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Review

Genetic Control of Lateral Root Formation in Cereals

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Cereals form complex root systems composed of different root types. Lateral root formation is a major determinant of root architecture and is instrumental for the efficient uptake of water and nutrients. Positioning and patterning of lateral roots and cell types involved in their formation are unique in monocot cereals. Recent discoveries advanced the molecular understanding of the intrinsic genetic control of initiation and elongation of lateral roots in cereals by distinct, in part root-type-specific genetic programs. Moreover, molecular networks modulating the plasticity of lateral root formation in response to water and nutrient availability and arbuscular mycorrhizal fungal colonization have been identified. These novel discoveries provide a better mechanistic understanding of postembryonic lateral root development in cereals.

Trends

Lateral root formation in cereals is unique with respect to the involved cell types, their position relative to the vascular elements, their stochastic pattern of emergence and their root-type specificity.

Genetic analyses demonstrated that auxin signal transduction, polar auxin transport, auxin transport regulation and cell cycle regulation are key elements of lateral root formation in cereals.

High resolution tissue- and cell-type-specific transcriptome studies identified candidate genes and metabolic pathways associated with lateral root initiation in cereals.

Architectural remodeling of lateral root branching contributes largely to the adaptive plasticity of the root system in response to extrinsic abiotic and biotic factors such as water availability, nutrients status and interaction with arbuscular mycorrhizal fungi.

Morphology and Anatomy of Lateral Roots in Cereals

The three-dimensional architecture of plant root systems is a prerequisite for their anchorage in soil, the efficiency of capturing water and nutrients, and the establishment of beneficial plant–microorganism communities [1,2]. The initial blueprint of the plant root system is laid down during embryogenesis. After germination, the structure of the growing root stock is adjusted by sequentially formed postembryonic roots, which allow plants to exploit limited soil resources and to respond to changing environmental conditions [2,3]. The dicot model plant arabidopsis (*Arabidopsis thaliana*) forms a simple root system consisting of an embryonic primary root from which several orders of postembryonic lateral roots emerge. By contrast, monocot cereals such as maize (*Zea mays*) and rice (*Oryza sativa*) form a much more complex root system [4,5]. In addition to the embryonic primary root and a number of embryonic seminal roots in maize, these species develop an extensive shoot-borne root system not present in arabidopsis. Both embryonic roots and postembryonic shoot-borne roots of cereals have the capacity to form highly branched lateral roots [4,5]. Hence, despite the overall architectural difference of arabidopsis and cereal root systems [6–8], the substantial increase of the absorbing surface by lateral roots is conserved in all root systems of higher plants [9,10]. This review mainly focuses on the developmental plasticity of lateral root formation in maize and rice because of the limited data available on other cereal species.

In longitudinal orientation, roots can be divided into three functionally distinct zones which partially overlap [11] (Figure 1A). These zones are the meristematic zone where cells divide, the elongation zone where cells that have left the meristematic zone elongate, and the differentiation zone where cells become finally differentiated and root hairs and lateral roots are formed [11]. As a consequence, roots represent a gradient of development with the youngest and undifferentiated cells in the meristems of the root apex and the oldest cells in the proximal part of the root.

Lateral roots are initiated from specific cell types deep inside the cortical tissue. In arabidopsis, lateral roots are formed from pericycle cells, which represent the outermost cell layer of the

