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Chapter 1

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 thaliana2* (*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 CO_2 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].

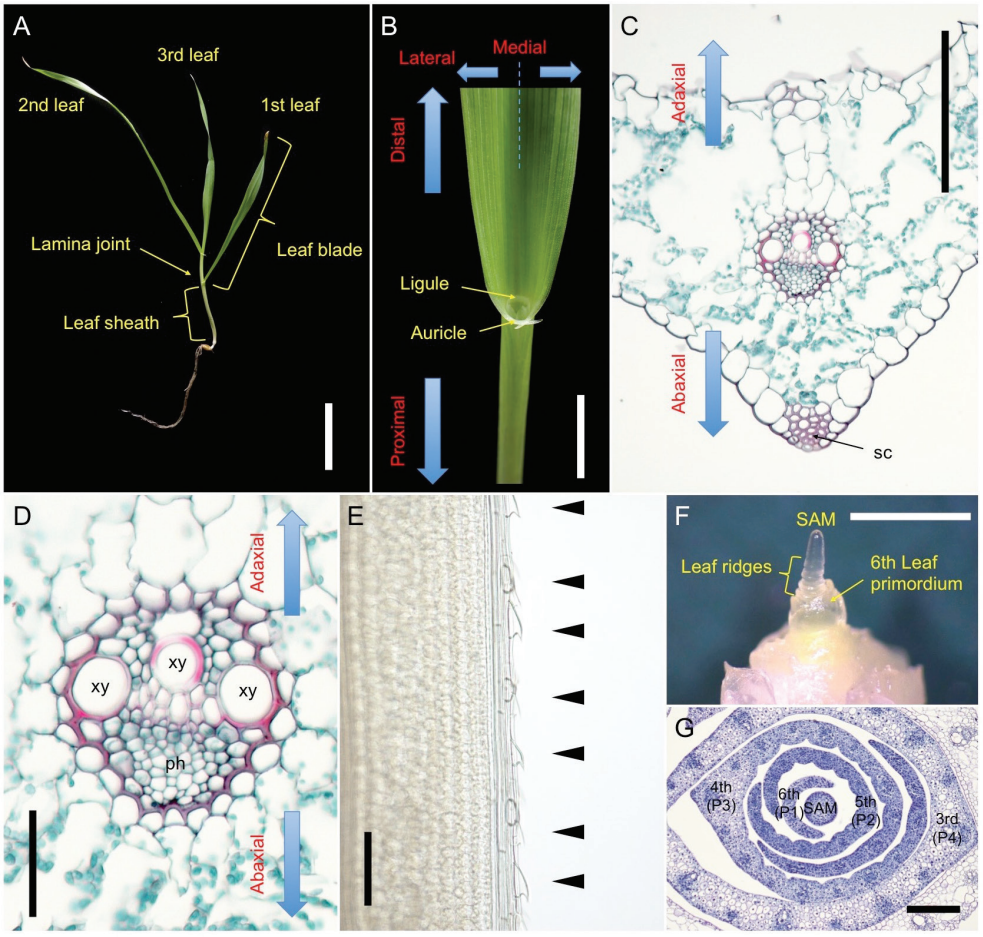

Figure 1. The shoot structure of normal barley (KN29). **(A)** A barley seedling at the second leaf stage. The leaf stage is defined by the number of fully expanded leaves. The first to third leaves are labeled. The leaf blade, leaf sheath, and lamina joint in the first leaf are indicated. **(B)** Close-up 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 μm **(C, G)**, 50 μm **(D)**, 100 μm **(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 arabidopsis (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

