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Narrow Leaf Mutants in the Grass Family

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Abstract

Leaf morphology is critical for the survival of plant species. After a leaf primordium is initiated at the flank of shoot apical meristem (SAM), the development along the medial-lateral direction enlarges the leaf-blades, leading to the increase of photosynthetic activities. Thus, the revelation of mechanisms that control development across a leaf is quite important for plant breeding. A variety of narrow leaf mutants have been identified in the grass family, which includes particularly important crops in the world. Here, the molecular mechanisms underlying the leaf development in the medial-lateral direction are discussed as we introduce the three major groups of narrow leaf mutants in the grass family: (1) auxin-related mutants, (2) cellulose synthase-like D (CSLD)-related mutants, and (3) polarity-related mutants. The results obtained from these analyses could be directly applied to the breeding of major cereal crops such as maize, rice, and barley; therefore, they could contribute to the increase of food production.

Keywords: barley, rice, maize, leaf morphogenesis, mutant, gene expression

1. Introduction

Leaves are the major photosynthetic organs in plants. The light-capture efficiency significantly differs depending on the leaf shapes, angles, and arrangements in the canopy. Steeper leaf angle allows more light to penetrate to the lower leaves, leading to the increase of carbon gain through assimilation [1]. To avoid self-shading, leaf arrangement (phyllotaxis) is highly regulated by the plant hormone auxin [2, 3]. Since carbohydrates used in living activities are largely derived from the photosynthesis in plants, leaf morphology is critical for the survival of plant species.

A leaf primordium is initiated at the flank of shoot apical meristem (SAM), in which cells are maintained an indeterminate state by *class I knotted1-like homeobox (KNOX)* genes. The *Arabidopsis thaliana* genome includes four *class I KNOX* genes; *shoot meristemless (STM)*, *brevipedicellus*

(*BP*), *KN1*-like in *Arabidopsis thaliana*2 (*KNAT2*), and *KNAT6* [4]. *STM* is expressed throughout the SAM and induces cytokinin biosynthesis via *isopentenyl transferase7* (*IPT7*) activation and negatively regulates gibberellin biosynthesis via *GA 20-oxidase1* (*GA20ox1*) repression [5]. The resulting high cytokinin and low gibberellin ratio promotes meristem maintenance [6]. Such *STM* expression is downregulated by plant hormone auxin [2, 3]. Auxin is unique in its polar transportation mediated by influx carriers represented by *AUXIN1* (*AUX1*) and *LIKE-AUX1* (*LAX*) proteins, and efflux carriers represented by *PIN-FORMED* (*PIN*) and ATP-binding cassette B (*ABCB*) proteins [7]. Once transported to SAM, auxin flows to the peripheral young leaf primordia, creating an auxin maximum in the region where leaf primordia do not exist in the meristem. Such auxin localization downregulates *STM* expression, leading to the low cytokinin and high gibberellin ratio, which promote the switch from an indeterminate to a determinate state [8]. The loss-of-function of *PIN1* results in the malformed leaf development such as fused or cup-shaped leaves, suggesting that localized auxin accumulation in the meristem determines the radial position of leaf initiation [9].

In SAMs, *STM* also downregulates the expression of the MYB transcription factor *asymmetric leaves1* (*AS1*) and lateral organ boundaries domain (LBD) transcription factor *AS2*. When *STM* is repressed due to the auxin localization, *AS1* and *AS2*, released from the negative regulation of *STM*, act together as a heterodimer to repress the expression of *BP*, *KNAT2*, and *KNAT6* to prevent cell fate from returning to meristem [10–12]. The loss-of-function of *AS1* resulted in the malformation of leaves due to the ectopic *BP* expression, which was enhanced with the additional loss-of-function of *auxin resistant1* (*AXR1*) encoding a subunit of the related to ubiquitin1 (*RUB1*) activating enzyme that affects auxin responses [13]. These results suggest that the expression of *AS1* together with auxin localization plays a pivotal role in conferring leaf fate and promoting leaf development. Interestingly, slight *KNOX* expression remains in leaf primordia in species with compound leaves [14]. In tomato, the class I *KNOX* genes *tomato knotted1* (*TKN1*) and *TKN2* are expressed in young leaf primordia [15, 16]. The repression of *TKN* activity quickens the transition of the leaf primordia from the initiation to the secondary morphogenesis, suggesting that *KNOX* proteins are involved in the delay of leaf maturation and enable leaflet formation within leaf primordia [16].

The morphogenesis of sophisticated leaf organs with high reproducibility is achieved through the development in accordance with three axes; the proximal-distal, adaxial-abaxial, and medial-lateral directions (**Figure 1A–E**) [8, 17]. The development along the medial-lateral direction enlarges the leaf-blades, leading to the increase of photosynthetic activities. Thus, the revelation of developmental mechanism along the medial-lateral direction is quite important for plant breeding. So far, a variety of narrow leaf mutants have been identified in the grass family, which includes particularly important crops in the world. The results obtained from these analyses could be directly applied to the breeding of major crops such as maize, rice, and barley; therefore, they could contribute to the increase of food production. In fact, erect and narrow-leafed rice mutants led to the higher photosynthetic CO₂ uptake and improved yield in dense planting [18]. Recently, it was revealed that the Quantitative Trait Locus (QTL) controlling flag leaf morphology and photosynthetic activity were allelic to the causal gene for narrow leaf mutant in rice, suggesting the availability of narrow leaf genes for breeding high-yield varieties [19–23].

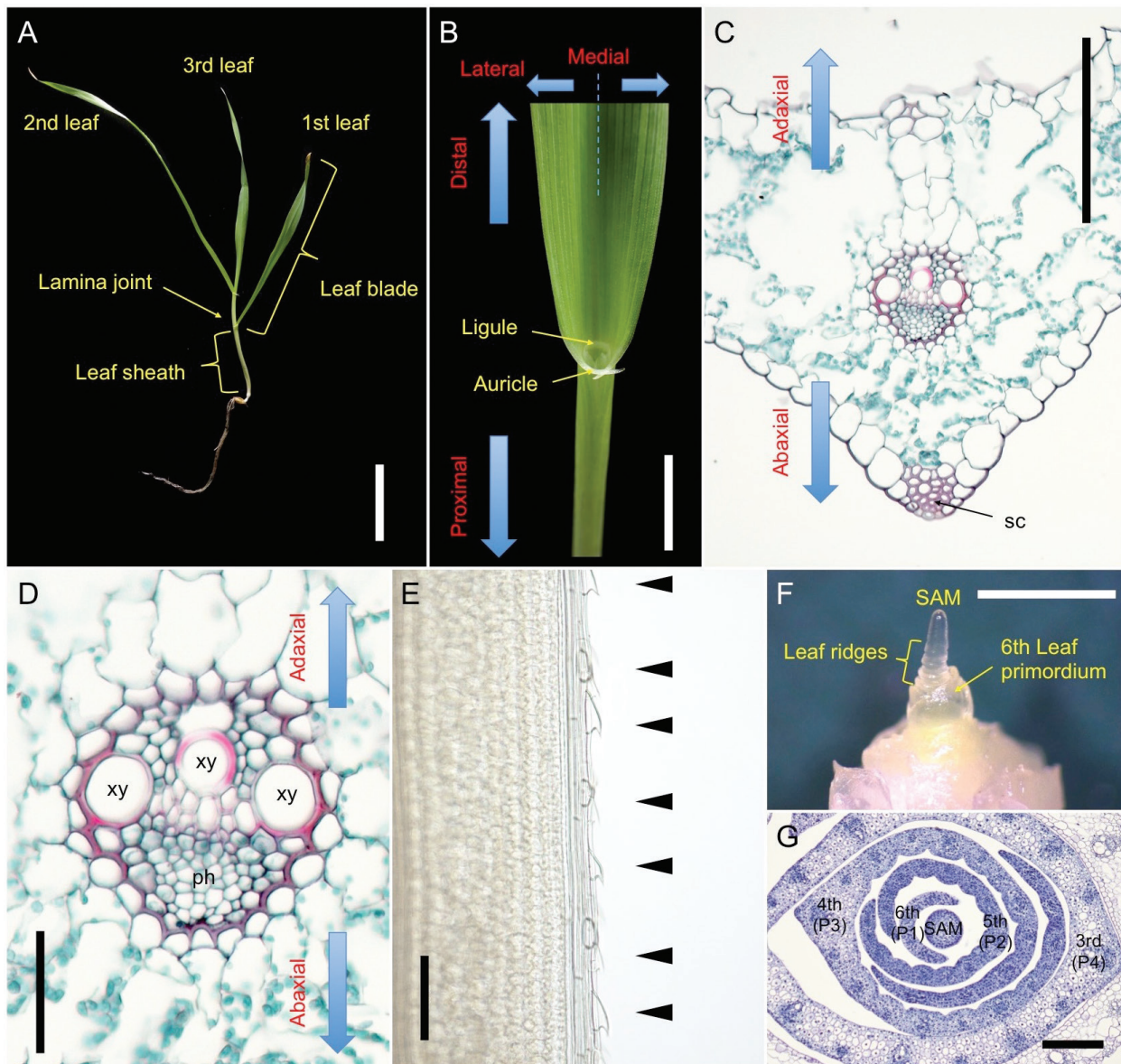


Figure 1. The shoot structure of normal barley (KN29). **(A)** A barley seedling at the second leaf stage. The leaf stage is defined by the number of fully expanded leaves. The first to third leaves are labeled. The leaf blade, leaf sheath, and lamina joint in the first leaf are indicated. **(B)** Close-up of the lamina joint in the second leaf. The ligule and auricle are pointed by arrows. **(C)** A cross section of the medial region in the second leaf blade. The section is double-stained in safranin and fast green. The lignified tissue is stained in red by safranin. “sc” indicates sclerenchymatous cells. **(D)** Close-up of the central vascular bundle in **(C)**. “xy” and “ph” indicate xylems and phloems, respectively. **(E)** The epidermal cells of the leaf margin in the second leaf blade. Arrow heads indicate the sawtooth hairs in the leaf margin. **(F)** A shoot apex of barley seedling at the second leaf stage. Matured leaves and leaf primordia are removed. The sixth leaf is initiating from the basal part of shoot apical meristem (SAM). Barley is unique in that leaf ridge formation precedes leaf primordium development. **(G)** A cross section of the shoot apex in barley seedling at the second leaf stage. The leaf positions (third to sixth) and the leaf primordial stages (P1–P4) are shown in the figure. Bars = 5 cm **(A)**, 5 mm **(B)**, 200 μ m **(C, G)**, 50 μ m **(D)**, 100 μ m **(E)**, 1 mm **(F)**.

Here, the molecular mechanisms underlying the leaf development in medial-lateral direction are discussed as we introduce the three major groups of narrow leaf mutants in grass family: (1) auxin-related mutants, (2) cellulose synthase-like D (CSLD)-related mutants, and (3) polarity-related mutants.

2. Auxin-related narrow leaf mutants

Auxin is a fundamental plant hormone and regulates a variety of plant growth and development. All parts of the young plant such as cotyledons, expanding leaves, and root tissues can potentially produce auxin although the youngest leaves exhibit the highest biosynthetic capacity [24–26]. Auxin is unique in its polar transportation (polar auxin transport (PAT)), as we mentioned above, mediated by influx carriers and efflux carriers [7]. The direction of auxin flow is the consequence of asymmetric localization of these carriers at plasma membrane [27, 28]. The resulting auxin localization within organs plays pivotal roles in phyllotactic patterning [29, 30], organogenesis [9, 31, 32], embryogenesis [33, 34], tropic response [35], and apical dominance [36]. At the cellular level, auxin regulates cell division, cell elongation, and cell differentiation [7, 37].