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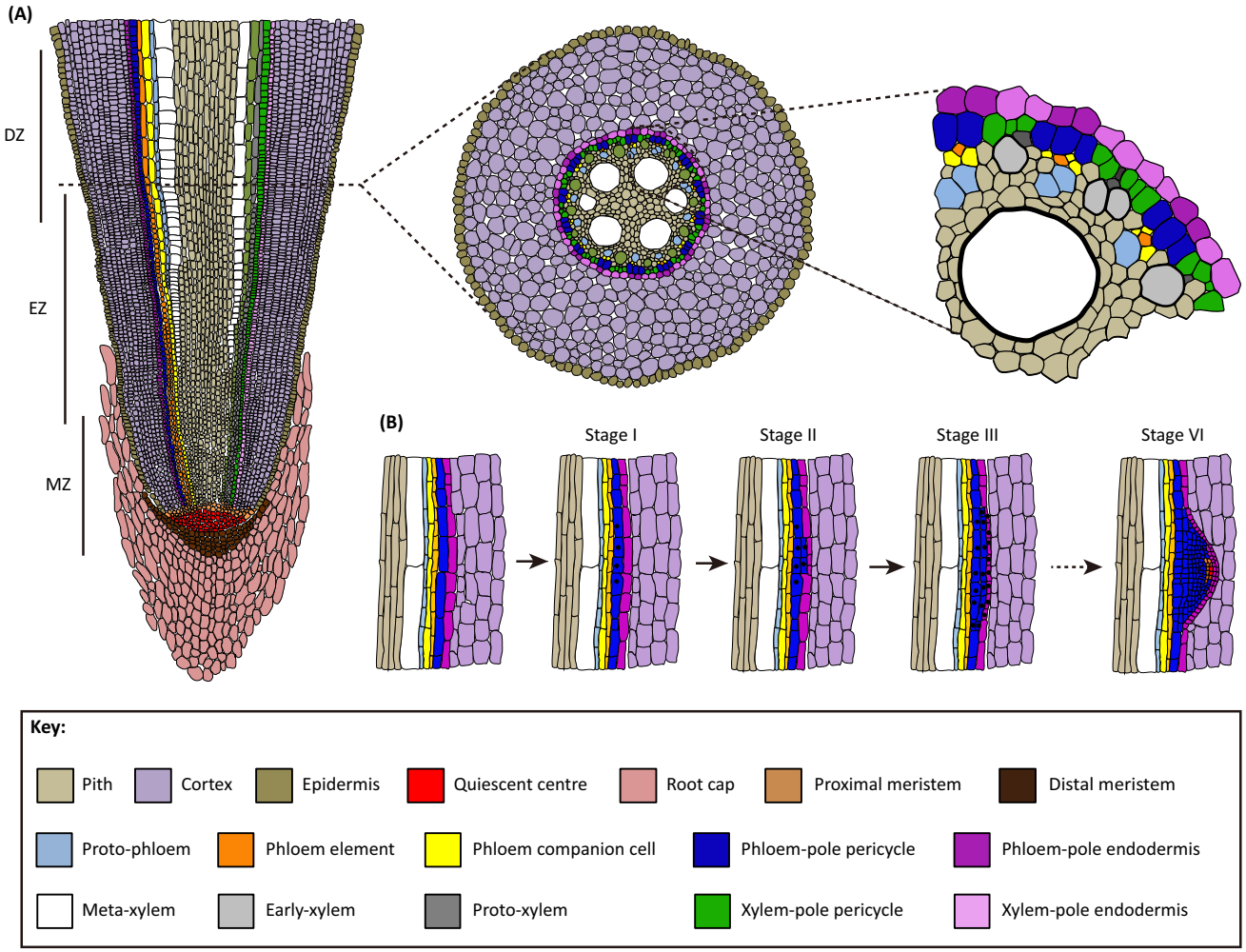


Figure 1. Cellular Organization of Maize Roots and Tissues Involved in Lateral Root Development. (A) Functionally distinct zones in the longitudinal orientation and transversal view of the differentiation zone of primary roots. Heterogeneously patterned pericycle cell types at the xylem and phloem poles are enlarged. (B) Stages of lateral root development: Stage I, asymmetric anticlinal divisions in two adjacent pericycle cells; Stage II, periclinal division resulting in a second cell layer; Stage III, endodermis cells divide and become involved in lateral root formation; and Stage VI, a mature lateral root primordium has formed. Cell types are color-coded as indicated in the key. Abbreviations: DZ, differentiation zone; EZ, elongation zone; MZ, meristem zone.

central vascular cylinder [12]. By contrast, both pericycle and endodermal cells contribute to lateral root formation in rice [13] and maize [14]. In maize, lateral root initiation is a multistep process (Figure 1B) starting with anticlinal cell divisions of phloem pole pericycle cells (stage I), followed by periclinal cell divisions of these cells (stage II) [15]. Subsequently, pericycle cells continue their periclinal divisions and endodermal cells start dividing anticlinally (stage III). In subsequent stages a combination of anticlinal and periclinal divisions give rise to the lateral root primordium as exemplified by stage VI in Figure 1B [15]. In maize, endodermal cells give rise to the epidermis and columella of the newly formed lateral roots, whereas all other cell types of developing lateral roots are formed by pericycle cells [14]. The radial positioning of lateral roots is another difference between cereals and arabidopsis. While in cereals lateral roots form at the phloem poles, lateral roots in arabidopsis are initiated from xylem pole pericycle cells (reviewed in [6]). Arabidopsis has only two xylem poles, where lateral roots are initiated in an alternating pattern at each pole. By contrast, ten or more phloem poles are formed in cereals (Figure 1A). As

a consequence, the radial branching pattern in cereals is much more complex and does not allow predicting the longitudinal positions of lateral roots (reviewed in [5,6]).

