



Dissection of Soybean Pod Shattering Mechanism from External Environment to Pod Micro-environment: A Review

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ABSTRACT

Pod shattering, also referred to as pod dehiscence, is a major domestication-related and agronomically important trait in soybean [*Glycine max* (L.) Merr.]. In wild soybean, pod opening is an adaptive seed-dispersal mechanism, whereas in cultivated soybean it may cause severe yield loss before or during harvest. The process is not controlled by a single factor, instead, it results from the interaction between environmental triggers, pod water status, mechanical tension in pod walls, pod morphology, anatomical differentiation of the dorsal and ventral sutures and molecular regulation of secondary cell wall formation and lignin deposition. Among environmental factors, air humidity and repeated wetting drying cycles are particularly important, as they regulate pod moisture content and thereby affect the accumulation of dehiscence force. Anatomically, soybean pods contain separation tissues at the sutures, but resistance to shattering is strongly associated with the structural reinforcement of the ventral suture, especially the lignification and secondary wall thickening of fiber cap cells. At the molecular level, genes such as *Pdh1*, *SHAT1-5*, *NST1A*, *Sh1* and recently reported *GmMYB26* homologs connect pod wall biomechanics with lignin, cellulose, hemicellulose and secondary wall biosynthesis. This review summarizes the current understanding of soybean pod shattering from environmental induction to anatomical and molecular mechanisms and proposes an integrated model in which dehydration induced tension exceeds the bonding strength of pod sutures prior to shattering.

Key words: Dehiscent, Enzymes, Hormones, Pod valves, Tension.

Pod shattering is the opening of mature pods along the dorsal or ventral sutures, resulting in seed dispersal (Dong and Wang, 2015; Funatsuki *et al.*, 2014). In wild soybean, this mechanism enhances ecological fitness by spreading seeds away from the maternal plant. In cultivated soybean, however, shattering is undesirable because it causes yield loss, reduces harvest efficiency and may increase volunteer plants in subsequent cropping seasons (Agrawal *et al.*, 2002; Bhor *et al.*, 2014; Parker *et al.*, 2020; Van der Merwe *et al.*, 2024). Therefore, resistance to pod shattering is considered a classical domestication trait and remains an important target in breeding programs, especially in regions where delayed harvest, drought, high temperature, or low humidity promote pod drying (Parker *et al.*, 2021a). As the most widely cultivated legume worldwide, pod shattering in soybean has been extensively studied (Parker *et al.*, 2021a) and this trait has accordingly emerged as a core breeding objective that attracts widespread attention in soybean genetic improvement (Nair *et al.*, 2023). Mechanistically, soybean pod shattering represents a balance between two opposing forces. The first is the driving force generated by dehydration of the pod wall, especially differential contraction and torsion in lignified tissues (Estornell *et al.*, 2013; Liljegren *et al.*, 2004). The second is the resistance force provided by the anatomical and biochemical strength of the sutures, particularly the ventral suture where two pod valves are joined (Dong *et al.*, 2014; Graham and Vance, 2003; Zhang *et al.*, 2018). Shattering occurs when dehydration induced mechanical tension surpasses the structural bonding

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strength of the dehiscence zone and adjacent reinforcing tissues (Christiansen *et al.*, 2002; Tu *et al.*, 2019). This concept explains that environmental conditions, pod water content, anatomical structure and gene regulated cell wall properties should be comprehensively analyzed instead of being studied separately.

Compared with cereals including rice and sorghum, in which seed shattering generally relies on abscission layer formation at the seed pedicel junction, soybean pod shattering is associated with the pod wall and sutures of dry dehiscent legume fruits (Ferrándiz, 2002). Studies have demonstrated that the abscission layer is not absent in

domesticated soybean cultivars. Instead, pod shattering resistance is achieved *via* strengthening surrounding tissues including fiber cap cells and altering the torsional properties of pod walls (Dong *et al.*, 2014; Dong *et al.*, 2017a; Tu *et al.*, 2019). This review article elucidates the mechanisms underlying soybean pod shattering by analyzing variations in tension induced by external environmental factors, as well as microscopic alterations in pod anatomical structures and physiological changes of pod sutures. The findings are expected to provide theoretical references for the breeding of shattering-resistant soybean cultivars.