The predominant form of auxin is indole-3-acetic acid (IAA). Genetic and biochemical analyses indicated that tryptophan (Trp) is the main precursor of IAA in plants, and four biosynthetic pathways for IAA from Trp have been assumed [38–40]. Among IAA biosynthetic enzymes revealed so far, the most important biosynthetic enzymes are the tryptophan aminotransferase of arabisopsis (TAA) family of aminotransferases and the YUCCA (YUC) family of flavin-containing monooxygenases [41, 42]. TAA1 catalyzes the conversion of Trp to indole-3-pyruvic acid (IPA) in the initial step of the IPA pathway, and YUC catalyzes the conversion of IPA to IAA, downstream of TAA, in *arabidopsis* [40, 42–45]. The inactivation of a single TAA or YUC gene showed no obvious defects, indicating overlapping functions among TAA or YUC family members. On the other hand, the simultaneous inactivation of TAA1 and its close homologs, TAA-related1 (TAR1) or TAR2 (**Figure 2A**), or inactivation of two or more YUC genes resulted in multiple growth defects together with a severe reduction in IAA level [43, 46]. Therefore, the IPA pathway, catalyzed by TAA and YUC, is considered to be the major auxin biosynthetic pathway in *Arabidopsis* [40].

The importance of the IPA pathway in IAA biosynthesis is also demonstrated in grass family. In maize, loss-of-function of *vanishing tassel2* (VT2) and *sparse inflorescence1* (SPI1), co-ortholog of TAA1 and YUC in maize, respectively (**Figure 2**), caused severe barren inflorescences and semidwarf vegetative phenotypes with fewer leaves together with the reduction in IAA content [47, 48]. Similar reduction in IAA levels was shown in the loss-of-function of *fish bone* (FIB) and *narrow leaf7* (NAL7), co-ortholog of TAA1 and YUC in rice, respectively (**Figure 2**) [49, 50]. Thus, the IPA pathway seems to be the major IAA biosynthetic pathway in plants.

The reduction in IAA levels gives rise to pleiotropic organ malformation together with severe narrow leaf phenotype in rice. *Tryptophan deficient dwarf1* (TDD1) encodes a protein homologous to the anthranilate synthase β -subunit, which catalyzes the initial step of the Trp biosynthesis pathway [51]. TDD1 mutant is embryonic lethal because of a failure to develop most organs during embryogenesis. Regenerated TDD1 plants exhibit pleiotropic malformations including dwarfing, narrow leaves, short roots, and abnormal flowers, together with a reduction in Trp and IAA content. Trp feeding and moderate expression of *OsYUC1* rescued the mutant phenotypes, indicating that abnormal phenotypes of TDD1 were caused mainly by Trp and IAA deficiency [51]. The loss-of-function of *constitutively wilted 1* (COW1), which encodes

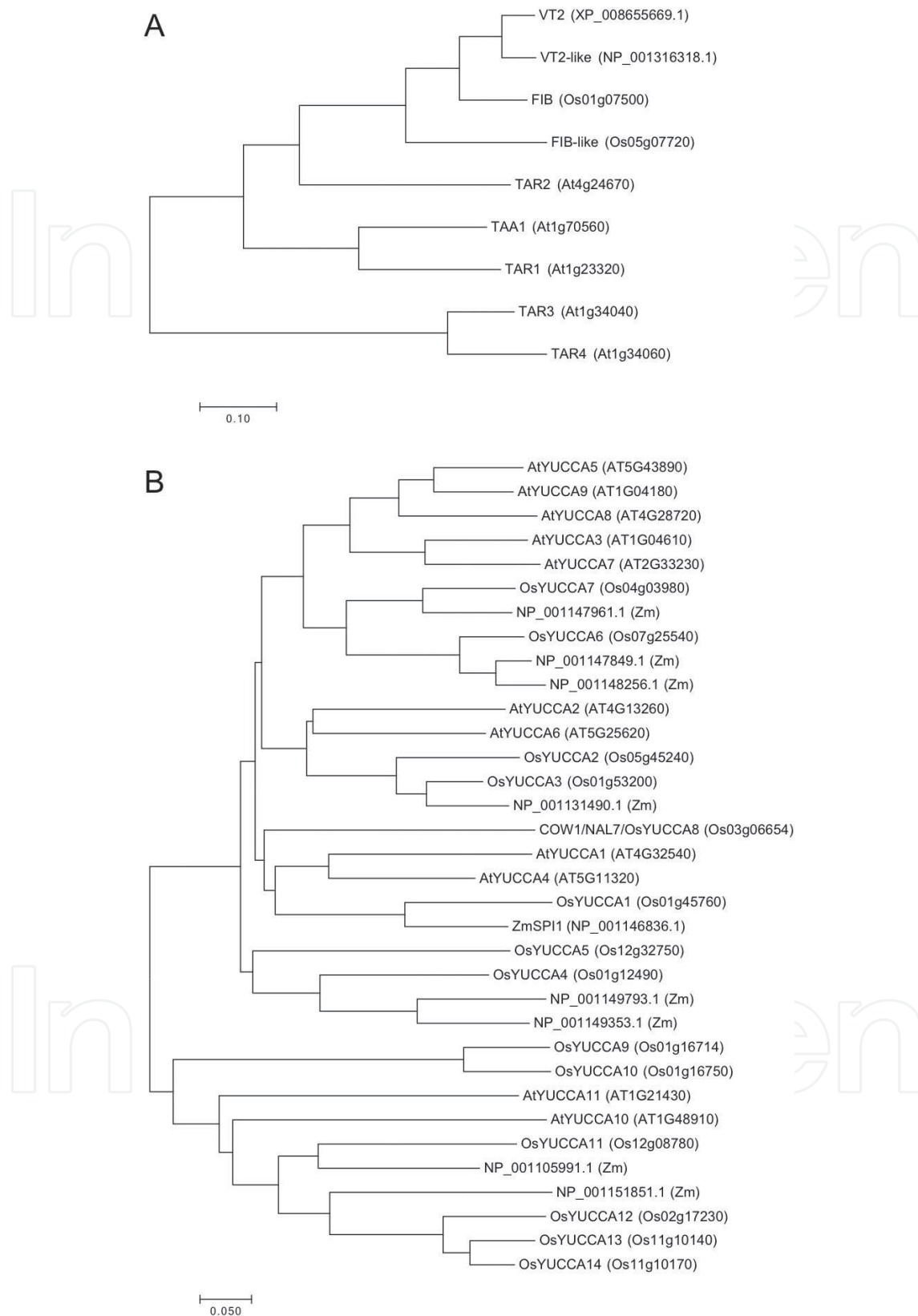


Figure 2. Phylogenetic tree of proteins involved in the IPA pathway. **(A)** TAA-related proteins in rice (FIB and FIB-like), maize (VT2 and VT2-like), and *Arabidopsis thaliana* (TAA1 and TAR1-4). **(B)** YUCCA-related proteins in rice (Os), maize (Zm), and *Arabidopsis thaliana* (At).

OsYUC8 (**Figure 2B**), was isolated from *TOS17* and T-DNA insertional rice mutants [52]. *COW1* mutants exhibited narrow leaves and a rolled leaf phenotype, which is likely attributable to insufficient water supply due to the small root-to-shoot ratio. Fujino et al. [49] identified another allele of *COW1*, *narrow leaf 7 (NAL7)*. The *NAL7* mutant shows a similar but milder phenotype compared with *COW1*, and the IAA content in *NAL7* was reduced compared to the wild type. In addition, overexpression of *NAL7* cDNA gave rise to overgrowth and abnormal morphology of the root, which was likely attributable to the overproduction of auxin. These results suggested that *NAL7/OsYUC8* is also involved in auxin biosynthesis. The importance of *TAA* gene in IAA biosynthesis in rice was demonstrated by *fish bone (FIB)* mutant [50]. *FIB* exhibited pleiotropic abnormal phenotypes including dwarfing, narrow and adaxially rolled leaves with large lamina joint angles, abnormal vascular development, and lack of crown and lateral roots. In addition, *FIB* also showed lack of gravitropism and aberrant phyllotaxy deviated from the normal distichous one. Map-based cloning revealed that *FIB* encodes co-ortholog of *TAA1* in rice (**Figure 2A**). Interestingly, loss-of-function of *FIB* resulted in not only the reduction in IAA level but also higher sensitivity to IAA and lower PAT activity. These results suggest that auxin biosynthesis, transport, and sensitivity are interrelated, which might be attributable to the pleiotropic abnormal phenotypes of *FIB* [50]. Rice genome includes 2 and 14 genes belong to the *TAA* and *YUC* families, respectively (**Figure 2**) [53]. While the inactivation of a single *TAA* or *YUC* gene showed no obvious defects in *arabidopsis*, distinct abnormal phenotypes were appeared in *FIB* or *COW1/NAL7* mutants in rice, suggesting that functional redundancy among *TAA* or *YUC* genes is less prevalent in rice than in *Arabidopsis*.

In contrast, rice *narrow leaf1 (NAL1)* encodes a trypsin-like serine and cysteine protease, whose relationship between auxin remains unknown, but *NAL1* mutant showed narrow leaves, dwarfing, and defective vascular patterns together with reduced PAT activity [54]. Surprisingly, several agronomic QTLs involved in flag leaf width (*qFLW4*; [19], *WFL*; [23]), photosynthesis rate (*GPS*; [21]), flag leaf shape (*qLSCHL4*; [22]), and spikelet number (*SPIKE*; [20]) were allelic to *NAL1*. The increased yield in *indica* rice varieties, which introduced these QTLs, suggests that *NAL1* is available in plant breeding. The latest study uncovered that *NAL1* functions in the regulation of cell division during leaf primordia initiation [55]. In *NAL1* mutant, expression of several G1- and S-phase specific genes were reduced, suggesting that *NAL1* affects cell-cycle regulation. In addition, the reduced expressions were also shown in *PIN1*, three *auxin response factor ARF* genes, and three *YAB* genes, but the expression of *YUC* genes were comparable to those of wild type. These results indicated that the inactivation of *NAL1* affects auxin transport and auxin response but not auxin biosynthesis [55].

Overall, auxin-related narrow leaf mutants exhibit pleiotropic abnormal phenotypes other than the reduction in leaf width. The representative phenotypes seem to be appeared in vascular patterning and root growth since auxin plays critical role in the development of these organs.

3. CSLD-related narrow leaf mutants

Cell walls are essential structures surrounding plant cells. While cells are expanding, primary cell walls fulfill the support and barrier functions. After cell expansions are completed, secondary cell

walls are formed between primary walls and plasma membranes, giving additional strength to cells. Cell wall is composed of polysaccharides, proteins, and phenolic compounds. Classically, polysaccharides are classified into cellulose, hemicelluloses, and pectins [56]. Cellulose synthase (CesA) protein contains a zinc finger domain at the *N*-terminus, eight transmembrane domains, and a central catalytic domain known as “D_D_D_QxxRW” motif. Although the mechanism by which CesA creates β -1,4-glucan chain is not fully revealed, it is plausible that glucan chain synthesized by the catalytic domain in the cytoplasm goes out of plasma membrane through the pores formed by the transmembrane domain [57]. It is likely that the zinc finger domain at the *N*-terminus is involved in CesA protein dimerization, leading to the higher-order structures [58, 59].