Intrinsic Genetic Control of Lateral Root Formation in Cereals

Mutant Analysis of Lateral Root Formation in Maize and Rice

Intrinsic genetic regulators and extrinsic environmental cues determine the formation of lateral roots in cereals. In recent years a number of maize and rice mutants with defects in intrinsic regulators of lateral root initiation, elongation, and reduced lateral root density have been characterized (Table 1). Remarkably, the genetically-encoded lateral root defects thus far identified in maize are confined to the embryonic primary and seminal roots. Lateral root formation in the shoot-borne root system is not affected in these mutants (Table 1). By contrast, in most rice mutants characterized by now, lateral root defects concern the primary but also the shoot-borne root system (Table 1). In most instances, maize and rice mutants defective in lateral root formation also display abnormal development of other root types, suggesting complex regulatory mechanisms controlling cereal root system architecture (Table 1).

For many of these mutants, the causal gene which conditions their aberrant phenotype has been cloned. In most instances these genes are involved in auxin-related processes such as signal transduction (Aux/IAA, LBD, CYCLOPHILIN), polar auxin transport, auxin transport regulation, and cell cycle regulation (Table 1).

Table 1. Monogenic Mutants Impaired in Lateral Root Initiation in Maize and Rice[d]

Species	Mutants	Formation of lateral roots on these root types			Type of lateral root defects	Defects in other root types	Molecular function	Refs
		Primary	Seminal	Crown				
Maize	*rum1*	no	–	yes	Initiation	Lack of seminal root initiation	Auxin signaling (Aux/IAA)	[17]
	lrt1	no	no	yes	Initiation	Lack of crown root initiation at coleoptilar node	Unknown	[90]
	slr1	no	no	yes	Elongation	–	Unknown	[91]
	slr2	no	no	yes	Elongation	–	Unknown	[91]
Rice	*iaa3*	no	–	n.d.	Elongation and density	Reduced seminal and crown root number and elongation	Auxin signaling (Aux/IAA)	[18]
	iaa11	no	–	no[a]	Initiation	–	Auxin signaling (Aux/IAA)	[19]
	iaa13	no	–	no[b]	Density	Longer primary root and l ess root hairs	Auxin signaling (Aux/IAA)	[20]
	iaa23	no	–	no[a]	Initiation	Reduced crown root initiation, lack of root cap	Auxin signaling (Aux/IAA)	[21]
	crl1/arl1	no	–	–	Density	Missing crown root initiation	Auxin signaling (LBD)	[27,28]
	lrt2/cyp2	no	–	no[c]	Initiation	Disorganized stele, reduced number of cortex cell layers	Degradation of Aux/IAA proteins (Cyclophilin)	[25,26]
	aux1	no	–	yes	Initiation	Reduced root hair elongation	Polar auxin transport	[32]
	nal2/3	no	–	no	Initiation	–	Auxin transport regulation	[35]
	orc3	no	–	no[a]	Emergence	Reduced primary root elongation	Cell cycle regulation	[39]
	nar2.1	no	–	no	Elongation and density	Reduced primary and shoot-borne root elongation	High-affinity NO_3^- transporter	[70]

[a]Chuanzao Mao, personal communication.
[b]Yoshiaki Inukai, personal communication.
[c]Xiaorong Mo, personal communication.
[d]Abbreviations: –, root types are not formed in these mutants (rice generally does not form seminal roots); n.d., not determined.

The maize *rum1* [16,17] and the rice *IAA3* [18], *IAA11* [19], *IAA13* [20] and *IAA23* [21] genes encode AUXIN/INDOLE-3-ACETIC ACID (Aux/IAA) proteins. Aux/IAA proteins interact with AUXIN RESPONSE FACTORs (ARFs) which bind to the promoters of downstream genes. Aux/IAA–ARF complexes repress the activity of downstream target genes at low auxin concentrations. At high cellular auxin levels Aux/IAA proteins are quickly degraded, thus activating transcription of downstream genes under their control (reviewed in [22]). All *aux/iaa* mutants with developmental defects in lateral root formation contain a mutation in their degron sequence, which is the portion of the protein that is important in regulation of protein degradation. These mutations inhibit interaction with the F-box protein TIR1 and thus stabilize the Aux/IAA proteins. The stabilization of Aux/IAA proteins constitutively represses the expression of downstream target genes and results in the described defects in lateral root formation. Despite their similar molecular mode of action, Aux/IAA proteins control diverse aspects of lateral root formation including initiation, elongation, and density (Table 1). Remarkably, many of these *Aux/IAA* genes also affect other morphological aspects of root formation such as seminal root initiation in maize (*rum1* [16]) or primary root and root hair elongation (*IAA13* [20]), crown root initiation and root cap formation (*IAA23* [21]), and crown root number and elongation (*IAA3* [18]) in rice. The variety of root developmental processes controlled by members of the Aux/IAA family is also underscored by the root-type- and tissue-specific developmental regulation of their expression and their molecular interactions observed in maize [23,24].

