REPORT

PLANT SCIENCE

Evolution of the grass leaf by primordium extension and petiole-lamina remodeling

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The sheathing leaf found in grasses and other monocots is an evolutionary innovation, yet its origin has been a subject of long-standing debate. Here, we revisit the problem in the light of developmental genetics and computational modeling. We show that the sheathing leaf likely arose through *WOX*-gene-dependent extension of a primordial zone straddling concentric domains around the shoot apex. Patterned growth within this zone, oriented by two polarity fields, accounts for wild-type, mutant and mosaic grass leaf development, whereas zone contraction and growth remodeling accounts for eudicot leaf development. In contrast to the prevailing view, our results suggest that the sheath derives from petiole, whereas the blade derives from the lamina of the eudicot leaf, consistent with homologies proposed in the 19th century.

he grass leaf is a conundrum. Unlike a eudicot leaf, which typically has a broad lamina, narrow petiole, and basal stipules (Fig. 1, A to C), the grass leaf has a cylindrical sheath supporting a straplike blade (Fig. 1, D to F). The encircling sheath, a derived feature of monocots (*I*, 2), allows grasses to grow in height during the vegetative phase without extending stem internodes, keeping the apical meristem protected close to the ground.

Evolution of the sheathing leaf presents two problems. First, unlike eudicot leaf primordia, which occupy a fraction of the apical meristem circumference, sheathing leaf primordia extend to encircle the meristem (1, 3, 4) (Fig. 1, G to J). It is unclear how this extension arose. Second, the origins of sheath and blade are uncertain. The grass sheath was originally considered homologous to petiole and blade to lamina: the "petiole-sheath" hypothesis (5, 6)(Fig. 1K). Later, the petiole-like parallel venation of grasses led to the idea that the grass leaf mainly derives from the petiole [phyllode theory (7-9); Fig. 1L] or from the petiole base: the current "petiole-leaf" hypothesis (1, 10-14) (Fig. 1M). Here, we revisit these problems through developmental genetics and computational modeling.

The grass leaf primordium emerges from a primordium zone (PZ) (Fig. 1N), which lacks *KNOX* expression (*15*). The PZ straddles concentric domains that will give rise to the adaxial (upper) and abaxial (lower) regions of the leaf which meet at a midplane boundary (green) (*16, 17*). The PZ is also subdivided mediolaterally into central, lateral, and marginal domains (*18*) (Fig. 1, O and P). Marginal identity depends on *NARROWSHEATH* genes (*NS1* and *NS2*), members of the *WUSCHEL-RELATED HOMEOBOX* (*WOX*) gene family (*19, 20*). *ns1/2* double-mutant primordia do not fully encircle the apex and produce narrow leaves (*21*).

To understand how these domains control leaf morphogenesis and to clarify hypothesis predictions, we modeled their growth. In simulations, morphology is an emergent property that depends on how specified local growth rates interact with mechanical tissue constraints.

To simulate primordium emergence from a dome-shaped apex, we built on a recently proposed model based on growth oriented by two polarity fields (22): an orthoplanar field running orthogonal to the tissue surface and a planar polarity field running parallel to the tissue surface. We first tried to model growth with orthoplanar polarity alone. Orthoplanar polarity ran from the tissue surface toward the ad-abaxial midplane to orient primordium emergence and toward an axial domain to orient apex growth (Fig. 2, A and B). Growth rates were specified in two orientations: K_{OP} , parallel to orthoplanar polarity, and K_{PER} , perpendicular to orthoplanar polarity. Setting K_{PER} greater than K_{OP} in the PZ generated a ring-shaped primordium encircling the apex (Fig. 2, C and D, and figs. S1A and S2, A to D).



Fig. 1. Eudicot and grass leaf. (A to F) Eudicot Arabidopsis [(A) to (C)] and grass Zea mays [(D) to (F)]. (A) and (D) are seedlings. SAM, shoot apical meristem. Scale bar, 1 cm. (B) and (E) are mature leaf. (C) and (F) are venation patterns. (G to J) Optical projection tomography of maize leaf primordia. (G) is plastchron 1 (P1) viewed from the side or top down. (H) and (I) are P2 and P3 viewed from the side. (J) P4/P5 with wrapped margins (front view). M. meristem. Dotted line indicates the primordium. Scale bar, 100 µm. (K to M) Proposed homologies between eudicot and grass leaves. (N to P) Domains in the grass leaf primordium. (N) The primordial zone (PZ, dotted line) straddles the midplane (green line) between the abaxial (orange) and adaxial (blue) domains. (O) and (P) The central (blue), lateral (red), and marginal (cyan) domains in the PZ and the mature leaf [modified from (18)]. Asterisk indicates the presumptive midvein tip.