Based on the sequence similarity to *CesA* genes, a large superfamily of at least 41 *cellulose synthase-like* (CSL) genes were found in the *Arabidopsis thaliana* genome [60]. They were classified into six subfamilies (*CSLA*, *B*, *C*, *D*, *E*, and *G*), and subsequent studies identified three additional CSL subfamilies (*CSLF*, *H*, and *J*) [61, 62]. CSL proteins contain sequence motifs that are characteristics of β -glycosyltransferases. The only difference of CSLs from CesAs is the lack of the zinc finger domains at the *N*-terminus, which seems to be particularly important to form higher-order structures. In addition, most CSL proteins appear to be localized not in the plasma membrane but in the Golgi, where hemicellulose synthesis takes place. From these characteristics, *CSL* genes are predicted to catalyze the biosynthesis of noncellulosic polysaccharides [60]. As far as we know, the first biochemical evidence was provided by the soybean somatic embryos, in which expression of guar *CSLA* candidate cDNA gave rise to the enhanced mannan synthase activity [63]. Subsequent studies demonstrated that the *CSLA* genes encode (gluco)mannan synthases [64, 65], and that the *CSLF* and *CSLH* genes encode mixed linkage glucan synthases [66, 67]. *CSLC* genes were predicted to be involved in the xyloglucan synthesis [68], but recent study reported that some *CSLC* genes of barley are targeted to the plasma membrane, suggesting that the *CSLC* subfamily contains more than one type of polysaccharide synthase [69].

The uneven distribution of *CSL* genes implies how *CSL* subfamilies have been evolved in parallel with the diversification of plant species. While *CSLB* and *CSLG* subfamilies are found only in eudicots, *CSLF*, *CSLH*, and *CSLJ* subfamilies are specific to Poaceae. Particularly, *CSLJ* subfamily is unique in that it is only found in certain grasses, such as barley, wheat, sorghum, and maize, but not in rice or *Brachypodium* [62]. In contrast, *CSLD* subfamily is commonly found in all land plants, and show the highest similarity to *CesA* family among *CSL* subfamilies at sequence levels. The small number of introns and the gene structure diversity within the subfamily imply the possibility that *CSLD* is the oldest gene family in the cellulose synthase superfamily [60, 70]. Genome database survey revealed that *CSLD* subfamily contains six *Arabidopsis* genes, five maize genes, five rice genes, three barley genes, five sorghum genes, and six *Brachypodium* genes, and subsequent phylogenetic analysis showed that they are further classified into three clades (**Figure 3**) [71, 72]. The first clade including *AtCSLD1* and *AtCSLD4* is specifically expressed in pollens and involved in pollen tube elongation [73], and the second clade including *AtCSLD2*, *AtCSLD3*, *OsCSLD1*, and *ZmCSLD5* is highly expressed in root tissues and involved in root hair development [73–77]. While these two clades are commonly involved in “tip-growing” development, the loss-of-function of the third clade including *AtCSLD5*, *OsCSLD4*, and *ZmCSLD1* exhibited different phenotypes.

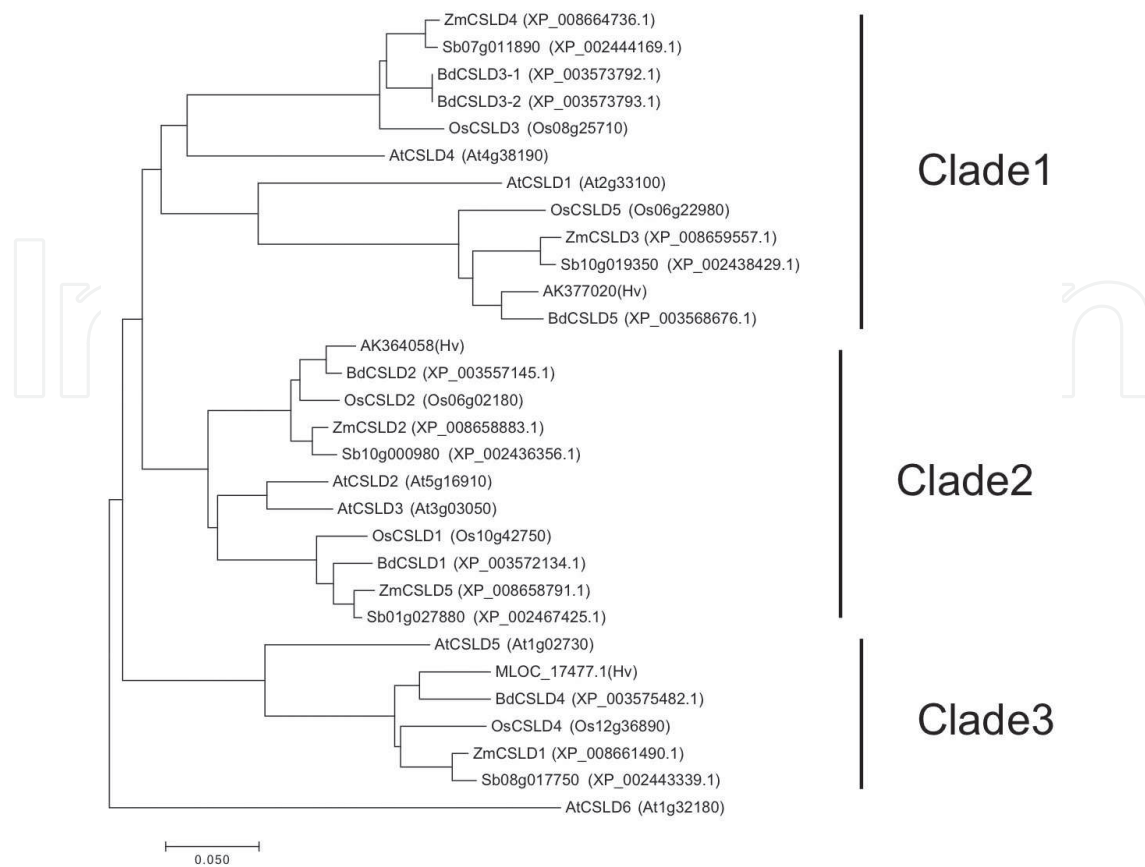


Figure 3. Phylogenetic tree of CSLD-related proteins in rice (Os), maize (Zm), barley (Hv), sorghum (Sb), *Brachypodium distachyon* (Bd), and *Arabidopsis thaliana* (At).

In rice, inactivation of *OsCSLD4* resulted in distinct narrow leaf phenotype. So far, several narrow leaf genes such as *narrow leaf and dwarf 1* [78], *narrow and rolled leaf 1* [79], *Oscd1* [80], *slender leaf 1* [72], *dwarf and narrowed leaf 1* [81], and *dwarf and narrow leaf 3* [82] were allelic to *OsCSLD4*. The mutants commonly exhibited narrow and rolled leaves and dwarfing phenotypes. The reduction in leaf-blade width and plant height was clearly attributable to the decrease of cell number, suggesting that *OsCSLD4* promotes cell proliferation activity. But if so, why is leaf-blade length less affected by the mutation than that of leaf-blade width? This question was solved by the increase of cell length in *OsCSLD4* mutant. Plants are able to compensate for a reduction in cell number with an increase in cell size [83], and the degree of compensation may differ depending on the direction. In fact, the number of cells was equally reduced in both length and width direction in *OsCSLD4* [72]. The expression analysis revealed that *OsCSLD4* is specifically expressed in M-phase cells in all developing organs, and loss-of-function of *OsCSLD4* resulted in the alteration of cell-cycle regulation. Interestingly, *OsCSLD4* included cells with 4C nucleus while such cells were not detected in normal rice. These results suggested that *OsCSLD4* plays a pivotal role in M-phase to progress cell proliferation [72].

The inactivation of *ZmCSLD1* also results in the narrow leaf and fine stem phenotype mainly due to the decrease of cell number [71]. In addition, wart-like cell clusters were formed on the leaf surface. The warts were attributable to the defects of cell division in leaf development, and

disrupted cross-wall formations were frequently observed in epidermal cells. Such defective developments of cell wall often appeared in cytokinetic mutants of *Arabidopsis*, such as *knolle* [84], *korrigan* [85], and *hinkel* [86], in which impairment of cytokinesis was caused by a failure of cell-plate formation. Considering the nature of *CSLD* as a wall-synthesizing enzyme, the *M*-phase specific expression, and the defective cell wall development in the mutant, it is speculated that *CSLD* may be involved in cell-plate formation. The existence of *CSLD* genes in all land plants also suggests the fundamental function of this subfamily. Recently, it was revealed that transiently expressed *AtCSLD5* is involved in mannan synthesis in tobacco leaves [87]. Distantly related *CSLA* subfamily also exhibits mannan synthase activity, but *CSLA* proteins readily use Guanosine diphosphate (GDP)-glucose as well as GDP-mannose and hence efficiently synthesize glucomannans [64, 88]. Since the mannosyltransferase activity of *AtCSLD5* was reduced by adding GDP-glucose together with GDP-mannose, *CSLD* subfamily is involved in a different kind of mannan synthesis from that catalyzed by *CSLA* subfamily [87]. Although mannans have been well studied as storage component, little information has been accumulated in relation to cytokinesis. Further analysis will reveal the detailed mechanism of plant cytokinesis and novel functions of hemicelluloses.

Overall, *CSLD*-related narrow leaf mutants exhibit a decrease in the whole plant size other than the reduction in leaf width. These phenotypes are directly attributable to the reduced cell proliferation activity, for *CSLDs* of the third clade are predicted to fulfill a function closely related to cytokinesis.

4. Polarity-related narrow leaf mutants

Most plant leaves are asymmetrical in all directions. Grass family leaves include leaf-blade in the distal side, leaf-sheath in the proximal side, and lamina-joint between the leaf-blade and leaf-sheath. The bulliform cells, which curl leaf-blades to prevent over transpiration, and xylems are formed only on the adaxial side, and the phloems on the abaxial side. The midrib, which functions as a physical support for the leaves, and ligule are formed in the medial side, and the sawtooth hairs and auricle in the lateral side (**Figure 1A–E**) [89]. For the construction of such a sophisticated organ, the proximal-distal, adaxial-abaxial, and medial-lateral polarities must be constructed as soon as cells acquire leaf fate in SAM (**Figures 1F and G**).

Among the three polarities, the molecular mechanism of adaxial-abaxial polarity is well studied using *Arabidopsis*. Through the loss-of-function and/or gain-of-function analyses, it has been revealed that adaxial identity is regulated by class III homeodomain-leucine zipper (HD-Zip) family genes and *asymmetric leaves2* (*AS2*), and that abaxial identity by *yabby* (*YAB*) family genes, *kanadi* (*KAN*) family genes, and *auxin response factor* (*ARF*) family genes [90]. The adaxial or abaxial specific expression of these genes is crucial for the establishment of the organ polarity, and these regulators are interacting antagonistically [17, 90]. In addition, small RNAs are also involved in the negative regulation of these regulators to maintain the expression regions [90–92]. In rice, the loss-of-function of *shallot-like 1* (*SLL1*)/*rolled leaf 9* (*RL9*), which encodes SHAQKYF class MYB transcription factor belonging to the *KAN* family, resulted in

the suppression of abaxial development while enhanced expression led to the abaxialized leaf phenotypes [93, 94]. Moreover, in maize, the accumulation of miR166, which is involved in the cleavage of class III *HD-Zip* transcripts, defined the expression region of the *rolled leaf 1 (RLD1)* belonging to the class III *HD-Zip* family, promoting the establishment of adaxial-abaxial polarity [95]. Despite the morphological differences from dicots, these genes homologous to *KAN* or class III *HD-Zip* seem to fulfill similar regulation in grass family.