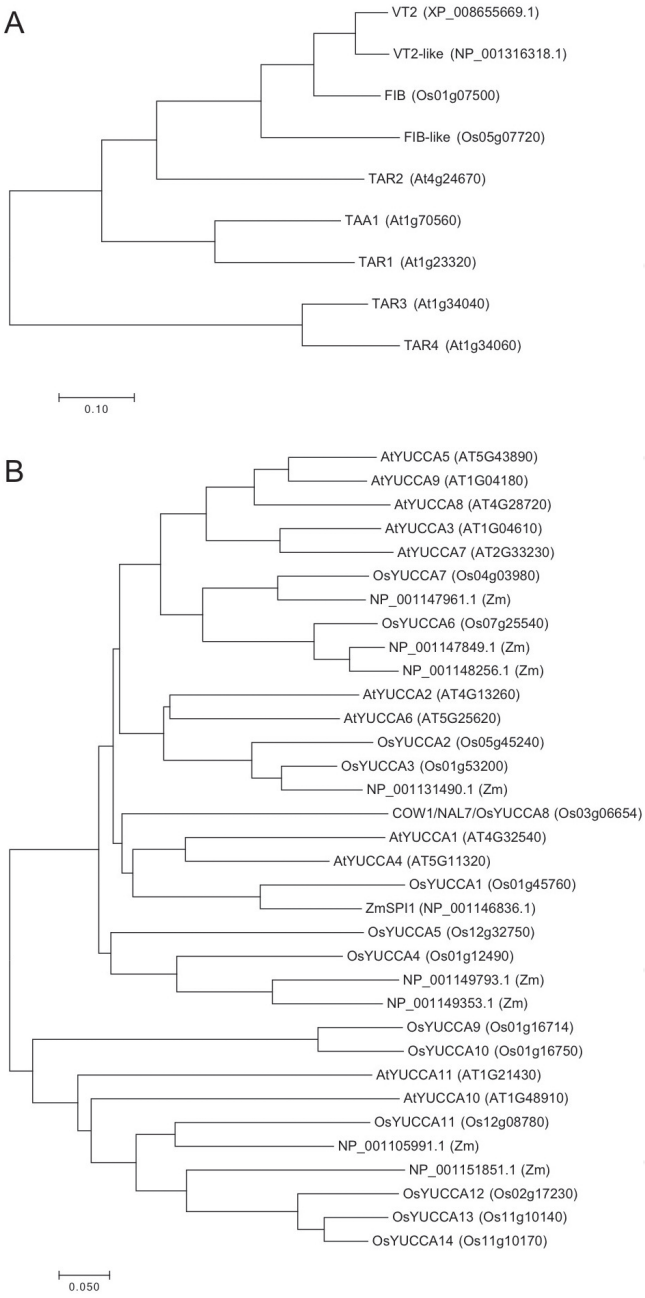

Figure 2. Phylogenetic tree of proteins involved in the IPA pathway. **(A)** TAA-related proteins in rice (FIB and FIB-like), maize (VT2 and VT2-like), and *Arabidopsis thaliana* (TAA1 and TAR1-4). **(B)** YUCCA-related proteins in rice (Os), maize (Zm), and *Arabidopsis thaliana* (At).

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 2**A). 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.

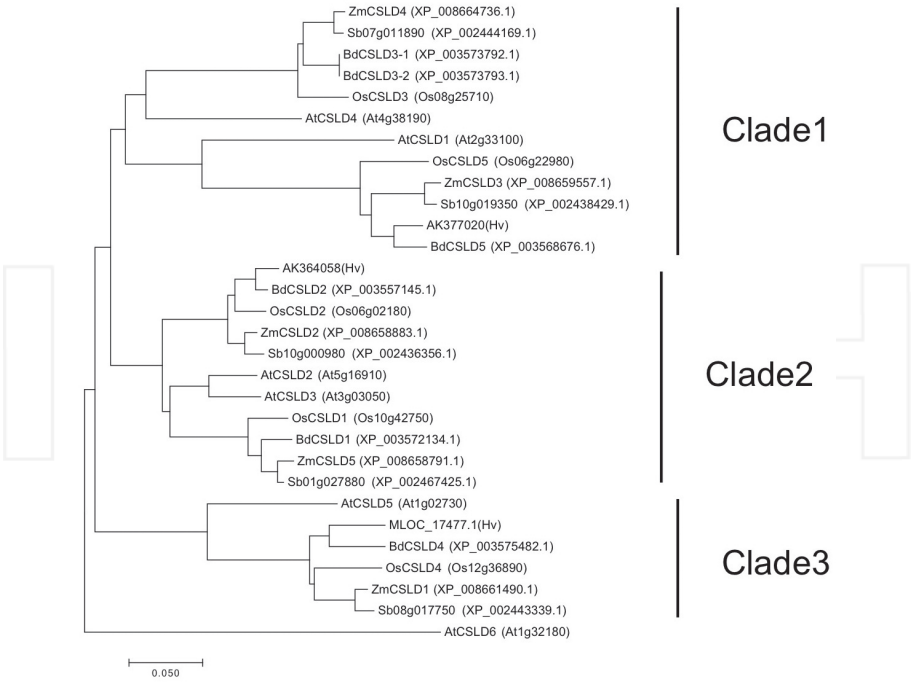

Figure 3. Phylogenetic tree of CSLD-related proteins in rice (Os), maize (Zm), barley (Hv), sorghum (Sb), *Brachypodium distachyon* (Bd), and *Arabidopsis thaliana* (At).

