Cellular and Molecular Life Sciences (2018) 75:3329–3338
https://doi.org/10.1007/s00018-018-2861-5

REVIEW

Pivotal role of *LBD16* in root and root-like organ initiation

Wu Liu[1] · Jie Yu[1] · Yachao Ge[1,2] · Peng Qin[3] · Lin Xu[1]

Received: 19 March 2018 / Revised: 17 June 2018 / Accepted: 21 June 2018 / Published online: 25 June 2018

Abstract

In the post-embryonic stage of *Arabidopsis thaliana*, roots can be initiated from the vascular region of the existing roots or non-root organs; they are designated as lateral roots (LRs) and adventitious roots (ARs), respectively. Some root-like organs can also be initiated from the vasculature. In tissue culture, auxin-induced callus, which is a group of pluripotent root-primordium-like cells, is formed via the rooting pathway. The formation of feeding structures from the vasculature induced by root-knot nematodes also borrows the rooting pathway. In this review, we summarize and discuss recent progress on the role of *LATERAL ORGAN BOUNDARIES DOMAIN16* (*LBD16*; also known as *ASYMMETRIC LEAVES2-LIKE18*, *ASL18*), a member of the *LBD/ASL* gene family encoding plant-specific transcription factors, in roots and root-like organ initiation. Different root and root-like organ initiation processes have distinct priming mechanisms to specify founder cells. All these priming mechanisms converge to activate *LBD16* expression in the primed founder cells. The activation of *LBD16* expression leads to organ initiation via promotion of cell division and establishment of root-primordium identity. Therefore, *LBD16* might play a common and pivotal role in root and root-like organ initiation.

Keywords Root founder cell · Lateral root · Adventitious root · *LBD16* · Callus · Root-knot nematodes

Abbreviations

AR	Adventitious root
ARF	AUXIN RESPONSE FACTOR
ASL	ASYMMETRIC LEAVES2-LIKE
ATXR2	ARABIDOPSIS TRITHORAX-RELATED 2
Aux/IAA	AUXIN/INDOLE-3-ACETIC ACID
AuxRE	AUXIN RESPONSE ELEMENT
CIM	Callus-inducing medium
CRL1	CROWN ROTLESS1
eY1H	Enhanced yeast one-hybrid
FAD-BD	FAD-BINDING BERBERINE
LBD	LATERAL ORGAN BOUNDARIES DOMAIN
LR	Lateral root
PLT	PLETHORA
RIM	Root-inducing medium
RTCS	ROOTLESS CONCERNING CROWN AND SEMINAL ROOTS
SIM	Shoot-inducing medium
SLR	SOLITARY-ROOT
WOX	WUSCHEL-RELATED HOMEOBOX

Wu Liu and Jie Yu have contributed equally to this work.

✉ Lin Xu
xulin01@sibs.ac.cn

[1] National Key Laboratory of Plant Molecular Genetics, CAS Center for Excellence in Molecular Plant Sciences, Shanghai Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, Shanghai, China

[2] University of Chinese Academy of Sciences, Beijing, China

[3] Department of Instrument Science and Engineering, Shanghai Jiao Tong University, Shanghai, China

Introduction

In the post-embryonic stage of *Arabidopsis thaliana*, many types of roots can originate from the vasculature. Adventitious roots (ARs) can form from non-root organs, such as detached leaf or stem explants and the hypocotyl [1–8]. In a developing root, acropetal lateral roots (simply referred to LR in this review) form from the xylem-pole pericycle cells under the guidance of an oscillating auxin flux derived from the root cap [9–14]. An existing root can also produce adventitious lateral roots, mainly via the AR formation pathway [15–23].

Some root-like organs can also be initiated from the vasculature in *A. thaliana*. In tissue culture, callus can be induced on auxin-rich callus-inducing medium (CIM) [24–32]. Callus forms via the rooting pathway and the

cellular nature of the newly formed callus is a group of root-primordium-like cells [33–38]. Callus cells are pluripotent, because they are competent for shoot regeneration on cytokinin-rich shoot-inducing medium (SIM) or root regeneration on root-inducing medium (RIM). In addition, root-knot nematodes can induce the formation of feeding structures from the vasculature of *A. thaliana* in either roots or detached leaf explants [39, 40]. The formation of feeding structures has been proposed to borrow the rooting pathway [40–48]. Therefore, it is possible that feeding structures induced by root-knot nematodes are also root-like organs.

LATERAL ORGAN BOUNDARIES DOMAIN (*LBD*; also known as *ASYMMETRIC LEAVES2-LIKE*, *ASL*) transcription factor genes belong to a plant-specific family that is present in diverse taxa ranging from algae to seed plants. There are at least six classes of *LBD* genes in *A. thaliana* [49–54]. The class-IB, also known as the root-associated LBD/ASL clade, has ten members in *A. thaliana* [53, 54] (Fig. 1), and they are involved in many aspects of plant development. Here, we review recent progress in research on the role of *A. thaliana LBD16* (Fig. 1), which belongs to class-IB *LBD* genes, in root and root-like organ initiation.

LBD16 in LR initiation

When *A. thaliana* is grown vertically on the medium, the primary root usually produces LRs by an acropetal sequence. The formation of LR in *A. thaliana* involves successive steps of cell fate transitions [13, 14, 55–57] (Fig. 2a). Auxin is transported into and accumulates in the xylem-pole pericycle cells in the priming step for specification of a group of LR founder cells. After priming, the nuclei of the LR founder cells migrate to start the initiation step, and pairs of LR founder cells undergo asymmetric cell division to form the LR primordium. The LR primordium undergoes continuous cell division, and then, the LR primordium forms the LR apical meristem with functional domains in the patterning step [55].

The expression of *LBD16* is specifically induced in the primed LR founder cells before the nuclei migrate and asymmetric division occurs [58] (Fig. 2a). During the initiation step, *LBD16* expression continues in the LR primordium, but its expression gradually decreases during the patterning step to form the LR apical meristem ([9, 20, 58] and our unpublished data) (Fig. 2a). The *lbd16* mutant and *LBD16-SRDX* transgenic lines (in which the *LBD16* pathway was blocked) formed fewer LRs from the primary root than did wild type [9, 20, 58–60]. Specifically, blocking of the *LBD16* pathway resulted in defective polar nuclei migration in LR founder cells and defective asymmetrical cell division, but it did

