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REVIEW

Interplay between the shoot apical meristem and lateral organs

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Abstract Tissues and organs within a living organism are coordinated, but the underlying mechanisms are not well understood. The shoot apical meristem (SAM) continually produces lateral organs, such as leaves, from its peripheral zone. Because of their close proximity, SAM and lateral organs interact during plant development. Existing lateral organs influence the positions of newly formed organs to determine the phyllotaxis. The SAM not only produces lateral organs, but also influences their morphogenesis. In particular, the SAM promotes leaf polarity determination and leaf blade formation. Furthermore, lateral organs help the SAM to maintain homeostasis by restricting stem cell activity. Recent advances have started to elucidate how SAM and lateral organs patterning and growth are coordinated in the shoot apex. In this review, we discuss recent findings on the interaction between SAM and lateral organs during plant development. In particular, polar auxin transport appears to be a commonly used coordination mechanism.

Keywords Shoot apical meristem, Lateral organ, Morphogenesis, Sussex signal, Auxin

INTRODUCTION

The majority of the above-ground shoot comes from the shoot apical meristem (SAM). Established during embryogenesis, the SAM contains a mass of stem cells in the center. Stem cells in the SAM divide to maintain new stem cells and to provide cells that make new primordia on the periphery (Fletcher 2018; Shi and Vernoux 2019). During vegetative growth, leaves are the most common lateral organs produced by the SAM. Whereas seed plant leaves are determinate, which contrasts to the indeterminate SAM, axillary meristems (AMs) form in the leaf axil to enable branching (Wang and Jiao 2018). AMs share the same structure and developmental potential as the SAM. AMs produce their own lateral organs and make the shoot a ramifying system where the growth of new shoots can be initiated. After floral transition, the SAM generates floral primordia instead of leaf primordia in plants with a simple raceme, an indeterminate inflorescence, such as in *Arabidopsis*. A floral primordia contains a floral meristem that produces a limited number of floral organs, including sepals, petals, stamens and carpels, to make a flower. Although a flower is a modified, shortened, compacted branch, the floral primordium behaves in many ways similar to the leaf primordium. Thus, floral primordia are often treated as lateral organs (Long and Barton 2000).

In this review, we focus on the interplay of the SAM and lateral organs. We refer the readers to recent reviews on closely related subjects such as SAM function and homeostasis (Janocha and Lohmann 2018; Shi

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and Vernoux 2019; Wu et al. 2018), and lateral organ patterning (Conklin et al. 2019; Du et al. 2018; Maugarny-Cales and Laufs 2018).

SPATIOTEMPORAL PATTERNING OF LATERAL ORGANS AT THE SAM

The SAM includes a central zone (CZ) containing pluripotent stem cells and a peripheral zone (PZ) surrounding the CZ. Lateral organs, such as leaves and flowers originate from the PZ of the SAM. Plants have evolved feedback mechanisms to sustain and to restrict stem cell activities (Brand et al. 2000; Schoof et al. 2000). The organizing center (OC) is located below the CZ and functions as a stem cell niche that promotes stem cell maintenance. WUSCHEL (WUS) is expressed in the OC, and the protein migrates into the CZ to activate the expression of *CLAVATA3* (*CLV3*) (Daum et al. 2014; Yadav et al. 2011). *CLV3* encodes a secreted peptide which acts through *CLV1* and other putative receptors to inhibit *WUS* expression, forming a self-regulatory feedback loop (Brand et al. 2000; Fletcher et al. 1999).

Whereas the entire PZ has organogenesis potential and are competent to organ induction (Reinhardt et al. 2000), the positions of where lateral organs form are highly regular and predictable. The ordered positioning of organs relative to the main shoot and to another organ is termed phyllotaxis. For many plant species, including the model plant *Arabidopsis*, a new primordium is 137.5° away from the previous primordium (Fig. 1). It has long been noticed that the position of new leaf primordia is determined by the existing leaf primordia. Microsurgery experiments support the conclusion that the interaction between existing and upcoming primordia dictates the location where new primordia develop. When an emerging primordium is isolated by an incision between the SAM and the primordium, the position of the upcoming primordium will be closer to the isolated primordium (Reinhardt et al. 2005; Snow and Snow 1962). Many hypotheses have been proposed to explain this exciting patterning process. For example, it has been proposed that each emerging primordium around the SAM forms an inhibitory field that prevents the formation of the new primordium (Douady and Couder 1996; Snow and Snow 1962; Steeves and Sussex 1989).