Degradation of Aux/IAA proteins is regulated by the *CYCLOPHILIN* gene (*CYP2*) in rice. As illustrated by the phenotype of the allelic mutants *lrt2* [25] and *cyp2* [26], this gene controls asymmetric anticlinal division of pericycle cells during lateral root initiation. The regulation of auxin signaling by LRT2/CYP2 is highly conserved between dicots and monocots [25].

LATERAL ORGAN BOUNDARIES (LOB) domain proteins are another class of proteins involved in auxin signaling. Promoters of LOB domain proteins are direct targets of ARF transcriptional activators at high auxin concentrations, while ARF function is inhibited at low auxin concentrations by their interaction with Aux/IAA proteins. The allelic rice mutants *crown rootless 1* (*crl1*) and *adventitious rootless 1* (*arl1*) underscore that this LOB domain protein plays a crucial role in lateral root formation in rice [27,28]. In addition to their lateral root defects, these mutants are also defective in crown root initiation in rice [27,28]. Remarkably, the maize mutant *rtcs*, which is defective in the syntenic homolog of the rice gene *CRL1/ARL1*, is only affected in crown and seminal root initiation but not in lateral root formation [29]. It was suggested that the genetic redundancy of the duplicated maize paralogs *rtcs* and *rtcl* conditions normal lateral root development in these mutants [29].

Polar auxin transport plays a critical role in lateral root formation as demonstrated by the suppression of this process by polar auxin transport inhibitors in maize [15,30]. Directional transport of auxin results from the asymmetric distribution of different auxin membrane carriers, including the AUXIN TRANSPORTER PROTEIN 1 (AUX1) influx carrier family and the efflux carriers of the PIN-FORMED (PIN) family [12,31]. In rice, the mutant *aux1* displays a reduced number of lateral roots and reduced root hair length [32]. Overexpression of *AUX1* in rice results in an increased rate of lateral root initiation in response to local nitrate supply in rice plants [33]. This is in line with *in situ* hybridization experiments in which endodermis and pericycle specific expression of maize *AUX1* was demonstrated in the primary root [34]. Moreover, the rice *NARROW LEAF 2* (*NAL2*) and *NAL3* genes are paralogs that encode WUS-related HOMEOBOX 3A (WOX3A) transcriptional activators with identical amino acid sequences. The reduced number of lateral roots in the double mutant *narrow leaf2/narrow leaf3* (*nal2/3*) and expression studies suggest that these genes are involved in lateral root primordia formation likely by regulating *PIN1* and *PIN2* expression [35]. Overexpression of *PIN1* significantly increases lateral root density in rice [36], whereas rice plants overexpressing *PIN2* form less lateral roots [37].

These results demonstrate that the polar auxin transporters *AUX1* and members of the *PIN* family are also central checkpoints of lateral root formation.

Periodicity of lateral root initiation and spacing has been linked to auxin-efflux-carrier-mediated polar auxin transport and local auxin gradients [12,38]. Downstream molecular components controlling cell cycle progression are instrumental for lateral root initiation in arabidopsis [12,38]. The ORIGIN RECOGNITION COMPLEX (ORC) is a pivotal element in DNA replication, heterochromatin assembly, cell cycle checkpoint regulation, and chromosome assembly. In rice, mutations in the cell cycle regulator gene *ORIGIN RECOGNITION COMPLEX SUBUNIT 3* (*ORC3*) disrupt cell cycle progression and block lateral root emergence in primary roots [39].