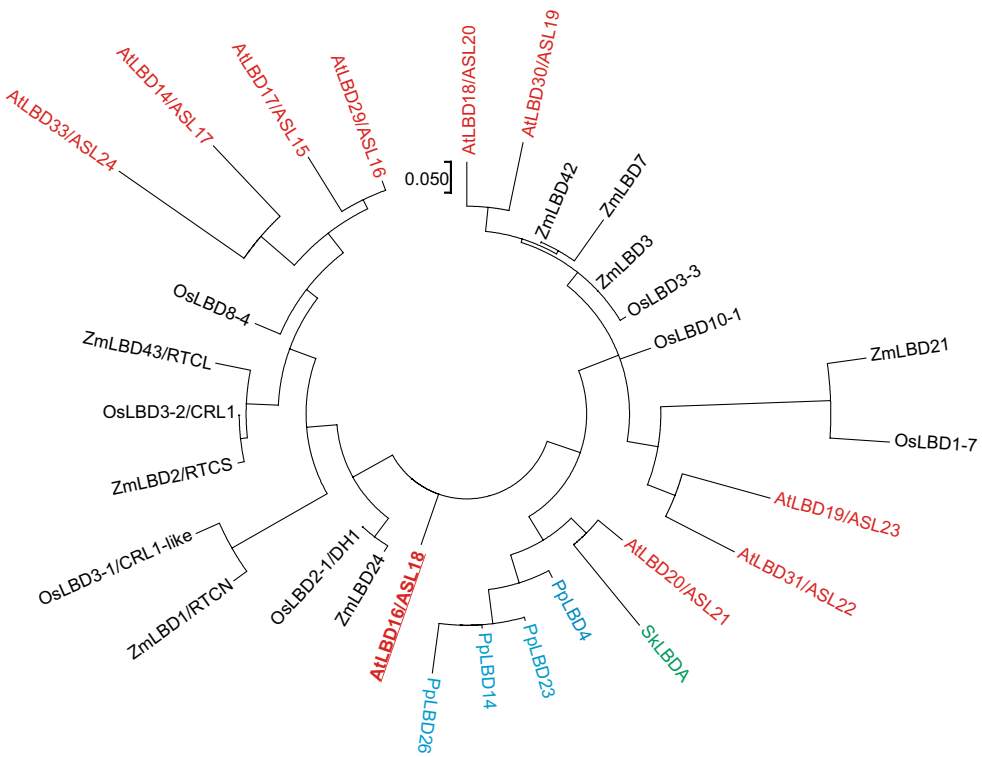

Fig. 1 Phylogeny of class-IB *LBD* genes in land plants. Phylogenetic analysis of protein sequences of class-IB LBDs from a bryophyte *Physcomitrella patens* (Pp, in blue), a lycophytes *Selaginella kraussiana* (Sk, in green), a dicot *Arabidopsis thaliana* (At, in red), and monocot *Oryza sativa* (Os, in black) and *Zea mays* (Zm, in black). Sequence of SkLBDA was obtained by analyzing RNA-seq and DNA-seq data published previously [91] (GenBank, MH107252). Other sequences were obtained from the published data [53]. Phylogenetic tree of full length of the LBD proteins was constructed using the maximum-likelihood method (the Poisson model) with MEGA7.0 and default parameters [92]

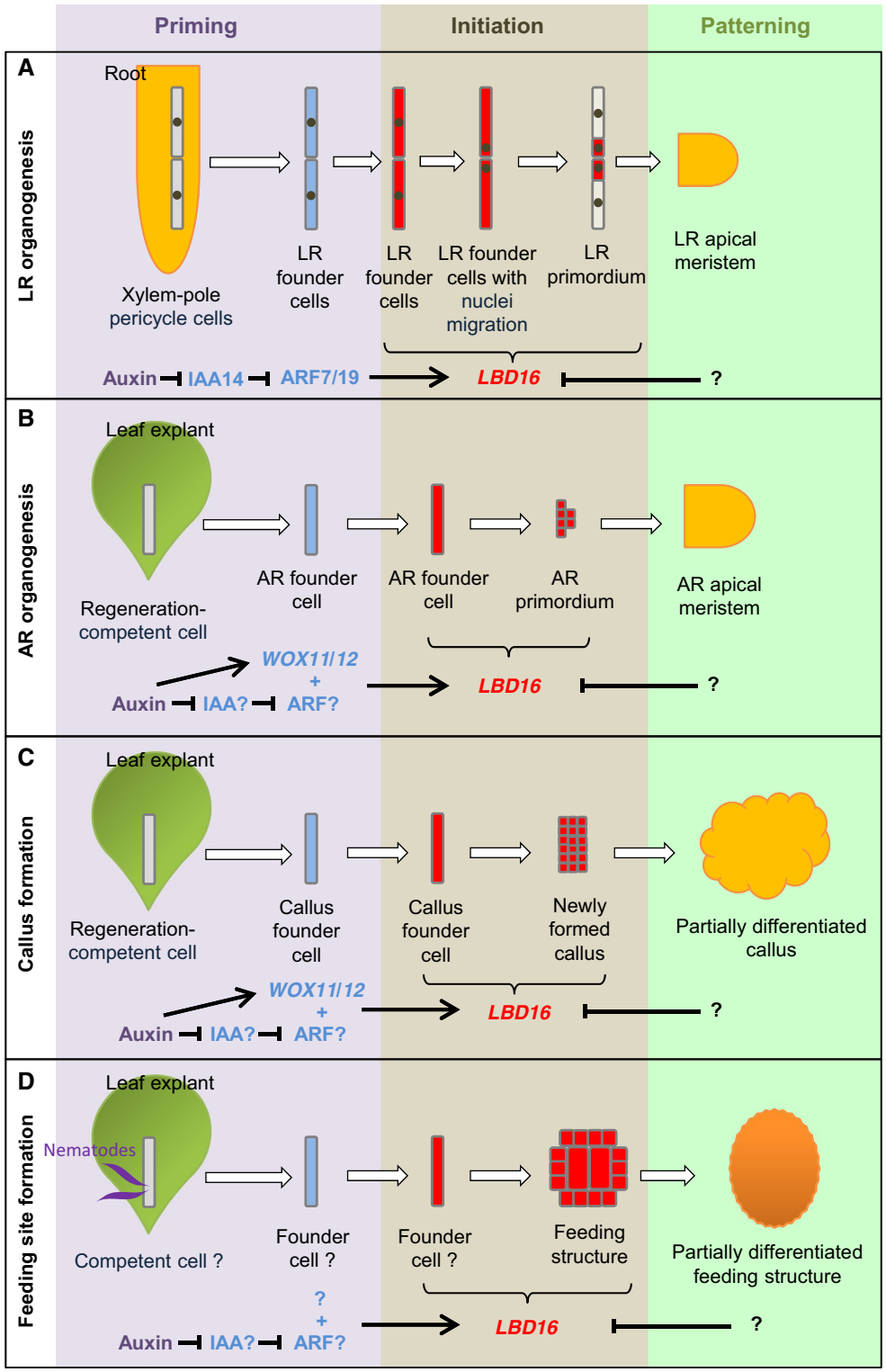

Fig. 2 Model of *LBD16* in root and root-like organ formation. Model summarizing the common role of *A. thaliana LBD16* in LR formation from primary root (**a**), AR formation from detached leaf explants (**b**), callus formation from detached leaf explant (**c**), and feeding structure formation from detached leaf explant (**d**). Cells and genes that are involved in the priming step are in blue, and those in the initiation step are in red

not affect the specification of LR founder cells with auxin accumulation in the priming step [58]. Therefore, *LBD16* seems to be specifically involved in the initiation of the LR primordium.

