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REVIEW

Patterning the embryo in higher plants: Emerging pathways and challenges

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Abstract **Embryogenesis, which establishes the basic body plan for the post-embryonic organs after stereotyped cell divisions, initiates the first step of the plant life cycle. Studies in the last two decades indicate that embryogenesis is a precisely controlled process, and any defect would result in abnormalities. Here we discuss the recent progresses, with a focus on the cellular pathways governing early embryogenesis in the model species *Arabidopsis*.**

Keywords *Arabidopsis* embryogenesis, auxin signaling, receptor-like kinases (RLKs), non-cell-autonomous transcription factors and microRNA

The stereotyped embryo development in higher plants

As a model plant, *Arabidopsis* is widely used to study the embryogenesis in higher plants. Research benefits from the simple organization and invariant division order in *Arabidopsis* embryo development, and thus, each tissue or organ can be easily traced back to specific initial cells in the embryo (West and Harada, 1993; De Smet et al., 2010). The fusion of egg and sperm produces a zygote which undergoes elongation phase and then division. The first division of zygote is transversal and asymmetric, generating a small apical and a large basal cell. The basal cell divides transversally to produce a single file of cells. The upper-most hypophyseal cell in this file contributes to the formation of the root apex, and the other cells compose the suspensor, which is a transient structure and will undergo degeneration. The apical cell featured with condensed cytoplasm and large nucleus, proliferates the most part of the embryo except the hypophyseal cell lineage. The apical cell undergoes two longitudinal divisions to form a quadrant embryo. A subsequent transversal division results in the upper and lower tires of the octant embryo. Each cell in the octant divides tangentially to form the dermatogen embryo, which comprises the outer protoderm and inner subprotoderm. The next round of division will form the early globular embryo, and when the number of cells in the globular embryo grows up to about two hundred, the embryo will enter into a heart embryo stage, a transition from the radical to the lateral symmetric pattern. The asymmetric growth at the top tire leads to the formation of a central shoot apical meristem in the middle and two flanking cotyledon primordia. The subprotoderm differentiates into the vascular primordium and ground tissue, together with the protoderm and the hypophyseal cell forming the embryonic radicle. The hypocotyl connecting the shoot and root apical meristems (SAM and RAM) becomes evident as a result of the elongation and transversal division. At the torpedo embryo stage, there is a refinement and further differentiation in every part of the embryo, and the differentiation in the hypocotyl and root is completed and the provascular bundle appears in the cotyledon. Until now, the embryo has established the apical-basal body axis consisting of cotyledon, hypocotyl and root meristem, as well as lateral axis including epidermis, ground tissue and vascular system, defining the blueprint for the post embryonic development.

The mechanism underlying the initial asymmetric division of zygote

Asymmetric division is a fundamental process that occurs in diverse contexts of plant development, which plays a crucial

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role in cell fate specification, tissue patterning and cellular renewal (Pillitteri et al., 2007; Abrash and Bergmann, 2009). Insights have been obtained from the analysis of mutants related to the first division of zygote, such as the *gnom/emb30*, *root-shoot-hypocotyl-defective* (*rsh*), *embryonic factor 1* (*fac 1*), and *yaozhe* (*yao*) (Shevell et al., 1994; Torres-Ruiz and Jurgens, 1994; Hall and Cannon, 2002; Li et al., 2010), however, the molecular mechanism underlying zygote asymmetric division is still largely unknown. Studies on animal systems suggest that the first division of zygote may requires both intrinsic and extrinsic cues to "direct and survey" this critical process. For instance, PARTITION (PAR) complexes, comprising PAR proteins and atypical protein kinases, serve as the determinant of asymmetry division through their polar distribution prior to division (Kemphues et al., 1988; Suzuki and Ohno, 2006; St Johnston and Ahringer, 2010). There are extrinsic cues involved in the asymmetric division as well, such as the WINGLESS AND INT (WNT) signaling components, which regulate the expression of the downstream genes that are essential for cell polarity and asymmetric division (Goldstein et al., 2006). No genes in the plant genome has been identified as the homolog of PARs, furthermore, whether the auxin or CLAVATA3 (CLV3)/ENDOSPERM SURROUNDING REGION (ESR) related (CLE) peptides act as the morphogen in plant, in a similar manner to WNT signaling in animal systems, is still unclear yet. Alternatively, plant may employ different intrinsic and extrinsic signals to mediate the asymmetric division (Menke and Scheres, 2009). Indeed, recent studies have confirmed that both the intrinsic and extrinsic cues are involved in asymmetric division during stomatal development in maize and *Arabidopsis*. BREAKING OF ASYMMETRY IN THE STOMATAL LINEAGE (BASL) acts as an intrinsic determinant of the *Arabidopsis* stomata lineage (Dong et al., 2009) whereas PANGLOSS1 (PAN1), a leucine-rich repeat receptor-like protein (LRR-RLK), may serve as the receptor of unidentified extrinsic signal to promote the asymmetric division in maize (Cartwright et al., 2009). Further investigation is required to clarify the function of BASL and PAN1, as well as the existence of extracellular signal promoting the zygote asymmetric division in *Arabidopsis*.