Findings in the past two decades have significantly advanced our understanding of this interplay between lateral organs. The phytohormone auxin plays a key role in lateral organ formation in the PZ. Only cells overlapping with auxin maxima are designated to develop into lateral organs (Reinhardt et al. 2000; Vernoux et al. 2000). Furthermore, auxin maxima are periodically formed at the PZ, and auxin maxima formation requires the auxin efflux carrier PINFORMED1 (PIN1)-mediated polar auxin transport (PAT) (Heisler et al. 2005; Okada et al. 1991; Reinhardt et al. 2000, 2003) (Fig. 2).

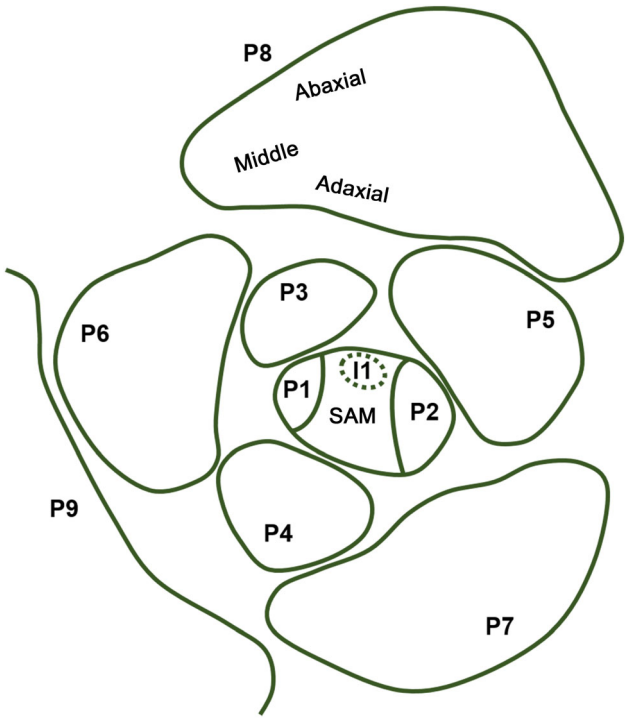

Fig. 1 A transverse section showing phyllotaxy of *Arabidopsis*. Primordia initiated at the PZ (peripheral zone) most distantly away from existing primordia. I1 denotes the incipient leaf primordium, and P1 denotes the youngest leaf primordium, followed by P2–P9. *SAM* meristem

Assuming that auxin has a positive feedback on PAT, several models have been proposed to explain phyllotaxis. The concentration-based model postulates that PIN1 in the epidermis of the SAM is polarized toward neighboring cells with higher auxin concentration (de Reuille et al. 2006; Jönsson et al. 2006; Smith et al. 2006). To resolve the difficulty of how cells compare their own auxin concentration with neighbors, a mechanical stress-based model has been proposed, in which PIN1 polarize toward expanding neighboring cells (Heisler et al. 2010). This model is supported by experiments showing that tensile stress on the membrane can stabilize PIN1 localization (Nakayama et al. 2012). Alternatively, a flux-based model assumes that the PIN1 membrane localization is strengthened by auxin flux and explains phyllotaxis with certain assumptions (Hartmann et al. 2019; Stoma et al. 2008). All existing models rely on certain assumptions that need further experimental testing. In addition to PIN1 polarization, auxin also promotes the transcription of