In LR formation, *LBD16* is activated by AUXIN RESPONSE FACTOR 7 (ARF7) and ARF19 (ARF7/19), two functionally redundant transcription factors [9, 58, 59, 61] (Fig. 2a). At a low auxin level, ARF7/19 form a protein complex with the AUXIN/INDOLE-3-ACETIC ACID (Aux/IAA) protein IAA14 (also known as SOLITARY-ROOT, SLR) [62]. The interaction with IAA14 represses the transcriptional activation activity of ARF7/19. In the priming step of lateral rooting, auxin is transported into and highly accumulates in LR founder cells. This results in the degradation of the IAA14 protein and, therefore, the release of ARF7/19. The release of ARF7/19 derepresses their transcriptional activator role. In the primed founder cells, ARF7/19 can directly bind to the *AUXIN RESPONSE ELEMENT*s (*AuxRE*s) on the promoter of *LBD16* to activate transcription [9, 58, 59, 63]. The *arf7 arf19* double mutant showed defective LR initiation and a loss of *LBD16* expression when the plants were vertically cultured on growth medium. Overexpression of *LBD16* in the *arf7 arf19* double mutant background partially rescued the LR formation defect, suggesting that *LBD16* acts downstream of *ARF7/19* [9].

Overall, during LR organogenesis, ARF7/19 activate *LBD16* expression in the primed LR founder cells, and then, *LBD16* promotes cell division and fate transition during the initiation of LR primordium.

LBD16 in AR initiation

In *A. thaliana*, ARs can form from many tissues after wounding or in response to environmental signals [1–8]. By studying de novo root regeneration from detached *A. thaliana* leaf explants [64], the role of *LBD16* in AR initiation was analyzed [8, 20, 36, 65] (Fig. 2b). After detachment of leaf explants, endogenous auxin is produced and polar-transported into regeneration-competent cells (i.e., procambium cells and some vascular parenchyma cells) near the wounded site. Accumulation of auxin in a regeneration-competent cell activates the expression of two partially redundant transcription factor genes, *WUSCHEL-RELATED HOMEOBOX11* (*WOX11*) and *WOX12* (*WOX11/12*), resulting in the priming step, i.e., cell fate transition from a regeneration-competent cell to an AR founder cell [36]. In the initiation step, the AR founder cell divides to form the AR primordium. To date, there is no solid evidence that nucleus migration and asymmetrical cell division of pairs of founder cells occur during the initiation of the AR primordium. Further analysis of the first round of cell division in AR formation from *A. thaliana* leaf explants will clarify how the AR primordium is initiated in the future.

LBD16 is specifically induced in the primed AR founder cell during the initiation step ([65] and our unpublished data) (Fig. 2b). *LBD16* expression continues in the AR primordium and gradually decreases when the AR primordium enters the patterning step to differentiate into the AR apical meristem [20, 36, 65] (Fig. 2b). The *lbd16* mutant showed defects in AR organogenesis from leaf explants [20], suggesting that *LBD16* is required for AR initiation.

During AR formation from leaf explants, *LBD16* is not activated by ARF7/19 [20, 36]. The *arf7 arf19* double mutant was able to form ARs from detached leaf explants, suggesting that AR initiation from leaf explants is not strictly dependent on *ARF7/19*, in contrast to LR initiation [20]. Therefore, other upstream activators may induce *LBD16* expression during AR formation. *WOX11/12* were proposed to directly activate *LBD16* [20]. In the *WOX11–SRDX* transgenic lines, *LBD16* expression was not upregulated in the primed AR founder cells or the AR primordium. There are two WOX-binding elements on the *LBD16* promoter, and WOX11 can directly bind to these elements. Mutations in the WOX-binding elements resulted in the loss of the *LBD16* expression during AR initiation, suggesting that WOX11/12 are key upregulators of *LBD16* in AR formation. Activation of *LBD16* by WOX11/12 requires the presence of auxin, suggesting that the upregulation of *LBD16* in the primed AR founder cells may require ARF proteins other than ARF7/19. Those ARFs may cooperate with WOX11/12 to upregulate *LBD16* during AR primordium initiation from leaf explants [8] (Fig. 2b).

Although *ARF7/19* do not regulate *LBD16* expression during AR formation from leaf explants, the two ARFs have been shown to control AR formation from hypocotyls [66], indicating that different priming mechanisms might be involved in AR formations from different organs. It will be interesting to determine whether the auxin signaling pathways involved in AR formation differ between leaf explants and hypocotyls in the future.

WOX11/12 did not regulate *LBD16* during LR formation when *A. thaliana* was vertically grown on the medium [20]. *WOX11/12* are not expressed in LR founder cells; therefore, they cannot be responsible for *LBD16* upregulation during LR initiation. Interestingly, ectopic *WOX11-SRDX* expression under the control of the 35S promoter in LR founder cells did not block *LBD16* activation by ARF7/19, suggesting that there is some unknown mechanism to abolish the function of the WOX11 protein in the LR founder cells [20].

The *A. thaliana* primary root can produce not only LRs but also adventitious lateral roots [20–23]. The priming of founder cells during adventitious lateral rooting is more likely to follow the AR pathway than the LR pathway, i.e., involving *WOX11/12* but not *ARF7/19* [20]. It is possible

that *LBD16* could also be involved in the initiation step of adventitious lateral rooting, as it is in AR formation. Further research on the role of *LBD16* in adventitious lateral root formation is required to test this hypothesis.

Overall, during AR organogenesis from leaf explants, *WOX11/12* together with ARFs activate *LBD16* expression in the primed AR founder cells. *LBD16* then promotes the initiation of AR primordium.

LBD16 in callus initiation and pluripotency acquisition

De novo shoot regeneration (also known as de novo shoot organogenesis) in tissue culture usually experiences two phases: first, callus forms from detached explants on auxin-rich CIM; then, callus is moved to cytokinin-rich SIM for adventitious shoot induction [24–32]. The results of recent studies have suggested that the newly formed callus on CIM is a group of root-primordium-like cells and the process of callus initiation borrows the rooting pathway [33–38].

Using callus formation from *A. thaliana* leaf explants as an example, the priming and initiation steps of callus formation are similar to those that occur during AR formation [34, 36, 38, 67–70] (Fig. 2c). In the priming step, exogenous auxin in the medium activates *WOX11/12* expression to trigger fate transition from a regeneration-competent cell to a callus founder cell [36, 38, 69]. Then, the callus founder cell undergoes division to become the newly formed callus cells, which have root-primordium-like features at the molecular level [36–38, 69]. When callus is cultured on CIM for a long time, partial differentiation into root apical meristem-like tissue can occur (i.e., the formation of partially differentiated callus) [69].

LBD16 expression is specifically induced in the primed callus founder cell in the initiation step on CIM ([34, 38] and our unpublished data) (Fig. 2c). *LBD16* expression continues in the root-primordium-like newly formed callus [38]. The *lbd16* mutant exhibited slowed cell division during callus initiation, indicating that *LBD16* is required for proper cell division [34, 38]. When the callus is continuously cultured on the CIM for a long time, *LBD16* expression level decreases in root apical meristem-like partially differentiated callus ([34, 69] and our unpublished data) (Fig. 2c).

When newly formed callus is moved to SIM, *LBD16* expression sharply decreases and then disappears, suggesting that cytokinin might have a role in repressing *LBD16* expression on SIM [38]. Interestingly, the callus of the *lbd16* mutant showed defective shoot formation on SIM, suggesting that *LBD16* is also required for the acquisition of pluripotency in the newly formed callus during its initiation [38]. The cellular basis of pluripotency in the newly formed callus was proposed to be the root-primordium identity [37, 38]. Therefore, *LBD16* promotes establishment of the root-primordium cell fate identity in newly formed callus.