Pathways involved in specification of the apical and basal cell fate

The apical and basal progeny from the zygote asymmetric division have different cell fates as far as the pattern of cell division and transcriptional profiles. Some progress has been made in exploring the mechanism controlling the cell fate of the apical and basal cells. The best known is the SHORT SUSPENSOR (SSP)-activated and YODA (YDA)-dependent MAPK kinase pathway. Mutations in *SSP* or *YDA* suppress zygote elongation, especially the basal lineage, whereas the gain of function of either *SSP* or *YDA* promotes the suspensor cell lineage and repress the embryonic fate (Lukowitz et al., 2004; Bayer et al., 2009).

*WOX*s are a class of plant unique *WUSHEL* homeobox genes, marking different parts of early embryo development (Haecker et al., 2004). Both of *WOX2* and *WOX8* are initially expressed in zygote. Subsequently, *WOX2* is confined to the apical cell, and *WOX8* is expressed in the basal cell. Recent studies showed that *WOX2* and *WOX8/WOX9* act as regulators to promote the specification of the apical and basal cells, respectively. More importantly, there is a cell-cell interaction between the apical and the basal cells, manifested by the lack of *WOX2* expression in the apical cell in *wox8 wox9* double mutant. This indicates that *WOX8/WOX9* exhibit a non-cell-autonomous effect on the *WOX2*-mediated apical cell specification (Breuninger et al., 2008).

Besides the above mechanisms, elements of auxin signaling, such as auxin transport facilitator and auxin responsive factors, may also participate in this process. PINFORMED7 (PIN7), one of the auxin efflux facilitators, is localized in the upper membrane of the basal cell and guides auxin efflux into the apical cell. Knockout of *PIN7* results in aberrant apical cell division (Friml et al., 2003). Moreover, two components of the auxin signaling, MONOPTEROS (MP) and AUXIN RESPONSE 6 (AXR6), are also implicated in the apical and basal fates, as *mp* mutant displays defects in the apical cell division (Hamann et al., 1999) and *axr6* mutant are abnormal in basal cell division (Willemsen et al., 1998).

Together, there are several cellular pathways involved in cell fate determination after the first asymmetric division of zygote. It is unknown that whether these pathways converge at some points or function in parallel during the apical and basal cell fate specification.

The establishment of the apical-basal axis by polar auxin transport

Apical-basal axis formation is one of the earliest patterning events in plant embryogenesis. The basic body plan is established upon this axis. The embryo is characterized with three parts: the shoot meristem and the adjacent cotyledons at the top, the root meristem at the basal, and the hypocotyl in the middle. Several experiments have showed that auxin signaling is essential for the embryo patterning. For example, any mutation in genes associated with auxin biogenesis, transport, perception and response, will lead to the abnormality of embryogenesis, especially in the establishment of apical-basal axis (Hamann et al., 1999; Willemsen et al., 1998; Friml et al., 2003; Cheng et al., 2007).