While detail genetic regulators of proximal-distal polarity remain unclear in *Arabidopsis*, morphological, and molecular analyses are proceeding in grass families for the convenience of distinct organ development along the proximal-distal axis. A number of dominant mutations which specifically affect proximal-distal patterning have been characterized in maize [96]. The dominant mutant *Knotted1 (Kn1)* was characterized by sheath-like cells in the leaf-blade [97]. *KN1* encodes a homeodomain protein, and *KN1* transcripts were localized in the meristem but excluded from the leaf initial cells [98, 99]. However, *KN1* proteins were detected outside of the *KN1*-transcript localized area, suggesting the noncell-autonomous nature of *KN1* gene [100]. In leaf primordia, *KN1* proteins were accumulated in the most proximal part, and ectopic expression of *KN1* in the distal leaf-blade gave rise to alteration into sheath cell identity [101, 102]. These results suggested that *KN1* is involved in the establishment of proximal identity in leaf development. Ectopic expressions of *KN1*-like *homeobox (KNOX)* genes also resulted in cell fate alterations in maize, barley, and *Arabidopsis*, suggesting the highly conserved function of *KNOX* genes [103–105]. On the other hand, *PIN1* proteins which mediate polar auxin transport (*PAT*) are highly expressed in the distal ends of developing leaf primordia. Auxin plays pivotal roles in leaf development as we mentioned above, and *PIN1* creates an auxin maximum in the distal end of leaf primordium [31, 106]. The subsequent canalization through the interior of leaf primordia leads to the development of primary vascular strand. Thus, the auxin gradient along the proximal-distal axis is likely to play pivotal role in leaf development. Maize *liguleless1 (LG1)* and *liguleless2 (LG2)* mutants lack both ligule and auricle between leaf-blade and leaf-sheath [107–109]. It was revealed that *LG1* encodes a squamosa-promoter binding protein, and that *LG2* encodes a basic leucine zipper protein [110, 111]. While *LG1* is specifically expressed in ligule initiating area, *LG2* shows earlier and broader expression pattern than that of *LG1* [112, 113]. The phenotype of *lg1 lg2* double mutant suggested that they act in the same pathway, implying the possibility of interaction between *LG1* and *LG2* [109]. In addition, other liguleless mutants have been identified such as *LG3* and *LG4*, which encode class I *KNOX* genes [114, 115]. These findings promote the construction of a hypothetical model of leaf-blade-sheath boundary formation [113].

Compared with other polarities, the molecular mechanism of the medial-lateral polarity is less understood. So far, it was revealed that *drooping leaf (DL)* plays pivotal role in the development of medial organs in rice. *DL* encodes a putative transcription factor belonging to the *YAB* family, and *DL* mutants showed defective development of a midrib in the leaf, leading to the drooped leaf phenotype [116]. The *DL* transcripts were localized in the central region of leaf primordia, and over-expression of *DL* resulted in the ectopic formation of midrib-like structures in the lateral regions as well as in the central region of the leaf. In contrast, the development of leaf lateral domains is highly regulated by *wuschel-related homeobox (WOX)* genes. In maize, the loss-of-function mutations in both *narrow sheath1 (NS1)* and *NS2* resulted in the

significant reduction in leaf width due to the lack of marginal regions in leaves [117–119]. *NS1* and *NS2* double mutants fail to downregulate KNOX proteins in the premarginal regions of leaf primordia, leading to the deletion of marginal region from the primordial stages [117, 119]. *NS1* and *NS2* encode the duplicated *WOX3* genes, and *NS* transcripts are accumulated in the marginal edges of initiating leaf primordia. From these results, it was suggested that *NS* genes play pivotal roles in the recruitment of leaf founder-cells by downregulating KNOX accumulation [120–122]. Genes belonging to *WOX3* family are largely classified into two clades (**Figure 4**), and the *NS*-related clade includes *narrow leaf2* (*NAL2*) and *NAL3* of rice, *narrow leafed dwarf 1* (*NLD1*) of barley, and *pressed flower1* (*PRS1*) of *Arabidopsis* [123].

The nucleotide sequences of *NAL2* and *NAL3* are identical, corresponding with the recent duplication of a large chromosomal segment in chromosomes 11 and 12 [124]. *NAL2/3* and *NLD1* mutants show the similar abnormal phenotypes to *NS1* and *NS2* such as distinct narrow leaf phenotype and defective marginal development, which are attributable to the lack of marginal regions (**Figure 5**) [123, 125, 126]. The expression patterns of *NAL2/3* and *NLD1* are also similar to that of *NS1 NS2*, suggesting the conserved function of *NS*-related genes in the development of lateral organs. Interestingly, no distinct abnormal phenotypes were observed in the leaf of *PRS1* mutant except for the deletion of the proximal lateral stipules [117]. This result supported the leaf-zonation model that the lower leaf zone of bifacial monocot leaves corresponds with the basal part of bifacial eudicot leaves including stipules [127]. It is, therefore, considered that *NS*-related *WOX3* genes are involved in the development of the lateral domain in the lower leaf zone.

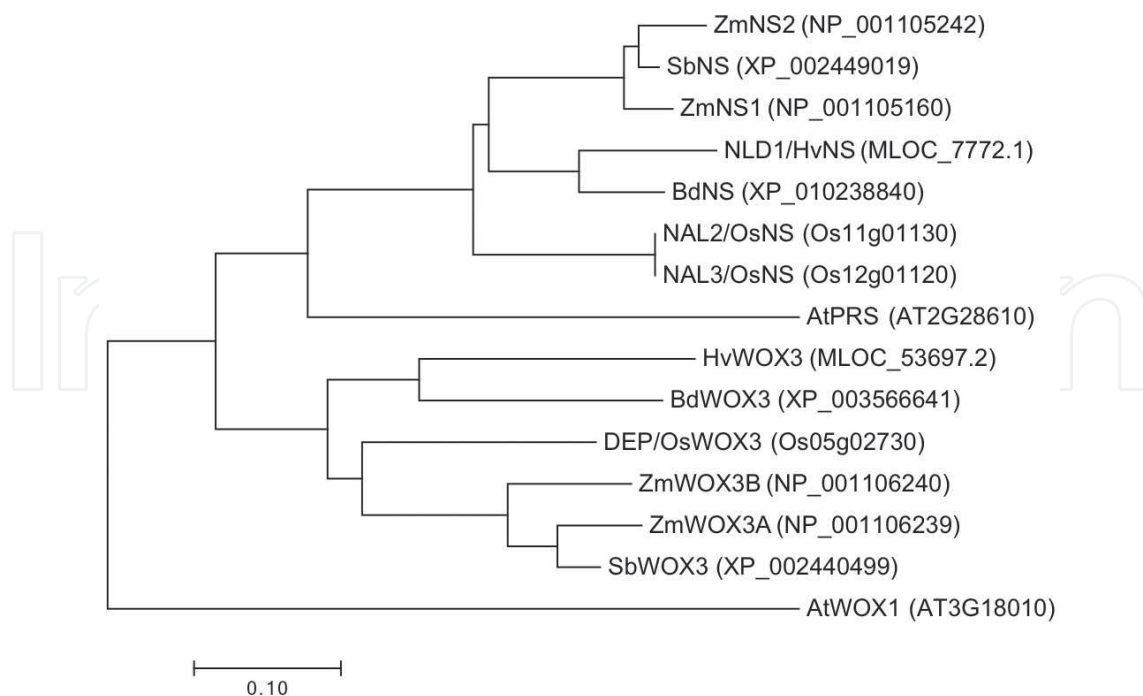


Figure 4. Phylogenetic tree of *WOX3*-related proteins in rice (*Os*), maize (*Zm*), barley (*Hv*), sorghum (*Sb*), *Brachypodium distachyon* (*Bd*), and *Arabidopsis thaliana* (*At*).

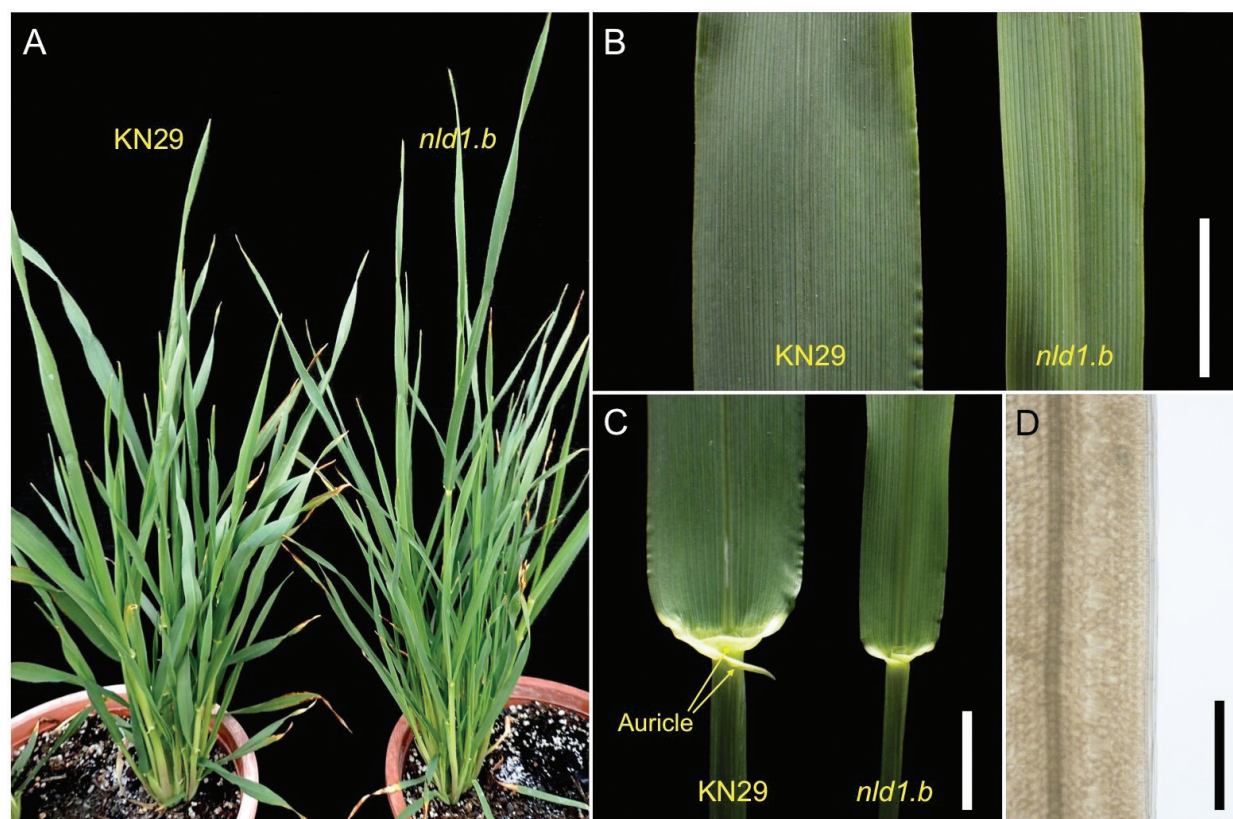


Figure 5. The narrow leaf phenotype of barley *narrow leaved dwarf1* (*NLD1*) mutant. (A–C) The whole shoots (A), the leaf-blades (B), and the lamina joints (C) in matured leaves of wild-type (KN29) and *NLD1.b* mutant. The auricles are pointed by arrows in (C). Auricles are significantly diminished in *NLD1.b* due to the defective development of the lateral domain. (D) The epidermal cells of the leaf margin in *NLD1.b* leaf-blade. Sawtooth hairs are rarely formed in the mutant unlike wild-type (Figure 1E). Bars = 1 cm (B, C), 200 μ m (D).

The width of *PRS* leaves was significantly reduced by the additional mutation of *WOX1*. *WOX1* is unique in that it belongs to the same clade of the *WOX3/PRS* family but seems to be absent in grasses (Figure 4) [128, 129]. *WOX1* and *PRS* double mutants exhibit not only the loss of leaf marginal tissues but also the confused adaxial-abaxial identity at leaf marginal regions [129, 130]. These results suggested that leaf margin functions as an adaxial-abaxial boundary, where adaxial and abaxial regulators are downregulated by *WOX* genes [90].

