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Grass awns: Morphological diversity arising from developmental constraint

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Grasses dominate agriculturally and ecologically. One hypothesized driver of this dominance is grasses' facility for grain dispersal and rapid seedling establishment. Dispersal and establishment are aided by the awned lemma - a modified bract associated with grass flowers. Awns have diverse forms, many proposed functions, and have been gained and lost repeatedly in grass evolution. Here we hypothesize that the evolution of awn emergence is underpinned by deep conservation of developmental genes. Awns are likely homologous to leaf blades. Because leaf blades are essential, every grass species likely has a latent developmental program available for awn development. This developmental program may be repeatedly reactivated in lemmas, resulting in the frequent appearance of awns. Because awns are inessential, they can be lost and modified without dire consequences to fitness, resulting in the frequent loss and diversity of awns. Replicated awn evolution reveals how developmental conservation can potentiate the evolution of diversity. Awns also present a powerful opportunity to dissect mechanisms of leaf development.

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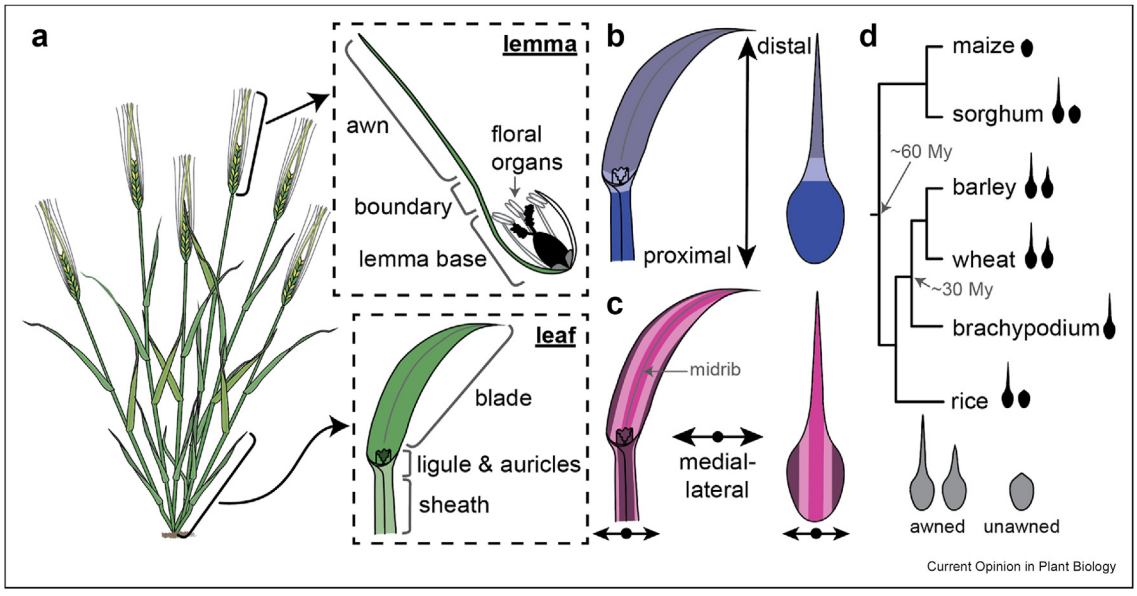
An organ produced by a meristem has vast potential for final form. Yet the same morphologies, such as succulent leaves and petal spurs, have repeatedly evolved [1]. This replicated evolution is often portrayed as natural selection driving adaptation to particular environments, constrained by development. However, deep conservation of developmental genes can also drive diversity and enable rather than constrain morphological evolution [2]. For example, soldier caste ants have evolved many times in divergent lineages, likely facilitated by a deeply conserved developmental program [3]. Here, we discuss a case in plants where replicated evolution and the evolution of morphological diversity may be facilitated rather than constrained by developmental conservation — the grass awn.

Awns have evolved many times in the grasses and vary extensively in form and hypothesized function [4,5]. Awns are, most frequently, distal bristle-like extensions of lemmas — outer protective organs of grass flowers (Figure 1a). Although not always adaptive, awns can have diverse roles, including in herbivore protection, diaspore dispersal, seed germination, and seed maturation [4–6]. For example, awns in wheat and barley contribute photosynthate to developing grains, thus boosting grain weight and potentially enhancing seedling survival [5,6]. Indeed, awns' roles in enhancing seedling survival and grass dispersal may have been important in the evolution of grass dominance, and in the origins of cereal agriculture in the fertile crescent [7,8]. In *Oryza sativa* (rice), awns were lost in many cultivars under domestication and crop improvement, but have re-emerged in the evolution of weediness [9,10]. Awn development and evolution is therefore of both evolutionary and agronomic interest.

