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Multifaceted mechanisms controlling grain disarticulation in the Poaceae

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Abstract

Cereal shattering and threshability, both involving disarticulation of grains from the mother plant, are important traits for cereal domestication and improvement. Recent studies highlighted diverse mechanisms influencing shattering and threshability, either through development of the disarticulation zone or floral structures enclosing or supporting the disarticulation unit. Differential lignification in the disarticulation zone is essential for rice shattering but not required for many other grasses. During shattering, the disarticulation zone undergoes either abscission leading to cell separation or cell breakage. Threshability can be affected by the morphology and toughness of the enclosing floral structures, and in some species, by the inherent weakness of the disarticulation zone. Fine-tuning shattering and threshability is essential for breeding wild and less domesticated cereals.

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Keywords

Shattering, Threshability, Disarticulation, Abscission zone, Poaceae.

Shattering and threshing—processes leading to seeds separated from the plant

The first step of seed dispersal is the release of seeds or fruits from the mother plant, a process referred to as seed/fruit shattering or disarticulation. In Poaceae (the grass family), a spikelet consists of one to multiple flowers (florets) subtended by a pair of glumes. Each floret consists of a pair of bracts (palea and lemma), the lodicules (highly modified petals), and the reproductive organs, in which the female part develops into a caryopsis (fruit). Poaceae fruits rarely shatter by themselves, but often with additional structures such as floral bracts (glumes, lemma and palea) and stem segments (rachilla, pedicel and rachis) (Figure 1) [1,2]. In agriculture, pre-harvest fruit shattering causes yield loss, and therefore, cereal domestication often selected for natural mutations leading to non-shattering fruits.

Shattering often occurs via abscission, a physiological process leading to cell separation in pre-programmed cell layers, the abscission zone (AZ) [3,4]. However, recent investigations have revealed that shattering may also occur through cell breakage [5,6]. Therefore, we refer the cell region where shattering occurs as the disarticulation zone (DZ), while the AZ is a type of DZ (Box 1).