While the medial-lateral polarity is directly related to leaf width, mutation or over-expression of the genes regulating the proximal-distal or adaxial-abaxial polarity can also result in the reduction in leaf width together with the alteration of organ polarities. Recessive mutant *rough sheath 2* (*RS2*) of maize exhibits narrow/bladeless leaves with a disruption of the blade-sheath boundary [131]. In *RS2* mutant, class I KNOX proteins are ectopically accumulated, and it was revealed that *RS2* encodes an MYB-domain protein, an ortholog of *AS1* in *Arabidopsis*. Thus, it is likely that *RS2* is involved in the proximal-distal patterning by downregulating *KNOX* expression. *Liguleless* (*LG*) genes play pivotal role in the establishment of the boundary between leaf-blade and leaf-sheath in the proximal-distal axis. Recently, another *LG* gene *liguleless narrow* (*LGN*) was identified, and its semidominant mutant (*LGN-R*) showed narrow leaves with greatly reduced auricle and ligule and indefinite blade-sheath boundary [132]. *LGN* encodes a grass-specific kinase, which is broadly expressed in maize organ but affects *LG1* and *LG2* expression. The dominant mutant *Wavy auricle in blade 1* (*WAB1*) shows narrow leaves with

ectopic auricle and extended sheath in leaf-blade [112, 133]. In contrast to *LGN-R*, *LG1* was misexpressed in *WAB1*, and recently it was revealed that *WAB1* encodes a teosinte-branched1/cycloidea/PCF (TCP) transcription factor, which is necessary for *LG1* expression [134]. These genes play a pivotal role in the establishment of proximal-distal polarity, but affect leaf width indirectly. Thus, it was considered that proximal-distal patterning may link to medial-lateral growth.

On the other hand, Rice *SLL1/RL9* encodes KAN transcription factor as we mentioned above, and *sll1/rl9* mutants show rolled leaf phenotypes due to the defective development of the sclerenchymatous cells on the abaxial side together with the reduction in leaf width [93, 94]. Similar defective development was observed in *semi-rolled leaf 2 (SRL2)*, which exhibits narrow incurved leaves due to the defective development of sclerenchymatous cells on the abaxial side [135]. *SRL2* encodes a novel plant-specific protein of unknown biochemical function, and highly expressed in the abaxial cell layer in the leaf sheath. However, *SLL1/RL9* expression was unaffected in *SRL2*, and *SRL2 SLL1* double mutants showed more severe defective development of sclerenchymatous cells on the abaxial side together with the much narrower leaf phenotype than single mutants [135]. These results suggest that *SLL1/RL9* and *SRL2* function in distinct pathways to regulate the abaxial development. Overexpression of *OsHOX32*, a member of class III *HD-Zip* family, resulted in narrow and adaxially rolled leaves due to the reduction in bulliform cell number [136]. Among the six *OsYAB* genes, *OsYAB1*, *OsYAB2*, and *OsYAB6* were upregulated while *OsYAB3*, *OsYAB4*, and *OsYAB5* were downregulated in the overexpression plants, suggesting the direct or indirect interaction between *OsHOX32* and *OsYAB* genes. Similar defective development was observed by the overexpression of *OsLBD3-7*, which shows high similarity to *AS2* of *Arabidopsis*. *OsLBD3-7* overexpression plants exhibit narrow and adaxially rolled leaves due to the reduction in bulliform cell size and number [137]. Since the negative regulators of bulliform cell development were upregulated in overexpression plants, it was suggested that *OsLBD3-7* positively regulate these negative regulators in leaf development. The marginal expressions of *NS* genes are disappeared in maize *ragged seedling 2 (RGD2)* mutant, which exhibits thread-like narrow leaves [138]. *RGD2* encodes argonaute7 (*AGO7*)-like protein, which is involved in the synthesis of trans-acting short-interfering RNA (ta-siRNA) derived from *TAS3* in *Arabidopsis*. So far, several mutants for *TAS3* ta-siRNA pathway have been identified including *AGO7*-related genes (*RGD2* in maize; [138], *shootless4 (SHL4)/shoot organization2 (SHO2)* in rice; [139]), *SGS3*-related gene (*leafbladeless1 [LBL1]* in maize; [140, 141]), *RDR6*-related gene (*SHL2* in rice; [142, 143]), and *DCL4*-related gene (*SHO1* in rice; [143, 144]). Although maize and rice leaves are different morphologically, the loss-of-function of these genes commonly gave rise to thread-like narrow leaves which showed defective adaxial-abaxial and medial-lateral polarities. *TAS3* ta-siRNA is expressed on the adaxial side of developing leaf primordia and restricts the expression region of abaxial factor *ARF3a* and miR166 [141]. Since miR166 restricts the expression region of class III *HD-Zip* genes, inactivation of *TAS3* ta-siRNA pathway results in the upregulation of *ARF3a* and miR166, and downregulation of class III *HD-Zip* genes, leading to the abaxialization of leaf. Such a severe abaxialization might disturb the establishment of medial-lateral polarity. In *Arabidopsis*, triple mutation of *YAB* genes (*FIL YAB3 YAB5*) has resulted in the thread-like narrow leaves which showed defective adaxial-abaxial and medial-lateral polarities [145, 146]. These results suggest that the establishment and/or development of the medial-lateral polarity is regulated downstream of the adaxial-abaxial polarity.

Overall, polarity-related narrow leaf mutants exhibit distinct reduction in leaf-blade width together with the disruption of organ polarity. The loss-of-function of lateral identity is directly reflected in the reduction of leaf width, but the disruption of the proximal-distal or adaxial-abaxial polarities also affect the establishment or development along medial-lateral axis, suggesting the interactive development between the three polarities.

5. Conclusion

The reduction in leaf width is a subtle morphological alteration, but the analyses of narrow leaf mutants have uncovered molecular functional diversity of the causal genes. Through a variety of genetic approaches, it has been demonstrated that *NS*-related *WOX3* genes are critical for the development of leaf lateral domains. Although *NS*-related *WOX3* transcripts are strictly limited within the marginal edges, the phenotypic alteration of loss-of-function mutants occurs in more broad area, suggesting the noncell-autonomous nature of *NS*-related *WOX3* genes. This could be explained by the migration of either *WOX3* protein itself or the secondary signals derived from the marginal cells. Recently, it was reported that barley *NLD1* mutant exhibited malformation of commissural veins in the leaf lateral domain [123]. Since polar auxin transport plays an important role in determining vascular pattern in leaves, *nld1* may include some abnormalities in auxin transport. Therefore, it is quite interesting whether auxin functions as the secondary signal of *NS*-related *WOX3* genes. Auxin plays pleiotropic role in plant development, and at the cellular level, auxin regulates cell division, cell elongation, and cell differentiation. In addition, it is suggested that auxin biosynthetic *YUC* genes are expressed in response to the juxtaposition of adaxial and abaxial domains [147]. Thus, auxin biosynthesis at the adaxial-abaxial boundary partly contributes to leaf margin expansion, and this might explain the reduction in leaf width attributable to the disruption of the adaxial-abaxial polarity. At the downstream of these mechanisms, cell proliferation activity is maintained by *CSLD* genes of the third clade. The details of plant cytokinesis are not fully understood, particularly as to the components of cell plate. All we covered here is just a part of well-studied mutants, and there should be many hither-to unidentified narrow leaf mutants. Further study will give us a novel and detailed mechanism of leaf development in the grass family.

6. Materials and methods

6.1. Plant materials

For morphological observation of barley shoot, a wild type line Kanto Nijo 29 (KN29), which has two-rowed spike and covered caryopsis, and its gamma-ray induced *narrow leafed dwarf1* (*NLD1*) mutant, *NLD1.b*, were used. To promote germination, seeds were kept at 15°C on wet paper for 3 days. Then, imbibed seeds were sown on soil and grown under natural conditions.

6.2. Paraffin sectioning and histological analysis

Plant samples were fixed with FAA (formaldehyde:glacial acetic acid:50% ethanol [2:1:17]) for 24 h at 4°C for histological analysis. They were then dehydrated in a graded ethanol series,

substituted with 1-butanol, and embedded in Paraplast® Plus (McCormick Scientific). The samples were sectioned at 8 µm thickness using a rotary microtome. For the histological analysis, sections were stained in hematoxylin or double-stained in safranin and fast green. After staining, sections were mounted with Poly-Mount® (Polysciences, Inc.) and observed with a light microscope.

6.3. Epidermal cell observation

The leaf-blades were fixed with FAA (formaldehyde:glacial acetic acid:50% ethanol [2:1:17]) for 24h at 4°C. They were then dehydrated in a graded ethanol series. Dehydrated samples were incubated at 96°C in chloralhydrate dissolved in 100% ethanol until they were cleared, and observed with a light microscope.

6.4. Phylogenetic analysis

For the phylogenetic analysis of *TAA*-, *YUCCA*-, *CSLD*-, and *WOX3*-related genes, amino acid sequences were obtained from TIGR (<http://rice.plantbiology.msu.edu>) for rice, IPK Barley BLAST Server (<http://webblast.ipk-gatersleben.de/barley/>) for barley, NCBI (<https://www.ncbi.nlm.nih.gov>) for maize, sorghum, and *Brachypodium distachyon*, and TAIR (<https://www.arabidopsis.org>) for *Arabidopsis thaliana*. As for *YUCCA*-related maize proteins, amino acid sequences showing the highest similarity to *YUCCA* protein were searched using the protein blast in NCBI. The obtained sequences were analyzed with MEGA version 7 (available at <http://www.megasoftware.net>, [148]) to create the phylogenetic trees.

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References

- [1] Falster DS, Westoby M. Leaf size and angle vary widely across species: What consequences for light interception?. *New Phytologist*. 2003;**158**:509-525
- [2] Hay A, Craft J, Tsiantis M. Plant hormones and homeoboxes: Bringing the gap?. *BioEssays*. 2004;**26**:395-404
- [3] Fleming AJ. Formation of primordia and phyllotaxy. *Current opinion in Plant Biology*. 2005;**8**:53-58

- [4] Hake S, Smith HMS, Holtan H, Magnani E, Mele G, Ramirez J. The role of KNOX genes in plant development. *Annual Review of Cell and Developmental Biology*. 2004;**20**:125-151
- [5] Hay A, Tsiantis M. KNOX genes: Versatile regulators of plant development and diversity. *Development*. 2010;**137**:3153-3165
- [6] Hepworth SR, Pautot VA. Beyond the divide: Boundaries for patterning and stem cell regulation in plants. *Frontiers in Plant Science*. 2015;**6**:1052
- [7] Petrášek J, Friml J. Auxin transport routes in plant development. *Development*. 2009;**136**:2675-2688
- [8] Moon J, Hake S. How a leaf gets its shape. *Current Opinion in Plant Biology*. 2011;**14**:24-30
- [9] Křeček P, Skůpa P, Libus J, Naramoto S, Tejos R, Friml J, Zažímalová E. The PIN-FORMED (PIN) protein family of auxin transporters. *Genome Biology*. 2009;**10**:249
- [10] Byrne ME, Barley R, Curtis M, Arroyo JM, Dunham M, Hudson A, Martienssen RA. *Asymmetric leaves1* mediates leaf patterning and stem cell function in *Arabidopsis*. *Nature*. 2000;**408**:967-971
- [11] Guo M, Thomas J, Collins G, Timmermans MCP. Direct repression of KNOX loci by the *ASYMMETRIC LEAVES1* complex of *Arabidopsis*. *The Plant Cell*. 2008;**20**:48-58
- [12] Li Z, Li B, Shen WH, Huang H, Dong A. TCP transcription factors interact with *AS2* in the repression of class-I KNOX genes in *Arabidopsis thaliana*. *The Plant Journal*. 2012;**71**:99-107
- [13] Hay A, Barkoulas M, Tsiantis M. *ASYMMETRIC LEAVES1* and auxin activities converge to repress *BREVIPEDICELLUS* expression and promote leaf development in *Arabidopsis*. *Development*. 2006;**133**:3955-3961
- [14] Tsiantis M, Hay A. Comparative plant development: the time of the leaf? *Nature Reviews Genetics*. 2003;**4**:169-180
- [15] Hareven D, Gutfinger T, Parnis A, Eshed Y, Lifschitz E. The making of a compound leaf: Genetic manipulation of leaf architecture in tomato. *Cell*. 1996;**84**:735-744
- [16] Shani E, Burko Y, Ben-Yaakov L, Berger Y, Amsellem Z, Goldshmidt A, Sharon E, Ori N. Stage-specific regulation of *Solanum lycopersicum* leaf maturation by class 1 *KNOTTED1-LIKE HOMEODOMAIN* proteins. *The Plant Cell*. 2009;**21**:3078-3092
- [17] Scarpella E, Barkoulas M, Tsiantis M. Control of leaf and vein development by auxin. *Cold Spring Harbor Perspectives in Biology*. 2010;**2**:a001511
- [18] Yamaguchi H, Watanabe M, Sato S, Kanbayashi Y. Yielding ability of erect- and narrow-leaved rice mutant in heavy manuring and dense planting culture. *Radioisotopes*. 1979;**28**:734-738
- [19] Chen M, Luo J, Shao G, Wei X, Tang S, Sheng Z, Song J, Hu P. Fine mapping of a major QTL for flag leaf width in rice, *qFLW4*, which might be caused by alternative splicing of *NAL1*. *Plant Cell Reports*. 2012;**31**:863-872