Despite variation in form and function and a complex evolutionary history, awns likely have simple developmental origins. Awned lemmas are homologous to leaves and are likely modified bracts [11,12]. Structurally, they are similar to grass leaves, with three morphologically and genetically distinct compartments from their base to tip: the lemma, the lemma/awn boundary, and the awn [12]. The base of the lemma is likely homologous to the grass leaf sheath, and the awn to the grass leaf blade (Figure 1a). In this case, an awnless lemma lacks a blade domain. Although awnless lemmas are common, there are no reported grass

Figure 1



Awns are likely homologous to leaf blades and have a complex evolutionary history in the grasses. (**a**) Awns are distal bristle-like extensions of the lemma, which is a modified bract that subtends the grass flower. Lemmas and vegetative leaves are serial homologs and can be divided into three compartments along the proximal-distal axis. (**b–c**) Cartoons representing vegetative leaf (left) and awned lemma (right) domains along the (**b**) proximal-distal and (**c**) medial-lateral axes. (**d**) Relationships and divergence times of species are discussed in the text. Awn presence, absence, and length varies over both shallow and deep evolutionary timescales.

species entirely lacking blade domains in vegetative leaves [13]. This suggests conservation of a blade developmental program across the grasses. This conserved "blade" developmental program may have been repeatedly suppressed and re-activated, thus driving the repeated gain and loss of awns. The suppression and activation of a blade domain could occur through many mechanisms, including changes in gene expression over the course of development. Once an awn emerges, selection could then act to shape awn form and diversify awn function. Importantly, our hypothesis for awn emergence does not require an awn to have any particular function. Therefore, we do not discuss awn function here and refer to the reader to reviews on the subject [4–6].

Our developmental hypothesis for awn emergence leads to many predictions, three of which are: (1) leaf patterning genes should have pleiotropic mutant phenotypes, impacting vegetative leaves and awned lemmas; (2) awn loss should be reversible as the blade developmental network is essential; (3) genetic networks controlling awn development should be conserved. Here, we evaluate the evidence in support of replicated awn evolution through suppression and reactivation of a blade domain, and discuss the recent literature in light of predictions arising from our hypothesis.

Leaf patterning mutants can have pleiotropic vegetative leaf and lemma phenotypes

Leaves have distinct, genetically defined domains across 3 axes: abaxial-adaxial, medial-lateral, and proximal-distal (Figure 1b–c). Differential growth and cell fate determination in these domains define the shape and function of the leaf [14]. If awned lemmas are homologous to grass leaves, we would expect mutations in genes essential for patterning of these domains to impact the awned lemma development. Although lemmas are often overlooked in studies focused on vegetative leaves, and vegetative leaf phenotypes are not often carefully assessed in studies focused on awns, there are leaf patterning mutants with reported lemma phenotypes.

There are three domains along the medial-lateral axis in grass leaves: a central domain encompassing the midrib; lateral domains; and marginal domains (Figure 1c) [14]. *WUSCHEL-LIKE-HOMEOBOX (WOX)* genes are essential in defining the lateral and marginal domains and regulate lateral outgrowth [14–16]. *WOX* mutants in maize (*narrowsheath1/2)*, barley (*narrow leafed dwarf1)*, and rice (*narrow leaf 2* and *3)*, all have very narrow leaves, lacking marginal and lateral domains [17–19]. In barley and rice *WOX* mutants, lemmas are also narrow, consistent with our prediction. Interestingly, the narrow

lemmas of barley and rice *WOX* mutants still form marginal tissue [17,19]. This suggests that although *WOX* function in medial-lateral patterning is broadly conserved, lemmas do not rely entirely upon *WOX* function to define their margins.

In the central domain, *WOX*-independent differentiation of the midrib is crucial for structural support of the leaf blade. Orthologs of the YABBY transcription factor DROOPING LEAF (DL) control the formation of the blade midrib in brachypodium, maize, and rice [20—22]. Our hypothesis predicts that *DL* mutants will also have awn defects. Maize *DL* mutants have no reported lemma phenotype [20]. This may be because awn development is suppressed and, like the leaf sheath, the lemma does not rely upon *DL* activity. However, *DL* mutants in rice and brachypodium lack awns [22,23], suggesting that narrow awns require central domain, and particularly midrib, identity. In barley, awns are wider and have more veins, and *DL* mutants have shorter awns with narrower midribs [24]. Lemmas in these barley *DL* mutants resemble maize and rice *DL* leaf blade mutants, where the central midrib vein resembles lateral veins [20,21,24]. Taken together, pleiotropic *DL* phenotypes support conservation of gene function in medial-lateral patterning in leaves and lemmas.