Transcriptomic Analysis of Lateral Root Initiation in Maize and Rice

Comparative transcriptome analyses of wild-type and mutant root systems in maize and rice have helped to reveal molecular functions involved in lateral root formation [32,40,41]. Comparative transcriptome analyses of the lateral root initiation mutants *aux1* in rice [32] and *rum1* in maize [40] with their wild-type siblings revealed similar sets of differentially expressed genes in primary roots. In both studies, genes involved in auxin signaling and cell cycle regulation were significantly downregulated, suggesting an evolutionary conservation of these key processes of lateral root initiation [32,40].

Laser capture microdissection (LCM) allows isolating specific cell types from complex composite tissues for subsequent cell-type specific transcriptome analyses [42]. Microarray analyses of captured maize pericycle cells suggest that specification and lateral root initiation might be controlled by a different set of genes involved in signal transduction, transcription, and the cell cycle [16,43]. Moreover, recent pericycle cell-specific RNA-Seq analyses indicate a role for auxin-related genes and cell cycle regulation during lateral root initiation in both rice and maize [41,44]. Notably, root type-specific transcription factors, such as MYB and MYB-related, HOMEOBOX and bHLH, were specifically identified in either primary or crown roots, which might explain the differential regulation of lateral root initiation in these two root types in maize [41].

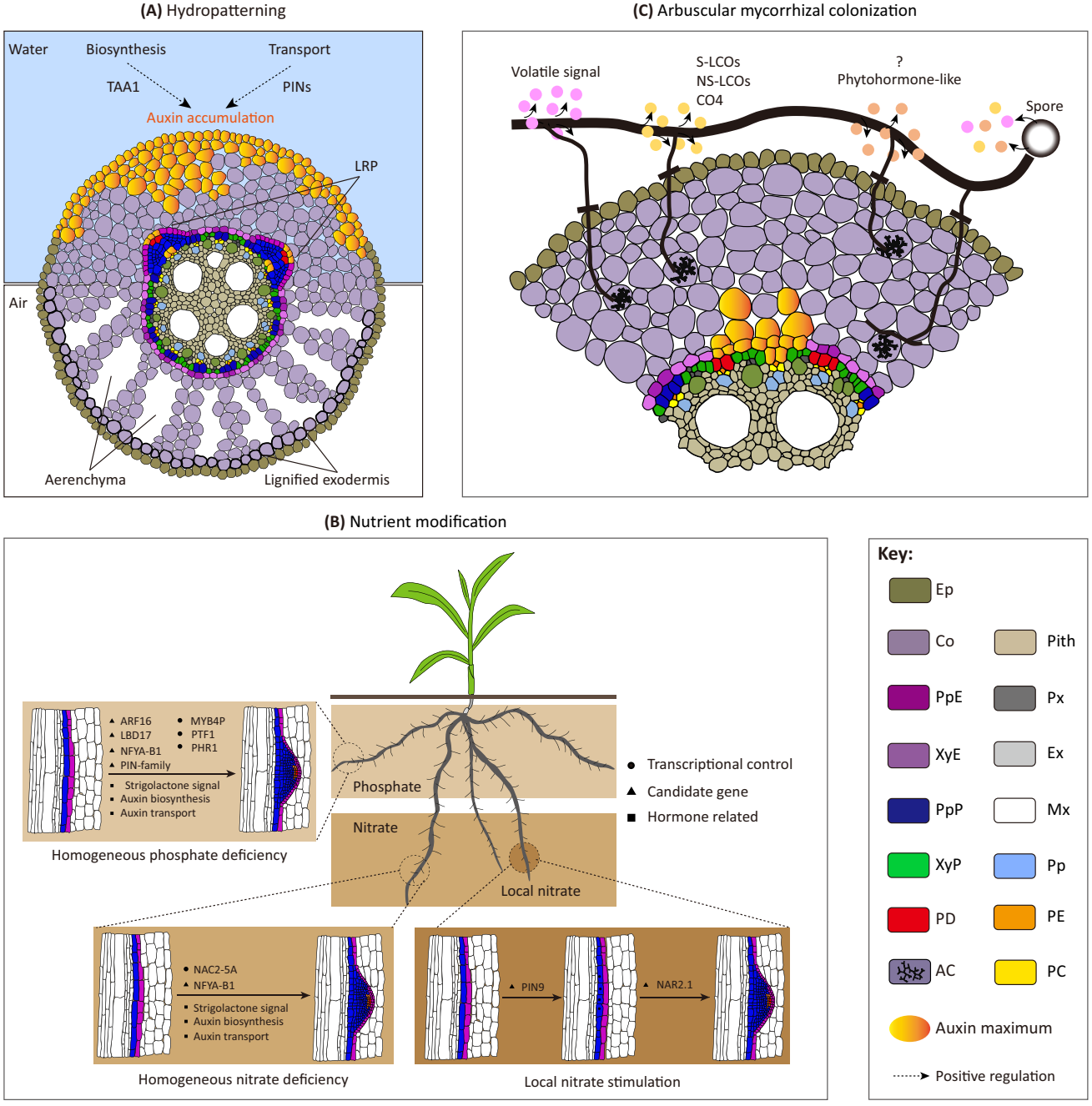
Environmental Control of Lateral Root Plasticity in Cereals