During callus formation from *A. thaliana* detached leaf explants on CIM, *LBD16* expression is upregulated by auxin together with *WOX11/12* [34, 38] (Fig. 2c), similar to the case during AR formation. The previous studies have indicated that ARF7/19 might be involved in activating *LBD16* during callus initiation [34, 71]. However, *LBD16* expression was not completely abolished in the *arf7 arf19* double mutant background when callus was initiated from leaf explants (our unpublished data), suggesting that at least some other ARF proteins are also involved in the activation of *LBD16* during this process (Fig. 2c). In addition, the chromatin factor ARABIDOPSIS TRITHORAX-RELATED 2 (ATXR2), a putative histone methyltransferase, acts as a co-activator with ARFs to upregulate *LBD16* [71]. ATXR2 might regulate *LBD16* expression via deposition of histone H3 lysine 36 trimethylation (H3K36me3) epigenetic markers on the *LBD16* locus, thereby facilitating its transcription. Consistent with the molecular role of ATXR2, the *atxr2* mutant showed partially defective callus formation from leaf explants, and the *LBD16* expression level was lower in *atxr2* leaf explants than in the wild-type leaf explants during callus initiation. Therefore, *WOX11/12* and the auxin-mediated *ARF* pathway together with chromatin factors could act together to upregulate *LBD16* during callus initiation on CIM. A recent study using enhanced yeast one-hybrid (eY1H) screening showed that *LBD16* is involved in a complex gene regulatory network involving multiple key transcription factors related to regeneration [72].

The AtbZIP59 transcription factor interacts with LBD16 during callus formation [70]. Like *LBD16* overexpression [34], *AtbZIP59* overexpression induced autonomous callus formation in the absence of exogenous auxin [70]. The AtbZIP59–LBD16 complex was shown to directly regulate the expression of *FAD-BINDING BERBERINE* (*FAD-BD*), which encodes a BBE-like enzyme involved in cell wall metabolism during LR emergence [70, 73].

Therefore, callus initiation from leaf explants may borrow the AR formation pathway. Similarly, it is possible that callus formation from root explants may borrow the acropetal lateral rooting pathway or adventitious lateral rooting pathway. Regardless of the founder cells from different rooting pathways, *LBD16* is the pivotal gene to be induced during callus initiation, and is required for the establishment of pluripotency (i.e., root-primordium identity) in the newly formed callus.

LBD16 in root-knot nematode feeding site formation

Root-knot nematodes, a type of plant endoparasitic nematode, can induce the formation of feeding structures from the vasculature in roots or in other organs (e.g., detached leaf

explants) [39, 40]. Giant cells, the most commonly formed feeding cells in the feeding structures, are initiated from the vasculature and undergo repeated mitosis with aborted cytokinesis induced by nematode effectors [48].

Using *A. thaliana* roots and detached leaf explants as the model systems, a series of studies revealed the role of *LBD16* in the formation of the feeding structures [40, 47, 48] (Fig. 2d). At the transcriptome level, the early stages of the formation of the feeding structure gall in *A. thaliana* roots resemble those of the formation of the root primordium [47]. In addition, in *A. thaliana* leaf explants, root-knot nematodes can feed on giant cells within a callus-like structure induced from the vasculature, similar to the gall induced in roots [40]. The formation of giant cells within these feeding structures (galls in roots or callus-like structures in leaf explants) is likely to borrow the root organogenesis pathways. The cells that are initiated to form the feeding structures have high auxin levels and express *LBD16* [40, 47, 48] (Fig. 2d). Mutation of *LBD16* led to partially defective feeding structure formation in roots and leaf explants [40, 47, 48]. The *LBD16* expression level decreases when the feeding structures are partially differentiated [40, 47] (Fig. 2d). These observations suggested that the auxin signaling pathway and the *LBD16*-mediated molecular network are adopted for the formation of feeding structures induced by root-knot nematodes.

Interestingly, *ARF7/19* are not strictly involved in the formation of giant cells and feeding structures. Primary roots of the *arf7 arf19* double mutant were able to form feeding structures in response to root-knot nematodes [40]. Thus, upregulation of *LBD16* and the formation of feeding structures either from the roots or leaf explants may occur mainly through the AR pathway instead of the LR pathway. At present, it is unclear which ARFs are involved in this process (Fig. 2d).

It is plausible to speculate that the initiation step of feeding structures is based on the AR formation mechanism involving auxin-induced *LBD16* expression. In future research, it will be interesting to test whether *WOX11/12* are also involved in this process.

Conclusion and perspectives

The common role of *LBD16* in root and root-like organ formation is at the initiation step (see models in Fig. 2). Expression of *LBD16* is induced in the specified founder cells after the priming step, and it continues to be expressed in the root primordium, the newly formed callus, or feeding structures. Its expression gradually decreases when the patterning step begins. The roles of *LBD16* in root and root-like organ initiation may be to control cell division and to determine root-primordium identity.

Although *LBD16* is upregulated in the initiation step during the formation of roots and root-like organs, the upstream mechanisms that activate *LBD16* differ depending on the process. First, different ARFs are required to fulfill the auxin-mediated signaling pathway: ARF7/19 for LRs and other ARFs for ARs or AR-like organs (e.g., adventitious lateral roots from the primary root, callus from leaf explants, or feeding structures). Second, *WOX11/12* are required for *LBD16* upregulation in ARs or AR-like organs, but not LRs. The different molecular events' upstream of *LBD16* in the priming step might be due to the different status of founder cells in LR or AR organogenesis. While LR organogenesis requires several pairs of founder cells with nuclei migration and asymmetric founder cell division, there is no conclusive evidence that these factors are required for AR organogenesis or AR-like organ formation. Therefore, different molecular mechanisms operate in different LR and AR founder cells. One hypothesis was that *WOX11/12*-mediated AR organogenesis could be inherited from the ancient ability of intermediate-clade *WOX* (IC-*WOX*) genes in root founder cells [74]; because similar IC-*WOX*-mediated root organogenesis was also observed in a fern [75].

In summary, in the formation of root and root-like organs, diverse upstream priming mechanisms for the specification of founder cells may converge to activate *LBD16* expression to achieve cell division and fate transition in organ initiation (see models in Fig. 2).