The role of PINs-mediated auxin transport in generating the apical-basal axis has been elucidated with *in vitro* culture of *Arabidopsis* embryos (Friml et al., 2003; Sauer and Friml, 2004; Wisniewska et al., 2006). There are two directions of auxin flux during early *Arabidopsis* embryogenesis, the

acropetal auxin flux mediated by PIN7and PIN1 dependent basipetal auxin flux. Data show that these two auxin fluxes are required for the specification of the apical cell and hypophysis, respectively (Friml et al., 2003). Molecular analysis of the *pins* mutants reveals that the formation of the apical-basal axis correlates with the dynamics of auxin transport and then the apical-basal auxin gradient (Leyser, 2005). Because of genetic redundancy in the PIN family, loss of one member only leads to mild, variable defects in the early embryo development. The embryonic development, however, is severely impaired in multi mutants of *pins*, as they showed misplaced or fused cotyledons, disappearance of apical structures and severe defects in root initiation in many cases, or even a ball-shaped embryo without the apical-basal patterning in extreme cases (Friml et al., 2003).

Since PINs serve as the main regulator of auxin spatial and temporal distribution essential to the patterning and organogenesis (Sabatini et al., 1999; Benkováet al., 2003; Blilou et al., 2005), mechanisms on how polar distribution of PINs are established is critical to embryo patterning too. Several studies reveal that many factors are involved in regulating the asymmetric distribution of PINs, including the constitutive cycling and protein phosphorylation modification (Geldner et al., 2003; Friml et al., 2004; Michniewicz et al., 2007; Grunewald and Friml, 2010; Huang et al., 2010; Zhang et al., 2010). PINOID (PID) kinase and PROTEIN PHOSPHATASE 2A (PP2A) act antagonistically to control the asymmetric localization of PIN1 by regulating its phosphorylation status. The phosphorylated PIN1 targets to the apical membrane, whereas the dephosphorylated PIN1 will result in a reversal targeting to the basal membrane (Friml et al., 2004; Michniewicz et al., 2007). In addition, the cellular constitutive cycling process may also impinge on the PINs polar localization. *GNOM/EMB30*, encoding an endosomal and BFA-sensitive ADP ribosylation factor GDP/GTP exchange factors (ARF GEF), plays a role in the PINs endocytic process (Steinmann et al., 1999). *gnom/emb30* mutation impairs the intracellular cycling of PINs (Dhonukshe et al., 2008), resulting in an obvious embryonic defect that similar to the phenotype of multi-mutations in the PINs family (Friml et al., 2003). Furthermore, ICR1, an interacting partner of constitutive Rho of plant1 (ROP1), is supposed to work with ROP1 to recruit cargoes, such as the PINs, to specific sites at the membrane during exocytosis (Hazak et al., 2010), complementary to the GNOM-mediated endocytic process.

It is possible that both phosphorylation and constitutive cycling may cooperate to regulate the polar localization of PINs. Indeed, recent evidence shows that the phosphorylation status of PINs determines whether they enter a GNOM-dependent or independent cycling pathway. As the phosphorylated PINs by PID kinase will recruit a GNOM-independent pathway to fulfill their polar localization, the dephosphorylated PINs will enter the GNOM-dependent intracellular cycling (Kleine-Vehn et al., 2009).

The establishment of shoot and root apexes

Shoot and root come from distinctive cell lineages with different program. The SAM originates from the inner cells of the upper tires, and the RAM is derived from hypophysis and part of cell of embryo lower tires. The polarity of apical-basal axis is established upon the cell specification of shoot and root apexes (West and Harada, 1993). Results of mutants with defects in the root or shoot meristem (RM or SM) have provided insights into the mechanism underlying meristem patterning. Both of SM and RM need a master regulator to start the embryonic and post-embryonic development, respectively (Aida et al., 2004; Smith and Long, 2010). Furthermore, regulators determining the root and shoot fate may act antagonistically to delimit the specification (Smith and Long, 2010).