To generate a primordium that slopes down from the midvein tip (Fig. 1H), we modulated K_{PER} such that it decreased mediolaterally. The resulting primordium was sloped but lacked an upwardly growing tip (Fig. 2, E and F, and fig. S2, E and F), suggesting that planar polarity may be required for proper shaping.

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Fig. 2. Grass leaf primordium emergence models. (A) Meristem apex with abaxial (orange) and adaxial (blue) identities. The PZ (dotted line) straddles the abaxial-adaxial midplane (green). (B) Section through (A). Orthoplanar polarity (OP) (black arrows) runs from the surface toward midplane and axial (dark blue) domains. (C and D) Fate of (A) if K_{PER} in PZ is high. (**E** and **F**) Same as (C) and (D) but with K_{PER} increasing toward the midvein. (G and H) Whole-mount immunolocalization of SoPIN1 (green) in barley P1/P2 primordia without (G) or with (H) cell wall signal (CW, magenta). White arrows indicate the SoPIN1 polarity (n = 4). (I) Central (blue), lateral (red), and marginal (cyan) domains. PD polarity field (blue arrows) runs from the PZ boundary toward the presumptive midvein tip (*) and apex ("A"). Axes illustrate specified growth rate orientations. (J to L) Model output at P1 [rear (J) or oblique (K) views] and P2 (L). (M and N) ZmCUC2 in situ hybridization in transverse sections of wild-type (M) and narrowsheath1/2 (N) vegetative maize meristems (n = 4). Dotted line indicates the primordium. (0) ns1/2 domains. (P and **0**) PZ truncation by marginal domain removal (arrowhead). Scale bars, 100 µm. Asterisk indicates presumptive midvein tip.



To determine the orientation of planar polarity, we analyzed an early indicator of epidermal polarity in grasses: the auxin transporter SISTER-OF-PINFORMED1 (SoPIN1) (23). Whole-mount immunolocalization of SoPIN1 in barley (24) revealed epidermal polarity converging at the primordium midpoint (Fig. 2, G and H). We therefore introduced a proximodistal polarity field (blue arrows in Fig. 2I and fig. S3) pointing from the PZ boundary toward the midpoint. Local growth rates could then be specified in three orientations: (i) parallel to orthoplanar polarity (K_{OP}), (ii) parallel to proximodistal polarity (K_{PD}), and (iii) perpendicular to both (K_{PER}) (Fig. 2I). Low K_{OP} combined with modulation of K_{PD} and K_{PER} (figs. S1 and S2, G and H) generated a sloping ring primordium with a shape and polarity pattern resembling that observed experimentally (Fig. 2, I to L).

To test whether this model could account for *ns1/2*, we first determined PZ extent using the *CUP-SHAPED-COTYLEDON2* (*CUC2*) boundary gene (25). In the wild type, *CUC2* expression encircled the meristem, whereas in *ns1/2*, the PZ was truncated by a *CUC2* expression boundary (Fig. 2, M and N). To model the *ns1/2* mutant, we similarly truncated the PZ by removing the marginal domain (Fig. 2O). This removal generated a primordium morphology similar to that observed experimentally at this stage (20) (Fig. 2, P and Q).

We next studied the formation of sheath and blade. The sheath margin derives from an overlapping domain, evidenced by clonal sectors that mark both sheath margins, with unmarked regions in between (*3*, *21*) (Fig. 3A, yellow-green-yellow sector). To clarify how overlap arises, we localized *CUC2* expression after primordium emergence. Instead of a continuous ring (Fig. 2M), we observed a diagonal line of *CUC2* expression in the marginal domain, delimiting overlapping PZ ends (Fig. 3B). In *ns1/2*, the PZ had blunt ends delimited by *CUC2* (Fig. 3C). Thus, NS1/2 are needed to extend the PZ and establish overlapping ends.

We incorporated these findings into a model for later developmental stages by considering the primordium as a ring-shaped tissue with overlapping ends (Fig. 3D and fig. S4). Tissue was modeled as a sheet, with K_{PD} and K_{PER} corresponding to planar growth rates and K_{OP} to growth rate in sheet thickness. A clonal sector (Fig. 3D, yellow) was introduced to allow comparison with experimentally observed sectors.