Tension in environmental regulation

Why field conditions matter

Environmental conditions influence pod shattering mainly by changing the water status of mature pods (Esau, 1977). As soybean pods mature, they lose water and become increasingly sensitive to drying. Low relative humidity, high temperature, strong sunlight and dry wind can accelerate pod dehydration (Maity *et al.*, 2021). Under field conditions, this explains why shattering is often more severe in dry regions, during delayed harvest, or after sudden transitions from wet to dry weather. Compared with the combination of high temperature and low humidity, low temperature paired with high humidity markedly lowers pod shattering rate of the lotus plants grown under conventional field conditions for this experiment, according to existing research (Grant, 1996). Drought stress-induced pod shattering in rapeseed adversely affects crop yield, which is largely caused by changes in the torsional force of pod walls and structural strength of the pod dehiscence zone, resulting in pod rupture, seed shedding and eventual yield loss (Parker *et al.*, 2021a).

Drought conditions negatively affect multiple morphological traits of plants, including reduced water content, fewer branches and decreased biomass yield (Singh *et al.*, 2022). The relationship between environment and genetics is especially clear for *Pdh1* and *PvPdh1*. Functional *Pdh1* regulates lignin arrangement in pod walls to drive pod twisting under dry conditions, while its mutant alleles weaken such torsion and mitigate pod shattering (Funatsuki *et al.*, 2014). Accordingly, the phenotypic role of *Pdh1* is highly dependent on ambient humidity (Parker *et al.*, 2021a). Studies indicate that orthologous *Pdh1* genes originated specifically in warm season legumes and their LoF alleles underwent parallel selection during legume crop domestication (Yong *et al.*, 2023). The *PvPdh1* locus, located on chromosome Pv03, has been identified as a key regulator of pod shattering in common bean. This gene greatly curtails crop yield particularly under arid environments and its functional allele inhibits pod valve torsion (Parker *et al.*, 2021b). Further exploration of these genes plays a vital role in enhancing drought tolerance of staple food crops across the globe. A genotype that performs acceptably in a humid, manually harvested region may suffer serious losses if introduced into a drier region or a

system with delayed mechanized harvest. This genotype-by-environment-by-management interaction should be considered when evaluating pod shattering resistance.

Relative humidity and pod moisture

Different from the climatic factors mentioned above, relative humidity is considered to play a regulatory role. Relative humidity is particularly important because it directly affects the equilibrium moisture content of pods. Could artificially increasing atmospheric relative humidity and pod moisture content effectively inhibit field pod shattering? Alternating wetting and drying of pods slightly increased the pod shattering rate under relative humidity of 30% and 40% (Caviness, 1965). Extension observations also indicate that pre-harvest pod shatter can occur when dry pods are re-wetted and later dry again, while harvest loss increases as grain moisture decreases below the recommended harvest range. Relative humidity serves as a key environmental factor, which exerts remarkable regulatory effects on pod structure development and further modulates soybean pod shattering susceptibility (Gao and Zhu, 2013; Maity *et al.*, 2021). A large-scale genetic and geo-climatic analysis further demonstrated that relative humidity has shaped the geographic distribution of pod-indehiscent alleles in soybean. In Chinese soybean landraces, the frequency of the indehiscent *Pdh1* allele showed a strong correlation with regional relative humidity during the harvest season (Yong *et al.*, 2023; Zhang and Singh, 2020).