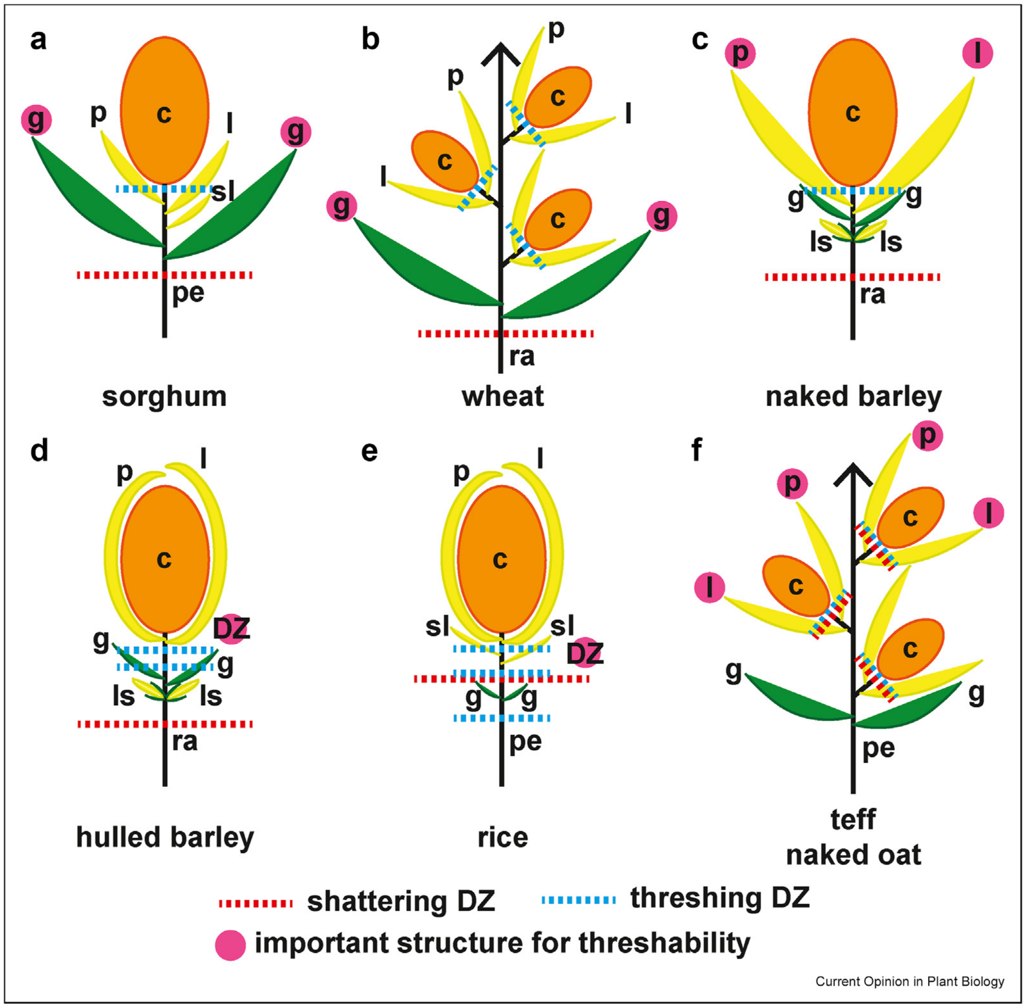
Post-harvest, the grain must be forcibly released from the attached or enclosed floral bracts or stems at organ junctions in a process known as threshing (Box 1). Threshability is often determined by the morphology and toughness of the enclosing floral bracts [7], but in some circumstances, it can be determined by the inherent weakness of the organ junction where disarticulation occurs [7]. The DZ in the threshing process can be located at various positions, sometimes overlapping with the shattering DZ (Figure 1). If the threshing DZ is physically too weak, grains will drop before harvest due to physical forces such as wind [8], while if threshing is too difficult, the required physical force will damage the grain, leading to yield loss.

Recent studies have revealed diverse mechanisms regulating shattering and threshability among grass species. Here, we describe recent advances in representative species and discuss the connections between shattering and threshing.

Differential lignification as a key mechanism in rice shattering

The DZ of rice is a thin layer of small and non-lignified cells surrounded by large and lignified cells, resembling a canonical AZ. No direct evidence has shown that shattering in rice is through abscission. Instead, most identified genes regulating this process are transcription

Figure 1



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Disarticulation zone (DZ) positions vary among grasses. Note particularly differences in the size and position of the lemma and palea (yellow structures) and glumes (green). (**a**) A sorghum spikelet consists of one fertile floret and one sterile floret that is reduced to a sterile lemma (sl). The shattering DZ is in the pedicel (pe) and threshing DZ is below the caryopsis (c). Glumes (g) are the major structure that determines threshability. (**b**) A wheat spikelet consists of multiple fertile florets. The shattering DZ is in the rachis (ra) and threshing DZ is below the caryopsis. Glumes are the major structure that determines threshability. (**c**,**d**) A barley spikelet consists of one floret. The glumes are much smaller than the lemma (l) and palea (p). The shattering DZ is in the rachis below a cluster of three spikelets, including a central spikelet and two lateral spikelets (ls). (**c**) In naked barley, the threshing DZ is below the caryopsis, and the lemma and palea are the major structures that determine threshability. (**d**) In covered barley, the lemma and palea adhere to the caryopsis; the threshing DZ is below the lemma and palea, and is the major structure that determines threshability. (**e**) A rice spikelet consists of a fertile floret and two lateral florets that are reduced to sterile lemmas (sl). The glumes are very small compared with the palea and lemma. The shattering DZ is above the glumes and below the sterile lemmas. The threshing DZ can overlap with the shattering DZ, or be in the rachilla above the sterile lemmas or in the pedicel below the glumes. DZ is the major structure that determines threshability. (**f**) Both teff (*Eragrostis tef*) and naked oat (*Avena nuda*) have multiple florets in a spikelet (normally two in oats). Both species possess DZ below the caryopsis for both shattering and threshing. The palea and lemma are the major structures that determine threshability.

factors (TFs) that prevent lignification of the DZ [9,10], presumably required for forming a weak zone for breakage. Here we focus on recent findings of these TFs and their interacting partners that regulate lignin biosynthetic genes.