Using growth patterns similar to those above generated a sloping primordium (Fig. 3E and fig. S5 and S6A), and subsequent modulation of $K_{\rm PD}$ and $K_{\rm PER}$ led to a wrapped primordium (Fig. 3F). SHEATH identity was then introduced (Fig. 3G), consistent with the timing of sheath margin emergence (3, 4), and further modulated growth rates. The result was a leaf with typical grass morphology and a yellow-green-yellow sector (Fig. 3H).

As a further test of the model, we removed marginal identity. The result was a more open primordium shape (Fig. 3, I to K), a mature leaf with a narrow sheath and proximal blade (Fig. 3L), and a clonal sector marking a single sheath margin, all features observed experimentally in ns1/2 mutants (20, 21).

Taken together, our findings suggest two roles for NS1/2 in the marginal domain: (i) extension of the PZ and midplane to encircle the meristem and (ii) growth promotion perpendicular to orthoplanar polarity to drive primordium emergence and planar growth, which is shaped through differential regulation of $K_{\rm PD}$ and $K_{\rm PER}$.

To explore the relationship between grass and eudicot leaves, we modified the grass models to produce a eudicot leaf. In the eudicot *Arabidopsis thaliana*, *PRESSED FLOWER* (*PRS*) is the ortholog of maize *NSI/2*. *prs* mutants lack stipules, and *wox1* mutations Fig. 3. Grass leaf tissue sheet model. (A) A clonal sector (yellow) can mark both margins of the leaf with an intervening unmarked region [green, arrowhead, adapted from (21)]. (**B** and **C**) ZmCUC2 in situ hybridization in transverse sections of wild-type (B) and narrowsheath1/2 (C) vegetative maize meristems (n = 4). Dotted line indicates P4/5. Arrowhead indicates the sheath margin. Scale bars, 100 μ m. (**D** to **L**) Tissue sheet models. (D) the initial ring with overlapping margins, clonal sector (yellow), central (blue), lateral (red), and marginal (cyan) domains. PD polarity (blue arrows) runs from the PZ boundary towards the presumptive midvein tip (*). Axes illustrate specified growth rate orientations. (E) and (F) show model output at P2 and P3. Upper leaf domains are shown in orange and purple. (G) shows introduced SHEATH identity (dark overlay and bracket). (H) is the final output of the emerging leaf with sector marking both margins with intervening unmarked region (arrowhead). In (I) to (L), the marginal domain removal generates a nonwrapping primordium and a leaf with a narrow sheath and proximal blade, with the sector marking one sheath margin. Pesumptive midvein tip (*).



enhance this phenotype to produce narrow leaves (26, 27). Early *prs wox1* primordia are narrower than those of the wild type and do not produce stipules (28) (fig. S7). We therefore modeled the *Arabidopsis* leaf primordium by contracting the PZ, assigning stipule identity to the marginal domain, and creating an outer lateral domain (Fig. 4, A to C). The result was a eudicot primordium (Fig. 4D and fig. S2, I and J). Removing the marginal domain gave the *prs* mutant (Fig. 4, E and F), and further removing the outer lateral domain gave *prs wox1* (Fig. 4, G and H).

To determine whether the model could account for mutants that lack ad-abaxial distinctions, we truncated the PZ to the central domain, replaced adaxial with abaxial identity, and replaced the midplane with an axial domain (Fig. 4, I to K, and fig. S2, K and L). This led to a radialized leaf, as observed in abaxialized mutants (29) (Fig. 4K). Thus, adabaxial genes may normally act to extend an axial domain to a midplane and promote planar growth (22, 27).

To simulate later stages of eudicot leaf development, we first modeled the petiolesheath hypothesis (Fig. 1K), with SHEATH corresponding to petiole, and BLADE to lamina (Fig. 4, L to O, and fig. S8). We next modeled the petiole-leaf hypothesis (Fig. 1M) by subdividing the primordium domain fated to form the grass leaf tip into two subdomains (Fig. 3, E to H, orange and purple), and inhibiting K_{PAR} proximal to this (Fig. 4, P to S, and fig. S9). In both models, growth was inhibited at the marginal-lateral boundary leading to stipule formation (Fig. 4, O and S, and figs. S6 C to F, S8, and S9).