- [20] Fujita D, Trijatmiko KR, Tagle AG, Sapasap MV, Koide Y, Sasaki K, Tsakirpaloglou N, Gannaban RB, Nishimura T, Yanagihara S, Fukuta Y, Koshiha T, Slamet-Loedin IH, Ishimaru T, Kobayashi N. NAL1 allele from a rice landrace greatly increases yield in modern indica cultivars. *Proceedings of the National Academy of Sciences*. 2013;**110**:20431-20436
- [21] Takai T, Adachi S, Taguchi-Shiobara F, Sanoh-Arai Y, Iwasawa N, Yoshinaga S, Hirose S, Taniguchi Y, Yamanouchi U, Wu J, Matsumoto T, Sugimoto K, Kondo K, Ikka T, Ando T, Kono I, Ito S, Shomura A, Ookawa T, Hirasawa T, Yano M, Kondo M, Yamamoto T. A natural variant of NAL1, selected in high-yield rice breeding programs, pleiotropically increases photosynthesis rate. *Scientific Reports*. 2013;**3**:2149
- [22] Zhang GH, Li SY, Wang L, Ye WJ, Zeng DL, Rao YC, Peng YL, Hu J, Yang YL, Xu, J, Ren DY, Gao ZY, Zhu L, Dong GJ, Hu XM, Yan MX, Guo LB, Li CY, Qian Q. LSCHL4 from Japonica Cultivar, which is allelic to NAL1, increases yield of indica super rice 93-11. *Molecular Plant*. 2014;**7**:1350-1364
- [23] Taguchi-Shiobara F, Ota T, Ebana K, Ookawa T, Yamasaki M, Tanabata T, Yamanouchi U, Wu J, Ono N, Nonoue Y, Nagata K, Fukuoka S, Hirabayashi H, Yamamoto T, Yano M. Natural variation in the flag leaf morphology of rice due to a mutation of the NARROW LEAF 1 gene in *Oryza sativa* L. *genetics*. 2015;**201**:795-808
- [24] Ljung K, Bhalerao RP, Sandberg G. Sites and homeostatic control of auxin biosynthesis in *Arabidopsis* during vegetative growth. *The Plant Journal*. 2001;**28**:465-474
- [25] Benjamins R, Scheres B. Auxin: The looping star in plant development. *Annu. Rev. Plant Biol.* 2008;**59**:443-465
- [26] Finet C, Jaillais Y. AUXOLOGY: When auxin meets plant evo-devo. *Developmental Biology*. 2012;**369**:19-31
- [27] Zažimalová E, Murphy A, Yang H, Hoyerová K, Hošek P. Auxin transporters: why so many?. *Cold Spring Harbor Perspectives in Biology*. 2010;**2**:a001552
- [28] Leyser O. Auxin, self-organisation, and the colonial nature of plants. *Current Biology*. 2011;**21**:331-337
- [29] Vernoux T, Kronenberger J, Grandjean O, Laufs P, Traas J. PIN-FORMED 1 regulates cell fate at the periphery of the shoot apical meristem. *Development*. 2000;**127**:5157-5165
- [30] Bainbridge K, Guyomarc'h S, Bayer E, Swarup R, Bennett M, Mandel T, Kuhlemeier C. Auxin influx carriers stabilize phyllotactic patterning. *Genes and Development*. 2008;**22**:810-823
- [31] Scarpella E, Marcos D, Friml J, Berleth T. Control of leaf vascular patterning by polar auxin transport. *Genes & Development*. 2006;**20**:1015-1027
- [32] Kitomi Y, Ogawa A, Kitano H, Inukai Y. CRL4 regulates crown root formation through auxin transport in rice. *Plant Root*. 2008;**2**:19-28
- [33] Möller B, Weijers D. Auxin control of embryo patterning. *Cold Spring Harbor Perspectives in Biology*. 2009;**1**:a001545

- [34] Forestan C, Meda S, Varotto S. ZmPIN1-mediated auxin transport is related to cellular differentiation during maize embryogenesis and endosperm development. *Plant Physiology*. 2010;**152**:1373-1390
- [35] Mei Y, Jia WJ, Chu YJ, Xue HW. Arabidopsis phosphatidylinositol monophosphate 5-kinase 2 is involved in root gravitropism through regulation of polar auxin transport by affecting the cycling of PIN proteins. *Cell Research*. 2012;**22**:581-597
- [36] Prusinkiewicz P, Crawford S, Smith RS, Ljung K, Bennett T, Ongaro V, Leyser O. Control of bud activation by an auxin transport switch. *Proceedings of the National Academy of Sciences*. 2009;**106**:17431-17436
- [37] Vanneste S, Friml J. Auxin: A trigger for change in plant development. *Cell*. 2009;**136**:1005-1016
- [38] Sugawara S, Hishiyama S, Jikumaru Y, Hanada A, Nishimura T, Koshiba T, Zhao Y, Kamiya Y, Kasahara H. Biochemical analyses of indole-3-acetaldoxime-dependent auxin biosynthesis in Arabidopsis. *Proceedings of the National Academy of Sciences*. 2009;**106**:5430-5435
- [39] Zhao Y. Auxin biosynthesis and its role in plant development. *Annual Review of Plant Biology*. 2010;**61**:49-64
- [40] Mashiguchi K, Tanaka K, Sakai T, Sugawara S, Kawaide H, Natsume M, Hanada A, Yaeno T, Shirasu K, Yao H, McSteen P, Zhao Y, Hayashi K, Kamiya Y, Kasahara H. The main auxin biosynthesis pathway in Arabidopsis. *Proceedings of the National Academy of Sciences*. 2011;**108**:18512-18517
- [41] Zhao Y, Christensen SK, Fankhauser C, Cashman JR, Cohen JD, Weigel D, Chory J. A role for flavin monooxygenase-like enzymes in auxin biosynthesis. *Science*. 2001;**291**:306-309
- [42] Won C, Shen X, Mashiguchi K, Zheng Z, Dai X, Cheng Y, Kasahara H, Kamiya Y, Chory J, Zhao Y. Conversion of tryptophan to indole-3-acetic acid by TRYPTOPHAN AMINOTRANSFERASES OF ARABIDOPSIS and YUCCAs in Arabidopsis. *Proceedings of the National Academy of Sciences*. 2011;**108**:18518-18523
- [43] Stepanova AN, Robertson-Hoyt J, Yun J, Benavente LM, Xie DY, Doležal K, Schlereth A, Jürgens G, Alonso JM. TAA1-mediated auxin biosynthesis is essential for hormone crosstalk and plant development. *Cell*. 2008;**133**:177-191
- [44] Stepanova AN, Yun J, Robles LM, Novak O, He W, Guo H, Ljung K, Alonso JM. The Arabidopsis YUCCA1 flavin monooxygenase functions in the indole-3-pyruvic acid branch of auxin biosynthesis. *The Plant Cell*. 2011;**23**:3961-3973
- [45] Dai X, Mashiguchi K, Chen Q, Kasahara H, Kamiya Y, Ojha S, DuBois J, Ballou D, Zhao Y. The biochemical mechanism of auxin biosynthesis by an Arabidopsis YUCCA flavin-containing monooxygenase. *Journal of Biological Chemistry*. 2013;**288**:1448-1457
- [46] Cheng Y, Dai X, Zhao Y. Auxin biosynthesis by the YUCCA flavin monooxygenases controls the formation of floral organs and vascular tissues in Arabidopsis. *Genes and Development*. 2006;**20**:1790-1799

- [47] Gallavotti A, Barazesh S, Malcomber S, Hall D, Jackson D, Schmidt RJ, McSteen P. sparse inflorescence 1 encodes a monocot-specific YUCCA-like gene required for vegetative and reproductive development in maize. *Proceedings of the National Academy of Sciences*. 2008;**105**:15196-15201
- [48] Phillips KA, Skirpan AL, Liu X, Christensen A, Slewinski TL, Hudson C, Barazesh S, Cohen JD, Malcomber S, McSteen P. vanishing tassel 2 encodes a grass-specific Tryptophan Aminotransferase required for vegetative and reproductive development in maize. *The Plant Cell*. 2011;**23**:550-566
- [49] Fujino K, Matsuda Y, Ozawa K, Takeshi N, Koshiha T, Fraaije MW, Sekiguchi H. NARROW LEAF 7 controls leaf shape mediated by auxin in rice. *Molecular Genetics and Genomics*. 2008;**279**:499-507
- [50] Yoshikawa T, Ito M, Sumikura T, Nakayama A, Nishimura T, Kitano H, Yamaguchi I, Koshiha T, Hibara K, Nagato Y, Itoh J. The rice FISH BONE gene encodes a tryptophan aminotransferase, which affects pleiotropic auxin-related processes. *The Plant Journal*. 2014;**78**:927-936
- [51] Sazuka T, Kamiya N, Nishimura T, Ohmae K, Sato Y, Imamura K, Nagato Y, Koshiha T, Nagamura Y, Ashikari M, Kitano H, Matsuoka M. A rice tryptophan deficient dwarf mutant, *tdd1*, contains a reduced level of indole acetic acid and develops abnormal flowers and organless embryos. *The Plant Journal*. 2009;**60**:227-241
- [52] Woo YM, Park HJ, Su'udi M, Yang JI, Park JJ, Back K, Park YM, An G. Constitutively wilted 1, a member of the rice YUCCA gene family, is required for maintaining water homeostasis and an appropriate root to shoot ratio. *Plant Molecular Biology*. 2007;**65**:125-136
- [53] Abu-Zaitoon YM, Bennett K, Normanly J, Nonhebel HM. A large increase in IAA during development of rice grains correlates with the expression of tryptophan aminotransferase *OsTAR1* and a grain-specific YUCCA. *Physiologia Plantarum*. 2012;**146**:487-499
- [54] Qi J, Qian Q, Bu Q, Li S, Chen Q, Sun J, Liang W, Zhou Y, Chu C, Li X, Ren F, Palme K, Zhao B, Chen J, Chen M, Li C. Mutation of the rice *Narrow leaf1* gene, which encodes a novel protein, affects vein patterning and polar auxin transport. *Plant Physiology*. 2008;**147**:1947-1959
- [55] Jiang D, Fang J, Lou L, Zhao J, Yuan S, Yin L, Sun W, Peng L, Guo B, Li X. Characterization of a null allelic mutant of the rice *NAL1* gene reveals its role in regulating cell division. *PLoS ONE*. 2015;**10**. DOI: 10.1371/journal.pone.0118169
- [56] Scheller HV, Ulvskov P. Hemicelluloses. *Annual Review of Plant Biology*. 2010;**61**:263-289
- [57] Richmond T. Higher plant cellulose synthases. *Genome Biology*. 2000;**1**:reviews3001.1-1.6.
- [58] Kurek I, Kawagoe Y, Jacob-Wilk D, Doblin M, Delmer D. Dimerization of cotton fiber cellulose synthase catalytic subunits occurs via oxidation of the zinc-binding domains. *Proceedings of the National Academy of Sciences*. 2002;**99**:11109-11114
- [59] Taylor NG. Cellulose biosynthesis and deposition in higher plants. *New Phytologist*. 2008;**178**:239-252