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 leaf*2 (*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.

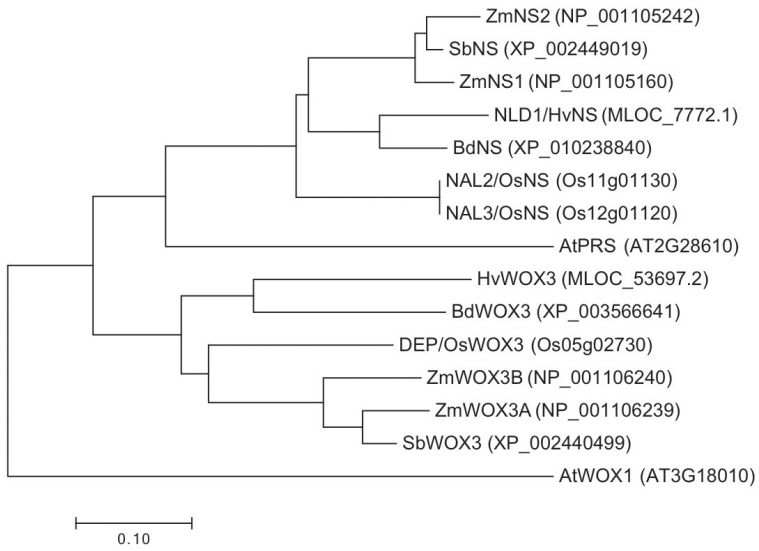

Figure 4. Phylogenetic tree of WOX3-related proteins in rice (Os), maize (Zm), barley (Hv), sorghum (Sb), *Brachypodium distachyon* (Bd), and *Arabidopsis thaliana* (At).

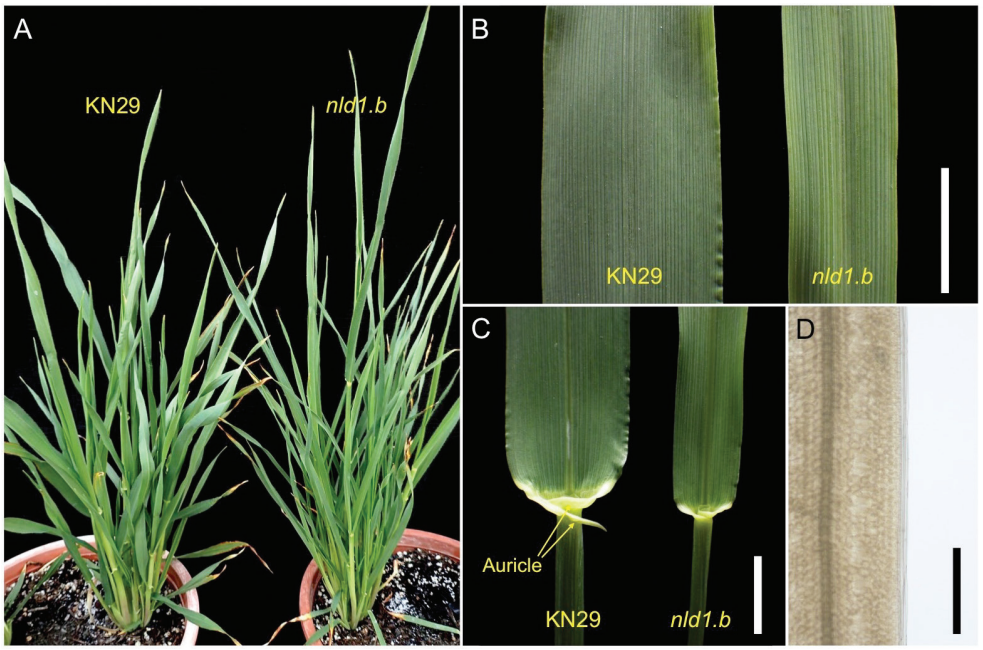

Figure 5. The narrow leaf phenotype of barley *narrow leafed dwarf1* (*NLD1*) mutant. **(A–C)** The whole shoots **(A)**, the leaf-blades **(B)**, and the lamina joints **(C)** in matured leaves of wild-type (KN29) and *NLD1.b* mutant. The auricles are pointed by arrows in **(C)**. Auricles are significantly 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 μm **(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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