The formation and specification of the embryonic root

Hypophysis is generated from transversal division of basal cell. It locates between the apical cell and suspensor. Hypophysis will adopt an embryo fate by incorporating into embryo (West and Harada, 1993). Many genes involved in this inductive progress have been identified through genetic screen, including *MP*, *BODENLOS* (*BDL*), *PLETHORA* (*PLT*), as well as the *PINs*, indicating an indispensable role of auxin in the embryonic root development (Hamann et al., 2002; Friml et al., 2003; Aida et al., 2004). MP is a member of auxin response factors and its mutation leads to a loss of basal structures such as root and hypocotyl due to the failure of hypophysis division. An AUX/IAA family member BDL can repress the expression of MP-dependent auxin responsive genes through interacting with MP and co-repressor TOPLESS (TPL) (Weijers et al., 2006; Szemenyei et al., 2008). The phenotype of *mp* is similar to that of *bdl* dominant negative mutant (Hamann et al., 2002; Weijers et al., 2006). However, MP or BDL accumulates in the progenies of the apical cell rather than the hypophysis in dermatogen embryo, suggesting that MP/BDL dependent pathway may have a non-cell-autonomous effect on hypophyseal specification (Weijers et al., 2006). It is suggested that cell-to-cell communication is important for cell specification in embryogenesis. It is proved that MP-dependent auxin accumulation and the non-cell-autonomous movement of TARGET OF MP 7 (TOM7) from adjacent cells to the hypophysis are required for hypophysis specification (Scheres, 2001; Weijers et al., 2006; Schlereth et al., 2010).

At the late globular embryo stage, the asymmetric division of the hypophysis gives rise to a lens-shaped apical cell and basal cell, which will develop into the quiescent center (QC) and the columellar cells, respectively (West and Harada, 1993). There are many factors involved in specifying the

QC-centered stem cell niche, including PLT, SCARECRAW (SCR), and WOX5. PLT, an AP2-like transcription factor, may act downstream of the auxin and require MP activity to pattern the root stem cell niche. PLT can induce the formation of secondary roots ectopically, which suggests that PLT is a master regulator of root initiation (Aida et al., 2004). Furthermore, PLT serves as an interpreter of positional information along the auxin gradient to elicit distinctive gene expression (Galinha et al., 2007). Similarly, during root radical pattern formation, a SHORT ROOT (SHR)/SCR-mediated pathway functions in maintaining the stem cell niche as well. The stele-originated SHR protein migrates outwards to the adjacent cell layer, including endodermis and QC, to promote the expression of *SCR*, whose mutation will result in a disorganized QC (Wysocka-Diller et al., 2000; Nakajima et al., 2001). Recently, evidences show that CLE40 and WOX5 may have an important role in the establishment of the stem cell niche as well (Stahl et al., 2009). CLE40, the counterpart of CLV3 in the root (Hobe et al., 2003), can be transferred from the columella cells to the columella stem cells to activate the ARABIDOPSIS CRINKLY4 (ACR4) kinase (De Smet et al., 2008). ACR4 represses the expression of *WOX5* which is exclusively expressed in QC and maintains the root stem niche (Sarkar et al., 2007).

Although there is a divergent and complicated regulation network to define the stem cell activity, it is most likely that the cellular pathways may converge at some points. For example, the expression pattern of *WOX5* is altered in *scr* mutant, but remained unchanged in *plt* mutant, indicating that SCR maintains the root stem cell activity via the WOX5-mediated pathway (Sarkar et al., 2007).

The establishment of shoot apical meristem

The CLV3 and WUS feedback loop acts as a main regulator of the specification and maintenance of the stem cell niche in shoot apex (Brand et al., 2000). WUS is a key player required for maintaining the stem cell niche (Mayer et al., 1998), whereas CLV3, the best characterized member of CLE family with a divergent role in plant development, such as vascular formation and epidermis specification (Hirakawa et al., 2008; Miwa et al., 2009; Etchells and Turner, 2010; Wang and Fiers, 2010), is proposed to repress *WUS* expression in the shoot organizer center via an LRR-RLK pathway (Willmann, 2000; Ogawa et al., 2008). CLV1, CLV2, CORYNE (CRN) and BARELY ANY MERISTERM (BAM) might serve as the receptors to perceive the CLV3 polypeptide signals (DeYoung et al., 2006; Deyoung and Clark, 2008; Müller et al., 2008). Genetic and biochemical studies demonstrate that there is a complicated regulation network to control the perception process. CRN may form hetero-oligomers with CLV2 through their transmembrane domain since it does not have extracellular domain (Müller et al., 2008). It is proposed that CLV1 work redundantly with CRN and CLV2 to control the shoot stem cell niche (De Smet et al., 2009). However, BAM1 and BAM2, predominantly localized in the periphery region of the stem cell niche, negatively regulate the CLV3-mediated signaling by sequestering CLV3 and preventing the ligand from moving to the central zone, ultimately promoting *WUS* expression and stem cell proliferation (Deyoung and Clark, 2008).

