shoot-borne-root formation is *crl2* [41,42], which forms fewer shoot-borne roots that stop growing shortly after germination. The remaining primary root shows an increased thickness and length as well as a reduced number of lateral roots.

Lateral root formation

Maize and rice form lateral roots on all major root types of the complex root stock. Identification of root-type-specific mutants in maize has revealed that there are at least two pathways of lateral root formation or at least two different sensitivities to signals involved in lateral root formation on the embryonic and post-embryonic roots [30,31]. This notion is supported by mutants specifically affecting lateral root initiation and elongation at specific root types. The mutant *lrt1* (Figure 3) is affected in early post-embryonic root development [30]. This developmental phase is confined to lateral roots initiated on embryonic roots and the formation of crown roots at the COLEOPTILAR NODE. The mutant *lrt1* shows normal crown root and lateral root formation from the second node onwards. The *slr1* [31] and *slr2* [31] mutants (Figure 3) also show reduced lateral root elongation only at the embryonic roots, and form normal lateral roots on the post-embryonic shoot-borne root system. In rice, the mutant *rm109* displays defects in lateral root initiation [43]. In *Arabidopsis*, a considerable number of mutants showing lateral root defects along with pleiotropic effects have been described [28]. In spite of considerable efforts, only a few *Arabidopsis* mutants with a lateral-root-specific phenotype (including the *alf* mutant series [44]) have been identified. This indicates either essential or redundant

genes controlling lateral root initiation in *Arabidopsis* [45]. The mutants *alf4* [44] and *slr* [46] do not initiate lateral roots under standard conditions, whereas the mutant *lin* [45] shows highly branched lateral roots in an environment with a high sucrose:nitrogen ratio, which usually suppresses lateral root initiation, indicating a role for this gene in coordinating lateral root initiation with environmental cues.

Reduced primary root elongation

Several mutants with reduced primary root length have been isolated in maize and rice. Although the available maize root elongation mutants [37,38] display pleiotropic seedling phenotypes, the rice mutants are root specific. The rice mutants that are affected only in primary root elongation are designated *rm1* [47], *rm2* [47], *rll1* [44], *rll2* [44] and *srt6* [48]. The mutant *srt5* [49], in addition to reduced primary root elongation, also shows reduced crown and lateral root elongation. A common feature of all these mutants is reduced cortical cell elongation. The *Arabidopsis* root mutants *scarecrow* (*scr*) and *short root* (*shr*) both display reduced primary root length. However, these phenotypes are not the result of reduced cortical root elongation but of degeneration or loss of cell division. The *scr* and *shr* genes are involved in radial patterning of the roots as indicated by the mutant phenotype, which displays only a single layer of ground tissue instead of the cortex and endodermis [50,51].

Root hair development

During root development, two cell types are formed in the epidermis that either form root hairs (trichoblasts) or do not (atrachoblasts). In *Arabidopsis*, immature epidermal cells that are located over the intercellular space between

underlying cortical cells develop into root hair cells. By contrast, epidermal cells located over a single cortical cell develop into non-root-hair cells [32]. However, it is difficult to predict root hair forming epidermal cells in cereals. In maize, three mutants have been identified with defects in root hair elongation (*rth1*, *rth2* and *rth3*) [52]. Interestingly, *rth2* and *rth3* grow normally, implying that root hairs might be dispensable under specific environmental conditions. This is particularly interesting given that the previously mentioned rhizosheath structure, which plays a major role in water and nutrient uptake, is greatly reduced or missing in these mutants. Furthermore, one rice root hair mutant has been identified (*rh2*) [53] that lacks any root hair formation. Compared with the extensive work on *Arabidopsis* root hair initiation and morphogenesis [32], these mutants are only a starting point for a more detailed analysis of root hair development and might bring insights into root-type-specific regulation of root hairs in cereals.

Molecular analysis of root formation

The various embryonic and post-embryonic root-types within a species have similar anatomical organization, and so pattern formation and morphogenesis of these different roots are probably regulated by a similar set of genes. However, it is assumed that different genes are involved in the initiation of these root types, because each root type is initiated from different tissues during embryogenesis and post-embryonic development [13]. The different morphological and anatomical organization of cereal and *Arabidopsis* roots is likely to be mirrored on the molecular level. This might be particularly true for genes specifically expressed in the shoot-borne root system, which is only present in cereals. A comparison of gene expression profiles of shoot-borne roots from two inbred maize lines with significant differences in root lodging resistance revealed a considerable number of lodging resistance related genes [54].