Cereal root systems display an enormous plasticity to adapt to changing environmental conditions. Root stocks can perceive extrinsic environmental signals and translate them into changes of their complex architecture and physiology during their whole life cycle. Lateral root initiation and elongation allow for flexible readjustment of root system architecture to suboptimal environmental conditions such as limited availability of water [45] or macronutrients including phosphate and nitrate (reviewed in [46]) and to beneficial interaction partners such as arbuscular mycorrhizal fungi (reviewed in [47]).

Drought and Hydropatterning Modulate Lateral Root Initiation

Drought is a major limitation of maize productivity [48]. Maize genotypes with reduced lateral root density perform better under drought conditions than other genotypes [1,49,50]. It has been demonstrated that lateral root initiation is repressed by transient water deficit in maize and barley (*Hordeum vulgare*) [51]. Upon water deficit, pericycle founder cells are blocked irreversibly at the asymmetric division stage in barley and at various later stages in maize [51]. On the anatomical level, root cortical aerenchyma and hydraulic barriers such as lignified exodermis cells, which limit water loss, develop preferentially on the side which is exposed to limited water access [52] (Figure 2A).

Recently, it has been demonstrated that arabidopsis, rice and maize can sense heterogeneity in water availability in transverse orientation at the sub-organ or cellular level. This phenomenon is



Trends in Plant Science

Figure 2. Summary of Lateral Root Initiation and Interaction with Environmental Cues in Cereals. (A) Anatomical adaptation and hydropatterning of lateral root initiation in response to the availability of water. (B) Hormonal and transcriptional regulation of lateral root initiation by phosphate and nitrate status. (C) Signals from arbuscular mycorrhizal fungi which trigger lateral root formation. Abbreviations: AC, arbuscule-containing cell; ARF16, AUXIN RESPONSE FACTOR 16; Co, cortex; CO4, TETRAACETYL CHITOTETRAOSE; Ep, epidermis; Ex, early-xylem; LBD17, LATERAL ORGAN BOUNDARY DOMAIN 17; LRP, lateral root primordium; Mx, meta-xylem; NS-LCOs, nonsulfated lipochitooligosaccharides; MYB, V-MYB AVIAN MYELOBLASTOSIS VIRAL ONCOGENE HOMOLOG; NAC, NAM, ATAF1/2, CUC2; NAR2.1, NITRATE ASSIMILATION RELATED2.1; NFYA, NUCLEAR FACTOR Y A; PC, phloem companion; PD, pericycle divisions; PE, phloem element; PHR1, PHOSPHATE STARVATION RESPONSE 1; PIN, PIN-FORMED; Pp, proto-phloem; PpE, phloem-pole endodermis; PpP, phloem-pole pericycle; PTF1, PHOSPHATE STARVATION INDUCED TRANSCRIPTION FACTOR 1; Px, proto-xylem; S-LCOs, sulfated lipochitooligosaccharides; TAA1, TRYPTOPHANE-PYRUVATE AMINOTRANSFERASE 1; XyE, xylem-pole endodermis; XyP, xylem-pole pericycle.

designated hydropatterning [53]. In soil this heterogeneity is constituted by local pockets in which roots are locally in contact with water and air. As a morphogenetic adaption to this heterogeneity, lateral roots only form on the side where the main root is in contact with water. It has been demonstrated that hydropatterning is preceded by PIN-mediated auxin efflux and TAA1 (TRYPTOPHANE-PYRUVATE AMINOTRANSFERASE 1)-mediated auxin biosynthesis to determine pre-branch sites of lateral roots [53] (Figure 2A). The process of hydropatterning is independent of endogenous abscisic acid signaling, thus distinguishing it from a classical drought response [53].