Class III homeodomain leucine zipper (HD-ZIP III) transcription factors possibly act in parallel with the CLV3-mediated pathway to control WUS activity. There are five HD-ZIP III transcription factors in *Arabidopsis*, named REVOLUTA (REV), PHAVOLUTA (PHV), PHABULOSA (PHB), CORONA (CNA), and ATHB8. The CNA is involved in stem cell niche and its mutation enhances the phenotype of *clv3* (Green et al., 2005). Whereas the *cna* only shows subtle defects in shoot meristem, and the *cna phb phv* triple mutant has an enlarged meristem, similar to that of the *clv* mutants (Prigge et al., 2005). This suggests that they act redundantly in SM. Recently, PHB is identified as a suppressor of root formation in dominant-negative *tpl* mutants, which can transform the shoot apical meristem to a secondary basal meristem (Long, 2006; Smith and Long, 2010). Furthermore, PLT and HD-ZIP III transcription factors act antagonistically to ensure the proper apical-basal axis in embryogenesis, besides the control of TPL and microRNA 165/166 (Szemenyei et al., 2008; Carlsbecker et al., 2010; Smith and Long, 2010). Notably, ZWILLE, a member of the ARGONAUTE family which has been revealed as an indispensable element of RNA-induced silencing complex (RISC), is mainly localized in the vascular primordium. ZWILLE can influence the WUS activity by exerting a non-cell-autonomous signal to the upper zone during embryogenesis (Moussian et al., 1998; Tucker et al., 2008).

The development of cotyledon

During the heart embryo stage, cotyledon is formed by the periclinal division of flanking cells. The formation of cotyledons marks a transition from the radical symmetry to the bilateral symmetry (West and Harada, 1993). Many cellular pathways are involved in the generation of cotyledon, including auxin dependent response and RLKs signaling (Aida et al., 2002; Friml et al., 2003). The role of auxin in the outgrowth of cotyledon mainly depends on the PIN1-mediated auxin accumulation in the cotyledon primordia. PIN1 is localized in the lateral membrane of epidermis cells in the upper tires (Friml et al., 2003). The most severe defects in *pins* multi mutants are the complete loss of cotyledon (Aida et al., 2002; Furutani et al., 2004). Thus, mutations in genes associated with PINs activity will obviously result in cotyledon defects. Moreover, two homologous transcription factors, CUP-SHAPED COTYLEDON 1 (CUC1) and CUC2, function redundantly in cotyledon separation. Expression of *CUC1* and *CUC2* is altered in *pin1 mp* mutant, suggesting

that they may be the targets of auxin signaling (Aida et al., 2002). *CUC1* and *CUC2* are negatively regulated by auxin and microRNA164, which can contain their expression in the medial domain and degrade *CUC* transcripts via microRNA mediated pathway, respectively (Aida et al., 2002; Laufs et al., 2004; Mallory et al., 2004).

Recent studies also show that DORNROSCHEN (DRN) and DORNROSCHEN-LIKE (DRNL) are involved in cotyledon development. Data of chromatin immuno-precipitation experiment indicate that MP interacts with the promoter of *DRNs* by binding its Auxin response elements (AuxRE) sequence, and this suggests that MP directly regulates DRNs activity (Cole et al., 2009). Additionally, DRNs can dimerize with the HD-ZIP III transcription factors (Chandler et al., 2007), a module embracing upstream auxin and downstream transcription factors which are specifically expressed during cotyledon development is emerging.

Furthermore, the RLKs-mediated pathway may be linked to cotyledon development as well. TOADSTOOL 2 (TOAD2) and RECEPTOR LIKE PROTEIN KINASE 1 (RPK1), which function redundantly in the radical patterning, also play roles in the initiation of cotyledon (Nodine et al., 2007). Loss of *TOAD2* and *RPK1* will damage the central domain of the protoderm, and subsequently a non-cell-autonomous signal is sent to the peripheral domain, the origin of cotyledon. The failure of cotyledon formation in the peripheral domain is linked to the loss of non-cell-autonomous signal. However, this non-cell-autonomous signal, together with the downstream genes of RLKs pathway remains to be unveiled (Nodine and Tax, 2008).