Developmental plasticity during root development is regulated not only by endogenous genetic programs but also by exogenous environmental stimuli such as hormones or nutrients. In *Arabidopsis*, an increasing amount of molecular data on auxin and auxin transport has recently become available [55]. It will be interesting to see how much of this work can be reproduced in cereals by, for example, the identification and characterization of homologous genes [56]. In deep-water rice, ethylene (another plant hormone) is involved in the emergence of shoot-borne roots at nodes that are submerged under flooded conditions. Root formation at these nodes is mediated by ethylene, not by other plant hormones [57]. Moreover, ethylene plays a role in the emergence of the newly induced roots by inducing cell death at the node where the adventitious root primordia are developing [58]. The influence of externally applied phosphate and nitrate supplies in a highly localized fashion on the control of the initiation and architecture of the barley root system was studied by Malcolm Drew and Leslie Saker in the 1970s [59,60]. These studies have recently been extended to *Arabidopsis* by Hanma Zhang and Brian Forde [61,62], and led to the finding that nitrate acts not only as a

nutrient but also as a signal that locally modulates root branching via a regulatory cascade in which the MADS box gene *ANR1* is involved.

Although little is known thus far about genes involved in cereal root formation, there are already clues for genes specifically involved in root formation of cereals that are absent in *Arabidopsis*. Examples include several glycine-rich putative cell wall proteins (including *Zm123A* [63], *ZmGRP3* [64] and *ZmGRP4* [65]) that are produced in the columella and epidermis of the root tip. Microsurgical and molecular data indicate that the positional and structural production of *Zm123A* in the root cap might be controlled by the QC and the root cap initials [63]. No homologues of these root-specific genes were found in *Arabidopsis*. Genes involved in *Arabidopsis* root formation that have already been cloned were reviewed recently [13,66].

Currently, only a few orthologous genes involved in root formation of cereals and *Arabidopsis* are available. An example of such a gene is *scr*, which, in *Arabidopsis*, is involved in radial pattern formation and is expressed in the cortex/endodermis initial and the endodermal cell lineage, but not in the QC [50]. The corresponding *Arabidopsis scr* mutant is characterized by the formation of a single cell layer instead of the cortex and endodermis cell layers, and by a reduced root length [50]. Interestingly, the expression of the maize orthologue of the *scr* gene extends through the QC [67]. This is of particular interest because, in *Arabidopsis*, the QC is thought to lack radial patterning information and to be positioned by the *scr* gene itself [68]. No mutant phenotype for the maize *scr* orthologue is yet available.

In addition to the analysis of individual genes involved in root formation, new approaches allow the parallel analysis of the accumulation of hundreds of proteins or thousands of mRNAs in cereal root proteomes and transcriptomes [69]. These studies will help to identify additional molecular components involved in root formation for which no mutants are yet available.

Prospects

At present, more and more cereal mutants are becoming available that are specifically affected in root development. This will pave the way for more detailed genetic and molecular analyses of cereal root systems that are different from the simple architecture of the *Arabidopsis* root stock; this will also allow the comparison of root formation between different cereal species. High-resolution genetic and physical maps, and the availability of molecular tools such as BACTERIAL ARTIFICIAL CHROMOSOME (BAC) collections anchored to these maps will soon allow the cloning of the genes using map-based approaches, even in genomes with highly redundant repetitive content (such as maize) [1]. Isolation of the impaired genes in these mutants will allow the discovery of root-development-specific checkpoints present only in monocot cereals. The identification of cereal-specific genes will be facilitated by the already available rice and *Arabidopsis* genome databases [70–72] and the upcoming sequences of the maize genome [1,73]. Transcriptome- and proteome-wide analyses of specific mutants will reveal downstream components involved in the complex network of cereal root formation. Emerging

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Gro Harlem Brundtland, director-general for the WHO, said that this initiative was 'perhaps the biggest step ever taken towards reducing the health information gap between rich and poor countries'.

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