Many questions about *LBD16* remain unanswered. First, it is largely unclear how other class-IB *LBD* genes interact with *LBD16* during root and root-like organ formation. It will be interesting to test whether class-IB *LBD* genes have partially redundant or unique functions. For example, *LBD29* is expressed in the root primordium during LR and AR formation [9, 36, 60, 76, 77], and its homologs CROWN ROTLESS1 (CRL1) in rice and ROOTLESS CONCERNING CROWN AND SEMINAL ROOTS (RTCS) in maize are involved in adventitious root (crown root) formation [78–82]. In addition, many class-IB *LBD* genes are upregulated during LR formation from the primary root or during callus formation on CIM [34, 36, 59, 73, 77, 83–87]. Furthermore, class-IB LBD proteins may form complexes to regulate downstream targets [88]. Further research is required to explore the shared and common roles of class-IB *LBD* genes. Second, it will be interesting to determine which ARF protein upregulates *LBD16* expression in AR organogenesis and AR-like organ formation. Why different ARF proteins function in different types of founder cells is an interesting question. Third, the genome-wide target analysis of LBD16 will provide new insights into how it regulates organ initiation. Fourth, the mechanism that downregulates *LBD16* expression in the patterning step is unclear. Fifth, further analysis of the protein complex involving LBD16 will provide new information about how LBD16 regulates

gene expression in the specific context of organ initiation. Sixth, it will be important to determine how the *LBD16* pathway acts synergistically with other pathways, for example the *PLETHORA*s (*PLT*s) and *WOX5/7* pathways, in root and root-like organ formation. *PLT3/5/7* and *WOX5/7* are all expressed in the root primordium or newly formed callus [33, 36, 37]. Mutations in either *PLT3/5/7* or *WOX5/7* resulted in abnormal root-primordium development or the loss of pluripotency in callus cells ([37, 89, 90] and our unpublished data). It is unclear how *LBD16*, *PLT3/5/7*, and *WOX5/7* form a regulatory network in this process [38]. Seventh, it will be interesting to explore how class-IB *LBD* genes have evolved and how and when were they recruited into root organogenesis, together with other rooting-related genes (e.g., *ARF*s and *WOX*s) [51–54, 74]. Answers to these questions will improve our understanding of root and root-like organ initiation and evolution.

Acknowledgements We apologize for references not cited due to space limitations. This work was supported by grants from the National Natural Science Foundation of China (31630007), National Basic Research Program of China (973 Program, 2014CB943500), the Key Research Program of CAS (QYZDB-SSW-SMC010), the Strategic Priority Research Program "Molecular Mechanism of Plant Growth and Development" of CAS (XDPB0403), and National Key Laboratory of Plant Molecular Genetics.

Compliance with ethical standards

Conflict of interest No conflicts of interest declared.

References

1. Falasca G, Altamura MM (2003) Histological analysis of adventitious rooting in *Arabidopsis thaliana* (L.) Heynh seedlings. Plant Biosyst 137(3):265–274
2. da Costa CT, de Almeida MR, Ruedell CM, Schwambach J, Maraschin FS, Fett-Neto AG (2013) When stress and development go hand in hand: main hormonal controls of adventitious rooting in cuttings. Front Plant Sci 4:133. https://doi.org/10.3389/fpls.2013.00133
3. Atkinson JA, Rasmussen A, Traini R, Voss U, Sturrock C, Mooney SJ, Wells DM, Bennett MJ (2014) Branching out in roots: uncovering form, function, and regulation. Plant Physiol 166(2):538–550. https://doi.org/10.1104/pp.114.245423
4. Bellini C, Pacurar DI, Perrone I (2014) Adventitious roots and lateral roots: similarities and differences. Annu Rev Plant Biol 65:639–666. https://doi.org/10.1146/annurev-arplant-050213-035645
5. Verstraeten I, Schotte S, Geelen D (2014) Hypocotyl adventitious root organogenesis differs from lateral root development. Front Plant Sci 5:495. https://doi.org/10.3389/fpls.2014.00495
6. Birnbaum KD (2016) How many ways are there to make a root? Curr Opin Plant Biol 34:61–67. https://doi.org/10.1016/j.pbi.2016.10.001
7. Steffens B, Rasmussen A (2016) The physiology of adventitious roots. Plant Physiol 170(2):603–617. https://doi.org/10.1104/pp.15.01360
8. Xu L (2018) *De novo* root regeneration from leaf explants: wounding, auxin, and cell fate transition. Curr Opin Plant Biol 41:39–45. https://doi.org/10.1016/j.pbi.2017.08.004
9. Okushima Y, Fukaki H, Onoda M, Theologis A, Tasaka M (2007) ARF7 and ARF19 regulate lateral root formation via direct activation of *LBD/ASL* genes in *Arabidopsis*. Plant Cell 19(1):118–130. https://doi.org/10.1105/tpc.106.047761
10. Moreno-Risueno MA, Van Norman JM, Moreno A, Zhang J, Ahnert SE, Benfey PN (2010) Oscillating gene expression determines competence for periodic *Arabidopsis* root branching. Science 329(5997):1306–1311. https://doi.org/10.1126/science.1191937
11. Xuan W, Audenaert D, Parizot B, Moller BK, Njo MF, De Rybel B, De Rop G, Van Isterdael G, Mahonen AP, Vanneste S, Beeckman T (2015) Root cap-derived auxin pre-patterns the longitudinal axis of the *Arabidopsis* root. Curr Biol 25(10):1381–1388. https://doi.org/10.1016/j.cub.2015.03.046
12. Xuan W, Band LR, Kumpf RP, Van Damme D, Parizot B, De Rop G, Opdenacker D, Moller BK, Skorzinski N, Njo MF, De Rybel B, Audenaert D, Nowack MK, Vanneste S, Beeckman T (2016) Cyclic programmed cell death stimulates hormone signaling and root development in *Arabidopsis*. Science 351(6271):384–387. https://doi.org/10.1126/science.aad2776
13. Du Y, Scheres B (2018) Lateral root formation and the multiple roles of auxin. J Exp Bot 69(2):155–167. https://doi.org/10.1093/jxb/erx223
14. Stoeckle D, Thellmann M, Vermeer JE (2018) Breakout-lateral root emergence in *Arabidopsis thaliana*. Curr Opin Plant Biol 41:67–72. https://doi.org/10.1016/j.pbi.2017.09.005
15. Esau K (1965) Plant anatomy, 2nd edn. Wiley, New York
16. Barlow PW (1986) Adventitious roots of whole plants: their forms, functions, and evolution. In: Jackson MB (ed) New root formation in plants and cuttings. Martinus Nijhoff, Hingham, pp 67–110
17. Charlton WA (1996) Lateral root initiation. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half, 2nd edn. Marcel Dekker Inc., New York, pp 149–173
18. Paolillo DJ Jr, Zobel RW (2002) The formation of adventitious roots on root axes is a widespread occurrence in field-grown dicotyledonous plants. Am J Bot 89(9):1361–1372. https://doi.org/10.3732/ajb.89.9.1361
19. Hou G, Hill JP, Blancaflor EB (2004) Developmental anatomy and auxin response of lateral root formation in *Ceratopteris richardii*. J Exp Bot 55(397):685–693. https://doi.org/10.1093/jxb/erh068
20. Sheng L, Hu X, Du Y, Zhang G, Huang H, Scheres B, Xu L (2017) Non-canonical *WOX11*-mediated root branching contributes to plasticity in *Arabidopsis* root system architecture. Development 144(17):3126–3133. https://doi.org/10.1242/dev.152132
21. Xu D, Miao J, Yumoto E, Yokota T, Asahina M, Watahiki M (2017) *YUCCA9*-mediated auxin biosynthesis and polar auxin transport synergistically regulate regeneration of root systems following root cutting. Plant Cell Physiol 58(10):1710–1723. https://doi.org/10.1093/pcp/pcx107
22. Baesso B, Chiatante D, Terzaghi M, Zenga D, Nieminen K, Mahonen AP, Siligato R, Heliariutta Y, Scippa GS, Montagnoli A (2018) PRE3 and WOX11 transcription factors are involved in the formation of new lateral roots from secondary growth taproot in *A. thaliana*. Plant Biol (Stuttg). https://doi.org/10.1111/plb.12711
23. Ge Y, Fang X, Liu W, Sheng L, Xu L (2018) Adventitious lateral rooting: the plasticity of root system architecture. Physiol Plant. https://doi.org/10.1111/ppl.12741
24. Duclercq J, Sangwan-Norreel B, Catterou M, Sangwan RS (2011) De novo shoot organogenesis: from art to science. Trends Plant Sci 16(11):597–606. https://doi.org/10.1016/j.tplants.2011.08.004
25. Sugimoto K, Gordon SP, Meyerowitz EM (2011) Regeneration in plants and animals: dedifferentiation, transdifferentiation, or

