distortion system present in the ancestor, or it was evolved *de novo* to allow the production of males, which would be favoured by selection when sexual reproduction is advantageous. It would be interesting to determine the mechanism by which *S. ratti* produce all-female offspring from matings between males and females, as this scenario predicts that sperm that lack an X should be dysfunctional or lacking, just as in *S. papillosus*, perhaps as a result of chromatin diminution. In addition, we would expect to see evidence for dosage compensation of X-linked genes in males, possibly using the same mechanisms as in *C. elegans* [17].

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Plant Development: Early Events in Lateral Root Initiation

How are the lateral root founder cells specified in the pericycle to initiate lateral root development? An Aux/IAA28 signaling module activates transcription factor *GATA23* to control founder cell identity.

Shri Ram Yadav, Anthony Bishopp, and Ykä Helariutta*

Higher plants have a branched root system that anchors them in the soil, allowing the uptake of essential nutrients and water. This root system consists of the primary root, which exhibits several branching mechanisms, including the formation of lateral roots. In *Arabidopsis,* lateral roots originate after embryogenesis from the root pericycle layer and emerge in the differentiation zone [1]. The pericycle layer consists of quiescent cells at the phloem pole and cells competent to initiate cell division at the xylem pole [2]. Genetic analysis has shown that the pericycle heterogeneity and diarch vascular organization are set up early in the root meristem and are regulated by the same genetic pathway [3,4]. Primary root growth is driven by a group of stem cells at the root apex. New daughter cells are continuously produced and displaced further away from the root tip. Therefore, there is a chronology of cells where the youngest occupy the meristematic zone and older cells pass through the elongation zone where they attain their final size before they differentiate at the differentiation zone [5]. Although the earliest cellular events in lateral root initiation are only detected several millimeters distal to the root meristem [2,6], the decision by xylem pole pericycle (XPP) cells to develop lateral roots is taken in the 'basal meristem', the region at the transition between the root meristem and the elongation zone (Figures 1A,B) [7,8].

The role of the phytohormone auxin as an important factor controlling lateral root development is well established. The Aux/IAA family of auxin signaling inhibitors represses the activity of a group of transcription factors called auxin response factors (ARFs), which initiate transcription of auxin-responsive genes. Auxin regulation is achieved by rapidly modulating levels of Aux/IAAs throughout development. Auxin binds to the F-box protein TIR1, which forms part of the SCF^{TIR1} ubiquitin ligase complex. When bound to auxin, the SCF^{TIR1} complex targets Aux/IAA proteins for proteolytic degradation, which releases the ARFs from Aux/IAA-mediated repression [9]. In *Arabidopsis*, Aux/IAA and ARF proteins are represented by large gene families and specific responses between co-expressed ARFs and IAAs can mediate different developmental responses [10,11].

During lateral root development auxin functions through successively acting regulatory modules: the SOLITARY ROOT (SLR/IAA14)–AUXIN REPONSE FACTOR (ARF7–ARF19)–LATERAL ORGAN BOUNDERIES DOMAINS (LBD/ASL) module regulates the division of XPP cells during lateral root initiation and the successive BODENLOS (BDL/IAA12)–ARF5 module regulates lateral root organogenesis (Figure 1B) [12–14]. Which factor(s) decides the founder cell