A MYB TF, SEED SHATTERING 11 (OgSH11), binds to the promoter and suppresses the expression of *GOLD HULL AND INTERNODE2* (*GH2*), which encodes a cinnamyl-alcohol dehydrogenase (CAD) that catalyzes the final step in the biosynthesis of monolignol, the main component of lignin [11]. OSH15, a KNOTTED1-Like Homeobox (KNOX) TF, physically interacts with BEL1-Like (BELL) homeobox TFs, SH5 and qSH1. Both SH5 and OSH15 directly suppress the expression of *CAD2* [13,14]. Similarly, OSH15, qSH1 and an APETALA2 (AP2)-LIKE TF SUPERNUMERARY BRACT (SNB) suppress *4-COUMARATE: COENZYME*

A LIGASE 3 (*4CL3*) by binding to its promoter [15]. SNB also directly activates the expression of *qSH1* and *SH5* (Figure 2) [16].

Box 1. Definition of terms used in this review. Some of the following terms are used interchangeably in the literature. However, they refer to slightly different processes. Here, we redefine the terms to clarify their differences and unify their usage in the research community.

Abscission: detachment of organs in specialized cell layers that undergo physiological changes including activating cell wall modifying and degrading enzymes upon stimuli, leading to cell separation.

Abscission zone: differentiated cell layers where abscission occurs.

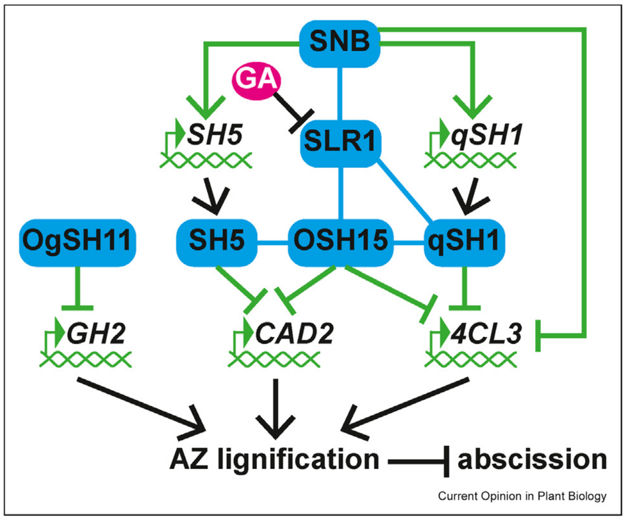
Disarticulation: detachment of organs, often at junctions between the organ and main plant, through either cell separation or cell breakage. It can be induced physiologically or physically.

Disarticulation zone: the region of cells where disarticulation occurs.

Shattering: detachment of organs from the mother plant in nature, usually referring to undesirable fruit or seed shedding in agriculture.

Threshing: release of fruits or seeds from other floral structures by manual or mechanical force in post-harvest agricultural practice.

Figure 2



Rice shattering genes directly involved in lignin biosynthesis. SLENDER RICE1 (SLR1), a negative regulator in the GA pathway, physically interacts with SUPERNUMERARY BRACT (SNB), qSH1 and OSH15. OSH15 also physically interacts with SH5 and qSH1. SNB activates the expression of *SH5* and *qSH1* by directly binding to their promoters. Both SH5 and OSH15 bind to the promoter of *CINNAMYL-ALCOHOL DEHYDROGENASE 2* (*CAD2*) and supress its expression. SNB, OSH15 and qSH1 individually suppress the expression of *4-COUMARATE: COENZYME A LIGASE 3* (*4CL3*) by binding to its promoter. OgSH11 directly suppresses the expression of *GOLD HULL AND INTERNODE2* (*GH2*). GH2, CAD2 and 4CL3 are key enzymes in the lignin biosynthetic pathway, and are supressed in the disarticulation zone (DZ), leading to a functional DZ without lignin deposition.