Essentially, relative humidity ultimately affects pod water status and dehydration degree, which further regulates pod shattering behavior. Reduced moisture level in pod valves leads to more severe yield losses due to soybean pod shattering during harvesting (Philbrook and Oplinger, 1989). Since pod moisture content is a crucial factor in the tension that drives pod shattering, does shading reduce the shattering rate? Studies have shown that pods located at the lower part of the stem exhibit the highest shattering rate (Krisnawati *et al.*, 2021) and an umbrella-shaped, closed canopy plant architecture is more prone to shattering (Tu *et al.*, 2025b). Ultimately, variations in pod moisture content are far more critical to the occurrence of pod shattering. The pod dehydration rate of shattering-susceptible vegetable soybean was significantly higher than that of shattering-resistant grain soybean from the R6 to R8 growth stage (Tu *et al.*, 2025a). In rapeseed siliques, higher seed water content contributes to lower pod shattering susceptibility (Zhang *et al.*, 2023). In Xinjiang, a semi-arid region of China, soybean pods exhibit low moisture content and poor mechanical strength at harvest, resulting in severe pod rupture and substantial yield losses during mechanical harvesting (Chen *et al.*, 2025). Once pod moisture falls below a critical range, the pod wall begins to shrink unevenly and mechanical tension accumulates.

Tension in the soybean pod

Pod shattering is fundamentally a biomechanical event. The mature soybean pod can be viewed as a pre-stressed

structure. During maturation and drying, the pod wall accumulates elastic energy. When the energy stored in the valves exceeds the resistance of the suture tissues, the pod opens rapidly and seeds are released (Zhang *et al.*, 2018). Therefore, one question is central: how is tension generated? Tension is generated mainly through dehydration-induced shrinkage of soybean pod wall tissues (Davies and Bruce, 1997; Estornell *et al.*, 2013). Studies suggest that differences between the endocarp and exocarp generate mechanical tension during pod dehydration and shrinkage (Bennett *et al.*, 2011). The tension triggering pod dehiscence mainly originates from pod walls, which is jointly regulated by the mechanical property differences between lignified and non-lignified tissues as well as turgor pressure changes during fruit maturation (Liljegren *et al.*, 2004). Several layers of lignified cells are present on the ventral sutures of mature dehiscent common bean pods, yet these cell layers are not thick enough. Pods may require differential cell wall thickening along the sutures to generate the mechanical tension necessary for pod dehiscence (Di Vittori *et al.*, 2021). The inner sclerenchyma layer is particularly important because it is lignified and mechanically stiff. However, the tension mechanism between the lignified cell wall layers and separation layers remains poorly understood (Liu *et al.*, 2024). We also attempted to identify the orientation of tension sources by observing fiber arrangement in pods, yet this attempt ended in failure. Nevertheless, it is certain that the formation of pod shattering tension is induced by environmental factors and it is closely associated with pod anatomical structures, including cell morphology of endocarp and exocarp as well as lignified cell layers.

Pod morphological traits including pod length, pod width, pod wall thickness, pod curvature and seed number per pod as well as seed size affect pod shattering to varying degrees (Adie *et al.*, 2022; Li *et al.*, 2017). These characteristics can alter the distribution of mechanical stress during desiccation, determine the force threshold for pod dehiscence and regulate the initiation probability of sutural cracks. Some researchers have even investigated the phenotypic syndrome of soybean pod shattering at the pod level (Tu *et al.*, 2025b). However, the relationships between seed size, pod length and width and the generation of pod shattering tension remain to be further explored.

In leguminous plants, tension triggers the separation of two pod valves accompanied by varying degrees of torsion, thereby resulting in twisting and non-twisting phenotypes. Twisting and non-twisting states are not absolute. Researchers from India have classified the pod dehiscence responses of common legumes into ten grades, including 20%, 40%, 60% and 80% torsion levels (Fatima *et al.*, 2023). Researchers have analyzed the twisting phenotype during pod shattering identification in common bean (Bijarniya *et al.*, 2024; Murgia *et al.*, 2017). Although soybean pods also undergo torsion, the degree

of twisting is far less pronounced compared with legume species that possess longer pods (Tu *et al.*, 2025b). It remains unclear whether the magnitude and generation pattern of tension underlying twisting and non-twisting pod dehiscence are identical. Moreover, it still needs further investigation to verify whether pod twisting is caused by the softening of pod fibers.