Proximal-distal patterning in the leaf results in the specification of the proximal sheath, the middle sheath/blade boundary where the ligule and auricles form, and the distal blade (Figure 1b) [25]. Our hypothesis predicts that mutations in sheath development genes will affect the base of the lemma, and mutations in blade development genes will affect the awn. The *BLADE ON PETIOLE (BOP)* genes promote sheath development and suppress blade development [26,27]. In rice, triple *BOP* mutants fail to develop sheaths in vegetative leaves. Consistent with a loss of blade suppression, some normally awnless lemmas also form awn-like bristles in these mutants. More commonly, these triple *BOP* mutants develop leaf-like lemmas with distinct sheath, ligule, and blade tissues [27]. The retention of the lemma base in these *bop* mutants suggests that, at least in rice, there are additional genes specifically involved in the promotion of lemma base formation that can compensate for the loss of *BOP* gene function. In barley and brachypodium, there are two *BOP* orthologs, *uniculme4 (cul4)* and *laxatum-a (lax-a)*. *Uniculme4* has a disrupted leaf sheath/blade boundary, indicative of a proximal-distal patterning defect, but has no described lemma phenotype [28]. Conversely, *laxatum-a* (*lax-a*) has no reported leaf phenotype but has narrower lemmas with thickened awn bases [29], indicative of a lemma proximal-distal patterning defect. In brachypodium, double *cul4/lax-a* mutants have severe defects, with spikelets replaced by leaf-like organs reminiscent of the rice triple *BOP* mutant [27,30]. These mutant phenotypes suggest that core proximal-distal patterning genes have conserved roles in leaves and lemmas, consistent with our prediction.

Abaxial-adaxial patterning defines distinct epidermal surfaces and drives laminar outgrowth. In rice, the abaxial-adaxial patterning mutants *shootless1 (SHL1)*, *shl2*, *shoot organization 1 (SHO1), and SHO2/SHL4* all have thread-like vegetative leaves [31,32]. *SHL2*, *SHO2*, and *SHO1* encode orthologues of (1) RNA-dependent RNA polymerase 6, (2) ARGONAUTE 7 and (3) DICER-like 4, respectively; all essential for tasi-RNA biosynthesis. tasi-RNAs mediate adaxial-abaxial patterning by repressing auxin response factor (ARF) function [31,32]. In normally awnless domesticated rice varieties, mutations in *SHL1*, *SHO1, and 2* and the ARF gene *ETTIN2* trigger awn formation [23,31,32], suggesting that disrupting abaxial-adaxial patterning releases awn growth repression. In nondomesticated awned rice cultivars, weak *SHO2* mutants, including *rod-like lemma* (*ROL*) and RNAi knockdowns of *SHO2*, have normal awns but radialized lemma bodies, reminiscent of the thread-like leaves of stronger mutants [31,33,34]. These phenotypes suggest that the proximal lemma and distal awn in rice differ in their abaxial-adaxial patterning. Analysis of these abaxial-adaxial mutants in rice is again consistent with the prediction that vegetative leaf patterning genes have pleiotropic effects on lemma development.

Awn presence varies over shallow and deep evolutionary timescales

There are no described grass species that lack vegetative leaf blades, but there are many species with normal vegetative leaves and no awns [13]. This indicates that, even in species lacking awns, there is a functional blade developmental program (i.e. gene loss has not occurred). This is in contrast to other instances of trait loss, like the loss of roots in the Lemnaceae, where morphological loss is accompanied by gene loss, and is likely irreversible [35]. Thus, if a conserved, latent leaf blade developmental program is driving awn evolution, then we expect awn loss to be reversible. Indeed, there are frequent gains and losses of awns across the grass family [5,36], suggesting that the blade developmental program can be easily suppressed and reactivated in the lemma driving the evolution of morphological variation.