Gibberellic acid (GA) promotes rice grain shattering by suppressing DZ lignification [15]. SLENDER RICE1 (SLR1), a DELLA protein that is a core repressor in GA-mediated responses, physically interacts with and represses OSH15, qSH1 and SNB, which then cannot inhibit *4CL3* expression (Figure 2) [15]. Mutations of *SLR1* and GA metabolic genes alter grain shattering, as measured by breaking tensile strength (BTS), the force required to separate the grain from the plant. For example, *slr1* and *elongated uppermost internode-1* (*eui1*), which fail to suppress GA signalling and catabolize bioactive GA, respectively, both decrease BTS and increase shattering compared to wild-type (WT). In contrast, the GA biosynthesis deficient mutants *semidwarf 1* (*sd1*) and *dwarf 18* (*d18*), exhibit increased BTS compared to WT plants. Furthermore, overexpressing the GA biosynthetic gene *D18* (*GA 3-oxidase2*) and a GA catabolic gene *GA 2-oxidase1* in the DZ results in increased and decreased bioactive GA, and decreased and increased BTS, respectively [15]. Although these GA mutants may produce less lignin than WT, the difference is subtle compared with other shattering mutants [10], suggesting that increased endogenous GA alone is not sufficient to specify DZ lignification. Nevertheless, this study [15] highlighted that optimizing other agronomically important traits, such as plant height, may impact shattering via hormonal regulation.

Shattering through abscission in *Setaria viridis*

Not all grasses require differential lignification for shattering. In a survey of 17 grass species, only eight had differential lignification between the DZ and surrounding cells [17]. Consistent with this observation, orthologues of rice DZ genes exhibit divergent expression patterns in other grass species, suggesting different mechanisms controlling shattering [2]. In green millet (*S. viridis*), the wild progenitor of foxtail millet (*Setaria italica*), neither the shattering WT nor non-shattering mutants have a lignified DZ [6,18,19]. Instead, cell separation was observed in the DZ of WT, demonstrating the likelihood of abscission in *S. viridis* shattering [6].

Two genes have been identified to regulate shattering in *S. viridis*, a YABBY2 TF *SHATTERING1* (*SH1*) [6,19] and a MYB TF *LESS SHATTERING 1* (*LES1*) [18,20]; knockout mutants of both genes reduce shattering compared to WT. *SH1* is so far the only gene known to have been selected independently in multiple cereals for the loss of shattering during domestication, including foxtail millet, rice, sorghum, maize and white fonio

[19,21–24]. SvSH1 binds the promoter of *CAD2* and supresses its inflorescence expression [19]. However, as no lignin difference was observed in the AZ between WT and *Svsh1* [6], it is unlikely that lignification plays a major role in abscission of *Setaria.* In contrast, cell wall immunofluorescence reveals changes in the abundance of xylan and esterified homogalacturonan in the AZ before and during abscission in WT. Such changes were not observed in *Svsh1*, or between *Svsh1* and WT before abscission, suggesting that *SvSH1* is required for cell wall modification that leads to cell separation [6]. The molecular function of SvLES1 is so far unknown [18,20]. While *SvSH1* transcripts are enriched in the AZ compared to adjacent tissues throughout development, *SvLES1* is preferentially expressed in the AZ post-anthesis, and its expression is downregulated in the *Svsh1* mutant, suggesting *SvLES1* is downstream of *SvSH1* [2,6].