The formation of lateral axis

The lateral axis formation, occurring perpendicularly to the apical-basal axis, is another profound patterning event which gives rise to the basic tissue layers required for the postembryonic development. The lateral axis initiates at the transition from the octant to dermatogen embryo. In this transition, cells in the octant divides periclinally, to generate the outer protoderm and inner subprotoderm cells. During the globular embryo stage, the inner cells derived vascular primordium and ground tissue, together with the protoderm to form a fine lateral axis (West and Harada, 1993). Besides the auxin-dependent signaling pathway, several other pathways, including RLKs-mediated pathway, non-cell-autonomous movement of transcription factors, and microRNA regulation, are shown to contribute to the establishment of lateral pattern too (Nakajima et al., 2001; Nodine et al., 2007; Carlsbecker et al., 2010).

The specification of endodermis and cortex

SHR, a transcription factor of GRAS family, is one of the best characterize non-cell- autonomous proteins (NCAPs). *SHR* transcript is found in the vascular bundle, whereas its protein appears in the ground tissue to activate the expression of another GRAS member, *SCR*, a process that interprets positional information, which is required for the asymmetric division and ground tissue specification (Helariutta et al., 2000; Nakajima et al., 2001). *shr* or *scr* mutants fail to divide asymmetrically to differentiate into the endodermis and cortex, resulting in shrunken root with only a single ground tissue layer (Helariutta et al., 2000).

The establishment of vascular primordium

The vascular primordium generates from the subprotoderm and locates at the center of the embryo. MP is a key player in vascular development. MP functions in many aspects of plant development, for example, the development of the root, the outgrowth of cotyledon and the initiation of leaf (Weijers et al., 2006; Schuetz et al., 2008). MP is initially expressed in the apical cell, and later in the whole embryo. Subsequently, MP is confined to the central domain of the embryo and provascular primordium (Hardtke and Berleth, 1998; Weijers et al., 2006). Loss of MP results in the lack of vascular tissue. HD-ZIP III transcription factors are also involved in vascular development (Prigge et al., 2005). For example, *rev* mutant displays a defect in the vascular development and the *rev phv* double mutant shows more severe vascular defects, indicating that PHV and REV have overlapping function in the vascular development. However, *cna* or *athb* mutant in *rev* background will restore the vascular bundle, which can attribute to the antagonistic effect between the members of HD-ZIP III family (Prigge et al., 2005). Recently, a new cell-to-cell communication regulator, mobile microRNA165/166 is reported to participate in the vascular development (Carlsbecker et al., 2010). MicroRNA165/166 is generated in the endodermis via the SHR/ SCR pathway, and it can migrate from the endodermis to stele to target transcripts of HD-ZIP III genes, implying that HD-ZIP III members acts in a dosage manner to the vascular development (Carlsbecker et al., 2010).

It is tempting to investigate whether the MP-dependent auxin signaling and HD-ZIP III transcription factors function in the same, or parallel ways to mediate the vascular development. Consistent with the previous hypothesis, it is proved that a member of HD-ZIP III transcription factors, ATHB8, can be induced by MP (Mattsson et al., 2003), indicating that MP acts in the upstream of HD-ZIP transcription factors during vascular development.

The formation of epidermis

Epidermis is derived from the protoderm, the outer layer of embryo that produced as a result of periclinal division during

the transition from octant to dermatogen embryo. Epidermis is the first differentiated tissue that serves as the boundary between the embryo and the environment. Genes specifically expressed in this single cell layer (L1) are identified, such as the putative extracellular protein PROTODERMAL FACTOR 1 (PDF1), GLABRA2-type homeodomain transcription factors ARABIDOPSIS THALIANA MERISTEM LAYER 1 (ATML1) and PDF2 (Abe et al., 1999; Abe et al., 2003). These genes contain the L1 box in their promoter region, conferring there capability to express in the L1 layers of SM (Abe et al., 2003).