just differentiation? Trends Cell Biol 21(4):212–218. https://doi.org/10.1016/j.tcb.2010.12.004
26. Ikeuchi M, Sugimoto K, Iwase A (2013) Plant callus: mechanisms of induction and repression. Plant Cell 25(9):3159–3173. https://doi.org/10.1105/tpc.113.116053
27. Su YH, Zhang XS (2014) The hormonal control of regeneration in plants. Curr Top Dev Biol 108:35–69. https://doi.org/10.1016/B978-0-12-391498-9.00010-3
28. Xu L, Huang H (2014) Genetic and epigenetic controls of plant regeneration. Curr Top Dev Biol 108:1–33. https://doi.org/10.1016/B978-0-12-391498-9.00009-7
29. Ikeuchi M, Ogawa Y, Iwase A, Sugimoto K (2016) Plant regeneration: cellular origins and molecular mechanisms. Development 143(9):1442–1451. https://doi.org/10.1242/dev.134668
30. Kareem A, Radhakrishnan D, Sondhi Y, Aiyaz M, Roy MV, Sugimoto K, Prasad K (2016) De novo assembly of plant body plan: a step ahead of Deadpool. Regeneration (Oxf) 3(4):182–197. https://doi.org/10.1002/reg2.68
31. Lee K, Seo PJ (2018) Dynamic epigenetic changes during plant regeneration. Trends Plant Sci 23(3):235–247. https://doi.org/10.1016/j.tplants.2017.11.009
32. Sang YL, Cheng ZJ, Zhang XS (2018) iPSCs: a comparison between animals and plants. Trends Plant Sci. https://doi.org/10.1016/j.tplants.2018.05.008
33. Sugimoto K, Jiao Y, Meyerowitz EM (2010) *Arabidopsis* regeneration from multiple tissues occurs via a root development pathway. Dev Cell 18(3):463–471. https://doi.org/10.1016/j.devcel.2010.02.004
34. Fan M, Xu C, Xu K, Hu Y (2012) LATERAL ORGAN BOUNDARIES DOMAIN transcription factors direct callus formation in *Arabidopsis* regeneration. Cell Res 22(7):1169–1180. https://doi.org/10.1038/cr.2012.63
35. He C, Chen X, Huang H, Xu L (2012) Reprogramming of H3K27me3 is critical for acquisition of pluripotency from cultured *Arabidopsis* tissues. PLoS Genet 8(8):e1002911. https://doi.org/10.1371/journal.pgen.1002911
36. Liu J, Sheng L, Xu Y, Li J, Yang Z, Huang H, Xu L (2014) *WOX11* and *12* are involved in the first-step cell fate transition during de novo root organogenesis in *Arabidopsis*. Plant Cell 26(3):1081–1093. https://doi.org/10.1105/tpc.114.122887
37. Kareem A, Durgaprasad K, Sugimoto K, Du Y, Pulianmackal AJ, Trivedi ZB, Abhayadev PV, Pinon V, Meyerowitz EM, Scheres B, Prasad K (2015) *PLETHORA* genes control regeneration by a two-step mechanism. Curr Biol 25(8):1017–1030. https://doi.org/10.1016/j.cub.2015.02.022
38. Liu J, Hu X, Qin P, Prasad K, Hu Y, Xu L (2018) The *WOX11-LBD16* pathway promotes pluripotency acquisition in callus cells during de novo shoot regeneration in tissue culture. Plant Cell Physiol 59(4):734–743. https://doi.org/10.1093/pcp/pcy010
39. Kyndt T, Vieira P, Gheysen G, de Almeida-Engler J (2013) Nematode feeding sites: unique organs in plant roots. Planta 238(5):807–818. https://doi.org/10.1007/s00425-013-1923-z
40. Olmo R, Cabrera J, Moreno-Risueno MA, Fukaki H, Fenoll C, Escobar C (2017) Molecular transducers from roots are triggered in *Arabidopsis* leaves by root-knot nematodes for successful feeding site formation: a conserved post-embryogenic de novo organogenesis program? Front Plant Sci 8:875. https://doi.org/10.3389/fpls.2017.00875
41. Barthels N, van der Lee FM, Klap J, Goddijn OJ, Karimi M, Puzio P, Grundler FM, Ohl SA, Lindsey K, Robertson L, Robertson WM, Van Montagu M, Gheysen G, Sijmons PC (1997) Regulatory sequences of *Arabidopsis* drive reporter gene expression in nematode feeding structures. Plant Cell 9(12):2119–2134
42. Koltai H, Dhandaydham M, Opperman C, Thomas J, Bird D (2001) Overlapping plant signal transduction pathways induced by a parasitic nematode and a rhizobial endosymbiont. Mol Plant Microbe Interact 14(10):1168–1177. https://doi.org/10.1094/MPMI.2001.14.10.1168
43. Favery B, Complainville A, Vinardell JM, Lecomte P, Vaubert D, Mergaert P, Kondorosi A, Kondorosi E, Crespi M, Abad P (2002) The endosymbiosis-induced genes *ENOD40* and *CCS52a* are involved in endoparasitic–nematode interactions in *Medicago truncatula*. Mol Plant Microbe Interact 15(10):1008–1013. https://doi.org/10.1094/MPMI.2002.15.10.1008
44. Mathesius U (2003) Conservation and divergence of signaling pathways between roots and soil microbes-the Rhizobium-legume symbiosis compared to the development of lateral roots, mycorrhizal interactions and matode-induced galls. Plant Soil 255:105–119
45. Grunewald W, Karimi M, Wieczorek K, Van de Cappelle E, Wischnitzki E, Grundler F, Inze D, Beeckman T, Gheysen G (2008) A role for AtWRKY23 in feeding site establishment of plant-parasitic nematodes. Plant Physiol 148(1):358–368. https://doi.org/10.1104/pp.108.119131
46. Quentin M, Abad P, Favery B (2013) Plant-parasitic nematode effectors target host defense and nuclear functions to establish feeding cells. Front Plant Sci 4:53. https://doi.org/10.3389/fpls.2013.00053
47. Cabrera J, Diaz-Manzano FE, Sanchez M, Rosso MN, Melillo T, Goh T, Fukaki H, Cabello S, Hofmann J, Fenoll C, Escobar C (2014) A role for *LATERAL ORGAN BOUNDARIES-DOMAIN 16* during the interaction *Arabidopsis-Meloidogyne* spp. provides a molecular link between lateral root and root-knot nematode feeding site development. New Phytol 203(2):632–645. https://doi.org/10.1111/nph.12826
48. Cabrera J, Fenoll C, Escobar C (2015) Genes co-regulated with *LBD16* in nematode feeding sites inferred from in silico analysis show similarities to regulatory circuits mediated by the auxin/cytokinin balance in *Arabidopsis*. Plant Signal Behav 10(3):e990825. https://doi.org/10.4161/15592324.2014.990825
49. Iwakawa H, Ueno Y, Semiarti E, Onouchi H, Kojima S, Tsukaya H, Hasebe M, Soma T, Ikezaki M, Machida C, Machida Y (2002) The *ASYMMETRIC LEAVES2* gene of *Arabidopsis thaliana*, required for formation of a symmetric flat leaf lamina, encodes a member of a novel family of proteins characterized by cysteine repeats and a leucine zipper. Plant Cell Physiol 43(5):467–478
50. Shuai B, Reynaga-Pena CG, Springer PS (2002) The *lateral organ boundaries* gene defines a novel, plant-specific gene family. Plant Physiol 129(2):747–761. https://doi.org/10.1104/pp.010926
51. Yang Y, Yu X, Wu P (2006) Comparison and evolution analysis of two rice subspecies *LATERAL ORGAN BOUNDARIES* domain gene family and their evolutionary characterization from *Arabidopsis*. Mol Phylogenet Evol 39(1):248–262. https://doi.org/10.1016/j.ympev.2005.09.016
52. Majer C, Hochholdinger F (2011) Defining the boundaries: structure and function of LOB domain proteins. Trends Plant Sci 16(1):47–52. https://doi.org/10.1016/j.tplants.2010.09.009
53. Coudert Y, Dievart A, Droc G, Gantet P (2013) ASL/LBD phylogeny suggests that genetic mechanisms of root initiation downstream of auxin are distinct in lycophytes and euphyllophytes. Mol Biol Evol 30(3):569–572. https://doi.org/10.1093/molbev/mss250
54. Kong Y, Xu P, Jing X, Chen L, Li L, Li X (2017) Decipher the ancestry of the plant-specific *LBD* gene family. BMC Genom 18(Suppl 1):951. https://doi.org/10.1186/s12864-016-3264-3
55. Peret B, De Rybel B, Casimiro I, Benkova E, Swarup R, Laplaze L, Beeckman T, Bennett MJ (2009) *Arabidopsis* lateral root development: an emerging story. Trends Plant Sci 14(7):399–408. https://doi.org/10.1016/j.tplants.2009.05.002
56. Lavenus J, Goh T, Roberts I, Guyomarc'h S, Lucas M, De Smet I, Fukaki H, Beeckman T, Bennett M, Laplaze L (2013) Lateral root development in *Arabidopsis*: fifty shades of auxin. Trends Plant Sci 18(8):450–458. https://doi.org/10.1016/j.tplants.2013.04.006