Awn presence and absence also variy over shallower evolutionary timescales, both within species and under domestication. In hexaploid wheat, where awned and unawned varietals are both cultivated, the transcriptional repressor gene *AWN LENGTH INHIBITOR 1 (ALI1)* underpins the B1 locus that negatively regulates awn development [37,38]. Variation in *ALI1* expression levels and copy-number is correlated with variation in awn length, suggesting variation in *ALI1* might underlie awn length variation [37,38]. Identifying the downstream targets of ALI1 could help identify blade-promoting genes, which have remained elusive. Awn morphology

Table 1

Awn genes and mutants.

Subfamily	Species	Gene name or mutant name	Gene ID	Protein family	Ref.
Pooideae	Barley	*calcaroides a (cal-a)*	UNKNOWN	Unknown	[52]
Pooideae	Barley	*calcaroides b (cal-b)*	UNKNOWN	Unknown	[52]
Pooideae	Barley	*Calcaroides-C (Cal-C)*	UNKNOWN	Unknown	[52]
Pooideae	Barley	*HOODED (BARLEY KNOX3) (KAP1/BKN3)*	HORVU.MOREX.r2.4HG0282910	KNOX	[53]
Pooideae	Barley	*ROUGH AWN 1 (RAW1)*	HORVU5Hr1G086520.6	LOG1	[54]
Pooideae	Barley	*LAXATUM-A (LAX-A)*	MLOC_61451.6	BOP	[29]
Pooideae	Barley	*SHORT AWN 2 (LKS2)*	MLOC_54434.1	SRS (SHI)	[39]
Pooideae	Barley	*MADS-BOX TF 1 (MADS1)*	HORVU4Hr1G067680	MADS BOX	[24]
Pooideae	Barley	*APETALA2 (AP2)*	HORVU2Hr1G113880.23	AP2/ERF	[55]
Pooideae	Barley	*awnless1 (lks1)*	UNKNOWN	Unknown	[56]
Pooideae	Wheat	*DROOPING LEAF (DL)*	TraesCS2A02G275600	YABBY	[45]
Pooideae	Wheat	*TEOSINTE BRANCHED 1/CYCLOIDEA/PCF (TCP4/10)*	TraesCS6A02G23380; TraesCS2B02G392900	TCP	[43]
Pooideae	Wheat	*WHEAT FRIZZY PANICLE (WFZP)*	TraesCS2A01G116900; TraesCS2D01G118200	AP2/ERF	[45]
Pooideae	Wheat	*AWN LENGTH INHIBITOR 1 (B1/ALI1)*	TraesCS5A02G542800	C2H2 zinc finger	[37,38]
Pooideae	Wheat	*Tipped2 (B2)*	UNKNOWN	Unknown	[57]
Pooideae	*Brachypodium*	*AWNLESS1 (AWL1); BdDL*	Bradi1g69900	YABBY	[22,58]
Oryzoideae	Rice	*AWN-1 (REDUCED AWN ELONGATION 1) (AN-1/RAE1)*	Os04g0350700	bHLH	[47]
Oryzoideae	Rice	*DROOPING LEAF (DL)*	LOC_Os02g15230	YABBY	[23]
Oryzoideae	Rice	*ETTIN2 (ETTIN2)*	Os01g0670800	ARF	[23]
Oryzoideae	Rice	*REDUCED AWN ELONGATION 3 (RAE3)*	Os06g0695900	E3 ubiquitin ligase	[49]
Oryzoideae	Rice	*EPIDERMAL PATTERNING FACTOR LIKE 2 (EPFL2)*	LOC_Os02g51950	EPFL	[59]
Oryzoideae	Rice	*LONG AND BARBED AWN1 (LABA1/AN-2)*	LOC_Os04g43840	LOG1	[46,60]
Oryzoideae	Rice	*REDUCED AWN ELONGATION 2 (RAE2/GAD1/EPFL1)*	LOC_Os08g37890	EPFL	[10,44]
Oryzoideae	Rice	*SHOOTLESS1 (SHO1)*	LOC_Os04g43050	DICER-like 4	[31]
Oryzoideae	Rice	*SHOOT ORGANISATION2 (SHO2/SHL4)*	LOC_Os03g33650	ARGONAUTE (AGO) 7	[32]
Oryzoideae	Rice	*shoot organization 3 (SHO3)*	UNKNOWN	Unknown	[32]
Oryzoideae	Rice	*SUPER PISTIL1 (SPP1)*	UNKNOWN	Unknown	[61]
Oryzoideae	Rice	*TONGARI-BOUSHI1 (TOB1)*	Os04g0536300	YABBY	[62]
Oryzoideae	Rice	*WAVY LEAF1 (WAF1)*	LOC_Os07g06970	HEN1	[63]
Oryzoideae	Rice	*AWNLESS1 (AWN1)*	LOC_Os06g46030	ALOG	[41]
Oryzoideae	Rice	*GRAIN LENGTH AND AWN 1 (GLA1)*	LOC_Os05g02500	MAPK phosphatase	[64]
Oryzoideae	Rice	*SHOOTLESS2 (ROD-LIKE LEMMA) (SHL2/ROL)*	LOC_Os01g34350	RNA-dependent RNA polymerase	[34]
Oryzoideae	Rice	*BLADE ON PETIOLE (BOP)*	LOC_Os01g72020; LOC_Os11g04600	BOP	[27]
Andropogoneae	Sorghum	*AWNLESS1 (AWN1)*	Sobic.003G421300	ALOG	[41]
Andropogoneae	Sorghum	*DOMINANT AWN INHIBITION (DAI)*	Sobic003G421300	ALOG	[42]