Auxin inhibits abscission in multiple eudicot species [25–27], an effect conserved in *S. viridis*. Exogenous application of synthetic auxin 1-Naphthaleneacetic acid (NAA) and auxin transport inhibitor 2,3,5-triiodobenzoic acid (TIBA) both suppress shattering in WT *S. viridis*. Immunofluorescence using an indole-3-acetic acid (IAA) antibody showed comparable auxin content between WT and *Svsh1*. However, auxin signal was observed in the chloroplasts of the mutant in late development at a stage when the chloroplasts were already degraded in the AZ of the WT, indicating that auxin signalling may interact with chloroplast degradation during activation of abscission in *S. viridis*. Additionally, gene ontology enrichment analysis found auxin-related genes enriched in differentially expressed genes between WT and *Svsh1*, suggesting that *SvSH1* may activate abscission by regulating auxin signalling and homeostasis [6]. As SH1 functions in shattering in multiple grass species [19,21–24], the putative role of SH1 in activating cell separation through auxin signalling may explain its function in shattering among species with drastically different DZ anatomy and lignification patterns.

Shattering through cell breakage

Grain shattering in barley is controlled by two domestication genes, *Brittle rachis 1* (*Btr1*) and *Btr2*, that appear to function in the same genetic pathway [28]. DZs of both shattering wild barley and non-shattering domesticated barley are lignified throughout, but cell walls in the DZ of wild barley are only 25% as thick as domesticated ones, with both primary and secondary wall thickness reduced. The separated DZ surface reveals cell breakage in both wild and domesticated barleys, but the surface is smoother in wild barley perhaps due to its thin cell walls [28]. *Btr1* and *Btr2,* only present in the tribe Triticeae, are derived from ancient duplications of *Btr1-like* and *Btr2-like* [29]. In barley, *Btr1-like* and *Btr2-like* are exclusively expressed in developing anthers but their specific functions are unknown [30]. Whether both *Btr* and *Btr*-like genes function in cell wall composition but in different cell types remains to be discovered.

Species of the genus *Eragrostis*, including the Ethiopian crop teff (*Eragrostis tef*), have an DZ directly below the caryopsis (Figure 1f) [2,5]. The DZ of teff is indistinct and thin-walled, and lacks lignification, and in this respect is similar to that of *S. viridis*. Cell death occurs specifically in the DZ and its immediate surrounding cells upon grain maturity, and aging and cell death related genes are preferentially expressed in the DZ. In contrast to *S. viridis*, the DZ cells in teff break open, leaving a rough surface, suggesting that disarticulation in teff occurs through cell fracture, facilitated by a fragile cell wall and cell death of the DZ [5]. Consistent with these results, SH1 functions differently in teff compared to *S. viridis* or rice [6,23]. CRISPR knockout mutants of both homeologs of *SH1* in teff still shattered [5], suggesting that *SH1* may be involved in abscission but not in grain disarticulation mediated by cell breakage.

Divergent genetic controls of threshability

The structural determinants of cereal threshability depend on floral morphology and the inherent weakness of the threshing DZ. In most cases, paleas, lemmas and glumes are removed during threshing, and threshability is mainly determined by the toughness and size of the enclosing floral bracts [7,31,32]. However, in some species, such as covered barley, in which the lemma and palea tightly adhere to the caryopsis [33], and rice, in which the bracts are tough and fully enclosing without adherence [34], the lemma and palea stay attached to the caryopsis after threshing. In these cases, threshability is determined by the inherent weakness of the DZ (Figure 1).

The sorghum caryopsis is covered by tough glumes and papery lemma and palea, and the glumes are often the main obstacle for efficient threshing, although a tough threshing DZ beneath the caryopsis may also contribute to hard threshability by retaining grains on the plant (Figure 1a) [32]. Decreased glume size exposes the mature caryopsis, resulting in naked sorghum, and is a major contributor to easy threshability. One gene controlling glume coverage, *GLUME COVERAGE 1* (*GC1*), encodes an atypical Gγ subunit of the heterotrimeric G protein complex [35]. A C-terminal truncation of GC1 increases protein stability leading to fewer cells in the glumes, suggesting that GC1 negatively regulates cell proliferation in glumes. GC1 physically interacts with a membrane-localized patatin-like phospholipase AII-1 (SbpPLAII-1). Overexpressing *SbpPLAII-1* in foxtail millet (*S. italica*) leads to more cells and longer glumes, confirming the role of *SbpPLAII-1* in cell proliferation and thus indirectly in threshability [35].