Although the genes specifically expressed in the epidermis or protoderm have been characterized, the mechanism of confining the specific genes in the epidermis is largely unknown. ATML1 and its homolog PDF2 can bind the L1 box in the promoter region of several genes and regulate epidermal development. Interestingly, a L1 box is also present in both of *ATML1* and *PDF2* promoters, which suggests that a positive feedback loop may exist in *ATML1* and *PDF2* themselves (Abe et al., 2003). Recently, detail functional analysis demonstrates that, besides the L1 box, there are several other regulatory elements in *ATML1* promoter, such as WUS binding sites. It is possible that *ATML1* is downstream of some positional signals that regulate ATML1 activity by binding different regulatory sites in its promoter (Takada and Jürgens, 2007). Furthermore, some RLKs, including ACR4, ABNORMAL LEAF SHAPE 2 (ALE2), GASSHO1 (GSO1), GASSHO2 (GSO2), RPK1 and TOAD2, are supposed to act in the upstream of these transcription factors to promote the epidermis specification and differentiation (Watanabe et al., 2004; Tanaka et al., 2007; Tsuwamoto et al., 2008). The *Arabidopsis* homolog of maize CRINKLY, ACR4, and the recently identified ALE2, are two members of the RLKs family. These two RLKs function in the same process involved in the epidermis formation on the basis that they can phosphorylate each other *in vitro* and the phenotype of their double mutant is more similar to the *ale2* (Tanaka et al., 2007). Previous analysis indicates that the kinase domain of ACR4 is dispensable for its activity, however, it may form hetero-oligomer through interaction with other kinase in the signal transduction pathway (Berger and Altmann, 2000; Gifford et al., 2005). In this context, ALE2 is likely the first partner candidate of ACR4. Further proof of *in vivo* interaction between ACR4 and ALE2 is required to elucidate the role of this RLK pathway in the establishment of epidermis.

RPK1 and TOAD2 are two co-localized RLKs that function redundantly in lateral pattern formation. The subprotoderm markers expand to the protoderm during the dermatogen stage in *rpk1 toad2* double mutant, which indicates that RPK1 and TOAD2 are required for the specification of subprotodermal cells by restricting subprotoderm markers expression in the subprotoderm region (Nodine et al., 2007).

Interestingly, the genes expressed in the endosperm are also related to the development of epidermis (Tanaka et al., 2001). The endosperm localized ALE1 is a member of subtilisin-like serine proteases, which is involved in the conversion of inactive substrate into an active ligand in the animal system. Furthermore, *ZHOU PI*, another endosperm expressed gene, is proposed to act upstream of the *ALE1* through promoting the expression of *ALE1* specifically in the endosperm (Yang et al., 2008). It is most likely that the ligand from ZHOU PI and ALE1 signaling pathway may move out of the endosperm to activate the ACR4/ALE1 of protoderm surface. Subsequently, the protoderm specific genes are regulated by ACR4/ALE1. It is obvious that more studies are required for the identification of signals and mechanism underlying the epidermis development.

Conclusion remarks

As discussed above, multiple cellular pathways including the intercellular auxin signaling, the RLK-mediated pathway, the non-cell-autonomous movement of the transcription factors and microRNAs, are involved in patterning the apical-basal and the lateral axes, as which set up the basic body plan for the post-embryonic development. However, there are still other factors associated with embryogenesis, such as the parental effect which is essential for the embryogenesis and function mainly via the gene imprinting pathway (Grossniklaus et al., 1998; Gehring et al., 2006). In addition, the cell-cell communications during embryogenesis should not be neglected. For example, the dynamic change of size exclusion limit (SEL) of plasmodesmata is correlated with embryo patterning, indicating that plasmodesmata play a role in coordinating the whole embryo differentiation (Kim et al., 2005a; Kim et al., 2005b). Consistently, some mutants with altered plasmodesmata SEL have been identified in a screen for embryo-defective phenotypes which ultimately result in collapsed embryos (Kim et al., 2002; Kobayashi et al., 2007).

Although the mechanisms underlying the embryonic patterning have turned clear after intensive genetic and molecular analysis, much more aspects remain to elucidate before we get a whole regulating network of embryo development. The number of key regulators determining specific embryo differentiation process is still limited. Whether there are novel signaling pathways involved in embryogenesis and to what extent various signaling pathways integrate into a common mechanism that governs the embryo patterning, require further investigation. Undoubtedly, knowledge obtained from *Arabidopsis* will serve as an instructive framework in the studies of other species especially crop plants.

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