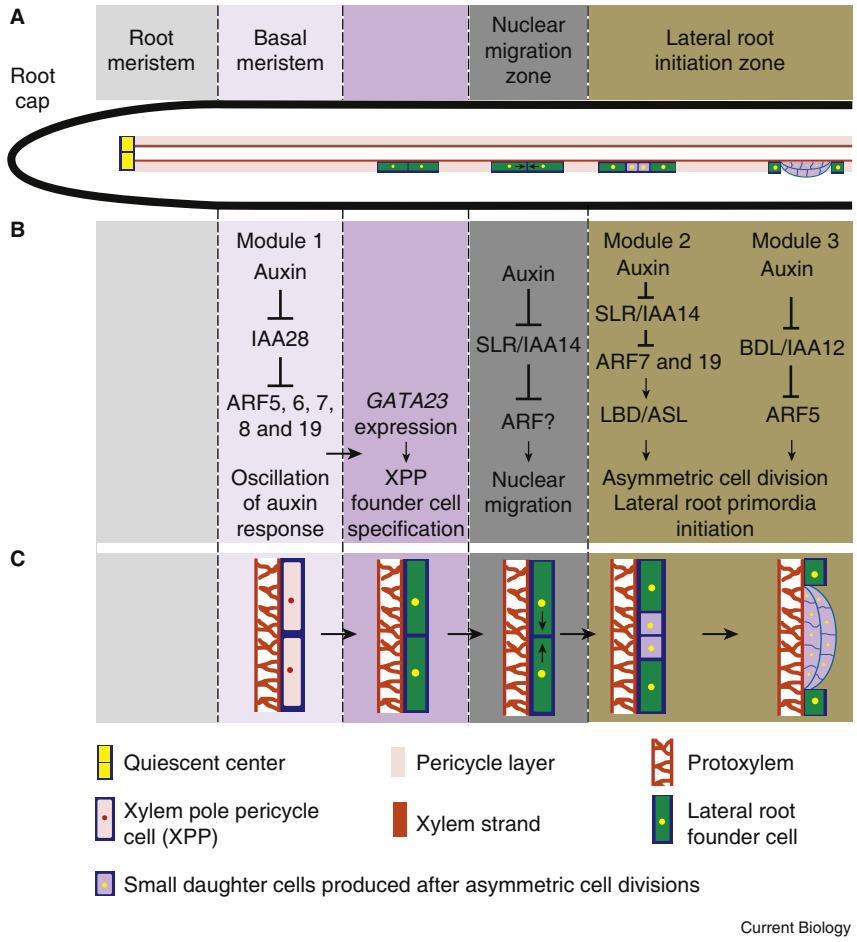

Figure 1. Auxin signaling modules and associated cellular events acting successively during *Arabidopsis* lateral root initiation.

(A) Schematic diagram showing different zones of the root. The quiescent centre of the root meristem is marked in yellow, red lines mark xylem strands and blue lines denote pericycle cell layers. XPP cells are marked in green, upon asymmetric division they produce smaller daughter cells (violet), which give rise to most of the lateral root primordium. (B) Schematic diagram illustrating the auxin-mediated molecular events acting in various regions of the root during lateral root initiation. Module 1 acts in the basal meristem and activates *GATA23*, which specifies XPP cells as founder cells of lateral roots. Modules 2 and 3 ensure the subsequent steps of lateral root development, such as nuclear migration and asymmetric cell divisions. (C) Schematic diagram showing various cellular events during lateral root initiation. A few XPP cells adopt founder cell identities due to the activity of *GATA23* and subsequently begin nuclear migration, followed by several rounds of anticlinal and periclinal cell divisions, resulting in lateral root primordia initiation.

identity and controls the longitudinal spacing of lateral roots? De Smet *et al.* [8] have demonstrated that the auxin response oscillates in the basal meristem, with auxin-responsive promoter activity peaking at regular intervals of 15 hours, correlating with the formation of consecutive lateral roots. They propose that this oscillation is an underlying mechanism for priming lateral root initiation. Alternatively, Laskowski *et al.* [15] have suggested mechanical stimuli as a primary cause for elevated auxin levels in the XPP cells located only on the outside of a root curve. Since the spacing of lateral root primordia is responsive to both environmental and endogenous signals, Peret *et al.* [2] suggested that both mechanisms may exist and function independently of the other. Although such recurrent auxin signaling events appear to regulate founder cell identity, the molecular basis was not known. In this issue of *Current Biology*, De Rybel *et al.* [16] report a novel auxin signaling module that acts at the earliest stage of lateral root development in the basal meristem and which establishes founder cell identity in a subset of XPP cells [16].

