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**Editorial**

# Molecular Insight into Polarity-Mediated Lamina Outgrowth

**Million Tadege***

*Department of Plant and Soil Sciences, Institute for Agricultural Biosciences, Oklahoma State University, USA*

***Corresponding author**
Million Tadege, Department of Plant and Soil Sciences, Institute for Agricultural Biosciences, Oklahoma State University, 3210 Sam Noble Parkway, Ardmore, OK 73401, USA, Email: million.tadege@okstate.edu

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The leaf lamina (blade) is a highly organized photosynthetic structure in which cells in the upper (adaxial) and lower (abaxial) surfaces are morphologically different associated with different functional specializations. The adaxial palisade mesophyll cells are specialized for solar energy capture and the abaxial spongy mesophyll cells are specialized for gas exchange, while the vascular bundles in the middle mesophyll are specialized for water and nutrient translocation in which the water and minerals conducting xylem vessels are positioned adaxial to the sugar transporting phloem. Because the lamina is essentially a solar panel where energy from the sun and carbon dioxide from the atmosphere are assimilated into chemical energy (sugars), its size and design are of fundamental interest to biology from the point of view of form, function, and environmental fitness. Leaf primordia are determinate lateral organs and arise from a small group of pluripotent stem cells in the shoot apical meristem (SAM). Once the leaf primordium initial cells are recruited from the SAM, the primordium organizes itself into well-defined cell layers through meticulously orchestrated cell division, cell expansion, and cell differentiation patterns forming a flattened blade with three distinct axes: proximodistal (length), mediolateral (width), and dorsoventral (thickness). How such a highly organized structure develops from undifferentiated cells of the SAM is a fundamental question in plant developmental biology.

Leaf primordium is initiated from the peripheral region of the SAM, perhaps specified by *PIN- FORMED1* (*PIN1*) polarity-directed auxin maxima [1,2]. This process requires down-regulation of Class I *KNOTTED1*-like home box (KNOX1) genes at the initiation site [3]. In the model plant *Arabidopsis thaliana*, KNOX1 members (*STM, BP/KNAT1, KNAT2*, and *KNAT6*) play important roles in the establishment and maintenance of the SAM [3-7]. KNOX1 genes promote meristematic activity by modulating the activity of phytohormones; activating cytokinin and repressing gibberellin biosynthesis [8-10], but they are removed from the emerging leaf primordium by factors that promote cell differentiation, primarily by repression with the *ASSYMETRIC LEAVES2* (*AS2*) and *AS1* complex [11-16] although they are reactivated in the leaf primordia of species with compound leaves [17,18]. Once the leaf primordium is established, polarity patterning along the dorsoventral (adaxial/abaxial) axis plays a critical role for lamina outgrowth. The origin of polarity is supposed to be a SAM-generated instructive signal [19,20] called the Sussex signal but its identity is unknown and even its existence is questioned by some. However, it is well established that juxtaposition of adaxial and abaxial cells is a prerequisite for proper development and expansion of the lamina [6,21-23], analogous to the dorsal and ventral cells in the imaginal discs of Drosophila wing development [24].