57. Goh T, Toyokura K, Wells DM, Swarup K, Yamamoto M, Mimura T, Weijers D, Fukaki H, Laplaze L, Bennett MJ, Guyomarc'h S (2016) Quiescent center initiation in the *Arabidopsis* lateral root primordia is dependent on the *SCARECROW* transcription factor. Development 143(18):3363–3371. https://doi.org/10.1242/dev.135319
58. Goh T, Joi S, Mimura T, Fukaki H (2012) The establishment of asymmetry in *Arabidopsis* lateral root founder cells is regulated by LBD16/ASL18 and related LBD/ASL proteins. Development 139(5):883–893. https://doi.org/10.1242/dev.071928
59. Lee HW, Kim NY, Lee DJ, Kim J (2009) LBD18/ASL20 regulates lateral root formation in combination with LBD16/ASL18 downstream of ARF7 and ARF19 in *Arabidopsis*. Plant Physiol 151(3):1377–1389. https://doi.org/10.1104/pp.109.143685
60. Feng Z, Zhu J, Du X, Cui X (2012) Effects of three auxin-inducible LBD members on lateral root formation in *Arabidopsis thaliana*. Planta 236(4):1227–1237. https://doi.org/10.1007/s00425-012-1673-3
61. Okushima Y, Overvoorde PJ, Arima K, Alonso JM, Chan A, Chang C, Ecker JR, Hughes B, Lui A, Nguyen D, Onodera C, Quach H, Smith A, Yu G, Theologis A (2005) Functional genomic analysis of the *AUXIN RESPONSE FACTOR* gene family members in *Arabidopsis thaliana*: unique and overlapping functions of *ARF7* and *ARF19*. Plant Cell 17(2):444–463. https://doi.org/10.1105/tpc.104.028316
62. Fukaki H, Tameda S, Masuda H, Tasaka M (2002) Lateral root formation is blocked by a gain-of-function mutation in the *SOLITARY-ROOT/IAA14* gene of *Arabidopsis*. Plant J 29(2):153–168
63. Ito J, Fukaki H, Onoda M, Li L, Li C, Tasaka M, Furutani M (2016) Auxin-dependent compositional change in mediator in ARF7- and ARF19-mediated transcription. Proc Natl Acad Sci USA 113(23):6562–6567. https://doi.org/10.1073/pnas.1600739113
64. Chen X, Qu Y, Sheng L, Liu J, Huang H, Xu L (2014) A simple method suitable to study de novo root organogenesis. Front Plant Sci 5:208. https://doi.org/10.3389/fpls.2014.00208
65. Hu X, Xu L (2016) Transcription factors WOX11/12 directly activate *WOX5/7* to promote root primordia initiation and organogenesis. Plant Physiol 172(4):2363–2373. https://doi.org/10.1104/pp.16.01067
66. Wilmoth JC, Wang S, Tiwari SB, Joshi AD, Hagen G, Guilfoyle TJ, Alonso JM, Ecker JR, Reed JW (2005) NPH4/ARF7 and ARF19 promote leaf expansion and auxin-induced lateral root formation. Plant J 43(1):118–130. https://doi.org/10.1111/j.1365-313X.2005.02432.x
67. Che P, Lall S, Howell SH (2007) Developmental steps in acquiring competence for shoot development in *Arabidopsis* tissue culture. Planta 226(5):1183–1194. https://doi.org/10.1007/s00425-007-0565-4
68. Atta R, Laurens L, Boucheron-Dubuisson E, Guivarc'h A, Carnero E, Giraudat-Pautot V, Rech P, Chriqui D (2009) Pluripotency of *Arabidopsis* xylem pericycle underlies shoot regeneration from root and hypocotyl explants grown in vitro. Plant J 57(4):626–644. https://doi.org/10.1111/j.1365-313X.2008.03715.x
69. Yu J, Liu W, Liu J, Qin P, Xu L (2017) Auxin control of root organogenesis from callus in tissue culture. Front Plant Sci 8:1385. https://doi.org/10.3389/fpls.2017.01385
70. Xu C, Cao H, Zhang Q, Wang H, Xin W, Xu E, Zhang S, Yu R, Yu D, Hu Y (2018) Control of auxin-induced callus formation by bZIP59-LBD complex in *Arabidopsis* regeneration. Nat Plants 4(2):108–115. https://doi.org/10.1038/s41477-017-0095-4
71. Lee K, Park OS, Seo PJ (2017) *Arabidopsis* ATXR2 deposits H3K36me3 at the promoters of *LBD* genes to facilitate cellular dedifferentiation. Sci Signal 10(507):eaan0316. https://doi.org/10.1126/scisignal.aan0316
72. Ikeuchi M, Shibata M, Rymen B, Iwase A, Bagman AM, Watt L, Coleman D, Favero DS, Takahashi T, Ahnert SE, Brady SM, Sugimoto K (2018) A gene regulatory network for cellular reprogramming in plant regeneration. Plant Cell Physiol. https://doi.org/10.1093/pcp/pcy013
73. Lee HW, Kim MJ, Kim NY, Lee SH, Kim J (2013) LBD18 acts as a transcriptional activator that directly binds to the *EXPANSIN14* promoter in promoting lateral root emergence of *Arabidopsis*. Plant J 73:212–224. https://doi.org/10.1111/tpj.12013
74. Liu W, Xu L (2018) Recruitment of IC-*WOX* genes in root evolution. Trends Plant Sci 23(6):490–496. https://doi.org/10.1016/j.tplants.2018.03.011
75. Nardmann J, Werr W (2012) The invention of WUS-like stem cell-promoting functions in plants predates leptosporangiate ferns. Plant Mol Biol 78(1–2):123–134. https://doi.org/10.1007/s11103-011-9851-4
76. Feng Z, Sun X, Wang G, Liu H, Zhu J (2012) LBD29 regulates the cell cycle progression in response to auxin during lateral root formation in *Arabidopsis thaliana*. Ann Bot 110(1):1–10. https://doi.org/10.1093/aob/mcs019
77. Porco S, Larrieu A, Du Y, Gaudinier A, Goh T, Swarup K, Swarup R, Kuempers B, Bishopp A, Lavenus J, Casimiro I, Hill K, Benkova E, Fukaki H, Brady SM, Scheres B, Peret B, Bennett MJ (2016) Lateral root emergence in *Arabidopsis* is dependent on transcription factor LBD29 regulation of auxin influx carrier *LAX3*. Development 143(18):3340–3349. https://doi.org/10.1242/dev.136283
78. Inukai Y, Sakamoto T, Ueguchi-Tanaka M, Shibata Y, Gomi K, Umemura I, Hasegawa Y, Ashikari M, Kitano H, Matsuoka M (2005) *Crown rootless1*, which is essential for crown root formation in rice, is a target of an AUXIN RESPONSE FACTOR in auxin signaling. Plant Cell 17(5):1387–1396. https://doi.org/10.1105/tpc.105.030981
79. Taramino G, Sauer M, Stauffer JL Jr, Multani D, Niu X, Sakai H, Hochholdinger F (2007) The maize (*Zea mays* L.) *RTCS* gene encodes a LOB domain protein that is a key regulator of embryonic seminal and post-embryonic shoot-borne root initiation. Plant J 50(4):649–659. https://doi.org/10.1111/j.1365-313X.2007.03075.x
80. Majer C, Xu C, Berendzen KW, Hochholdinger F (2012) Molecular interactions of ROOTLESS CONCERNING CROWN AND SEMINAL ROOTS, a LOB domain protein regulating shoot-borne root initiation in maize (*Zea mays* L.). Philos Trans R Soc Lond B Biol Sci 367(1595):1542–1551. https://doi.org/10.1098/rstb.2011.0238
81. Coudert Y, Le VA, Adam H, Bes M, Vignols F, Jouannic S, Guiderdoni E, Gantet P (2015) Identification of CROWN ROOTLESS1-regulated genes in rice reveals specific and conserved elements of post-embryonic root formation. New Phytol 206(1):243–254. https://doi.org/10.1111/nph.13196
82. Xu C, Tai H, Saleem M, Ludwig Y, Majer C, Berendzen KW, Nagel KA, Wojciechowski T, Meeley RB, Taramino G, Hochholdinger F (2015) Cooperative action of the paralogous maize lateral organ boundaries (LOB) domain proteins RTCS and RTCL in shoot-borne root formation. New Phytol 207(4):1123–1133. https://doi.org/10.1111/nph.13420
83. Berckmans B, Vassileva V, Schmid SP, Maes S, Parizot B, Naramoto S, Magyar Z, Kamei CL, Koncz C, Bogre L, Persiau G, De Jaeger G, Friml J, Simon R, Beeckman T, De Veylder L (2011) Auxin-dependent cell cycle reactivation through transcriptional regulation of *Arabidopsis E2Fa* by lateral organ boundary proteins. Plant Cell 23(10):3671–3683. https://doi.org/10.1105/tpc.111.088377
84. Kang NY, Lee HW, Kim J (2013) The AP2/EREBP gene *PUCHI* Co-Acts with *LBD16/ASL18* and *LBD18/ASL20* downstream of *ARF7* and *ARF19* to regulate lateral root development in