De Rybel *et al.* [16] began their study by performing a meta-analysis of all relevant available transcriptome data sets to identify regulatory genes involved in the early stages of lateral root initiation. The selected genes were differentially expressed between xylem and phloem pole pericycle cells but not expressed in other radial layers, were auxin responsive, and were predicted to have a role in asymmetric division but not in cell-cycle phase transition. By applying these criteria, the authors identified *GATA23*, a member of the GATA-type family of transcription factors, which are known to have several regulatory roles in cell fate specification both in animals [17] and plants [18]. The *GATA23* promoter was used to drive the expression of *GUS* (a reporter gene) and signal was observed in a subset of XPP cells prior to lateral root initiation and during early stages of lateral root formation. Next, the authors investigated the order of cellular events and auxin responses before the first asymmetric division. They confirmed the auxin response in two neighboring XPP cells [19] and observed *GATA23* expression in these cells. Following *GATA23* expression, the nuclei of these cells migrate towards the common wall and shortly after the first asymmetric cell divisions occur. The authors then showed that this synchronized migration of nuclei was SLR/IAA14-dependent.

To further understand the function of *GATA23,* De Rybel *et al.* [16] generated RNAi lines to down-regulate the expression of *GATA23*. They observed a strong reduction in the number of both emerged and non-emerged lateral root primordia. Interestingly, XPP-specific over-expression of *GATA23* caused an increase in the amount of non-emerged primordia due to excessive founder cell specification, indicating that *GATA23* is necessary and sufficient in controlling founder cell identity of XPP cells.

Since *GATA23* expression is regulated by auxin, the authors established the relationship between *GATA23* expression and auxin responses by monitoring the temporal expression of p*DR5*::GUS (a synthetic promoter marking auxin response) and p*GATA23*::GUS. They observed an oscillating p*DR5*::GUS maximum in the protoxylem cells of the basal meristem

and a concomitant patchy expression of p*GATA23*::GUS in XPP cells about 10 hours after each p*DR5*::GUS peak. This p*GATA23*::GUS expression requires TIR-mediated auxin signaling in the basal meristem. Since a previous study had shown that the auxin response in the basal meristem is independent of SLR/IAA14 [8], the authors sought to ascertain which TIR1-mediated auxin signaling module acts in the basal meristem. They examined the expression of *GATA23* in available *aux/iaa* mutants and showed that both the relative expression level and promoter activity of *GATA23* was reduced only in the *iaa28-1* gain-of-function mutant. Furthermore, *IAA28* expression was found to be associated with the basal meristem and there were a reduced number of lateral root primordia in *iaa28-1* mutants [20]. The authors also demonstrated that ectopic expression of *GATA23* in the XPP cells of *iaa28-1* complements the lateral root phenotype, indicating that *GATA23* acts downstream of the TIR1–IAA28 pathway [16].

Finally, De Rybel *et al.* [16] identified a set of ARFs that interact with IAA28 in yeast two-hybrid assays and are expressed in the basal meristem. The expression of *GATA23* is completely absent in *arf7arf19* double mutants, indicating a role of *ARF7* and *ARF19* in *GATA23* activation and lateral root initiation. Thus, De Rybel *et al.* [16] have identified the first molecular component of founder cell specification and a novel TIR1–IAA28-mediated auxin signaling module acting in the basal meristem to assign founder cell identity to XPP cells (Figures 1A–C). This is followed by a SLR/IAA14-dependent auxin signaling module that operates just above the basal meristem and guides the coordinated nuclear migration before asymmetric cell division.

As revealed by De Rybel *et al.* [16], *GATA23* expression is now the earliest known event associated with lateral root development. Therefore, the gene will serve as an important marker for further studies trying to define in more detail the early events of lateral root founder cell specification. It will next be interesting to analyze how the oscillating auxin maximum and *GATA23* expression are spatially specified in the domain above the root apical meristem. *GATA23* will also be informative in identifying the nature of the positional cues that make XPP cells distinct from other pericycle cells.

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Intracellular Transport: ER and Mitochondria Meet and Greet along Designated Tracks

A recent study shows that contacts between the endoplasmic reticulum and mitochondria occur preferentially on acetylated microtubules, providing physiological support for the microtubule track selectivity of molecular motors.

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Microtubules play a great variety of roles in the eukaryotic cell. Foremost, in interphase cells, microtubules act as the tracks upon which molecular motors traverse as they distribute myriad cellular cargoes throughout the cytoplasm. This microtubule-based transport is essential for any cell