Shattering resistance and cellular dissolution in pod anatomy

Dehiscence zone anatomy

Soybean pods consist of two valves, which are interconnected by ventral and dorsal sutures. The central cavity serves as the growth space for seeds (Tu *et al.*, 2019). A wedge-shaped dehiscence zone (DZ) exists in the ventral suture of soybean pods and most studies on pod shattering mainly focus on this zone (Dong *et al.*, 2014; Suzuki *et al.*, 2009). The ventral suture dehiscence zone is especially important because it is the region where the two pod valves are joined and where the abscission layer and fiber cap cells are located. Anatomical studies show that pod dehiscence depends on both the weakening of separation tissues and the ability of surrounding tissues to resist or transmit mechanical tension (Agrawal *et al.*, 2002; Christiansen *et al.*, 2002; Dong and Wang, 2015).

In the ventral suture dehiscence zone of shattering-susceptible *Vicia sativa*, vascular bundles are divided into two segments by the dehiscence zone. In contrast, shattering-resistant genotypes fail to form such a dehiscence zone, with their vascular bundles remaining intact (Dong 2017b). The outermost layer is made up of exocarp cells (EX) that firmly bind the fissure of the dehiscence zone together. Intact vascular bundles without separation by dehiscence zones provide strong resistance to tension formation.

Further studies have revealed that the ventral sutures of shattering-resistant *Vicia sativa* contain a specific cell type termed external valve margin cells (EVMC). These cells are arranged in parallel in groups of two to four and evenly distributed within both pod valves. Their outer cell walls are markedly thickened and such thickened EVMCs also serve as an effective barrier against pod shattering (Dong 2017a).

Neither exocarp cells (EX), thickened external valve margin cells (EVMC), intact vascular bundles nor absent dehiscence zones were detected in the ventral suture of shattering-resistant soybean pods. In contrast, thickened fiber cap cells (FCC) were abundantly distributed at dehiscence zone (Dong *et al.*, 2014). *SHAT1-5* encodes a NAC transcription factor related to secondary wall biosynthesis. It promotes secondary wall thickening and lignification of fiber cap cells (FCC) in the ventral suture. In cultivated soybean, increased expression of *SHAT1-5* is associated with thicker fiber cap cell walls and stronger binding between pod valves (Dong *et al.*, 2014).

Further studies have demonstrated that a longer and curved route extending from the route from the top of fiber

cap cells to the connecting point of the two valves (RFCV) was identified in shattering-resistant cultivated soybean (Tu *et al.*, 2019). This structure can effectively buffer tension generated from the pod wall. In contrast, shattering-susceptible cultivated soybean possesses short and straight RFCV, which renders pods prone to shattering. Soybean differs from some cereals because domesticated soybean resistance is not necessarily caused by complete disappearance of the abscission layer. Instead, the abscission layer may remain present, while shattering is prevented by reinforcement of adjacent cells, especially lignified fiber cap cells in the ventral suture.