Growth and cell differentiation in the adaxial and abaxial domain of the primordium is controlled by distinct regulatory factors. In *Arabidopsis*, the Class III Homeodomain Leucine Zipper (HD- ZIP III) family genes *PHABULOSA* (*PHB*), *PHAVOLUTA* (*PHV*), *REVOLUTA* (*REV*), and the LOB-domain family gene *AS2* are expressed in the adaxial cells and promote adaxial identity [25-30]. Meanwhile, the *KANADI* (*KAN1, 2, 3*), *YABBY* (*FIL, YAB2, 3, 5*) family genes, and *AUXIN RESPONSE FACTORS* (*ARF3*/*ETT* and *ARF4*) are expressed in the abaxial cells and promote the abaxial identity [31-35]. The adaxial and abaxial factors antagonistically regulate each other in multiple feedback loops to prevent activity across the boundary domain. The HD- ZIP III genes repress *KAN* in the adaxial domain, while *KAN* genes repress HD-ZIP III expression in the abaxial domain. Similarly, *AS2* represses *KAN1* and *ARF3/ETT* expression in the adaxial domain [36] and in return *KAN1* represses *AS2* expression in the abaxial domain [37]. A subset of this exquisite regulation is achieved through microRNAs (miRNAs) which also exhibit domain specific expression patterns. The miR165/166 is expressed in the abaxial side and degrades HD-ZIP III transcripts in the abaxial domain via mRNA cleavage [38-40], while adaxially expressed trans-acting small interfering RNA (tasiR-ARF) derived from the *TAS3* gene via the action of miR390 degrades *ARF3* and *ARF4* mRNA in the adaxial domain [41-43]. The balance of adaxial and abaxial activities through these mutually exclusive expression patterns and strictly reinforced border demarcations is important for flat lamina formation. Several polarity mutants showed that adaxialized or abaxialized primordia lead to malformed lamina including rods and curls although some species with unifacial leaves have flattened abaxialized lamina [44].

Nevertheless, not all leaf polarity factors are always on either side of the aisle. For example, *AS1* is an adaxial factor that forms a complex with *AS2* to repress KNOX1 activity in leaves. In fact, *AS1* is homolog of the snapdragon gene *PHANTASTICA* (*PHAN*), the first described polarity gene, whose loss-of-function mutant is characterized by temperature sensitive abaxialized and radialized lamina in the upper leaves [45]. But *AS1* is expressed in

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most parts of the cotyledon, except the cotyledon epidermis, and in the middle of the adaxial and abaxial region of leaf primordia [14]. Likewise, the expression pattern of *FILAMENTOUS FLOWER* (*FIL*) shows changes at different stages of development and for the most part extends from the abaxial domain well into the central region resulting in a broader expression domain than *KAN* [34, 35,46]. Furthermore, it has been recently reported that *FIL* and miR165/166 are initially expressed all over the initiating primordium at P0 stage and expression gradually shifts and becomes restricted to the abaxial side where *FIL* expressing miR165/166 free central region and *FIL* expressing miR165/166 active abaxial region become evident at later stages [47]. The timing of this shifting appears to be important for polarity patterning and is controlled by a plastid- generated retrograde signal [47] whose identity is unclear although candidates may be on the horizon [48]. We may have progressed from the meristem-derived to a plastid-derived signal in search of the elusive adaxializing factor, but whether the plastid-generated adaxializing signal requires the SAM and represents the Sussex signal or depends on differentiated cells from the primordium itself and represents a self-organizing signal remains to be shown. It is possible that the Sussex signal could originate in the leaf primordium and may have a self-patterning power, but may need to communicate with the meristem to generate a gradient dependent signal. Further research is needed to uncover the identity and source of the adaxializing factor.

In addition to domain specific transcription factors and miRNAs, recent data suggested that chromatin modification pathways may also be involved synergizing with the activities of at least some of the polarity factors. *AS1* has been reported to associate with *HISTONE DEACETYLASE6* (*HDA6*) in the regulation of Class I KNOX genes [49]. More recently, the AS1-AS2 complex is reported to physically interact and recruit the chromatin remodeling factor, Polycomb repressive complex 2 (PRC2) to stably silence *BP* and *KNAT2* in differentiated leaves [50]. The PRC2 complex has a methyltransferase activity and catalyzes trimethylation at lysine 27 of histone H3 (H3K27me3) associated with chromatin silencing [51-53]. The association of histone modifiers with the HD-ZIP III and KAN genes has not yet been reported and whether chromatin modification regulates lamina outgrowth through leaf polarity patterning is unknown. Most of the polarity factors including *AS2* and *KAN* are involved in the activation of either adaxial or abaxial characteristics, respectively, which requires cell differentiation but not necessarily cell proliferation. Obviously, lamina outgrowth requires both cell proliferation and cell differentiation, but the polarity factors have not been directly linked to activation of cell proliferation or to factors that control these processes such as the cell cycle. In fact, *AS2* and *KAN* repress cell proliferation in their respective domains [25]. This raises the question, how is cell proliferation coordinated with polarity factors? More importantly, as the leaf primordium (which in *Arabidopsis* contains about a dozen initial cells) grows away from the meristem, how are the proliferating cells maintained for sustained leaf growth?