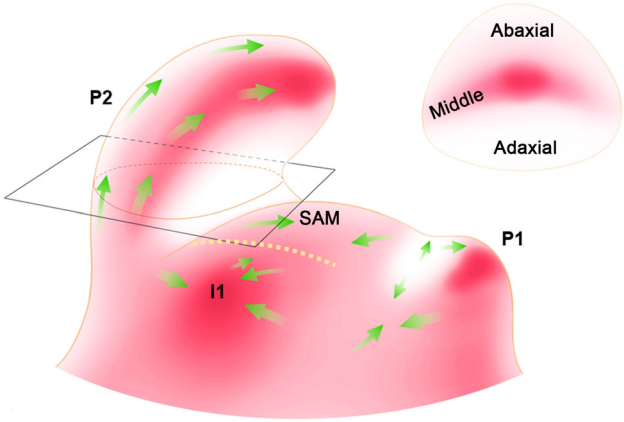

Fig. 2 Spatial auxin distribution and transport in the shoot apex. Summary of auxin levels, as reflected by the strength of red color, in the shoot apex. A cross section of a P2, as denoted by the rectangle, is also shown on top right. Auxin maxima precede leaf primordia in the PZ. Within a leaf primordium, auxin concentration is higher in the middle domain that encompass provascular tissue and leaf margins. Low auxin zones are detected in the organ boundary region and leaf adaxial domain. Green arrows show PAT direction and strength. Summarized according to (Shi et al. 2017). The dotted yellow line represents Sussex microsurgical incision site. After a microsurgical incision, I1, which is separated from the SAM, will form a radially symmetric leaf primordium. Printed with permission © Du Peng

PIN1 mRNA (Krogan et al. 2016), as well as *MONOPTEROS* (*MP*) encoding an auxin signaling component (Bhatia et al. 2016), forming additional feedback loops to stabilize auxin maxima formation.

The PAT-mediated auxin maxima formation is accompanied by auxin depletion around each primordium (Vernoux et al. 2011), precluding new auxin maxima formation in the vicinity of the emerging primordia. Thus, a competition for an activator of organogenesis leads to the phyllotaxis. The *Arabidopsis pin1* null alleles can still form leaves but not flowers (Guenot et al. 2012), suggesting that additional factors may contribute to organogenesis. It has long been speculated that physical stresses may explain phyllotactic patterning (Newell et al. 2008).

SAM INFLUENCES LATERAL ORGAN PATTERNING

At the shoot apex, stem cells not only produce lateral organs, but also regulate organ patterning. Classical microsurgical experiments indicated that the "Sussex signal", a SAM-derived signal, promotes leaf blade formation (Sussex 1951). When an incipient leaf is separated from the SAM through a microsurgical incision or laser ablation, it develops into a radially symmetric leaf (Reinhardt et al. 2005). Leaf blade formation requires adaxial-abaxial (also referred as dorsoventral) patterning of a leaf primordium (Waites and Hudson 1995). In isolated leaves, cells in the adaxial domain, i.e., the side closer to the SAM, acquire the opposite abaxial fate (Kuhlemeier and Timmermans 2016). Thus, it has been proposed that the Sussex signal passes from the SAM to the adaxial domain to promote the adaxial cell fate.

Prior to leaf primordium formation, the PZ of the SAM is already prepatterned with the inner domain expressing adaxial genes, such as *REVOLUTA* (*REV*), and the outer domain expressing abaxial genes, such as *KANADI1* (*KAN1*) (Caggiano et al. 2017; Husbands et al. 2009; Yu et al. 2017). Leaf primordia initiate at the junction between the two domains, and the middle domain is established in between the adaxial and abaxial domains. *WUSCHEL-RELATED HOMEOBOX* (*WOX*) genes are expressed in the middle domain to promote leaf blade formation (Nakata et al. 2012; Tadege et al. 2011). The Sussex signal maintains the adaxial cell fate and promotes the middle domain formation.

PAT provides an explanation for the Sussex experiment (Fig. 2). At the shoot apex, PIN1-mediated auxin transport occurs from the outside to the center of the SAM (Shi et al. 2017). During leaf primordium emergence, PIN1 directs auxin flow from both adaxial and abaxial sides to converge at the middle domain, where the leaf margins form, and finally to the leaf apex (Dong and Huang 2018; Shi et al. 2017). Auxin signaling promotes the expression of *Arabidopsis WOX1* and *WOX3/PRS* (Guan et al. 2017). On the other hand, lower auxin levels were detected in the adaxial domain, and to some extent in the abaxial domain, using the DII auxin sensor (Guan et al. 2019, 2017; Qi et al. 2014). Note that splitting the middle domain, which enriches auxin, and assigning each half to the adaxial and abaxial domains, respectively, would lead to a different conclusion (Bhatia et al. 2019).