Lateral Root Formation in Response to Nitrate and Phosphate Availability

Physiological experiments suggest that maize plants optimize their root architecture by regulating lateral root formation based on the availability of nitrate and phosphate. Sparsely spaced and long lateral roots are optimal for nitrate acquisition, while densely spaced and short lateral roots are optimal for phosphate acquisition in maize [1,54]. Poorly mobile phosphate is mainly distributed in the top soil layers and is therefore preferentially accessible by shallow roots, while deep roots can forage for mobile nitrate [49,50,55].

In rice, it has been demonstrated that nitrate- and phosphate-deficiency-dependent lateral root formation is controlled via the strigolactone biosynthesis genes *D10* and *D27* [56]. Moreover, the *D3* component of strigolactone signaling modulates transport of auxin from shoot to root by regulating the expression of members of the *PIN* family of auxin efflux carriers [56]. Similarly in wheat (*Triticum aestivum*), phosphate-deficiency-dependent lateral root formation is modulated by transcriptional regulation of members of the *PIN* family [57] (Figure 2B). Moreover, it has been observed that lateral root formation caused by phosphate and nitrate starvation in wheat is controlled by the *NFYA* (*NUCLEAR FACTOR Y A*)-*B1* gene, via the upregulation of auxin biosynthesis genes [58] (Figure 2B). Furthermore, it has been shown that the auxin signaling genes *ARF16* in rice [59] (Figure 2B) and *LBD17* in maize, plus several genes encoding auxin biosynthetic enzymes and genes involved in auxin transport, control phosphate-dependent lateral root formation [60] (Figure 2B). In summary, these findings suggest that conserved mechanisms of auxin signaling, biosynthesis, and transport control nitrate- and phosphate-dependent lateral root formation in cereals.

Transcription factors and transcriptional regulators also modulate lateral root formation in response to phosphate availability in cereals [61]. Phosphate-dependent lateral root formation is controlled by the transcription factors PTF1 in rice and maize [60,62,63] (Figure 2B), the MYB-like transcription factors PHR1-A1 in wheat [64], and MYB4P in rice [65] (Figure 2B). Moreover, the cereal-specific NAC transcription factor NAC2-5A controls nitrate-dependent lateral root formation in wheat [66] (Figure 2B).

In another series of experiments it has been demonstrated that local nitrate supply can considerably stimulate lateral root production in maize [67–69], rice [70], barley [71], and wheat [72]. It has been demonstrated that high-affinity nitrate transporters of the NRT2 family control nitrate-dependent lateral root formation by interacting with NAR2 proteins in rice [73,74]. NAR2 controls polar auxin transport from the shoot to the root system by controlling the transcription of the PIN family of auxin efflux carriers [70] (Figure 2B). Notably, the monocot-specific *PIN9* gene in phloem pole cells modulates auxin efflux to pericycle cells and subsequent cell cycle activation in maize [30]. Among the different root types of maize, brace roots display exceptional plasticity for lateral root formation compared to other root types upon changing nitrate concentrations. This is illustrated by an increased induction of lateral roots in brace roots by nitrate compared to other root types and is also reflected by their unique transcriptional control of cell cycle and MYB-related genes [75,76]. Taken together, these recent discoveries link transcriptional regulation and nutrient-signaling-triggered lateral root development in cereals.

Lateral Root Initiation in Response to Arbuscular Mycorrhizal Fungi

Lateral root formation is also influenced by soil microbes, which release signaling molecules and change the nutrient environment due to their metabolic activities or through direct nutrient delivery. In cereals most is known about the impact of arbuscular mycorrhizal fungi. These fungi colonize plant roots and release mineral nutrients, especially phosphate, to the plant, in return for organic carbon [77]. Arbuscular mycorrhiza influences the root system transcriptionally and morphologically. Root-type-specific transcriptional responses to root colonization have been observed in rice [78], while root system architecture changes have been reported for both rice and maize: most prominently an increase in lateral root formation but also an increase in crown root length [79,80]. Lateral roots are more strongly colonized as compared to crown roots [80] and the increase in lateral root numbers may favor symbiosis development.