In the legume model plant *Medicago truncatula*, a *WUSCHEL*-like transcription factor called *STENOFOLIA* (*STF*) is required for lamina outgrowth (mediolateral growth) as demonstrated by the *stf* loss-of-function mutant phenotype, which is characterized by a severely reduced narrow lamina [54, 55]. *STF* is homologue of the *WUSCHEL*-related homeobox1 (*WOX1)* in *Arabidopsis* [46, 56], *MAEWEST* (*MAW)* in petunia [56], *LATHROIDES* (*LATH*) in pea [57] and *LAM1* in tobacco [55]. Among these, the classical *bladeless lam1* mutant [58] exhibits the most severely affected lamina reduction phenotype while the *wox1* mutant is the least affected, where functional redundancy with *PRESSED FLOWER* (*PRS*) appeared to be insulating the effects [46,56]. *PRS* also called *WOX3* is homologue of the maize narrow sheath genes *NS1* and *NS2,* which redundantly function in regulating maize leaf lamina expansion [59]. While *lam1*, *maw*, *stf* and *lath* mutants representing both simple and compound leaves produce narrow lamina as single mutants, the *wox1* mutant appears to be an exception in requiring mutation at the *prs* locus to cause a similar phenotype. The reason for this phenotype difference between *Arabidopsis* and the other dicots has not been investigated. *STF* and its homologues, including *WOX1*, are expressed at the adaxial-abaxial boundary region of the leaf primordium both in the leaf margin and in the middle mesophyll [46,55,56], and regulate lamina expansion by controlling cell proliferation [46,55]. This led to the proposal of a three-domain model (adaxial, middle, abaxial) for lamina outgrowth in *Arabidopsis* [60]. These findings together suggest that a *WUS*-like function that resides in the middle domain is required for cell proliferation-mediated lamina outgrowth. Indeed, this function can be substituted in *stf* and *lam1* mutants by *Arabidopsis WUS* [55,61] indicating that *STF* and its homologues could establish and maintain a cell proliferation zone at the adaxial-abaxial junction during leaf morphogenesis [62].

Genetic evidence suggests that *Arabidopsis WOX1* may interact with adaxial and abaxial polarity factors, *AS2* and *KAN1*, in a mutually antagonistic manner [46] suggesting a mechanism for maintaining a cell proliferation zone protected from differentiation factors. It is therefore likely that the *WOX* genes in the middle keep cells in a proliferating state and supply cells for differentiation in the adaxial and abaxial domains thereby forming expanded planar lamina. In this context, *AS1* and *FIL* whose expression is expanded into the middle domain may have additional functions independent of *AS2* and *KAN*, respectively. For example, unlike *KAN, FIL* activates *AS1* and *WOX1* in the middle domain. Since the major players, *HD-ZIP III, AS1/AS2, KAN, FIL/YAB, ARF, and WOX* all encode transcriptional regulators, identifying their direct and indirect targets will enlighten our understanding. A recent progress in this area is pointing to the involvement of multiple phytohormones and sugar metabolites in the process [55,63-65], opening a window of opportunity to investigate how environmental, metabolic, and developmental signals are integrated at the dicot leaf primordium. Phylotactic arrangement of leaves, architecture of lobes and serrations at leaf margins, and leaflet placement in compound leaves appear to be modulated by the phytohormone auxin. Whether dorsoventral polaity patterning itself or the coordination of cell proliferation in the middle domain and cell differentiation in the adaxial and abaxial domains is controlled by phytohormones is yet to be established. Further studies using advanced techniques and integrated approaches in genetics, biochemical, cell biology, and metabolomics will uncover details of the network in the design and workings of the living solar panel, the lamina.

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