Auxin distribution and transport in the SAM suggest a model in which SAM-wide PAT leads to the middle domain and blade formation. In fact, PAT between the SAM and leaf primordia is essential for blade formation (Qi et al. 2014). In tomato, blocking PIN-mediated PAT between the SAM and leaf primordia by localized Brefeldin A or 1-*N*-naphthylphthalamic acid treatment leads to ectopic auxin signaling in the adaxial domain, and inhibition of leaf blade formation. Ectopic application of auxin or an auxin analog to the adaxial domain also leads to the identical phenotype (Qi et al. 2014), supporting that auxin distribution can affect blade formation.

In *Arabidopsis* where microsurgery or local chemical applications are not feasible, the role of auxin in leaf patterning is supported by *MPΔ* plants, in which MP is active in both the absence and presence of auxin. *MP* encodes an ARF protein functions as a transcriptional activator downstream of auxin signaling. MP is released by auxin to transcribe auxin response genes (Guilfoyle 2015). In very early leaf primordium, *MP* is expressed in the adaxial and middle domains, but auxin signaling, as indicated by the DR5 reporter, is restricted to the middle domain (Guan et al. 2017). In *MPΔ* leaves, both auxin signaling as well as the middle domain genes *WOX1* and *PRS* are ectopically expressed in the adaxial domain. Consistently, leaf blade formation is compromised (Guan et al. 2017; Krogan and Berleth 2012; Qi et al. 2014; Zhao et al. 2019). Low auxin levels explain the inactivation of normal MP in the adaxial domain. The abaxial domain also has lower auxin levels, as indicated by DII, than the middle domain. In addition, redundant ARF suppressors are expressed in the abaxial domain to inhibit *WOX* expression (Guan et al. 2017).

Together, the SAM-wide auxin transport provides an explanation for the SAM-mediated leaf patterning. PAT also explains how the middle domain is activated and restricted in the between of adaxial and abaxial domains. There is an alternative model for the middle domain formation independent of PAT. This model requires several assumptions: (i) a gap exists between the adaxial and abaxial domains to allocate the middle domain, (ii) adaxial HD-ZIPIII and abaxial KAN1 repress auxin signaling, and (iii) auxin promotes *HD-ZIPIII* expression and restricts *KAN1* expression (Caggiano et al. 2017; Heisler and Byrne 2020). These assumptions are not always consistent with experimental observations. An adaxial/abaxial gap does not exist prior to primordium formation (Caggiano et al. 2017), raising the question how this gap is established. HD-ZIPIII was found to promote *MP* expression and auxin signaling in the root (Müller et al. 2016). *MP* expression significantly overlaps with *REV* in leaves (Guan et al. 2017), which is incongruent with the model of HD-ZIPIII repression of auxin signaling. Furthermore, auxin signaling maxima, shown by DR5, and *REV* expression strongly overlap in floral primordia (Heisler et al. 2005). In fact, some assumptions are contradictory to each other: if auxin promotes *HD-ZIPIII* expression, why is *HD-ZIPIII* expression not enriched in the middle domain? Future research should address this important question.

In addition to auxin-mediated regulation, there are additional hypotheses explaining the Sussex experiment. Exogenous application of succinic semialdehyde (SSA), a GAMMA-AMINOBUTYRIC ACID AMINOTRANSFERASE (GABA) shunt metabolite, inhibits abaxial development. It has been proposed that SSA or its close derivatives are potential transmissible signaling molecules involved in leaf polarity morphogenesis (Toyokura et al. 2011). However, this hypothesis needs further experimentation. Since the adaxially expressed REV and related HD-ZIPIII transcription factors have a predicted mammalian sterol/lipid-binding (START) domain, lipophilic molecules have been proposed to be candidate organ patterning signals (McConnell et al. 2001). Wounding induces the expression of *KAN1*, and it has been proposed that the Sussex incision induces *KAN1* expression in the adaxial domain (Caggiano et al. 2017). However, this hypothesis does not explain the control experiments done by Sussex, in which partial microsurgical incisions had no effect on blade formation (Kuhlemeier and Timmermans 2016; Reinhardt et al. 2005; Sussex 1951).