It has been suggested that arbuscular mycorrhizal fungi influence root system architecture in several ways by the exudation of molecules that induce lateral root formation by changing the pattern of nutrient distribution inside the root through localized release of mineral nutrients at arbuscules (Figure 2C) and through localized consumption of organic carbon [47,63]. While little is known about the mechanisms by which nutrient patterns inside the root affect root system architecture more data is available for the role of signaling molecules. Treatment of roots with exudates from germinating fungal spores (germinating spore exudates) increases lateral root formation in both maize and rice [81] (Figure 2C). Germinating spore exudates contain so-called MYC factors which comprise chitin oligomers (chitotetraose CO4 and pentaose CO5 [82]) as well as sulfated and non-sulfated lipochito-oligisaccharides (S- and NS-MYC-LCOs [83]). Isolated CO4s, S-MYC-LCOs or NS-MYC-LCOs alone are sufficient to promote lateral root formation, crown root formation and crown root elongation in rice [84]. The increase in lateral and crown root development depends on *CCaMK/DMI3* [84], a calcium-calmodulin-dependent kinase-encoding gene, which is part of a signal transduction cascade (common SYM signaling) required for root colonization by arbuscular mycorrhizal fungi [85]. Common SYM signaling is triggered by MYC factor perception at the plasma membrane resulting in symbiotic response such as calcium spiking and gene expression [77]. Thus, symbiosis signaling seems to be directly linked with molecular mechanisms of lateral root formation. However, the molecular interconnecting node is currently unknown. Interestingly, it has been observed that presence of arbuscular mycorrhizal fungi and treatment with germinating spore exudates induces lateral root formation in several rice mutants (*pollux*, *ccamk*, *cyclops*) deficient in components of common SYM signaling [80,81]. Thus, it is likely that in addition to chitin-derived MYC factors, germinating spore exudates contain alternative molecules, which induce lateral root formation independent of common SYM signaling [47]. Since several fungi are known to produce plant hormones such as auxin, ethylene or gibberellin [86,87], it is possible that these molecules are lateral-root-inducing plant hormones, their mimics, or alternatively compounds that interfere with hormone signaling (Figure 2C). Interestingly, in the legume *Medicago truncatula*, induction of lateral root formation by germinating spore exudates required *SYMRK/DMI1* (encoding a receptor kinase) and *POLLUX/DMI2* (encoding a potassium channel), which act upstream of *CCaMK/DMI3* in common SYM signaling [81,88]. This indicates that *Medicago* may either not respond to these putative molecules or require them in higher concentrations than rice to trigger the alternative lateral root induction pathway. Using a split plate system showed that germinating spores of arbuscular mycorrhizal fungi also release volatile compounds, which induce lateral root formation in the legume *Lotus japonicus* [89]. This is independent of *CASTOR*, the paralog of *POLLUX*, which is also required for common SYM signaling [85]. However, in cereals the impact of volatiles released from arbuscular mycorrhizal fungi has not yet been studied. In summary, arbuscular mycorrhizal fungi influence root architecture in multiple ways, and it will be exciting to investigate in which way the various signals influence canonical mechanisms of lateral root formation.

Concluding Remarks and Outlook

Patterning of lateral roots in cereals is unique with respect to the involved cell types, their positioning relative to the vascular elements, and the unpredictable radial pattern of their emergence. An additional layer of complexity is added by the different root types that form throughout the life cycle of cereals, which all have the competence to form lateral roots. Genetic and transcriptomic analyses have revealed numerous genes and molecular functions involved in the intrinsic regulation of lateral root formation but also the environmental control that contributes to the plasticity of lateral root formation in cereals. In the future, cloning of quantitative trait loci (QTLs) associated with lateral root formation will further contribute to the molecular dissection of this developmental process. Despite the recent progress in the molecular understanding of lateral root formation in cereals, numerous questions still remain unanswered (see Outstanding Questions). For instance, it remains elusive which genes regulate the positioning of lateral roots in cereals and their random patterning. Similarly, it is unclear how pericycle and endodermis cells coordinate their contribution to emerging lateral roots. Moreover, it still remains enigmatic in most instances how intrinsic regulators of lateral root formation are modulated by environmental cues, and how these cues regulate the localized balance between cell division and differentiation in lateral root formation. In particular, it remains to be elucidated how a combination of different environmental factors simultaneously affect molecular networks involved in lateral roots, and how these synchronously acting cues are coordinated.

Outstanding Questions

Which molecular networks regulate the root type-specific formation of lateral roots in cereals?

Which genes regulate the positioning of cereal lateral roots at the phloem poles and their stochastic patterning?

How do pericycle and endodermis cells coordinate their contribution to emerging lateral roots in cereals?

How are intrinsic regulators of lateral root formation modulated by environmental cues and how do these cues regulate the localized balance between cell division and differentiation in lateral root formation?

How does a combination of different environmental factors simultaneously affect molecular networks involved in lateral roots and how are these synchronously acting cues coordinated?

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