Arabidopsis. Plant Cell Physiol 54(8):1326–1334. https://doi.org/10.1093/pcp/pct081

85. Lee HW, Kim J (2013) *EXPANSINA17* upregulated by LBD18/ASL20 promotes lateral root formation during the auxin response. Plant Cell Physiol 54(10):1600–1611. https://doi.org/10.1093/pcp/pct105
86. Lee HW, Cho C, Kim J (2015) *Lateral Organ Boundaries Domain16* and *18* act downstream of the AUXIN1 and LIKE-AUXIN3 auxin influx carriers to control lateral root development in *Arabidopsis*. Plant Physiol 168(4):1792–1806. https://doi.org/10.1104/pp.15.00578
87. Jeon E, Young Kang N, Cho C, Joon Seo P, Chung Suh M, Kim J (2017) *LBD14/ASL17* positively regulates lateral root formation and is involved in ABA response for root architecture in *Arabidopsis*. Plant Cell Physiol 58(12):2190–2201. https://doi.org/10.1093/pcp/pcx153
88. Lee HW, Kang NY, Pandey SK, Cho C, Lee SH, Kim J (2017) Dimerization in LBD16 and LBD18 transcription factors is critical for lateral root formation. Plant Physiol 174(1):301–311. https://doi.org/10.1104/pp.17.00013
89. Hofhuis H, Laskowski M, Du Y, Prasad K, Grigg S, Pinon V, Scheres B (2013) Phyllotaxis and rhizotaxis in *Arabidopsis* are modified by three PLETHORA transcription factors. Curr Biol 23(11):956–962. https://doi.org/10.1016/j.cub.2013.04.048
90. Du Y, Scheres B (2017) PLETHORA transcription factors orchestrate de novo organ patterning during *Arabidopsis* lateral root outgrowth. Proc Natl Acad Sci USA 114(44):11709–11714. https://doi.org/10.1073/pnas.1714410114
91. Ge Y, Liu J, Zeng M, He J, Qin P, Huang H, Xu L (2016) Identification of wox family genes in *Selaginella kraussiana* for studies on stem cells and regeneration in lycophytes. Front Plant Sci 7:93. https://doi.org/10.3389/fpls.2016.00093
92. Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Mol Biol Evol 33(7):1870–1874. https://doi.org/10.1093/molbev/msw054