also varies in undomesticated grasses. In *Microstegium vineum*, which is broadly distributed across eastern North America, short-awned variants are more common at higher latitudes, long-awned variants at lower latitudes, suggesting an adaptive advantage of awns at high temperatures, of no awns at low temperatures, or both, as has been suggested for both barley and wheat [6,39,40]. Similarly, twisted geniculate awns are strongly associated with savannah and grassland, straight awns with wetlands in the tropical grass genera *Themeda* and *Heteropogon* [36]. This evolutionary lability in awn presence and morphology may be because awns are expendable for plant survival, and the conserved blade gene regulatory network can be modulated specifically in developing inflorescences to drive awn morphological diversification.

Some awn initiation and patterning genes are conserved across grass subfamilies

In light of awned lemmas' homology to vegetative leaves, we predict that mutations in the same groups of genes will be responsible for the replicated gains and losses of awns across the grasses. Two parallel pathways regulate awn elongation in rice, one involving ETTIN, and the other DL [23]. Consistent with our prediction, both pathways are repeatedly implicated in awn elongation (Table 1) [22,24,39,41–44]. For example, in *Sorghum bicolor* (sorghum), the ALOG transcriptional repressor AWN1 drives awn loss, likely through repressing *DL* and *SHORT AWN2* (*LKS2)* [41,42]. In rice, which is distantly related to sorghum, mutants in an *AWN1* homolog have long awns, demonstrating conserved *AWN1* function across species [41]. In wheat, the B1 locus responsible for awn suppression does not contain any known awn genes but does repress *REGULATOR OF AWN ELONGATION2* (*RAE2)* and *LKS2*, which are awn elongation genes in rice and barley, respectively [39,43,44]. Similarly, WHEAT FRIZZY PANICLE (WFZP), which promotes awn elongation, regulates the conserved awn genes *DL*, *LONG AND BARBED AWN1 (LABA1)* and *RAE1* [45–47]. In barley, MADS1 regulates *HvDL* and *HvSHI* activity thus influencing awn elongation, differing from its role in rice in which it regulates floral organ identity [24,48]. In rice, although *RAE1, RAE2,* and *RAE3* have all had different histories of selection under domestication in Africa and Asia, their functions in regulating awn elongation are likely conserved across *Oryza* species [44,47,49,50]. Lastly, although not awn-specific, genes involved in prickle formation on awns are also deeply conserved [46,51]. These examples of conserved gene regulatory networks are consistent with our predictions. As awn genes are identified in species spanning grass diversity, it is likely that we will find significant conservation alongside species-specific modulation of the core awn/blade gene regulatory network linked to morphological diversity.

Viewing the development and genetic regulation of understudied organs through the lens of homology is a powerful approach to provide novel insight into their evolution and development. Here, we reveal significant support for the hypothesis that grass awns have been gained and lost through repeated suppression and reactivation of the blade gene regulatory network in lemmas. Awns are therefore an excellent example of morphological diversity arising because of (rather than in spite of) developmental conservation, providing a developmental mechanism underlying morphological innovation. Importantly, variation in awn morphology was likely possible because awns, unlike leaves, are not essential for survival, enabling diversification through stage-specific modulation of the blade gene regulatory network.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Madelaine Bartlett reports financial support was provided by National Science Foundation. Annis Richardson and Madelaine Bartlett reports financial support was provided by The Royal Society. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data were used for the research described in the article.

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