- [60] Richmond TA, Somerville CR. The cellulose synthase superfamily. *Plant Physiology*. 2000;**124**:495-498
- [61] Hazen SP, Scott-Craig JS, Walton JD. Cellulose synthase-like genes of rice. *Plant Physiology*. 2002;**128**:336-340
- [62] Fincher GB. Revolutionary times in our understanding of cell wall biosynthesis and remodeling in the grasses. *Plant Physiology*. 2009;**149**:27-37
- [63] Dhugga KS, Barreiro R, Whitten B, Stecca K, Hazebroek J, Randhawa GS, Dolan M, Kinney AJ, Tomes D, Nichols S, Anderson P. Guar seed beta-mannan synthase is a member of the cellulose synthase super gene family. *Science*. 2004;**303**:363-366
- [64] Liepman AH, Wilkerson CG, Keegstra K. Expression of cellulose synthase-like (Csl) genes in insect cells reveals that CslA family members encode mannan synthases. *Proceedings of the National Academy of Sciences*. 2005;**102**:2221-2226
- [65] Suzuki S, Li L, Sun YH, Chiang VL. The cellulose synthase gene superfamily and biochemical functions of xylem-specific cellulose synthase-like genes in *Populus trichocarpa*. *Plant Physiology*. 2006;**142**:1233-1245
- [66] Burton RA, Wilson SM, Hrmova M, Harvey AJ, Shirley NJ, Medhurst A, Stone BA, Newbigin EJ, Bacic A, Fincher GB. Cellulose synthase-like CslF genes mediate the synthesis of cell wall (1,3;1,4)-beta-D-glucans. *Science*. 2006;**311**:1940-1942
- [67] Doblin MS, Pettolino FA, Wilson SM, Campbell R, Burton RA, Fincher GB, Newbigin E, Bacic A. A barley cellulose synthase-like CSLH gene mediates (1,3;1,4)-beta-D-glucan synthesis in transgenic *Arabidopsis*. *Proceedings of the National Academy of Sciences*. 2009;**106**:5996-6001
- [68] Cocuron JC, Lerouxel O, Drakakaki G, Alonso AP, Liepman AH, Keegstra K, Raikhel N, Wilkerson CG. A gene from the cellulose synthase-like C family encodes a β -1,4-glucan synthase. *Proceedings of the National Academy of Sciences*. 2007;**104**:8550-8555
- [69] Dwivany FM, Yulia D, Burton RA, Shirley NJ, Wilson SM, Fincher GB, Bacic A, Newbigin E, Doblin MS. The Cellulose-synthase like C (CslC) family of barley includes members that are integral membrane proteins targeted to the plasma membrane. *Molecular Plant*. 2009;**2**:1025-1039
- [70] Roberts AW, Bushoven JT. The cellulose synthase (CESA) gene superfamily of the moss *Physcomitrella patens*. *Plant Molecular Biology*. 2007;**63**:207-219
- [71] Hunter CT, Kirienko DH, Sylvester AW, Peter GF, McCarty DR, Koch KE. Cellulose synthase-like D1 is integral to normal cell division, expansion, and leaf development in maize. *Plant Physiology*. 2012;**158**:708-724
- [72] Yoshikawa T, Eiguchi M, Hibara K, Ito J, Nagato Y. Rice SLENDER LEAF1 gene encodes cellulose synthase-like D4 and is specifically expressed in M-phase cells to regulate cell proliferation. *Journal of Experimental Botany*. 2013;**64**:2049-2061

- [73] Bernal AJ, Yoo CM, Mutwil M, Jensen JK, Hou G, Blaukopf C, Sørensen I, Blancaflor EB, Scheller HV, Willats WGT. Functional analysis of the cellulose synthase-like genes *Csld1*, *Csld2*, and *Csld4* in tip-growing *Arabidopsis* cells. *Plant Physiology*. 2008;**148**:1238-1253
- [74] Favery B, Ryan E, Foreman J, Linstead P, Boundonck K, Steer M, Shaw P, Dolan L. KOJAK encodes a cellulose synthase-like protein required for root hair cell morphogenesis in *Arabidopsis*. *Genes and Development*. 2001;**15**:79-89
- [75] Wang X, Cnops G, Vanderhaeghen R, De Block S, Van Montagu M, Van Lijsebettens M. *AtCSLD3*, a cellulose synthase-like gene important for root hair growth in *Arabidopsis*. *Plant Physiology*. 2001;**126**:575-586
- [76] Kim CM, Park SH, Je BI, Park SH, Park SJ, Piao HL, Eun MY, Dolan L, Han C. *OsCsld1*, a cellulose synthase-like D1 gene, is required for root hair morphogenesis in rice. *Plant Physiology*. 2007;**143**:1220-1230
- [77] Penning BW, Hunter CTIII, Tyengwa R, Eveland AL, Dugard CK, Olek AT, Vermerris W, Koch KE, McCarty DR, Davis MF, Thomas SR, McCann MC, Carpita NC. Genetic resources for maize cell wall biology. *Plant Physiology*. 2009;**151**:1703-1728
- [78] Li M, Xiong G, Li R, Cui J, Tang D, Zhang B, Pauly M, Cheng Z, Zhou Y. Rice cellulose synthase-like D4 is essential for normal cell-wall biosynthesis and plant growth. *The Plant Journal*. 2009;**60**:1055-1069
- [79] Hu J, Zhu L, Zeng D, Gao Z, Guo L, Fang Y, Zhang G, Dong G, Yan M, Liu J, Qian Q. Identification and characterization of NARROW AND ROLLED LEAF 1, a novel gene regulating leaf morphology and plant architecture in rice. *Plant Molecular Biology*. 2010;**73**:283-292
- [80] Luan W, Liu Y, Zhang F, Song Y, Wang Z, Peng Y, Sun Z. *OsCD1* encodes a putative member of the cellulose synthase-like D sub-family and is essential for rice plant architecture and growth. *Plant Biotechnology Journal*. 2010;**9**:513-524
- [81] Ding Z, Lin Z, Li Q, Wu H, Xiang C, Wang J. *DNL1*, encodes cellulose synthase-like D4, is a major QTL for plant height and leaf width in rice (*Oryza sativa* L.). *Biochemical and Biophysical Research Communications*. 2015;**457**:133-140
- [82] Shi L, Wei XJ, Adedze YM, Sheng ZH, Tang SQ, Hu PS, Wang JL. Characterization and gene cloning of the rice (*Oryza sativa* L.) dwarf and narrow-leaf mutant *dnl3*. *Genetics and Molecular Research*. 2016;**15**. DOI: 10.4238/gmr.15038731
- [83] Horiguchi G, Tsukaya H. Organ size regulation in plants: insights from compensation. *Frontiers in Plant Science*. 2011;**2**:1-6
- [84] Lukowitz W, Mayer U, Jürgens G. Cytokinesis in the *Arabidopsis* embryo involves the synthaxin-related *KNOLLE* gene product. *Cell*. 1996;**84**:61-71
- [85] Zuo J, Niu QW, Nishizawa N, Wu Y, Kost B, Chua NH. *KORRIGAN*, an *Arabidopsis* endo-1,4- β -glucanase, localizes to the cell plate by polarized targeting and is essential for cytokinesis. *The Plant Cell*. 2000;**12**:1137-1152

- [86] Strompen G, Kasmi FE, Richter S, Lukowitz W, Assaad FF, Jügens G, Mayer U. The Arabidopsis HINKEL gene encodes a kinesin-related protein involved in cytokinesis and is expressed in a cell cycle-dependent manner. *Current Biology*. 2002;**12**:153-158
- [87] Yin L, Verhertbruggen Y, Oikawa A, Manisseri C, Knierim B, Prak L, Jensen JK, Knox JP, Auer M, Willats WGT, Scheller HV. The cooperative activities of CSLD2, CSLD3, and CSLD5 are required for normal Arabidopsis development. *Molecular Plant*. 2011;**4**:1024-1037
- [88] Goubet F, Barton CJ, Mortimer JC, Yu X, Zhang Z, Miles GP, Richens J, Liepman AH, Seffen K, Dupree P. Cell wall glucomannan in Arabidopsis is synthesised by CSLA glycosyltransferases, and influences the progression of embryogenesis. *Plant J*. 2009;**60**:527-538
- [89] Itoh J, Nonomura K, Ikeda K, Yamaki S, Inukai Y, Yamagishi H, Kitano H, Nagato Y. Rice plant development: from zygote to spikelet. *Plant Cell Physiol*. 2005;**46**:23-47
- [90] Nakata M, Okada K. The leaf adaxial-abaxial boundary and lamina growth. *Plants*. 2013;**2**:174-202
- [91] Heisler MG, Ohno C, Das P, Sieber P, Reddy GV, Long JA, Meyerowitz EM. Patterns of auxin transport and gene expression during primordium development revealed by live imaging of the Arabidopsis inflorescence meristem. *Curr. Biol*. 2005;**15**:1899-1911
- [92] Vernoux T, Besnard F, Traas J. Auxin at the shoot apical meristem. *Cold Spring Harbor Perspectives in Biology*. 2010;**2**:a001487
- [93] Yan S, Yan CJ, Zeng XH, Yang YC, Fang YW, Tian CY, Sun YW, Cheng ZK, Gu MH. ROLLED LEAF 9, encoding a GARP protein, regulates the leaf abaxial cell fate in rice. *Plant Molecular Biology*. 2008;**68**:239-250
- [94] Zhang GH, Xu Q, Zhu XD, Qian Q, Xue HW. SHALLOT-LIKE1 is a KANADI transcription factor that modulates rice leaf rolling by regulating leaf abaxial cell development. *Plant Cell*. 2009;**21**:719-735
- [95] Juarez MT, Kui JS, Thomas J, Heller BA, Timmermans MC. microRNA-mediated repression of rolled leaf1 specifies maize leaf polarity. *Nature*. 2004;**428**:84-88
- [96] Freeling M. A conceptual framework for maize leaf development. *Journal of Developmental Biology*. 1992;**153**:44-58
- [97] Sinha N, Hake S. The Knotted leaf blade is a mosaic of blade, sheath, and auricle identities. *Developmental Genetics Journal*. 1994;**15**:401-414
- [98] Vollbrecht E, Veit B, Sinha N, Hake S. The developmental gene Knotted-1 is a member of a maize homeobox gene family. *Nature*. 1991;**350**:241-243
- [99] Smith L, Greene B, Veit B, Hake S. A dominant mutation in the maize homeobox gene, knotted-1, causes its ectopic expression in leaf cells with altered fates. *Development*. 1992;**116**:21-30
- [100] Jackson D, Veit B, Hake S. Expression of maize KNOTTED1 related homeobox genes in the shoot apical meristem predicts patterns of morphogenesis in the vegetative shoot. *Development*. 1994;**120**:405-413