LATERAL ORGANS FEEDBACK ON THE SAM SIZE

Initiating organs also provide feedback on stem cell homeostasis by affecting the SAM size (Sussex 1952). Inhibition of lateral organ primordium growth leads to the SAM enlargement (Emery et al. 2003; Goldshmidt et al. 2008; Tanaka et al. 2012). *YABBY* (*YAB*) genes are expressed in leaf primordia, but not the SAM, to promote growth, and *yab* mutants have enlarged SAM size (Goldshmidt et al. 2008; Lugassi et al. 2010; Tanaka et al. 2012). Therefore, it is unclear how leaf-expressed *YAB* genes act on the SAM homeostasis in a non-cell autonomous manner. Recent studies suggest that there are at least two parallel mechanisms mediating lateral organ feedback to the SAM homeostasis (Je et al. 2016; Shi et al. 2018).

A study in maize identified FASCIATED EAR3 (FEA3), a leucine-rich-repeat transmembrane receptor that is expressed in the SAM and participates in stem cell control. FEA3 responds to a CLV3/EMBRYO-SURROUNDING REGION-related (CLE) peptide signal, encoded by *ZmFCP1*, produced in organ primordia (Je et al. 2016). The maize *fea3* mutants have enlarged and fascinated meristems. The homologous *Arabidopsis CLV3* is expressed in the CZ of the SAM, and the CLV3 peptide moves downward toward the OC (Janocha and Lohmann 2018). CLV3 peptide is perceived by receptors, including the membrane-localized CLV1 receptor-like kinase, to restrict *WUS* expression. By contrast, the maize ZmFCP1 peptide is not expressed in the SAM but in leaf primordia. The encoded CLE signaling peptide moves from organ primordia to the SAM, where it is perceived by FEA3, a homolog of CLV1. Thus, the receptor-peptide

signaling system allows feedback regulation of SAM size from differentiating lateral organ primordia. Similar mechanism may also exist in *Arabidopsis* and other eudicots.

In parallel to the CLE peptide, PAT in inner cells, but not the epidermis as discussed above, balances auxin levels in the SAM and regulates its homeostasis. Whereas auxin is required for the SAM function, high level of auxin inhibits the SAM function (Luo et al. 2018; Ma et al. 2019). Perturbation of SAM auxin levels through ectopic expression of auxin biosynthesis genes or pharmacological experiments indicates that SAM size is negatively regulated by auxin levels (Shi et al. 2018). Therefore, auxin levels in the SAM need to be precisely regulated. By combine imaging and computational modeling, it has been shown that long-distance auxin transport in inner cells forms an auxin switch. Auxin flow from lateral organ primordia competes with auxin flow from the SAM. Because lateral organs, including leaf primordia and floral primordia, are much stronger auxin sources than the SAM, the earlier primordia inhibits auxin flows from the SAM (Shi et al. 2018). These model predictions are confirmed by experiments. Removal of floral or leaf primordia, by microsurgery or by genetic manipulation, results in enhanced auxin flow out of the SAM and reduced auxin levels in SAM. This in turn leads to an enlarged SAM, which produces more lateral organs in the PZ (Shi et al. 2018). The extra lateral organs then serve as stronger inhibiting auxin sources and the SAM size returns back to normal. Note that the auxin switch is also used by the primary shoot to inhibit lateral bud outgrowth, a phenomena termed apical dominance (Prusinkiewicz et al. 2009).

CONCLUSIONS AND FUTURE PERSPECTIVES

Organs and tissues are not isolated, and their growth is highly coordinated by complex chemical and mechanical signaling. Although we have started to understand the regulatory circuits and logic, we still know fairly little. For example, we need to analyze auxin transportation changes and gene expression changes after microsurgical incisions in species, such as tomato, to better understand the Sussex signals. It will also informative to test if other chemicals, especially phytohormones, move between leaf primordia and the SAM. Our understanding of plant development relies extensively on molecular genetics, in which causal genes for a developmental process are identified through positional cloning using corresponding mutants. Identifying genes specifically affecting organ and tissue coordination is expected to be difficult. Fortunately, cellular resolution live-imaging and computational modeling have been found to be very useful in dissecting interactions among organs and tissues. We expect further developmental in these two areas, as well as the identification of new genes, shed new light on our understanding of the interplay between the SAM and lateral organs.

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