In wheat, the threshing DZ is immediately beneath the caryopsis, and threshability is mainly determined by the morphology and toughness of the glumes (Figure 1b) [36]. Threshability has been mapped to three major loci, *soft glume* (*sog*) and *tenacious glume* (*tg*) on the short arm of chromosome 2 (chr2), and *Q* on chr5A [31,37]. Only *Q* has been cloned, which encodes an AP2 TF and is regulated by microRNA172 [37,38]. Compared to the easy-thresh *Q* alleles, the wild *q* allele or *Q* knockout mutant have more lignified and thicker glumes with more cell layers and thicker sclerenchyma cell walls, which may contribute to their toughness and firm attachment to the rachis [36]. Q physically interacts with the transcriptional co-repressor TOPLESS (TaTPL) [39] and a basic helix-loop-helix TF LAX PANICLE1 (TaLAX1) [40]. Overexpression lines of *TaLAX1* showed thickened glumes at the base and decreased threshability. Q and TaLAX1 antagonistically regulate the expression of lignin biosynthesis related genes, *KNOTTED ARABIDOPSIS THALIANA7* (*TaKNAT7-4D)* and *PHENYLALANINE AMMONIA-LYASE* (*TaPAL1-6B*), to control glume toughness and thus threshability [40].

Barley glumes are dramatically reduced compared to wheat, and the caryopsis is covered by the lemma and palea (Figure 1c and d). In naked barley with lemma and palea not adhered to the caryopsis, the threshing DZ is located directly beneath the caryopsis, and the toughness and morphology of the lemma and palea may contribute to threshability [41] (Figure 1c). GWAS for threshability identified loci on chr2H and chr3H [41]. It is unclear whether the locus on chr2H overlaps with the orthologue of *sog* or *tg* in wheat. In covered barley, the lemma and palea tightly adhere to the caryopsis and are threshed with it, and thus the threshing DZ is located below them and above the glumes (Figure 1d). Threshability in covered barley has been mapped to the *thresh-1* locus on chr1H, distinct from known threshability loci in wheat or naked barley [33]. However, the structural and developmental bases of weakness in the threshing DZ is unclear.

Similar to covered barley, the rice caryopsis is threshed with the hard lemma and palea [42]. The threshing DZ can be located at the shattering DZ, or other locations along the rachilla and pedicel that are physically weak (Figure 1e) [15]. Therefore, rice cultivars with a partially developed shattering DZ tend to be easily threshed [23]. Genes or alleles that play minor roles in DZ formation may be used to fine tune threshability. For example, Wu et al. (2023) showed that the rice cultivar Nipponbare with decreased *qSH1* activity had lower BTS than the *qsh1* knockout mutant [15], suggesting that a partially functional *qSH1* may facilitate threshing. It would be interesting to investigate whether a partially functional shattering DZ has been selected by humans for easy threshability during rice domestication.

Other factors that fine tune shattering and threshability

Floral bract morphology and inflorescence architecture may indirectly affect shattering. The lower seed drop rate in teff compared with its wild progenitor *Eragrostis pilosa* is due to its tough and persistent lemma that cradles the caryopsis. The lemma of *E. pilosa* naturally shatters at the base, although no obvious DZ was observed. The base of the lemma is much thicker in teff than that in *E. pilosa*, which may contribute to its toughness (Figure 1f) [5]. Similarly, in naked oat, shattering occurs directly beneath the caryopsis. Degree of shattering is not correlated with the BTS of the caryopsis itself, but rather the thickness and morphology of the lemma and palea (Figure 1f) [43]. These examples may be analogous to the control of threshability in sorghum and wheat.