- [101] Foster T, Veit B, Hake S. Mosaic analysis of the dominant mutant, Gnarley1-R, reveals distinct lateral and transverse signaling pathways during maize leaf development. *Development*. 1999;**126**:305-313
- [102] Ramirez J, Bolduc N, Lisch D, Hake S. Distal expression of knotted1 in maize leaves leads to reestablishment of proximal/distal patterning and leaf dissection. *Plant Physiology*. 2009;**151**:1878-1888
- [103] Müller KJ, Romano N, Gerstner O, Garcia-Maroto F, Pozzi C, Salamini F, Rohde W. The barley Hooded mutation caused by a duplication in a homeobox gene intron. *Nature*. 1995;**374**:727-730
- [104] Schneeberger RG, Becraft PW, Hake S, Freeling M. Ectopic expression of the knox homeobox gene rough sheath1 alters cell fate in the maize leaf. *Genes & Development*. 1995;**9**:2292-2304
- [105] Ha CM, Kim GT, Kim BC, Jun JH, Soh MS, Ueno Y, Machida Y, Tsukaya H, Nam HG. The BLADE-ON-PETIOLE 1 gene controls leaf pattern formation through the modulation of meristematic activity in Arabidopsis. *Development*. 2003;**130**:161-172
- [106] Bayer EM, Smith RS, Mandel T, Nakayama N, Sauer M, Prusinkiewicz P, Kuhlemeier C. Integration of transport-based models for phyllotaxis and midvein formation. *Genes & Development*. 2009;**23**:373-384
- [107] Becraft PW, Bongard-Pierce DK, Sylvester AW, Poethig RS, Freeling M. The liguleless-1 gene acts tissue specifically in maize leaf development. *Developmental Biology*. 1990;**141**:220-232
- [108] Becraft PW, Freeling M. Sectors of liguleless-1 tissue interrupt an inductive signal during maize leaf development. *Plant Cell*. 1991;**3**:801-807
- [109] Harper L, Freeling M. Interactions of liguleless1 and liguleless2 function during ligule induction in maize. *Genetics*. 1996;**144**:1871-1882
- [110] Moreno MA, Harper LC, Krueger RW, Dellaporta SL, Freeling M. liguleless1 encodes a nuclear-localized protein required for induction of ligules and auricles during maize leaf organogenesis. *Genes & Development*. 1997;**11**:616-628
- [111] Walsh J, Water CA, Freeling M. The maize gene liguleless2 encodes a basic leucine zipper protein involved in the establishment of the leaf blade-sheath boundary. *Genes & Development*. 1998;**12**:208-218
- [112] Foster T, Hay A, Johnston R, Hake S. The establishment of axial patterning in the maize leaf. *Development*. 2004;**131**:3921-3929
- [113] Johnston R, Wang M, Sun Q, Sylvester AW, Hake S, Scanlon MJ. Transcriptomic analyses indicate that maize ligule development recapitulates gene expression patterns that occur during lateral organ initiation. *Plant Cell*. 2014;**26**:4718-4732
- [114] Muehlbauer GJ, Fowler JE, Girard L, Tyers R, Harper L, Freeling M. Ectopic expression of the maize homeobox gene liguleless3 alters cell fates in the leaf. *Plant Physiol*. 1999;**119**:651-662

- [115] Bauer P, Lubkowitz M, Tyers R, Nemoto K, Meeley RB, Goff SA, Freeling M. Regulation and a conserved intron sequence of *liguleless3/4* knox class-I homeobox genes in grasses. *Planta*. 2004;**219**:359-368
- [116] Yamaguchi T, Nagasawa N, Kawasaki S, Matsuoka M, Nagato Y, Hirano HY. The YABBY gene *DROOPING LEAF* regulates carpel specification and midrib development in *Oryza sativa*. *Plant Cell*. 2004;**16**:500-509
- [117] Nardmann J, Ji J, Werr W, Scanlon MJ. The maize duplicated genes *narrow sheath1* and *narrow sheath2* encodes a conserved homeobox gene function in a lateral domain of shoot apical meristems. *Development*. 2004;**131**:2827-2839
- [118] Scanlon MJ, Freeling M. The narrow sheath leaf domain: a genetic tool used to reveal developmental homologies among modified maize organs. *The Plant Journal*. 1998;**13**:547-561
- [119] Scanlon MJ, Schneeberger RG, Freeling M. The maize mutant *narrow sheath* fails to establish leaf margin identity in a meristematic domain. *Development*. 1996;**122**:1683-1691
- [120] Scanlon MJ. *NARROW SHEATH1* functions from two meristematic foci during founder-cell recruitment in maize leaf development. *Development*. 2000;**127**:4573-4585
- [121] Scanlon MJ, Freeling M. Clonal sectors reveal that a specific meristematic domain is not utilized in the maize mutant *narrow sheath*. *Developmental Biology*. 1997;**182**:52-66
- [122] Scanlon MJ, Chen KD, McKnight IV CC. The narrow sheath duplicate gene: sectors of dual aneuploidy reveal ancestrally conserved gene functions during maize leaf development. *Genetics*. 2000;**155**:1379-1389
- [123] Yoshikawa T, Tanaka SY, Masumoto Y, Nobori N, Ishii H, Hibara K, Itoh J, Tanisaka T, Taketa S. Barley *NARROW LEAFED DWARF1* encoding a WUSCHEL-RELATED HOMEBOX 3 (*WOX3*) regulates the marginal development of lateral organs. *Breeding Science*. 2016;**66**:416-424
- [124] The Rice Chromosomes 11 and 12 Sequencing Consortia. The sequence of rice chromosomes 11 and 12, rich in disease resistance genes and recent gene duplications. *BMC Biology*. 2005;**3**:20
- [125] Cho SH, Yoo SC, Zhang H, Pandeya D, Koh HJ, Hwang JY, Kim GT, Paek NC. The rice *narrow leaf2* and *narrow leaf3* loci encode WUSCHEL-related homeobox 3A (*OsWOX3A*) and function in leaf, spikelet, tiller and lateral root development. *New Phytologist*. 2013;**198**:1071-1084
- [126] Ishiwata A, Ozawa M, Nagasaki H, Kato M, Noda Y, Yamaguchi T, Nosaka M, Shimizu-Sato S, Nagasaki A, Maekawa M, Hirano HY, Sato Y. Two WUSCHEL-related homeobox genes, *narrow leaf2* and *narrow leaf3*, control leaf width in rice. *Plant Cell Physiol*. 2013;**54**:779-792
- [127] Troll W. Concerning the morphological significance of the so-called *vorlaeufer Spitze* of monocot leaves. A contribution to the typology of monocot leaves. *Beitr. Biol. Pflanz*. 1955;**31**:525-558

- [128] Haecker A, Gross-Hardt R, Geiges B, Sarkar A, Breuninger H, Herrmann M, Laux T. Expression dynamics of WOX genes mark cell fate decisions during early embryonic patterning in *Arabidopsis thaliana*. *Development*. 2004;**131**:657-668
- [129] Vandebussche M, Horstman A, Zethof J, Koes R, Rijpkema AS, Gerats T. Differential recruitment of WOX transcription factors for lateral development and organ fusion in *Petunia* and *Arabidopsis*. *Plant Cell*. 2009;**21**:2269-2283
- [130] Nakata M, Matsumoto N, Tsugeki R, Rikirsch E, Laux T, Okada K. Roles of the middle domain-specific WUSCHEL-RELATED HOMEODOMAIN genes in early development of leaves in *Arabidopsis*. *Plant Cell*. 2012;**24**:519-535
- [131] Schneeberger R, Tsiantis M, Freeling M, Langdale JA. The rough sheath2 gene negatively regulates homeobox gene expression during maize leaf development. *Development*. 1998;**125**:2857-2865
- [132] Moon J, Candela H, Hake S. The Liguleless narrow mutation affects proximal-distal signaling and leaf growth. *Development*. 2013;**140**:405-412
- [133] Hay A, Hake S. The dominant mutant Wavy auricle in blade1 disrupts patterning in a lateral domain of the maize leaf. *Plant Physiol*. 2004;**135**:300-308
- [134] Lewis MW, Bolduc N, Hake K, Htike Y, Hay A, Candela H, Hake S. Gene regulatory interactions at lateral organ boundaries in maize. *Development*. 2014;**141**:4590-4597
- [135] Liu X, Li M, Liu K, Tang D, Sun M, Li Y, Shen Y, Du G, Cheng Z. Semi-Rolled Leaf 2 modulates rice leaf rolling by regulating abaxial side cell differentiation. *Journal of Experimental Botany*. 2016;**67**:2139-2150
- [136] Li YY, Shen A, Xiong W, Sun QL, Luo Q, Song T, Li ZL, Luan WJ. Overexpression of OsHox32 results in pleiotropic effects on plant type architecture and leaf development in rice. *Rice*. 2016;**9**:46. DOI: 10.1186/s12284-016-0118-1
- [137] Li C, Zou X, Zhang C, Shao Q, Liu J, Liu B, Li H, Zhao T. OsLBD3-7 Overexpression induced adaxially rolled leaves in rice. *PLoS One*. 2016;**11**:e0156413. DOI: 10.1371/journal.pone.0156413
- [138] Henderson DC, Muehlbauer GJ, Scanlon MJ. Radial leaves of the maize mutant ragged seedling2 retain dorsiventral anatomy. *Developmental Biology*. 2005;**282**:455-466
- [139] Itoh J, Sato Y, Nagato Y. The SHOOT ORGANIZATION2 gene coordinates leaf domain development along the central-marginal axis in rice. *Plant Cell Physiol*. 2008;**49**:1226-1236
- [140] Timmermans MC, Schultes NP, Jankovsky JP, Nelson T. Leafbladeless1 is required for dorsoventrality of lateral organs in maize. *Development*. 1998;**125**:2813-2823
- [141] Nogueira FT, Madi S, Chitwood DH, Juarez MT, Timmermans MC. Two small regulatory RNAs establish opposing fates of a developmental axis. *Genes & Development*. 2007;**21**:750-755

- [142] Satoh N, Itoh J, Nagato Y. The SHOOTLESS2 and SHOOTLESS1 genes are involved in both initiation and maintenance of the shoot apical meristem through regulating the number of indeterminate cells. *Genetics*. 2003;**164**:335-346
- [143] Nagasaki H, Itoh J, Hayashi K, Hibara K, Satoh-Nagasawa N, Nosaka M, Mukouhata M, Ashikari M, Kitano H, Matsuoka M, Nagato Y, Sato Y. The small interfering RNA production pathway is required for shoot meristem initiation in rice. *Proceedings of the National Academy of Sciences*. 2007;**104**:14867-14871
- [144] Itoh JI, Kitano H, Matsuoka M, Nagato Y. Shoot organization genes regulate shoot apical meristem organization and the pattern of leaf primordium initiation in rice. *Plant Cell*. 2000;**12**:2161-2174
- [145] Sarojam R, Sappl PG, Goldshmidt A, Efroni I, Floyd SK, Eshed Y, Bowman JK. Differentiating Arabidopsis shoots from leaves by combined YABBY activities. *Plant Cell*. 2010;**22**:2113-2130
- [146] Stähle MI, Kuehlich J, Staron L, von Arnim AG, Golz JF. YABBYs and the transcriptional corepressors LEUNIG and LEUNIG_HOMOLOG maintain leaf polarity and meristem activity in Arabidopsis. *Plant Cell*. 2009;**21**:3105-3118
- [147] Wang W, Xu B, Wang H, Li J, Huang H, Xu L. YUCCA genes are expressed in response to leaf adaxial-abaxial juxtaposition and are required for leaf margin development. *Plant Physiol*. 2011;**157**:1805-1819
- [148] Kumar S, Stecher G, Tamura K. MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*. 2016;**33**:1870-1874