These modeled hypotheses make different assumptions and predictions. The petiole-leaf hypothesis assumes additional proximal-distal domains and is therefore less parsimonious. The petiole-leaf hypothesis also predicts that petiole mainly derives from the middle of the early primordium (Fig. 4S, orange), whereas the petiole-sheath hypothesis predicts that petiole derives from the primordium base (Fig. 4O). Cell tracking shows that petiole derives from proximal primordium cells with high proximodistal growth rates, supporting the petiole-sheath prediction (30, 31). The petiole-leaf hypothesis predicts that the prs wox1 mutant has a narrow petiole base (Fig. 4T), whereas the petiole-sheath hypothesis predicts a narrow leaf (Fig. 4U), as was observed experimentally. The petiole-leaf hypothesis further predicts that homologs of petiole identity genes are expressed throughout the grass leaf, except the tip, whereas the petiole-sheath hypothesis predicts sheath-specific expression. Grass homologs of the Arabidopsis petiole identity gene BLADE ON PETIOLE (BOP) are expressed in sheath (Fig. 4V, maize TASSELS REPLACE UPPER EARS1, ZmTRU1) (32, 33), and rice triple knock-out bop mutants lack sheath but not blade development (32, 33). Taken together, these findings strongly support the petiole-sheath hypothesis.

We show how a common ground plan of identities may modulate specified growth rates to produce eudicot or grass leaf morphogenesis. In *Arabidopsis, WOX* genes act redundantly to extend the PZ and promote planar growth (27, 34, 35). Redundancy likely varies among eudicot species, because mutants in the *PRS* ortholog of tobacco, which normally lacks stipules, have very narrow leaves (36). A key step in grass evolution was the extension of primordium identity and *WOX* activity along the ad-abaxial boundary to encircle the apex. Further modulation of planar growth in the petiole and lamina domains led to grass sheath



Fig. 4. Eudicot leaf models. (**A**) PZ (dotted line) straddles the midplane (green line) between the abaxial (orange) and adaxial (blue) domains. (**B**) PZ central (blue), lateral (light red), outer lateral (dark red), and marginal (cyan) domains. (**C** to **K**) Volumetric primordium emergence models. (C) and (D) are the wild type, (E) and (F) are *prs*, (G) and (H) are *prs wox1*, and (I) to (K) are the abaxialized mutant. Blue arrows indicate proximodistal polarity, asterisks the presumptive midvein tip, and "A" the apex. Arrowhead indicates the missing domains. (**L** to **U**) Tissue sheet models. Upper leaf domains are shown in orange and purple. (L) to (O) are the petiole-sheath hypothesis. (P) to (S) are the petiole-leaf hypothesis. (N) and (R) SHEATH identity (dark gray overlay, bracket) introduced at P4. In (T) and (U), the *prs wox1* mutant generates a narrow petiole base in the petiole-leaf model (T) and a narrow leaf in the petiole-sheath model (U). Arrowhead indicates the missing domains. (**V**) is ZmTRU1 immunolocalization on a maize vegetative shoot apex longitudinal section (*n* = 4). Arrowhead indicates the ligule. P1 to P6 are the primordia plastochrons. Scale bar, 100 µm. Asterisk indicates presumptive midvein tip.

and blade morphogenesis, consistent with the 19th-century view of homology (Fig. 1K). Other anatomical traits, such as venation patterns, may represent further elaborations rather than being primary indicators of homology. Our findings are comparable to those from animal evo-devo studies, in which a discarded hypothesis, the notion that the ventral side of insects corresponds to the dorsal sides of vertebrates, was reinstated in the light of fresh developmental genetic evidence (*37*). We further provide a mechanistic link between the developmental genes involved and their morphogenetic effects.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abf9407 Materials and Methods Supplementary Text: Model Descriptions Figs. S1 to S10 Tables S1 to S4 References (38–44) Movies S1 to S7 MDAR Reproducibility Checklist

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Evolution of the grass leaf by primordium extension and petiole-lamina remodeling

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Shared systems in leaf development

The long, narrow leaves of grasses look rather different from the often shorter, flatter leaves of eudicot plants. Richardson *et al.* combined developmental genetics and computational modeling to reveal that these two types of leaves, which are widely separated by evolution, have more in common than expected. Expression of similar patterning genes in the primordial zone is confined to a wedge for the eudicot leaf but expanded to concentric domains in the grass leaf, driving development of the cylindrical, encircling sheath characteristic of grass leaves. Addition or removal of gene expression in a marginal zone contributes to the development of the broader leaf characteristic of eudicots. Thus, grass and eudicot leaves are diversified elaborations of shared toolkits. —PJH

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