In rice, the openness of the inflorescence and presence of awns contributes to shattering by affecting seed release, even when the DZ functions normally. An introgression line harboring the cultivated allele of *LIGULELESS1* (*OsLG1*) in the background of the wild rice *O. rufipogon* exhibited a closed panicle and long awns, especially on lower florets, increasing grain retention on the plant [44]. Simply introducing cultivated alleles of shattering domestication genes *sh4*, *qsh1* and *sh1* is not sufficient to reduce shattering in wild rice under field conditions, but introducing the cultivated allele of *OsLG1* does, suggesting that this cultivated *OsLG1* allele might have been selected for reduced shattering during domestication [44,45].

Both shattering and threshability are affected by environmental factors, such as wind speed, precipitation, and temperature [8,46,47]. In wheat cultivars, shattering was eliminated at the rachis during domestication; however, in extreme weather conditions at harvest time or delayed harvest, shattering still occurs below the caryopsis where grains normally break off during threshing, which accounts for significant yield loss. GWAS and quantitative trait loci (QTL) analysis identified loci close to *tg* and the semi-dwarf gene *Rht-B1*, suggesting that glume toughness and plant height may be associated with shattering degree [8]. In both weedy and cultivated rice, elevated CO_2 decreased grain BTS and altered DZ gene expression, suggesting that shattering and threshability may increase with climate change [48].

Conclusions and future perspectives

The need for crop diversification to meet the challenges of population growth and climate change require us to understand the mechanisms of shattering and threshability in cereal crops. Recent studies have revealed that grain shattering may be achieved through either abscission or cell breakage, and can be influenced by flower and inflorescence architecture, hormones regulating plant growth (e.g., GA and auxin), and environmental conditions. The divergent mechanisms of shattering pose challenges in manipulating this trait in less studied species, such as forage grasses or orphan crops that may require reduced shattering. More research is required to identify the common rules that regulate different types of shattering. For example, are genes regulating the activation of abscission conserved across species that shatter through abscission, regardless of their AZ anatomy and lignification pattern? Do the mechanisms of cell breakage converge in species that shatter through cell breakage, such as regulating cell death and cell wall structures? Do species with the same DZ anatomy and disarticulation mode share the same genetic mechanisms regardless of their phylogenetic distance? The increasing availability of genetic and genomic resources across different clades of grasses provide opportunities for cross-species comparisons to better understand the shattering mechanisms.

Threshability is rarely linked with shattering in the literature. However, we show that in some species, shattering and threshability rely on the same or similar mechanisms, such as inherently weak DZs that promote grain detachment (e.g., rice), or enclosing bracts that support the caryopsis (e.g., teff and naked oat). From a breeding perspective, fine tuning non-shattering and easy threshability is necessary to maximize grain yield and postharvest quality, especially in less domesticated crop varieties and crop wild relatives. It is also essential to understand how the optimization of plant architecture and growth may influence shattering and threshability.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

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

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** of outstanding interest

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This study reveals the cellular and molecular function of *SH1* in regulating shattering in *Setaria viridis*. The authors show that *SH1* does not regulate cell wall composition during AZ differentiation, but rather influences auxin dynamics and subcellular distribution during abscission. The paper provides insights into the molecular regulation of abscission activation, a process rarely described in other grasses.

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The authors identify a novel MYB TF, *OgSH11*, that controls shattering in African rice and show that OgSH11 represses the expression of a lignin biosynthesis gene, *GH2*, by directly binding to its promoter. This study provides new insights into the molecular regulation of shattering in rice.

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The authors identify that the GA negative regulator SLR1 physically interacts with known rice shattering proteins (OSH15, qSH1 and SNB) and interferes with their binding to the promoter of lignin biosynthesis genes. This is the first study to reveal the connection between two agronomically important traits, grain shattering and plant height, via GA signalling.

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