Cell lignification around the dehiscence zone and related genes

To achieve tissue separation, physical forces must trigger cell detachment within the abscission layer. This process involves reduced cell adhesion and diminished tension exerted by surrounding tissues or external substances. As discussed above, we focused on cell adhesion near the dehiscence zone, which serves as the physical resistance against pod shattering. The reduction in tension derived from surrounding tissues is closely associated with the degree of cellular lignification (Xueming *et al.*, 2025; Funatsuki *et al.*, 2014; Zhangsheng *et al.*, 2017). Unlike *SHAT1-5*, which acts mainly through sutural reinforcement, *Pdh1* acts mainly through pod wall torsion. The functional gene *Pdh1* was highly expressed in the lignin rich inner sclerenchyma of pod walls, particularly during the early stage of lignin deposition (Funatsuki *et al.*, 2014). GWAS and epistatic analyses have indicated that *NST1A* interacts with *Pdh1* and contributes to multi-level resistance. In particular, resistance conferred by *Pdh1* and *NST1A* together can be comparable to resistance involving all three loci *Pdh1*, *NST1A* and *SHAT1-5* (Zhang and Singh, 2020). This suggests that soybean shattering resistance is not simply additive; instead, epistatic interactions among secondary-wall regulatory genes and pod wall torsion genes shape the final phenotype. In wild soybean, *Sh1* promotes shattering by reducing secondary wall thickening of fiber cap cells. In cultivated soybean, selection of mutations in both *Sh1* and *Pdh1* contributed to shattering resistance. This finding integrates the two major mechanisms: reducing pod wall torsion through *pdh1* and increasing sutural reinforcement through derepression of *SHAT1-5* (Li *et al.*, 2024). Quadruple *GmMYB26* mutations were reported to enhance pod shattering resistance, with effects on lignin, cellulose and hemicellulose synthesis in

a tissue-specific manner (Takeshima *et al.*, 2025). This expands the molecular framework from the well-known *Pdh1–SHAT1-5* axis to a broader secondary cell wall regulatory network involving NAC and MYB transcription factors. Detailed information on soybean pod dehiscence-related genes is listed in Table 1. While research on molecular markers for pod shattering resistance in soybean has a long history (Thakare *et al.*, 2017), recent advancements have significantly enhanced its precision. A recent study demonstrates that combining genome-wide association study (GWAS) and genomic prediction (GP) analyses in soybean can greatly improve the efficiency of marker-assisted selection (MAS) for pod shattering resistance; furthermore, the validated GP models will be utilized for cross-population prediction (Mazkirat *et al.*, 2025).

Cell degradation in the dehiscence zone

The separation layer may become more susceptible to cell wall degradation and the balance between tissue weakening and tissue reinforcement determines whether the pod remains closed. Cell wall composition is a major physiological determinant. Lignin, cellulose, hemicellulose, pectin and soluble sugars can influence mechanical strength, flexibility and adhesion (Murgia *et al.*, 2017; Kuai *et al.*, 2016). Lignin increases rigidity and hydrophobicity, cellulose contributes tensile strength and pectin-rich middle lamellae are important for cell-to-cell adhesion (Zhang *et al.*, 2018; Zhu *et al.*, 2025). If pectin degradation weakens the separation layer while drying simultaneously generates torsion, pod opening becomes more likely. Conversely, stronger secondary walls in fiber cap cells can prevent separation even when the separation layer is developmentally competent (Dong *et al.*, 2014).

Cell wall-degrading enzymes are another important but underexplored component. Polygalacturonases, cellulases, expansins and other wall-modifying enzymes may reduce adhesion in the separation layer. Physical forces induce middle lamella breakdown within abscission layers (ALs) and facilitate the separation of lignified cells adjacent to these layers. In shattering-susceptible legume *Medicago ruthenica*, elevated activities of polygalacturonase and cellulase in pod ventral sutures are critical to accelerate autolysis of abscission layer cells (Guo *et al.*, 2022). In common vetch, these genes are predominantly enriched in hydrolase activity, cellular cytoplasm and carbohydrate metabolism pathways. Genes encoding cell wall modifiers and hydrolases including β -glucosidase and

Table 1: Summary of genes involved in the shattering in soybean.

Gene	Phenotypic	Function	References
<i>SHAT1-5</i>	Indehiscent	Thickening of fiber cap cells.	Dong <i>et al.</i> (2014)
<i>Pdh1</i>	Indehiscent	Regulate pod wall torsion.	Funatsuki <i>et al.</i> (2014)
<i>NST1A</i>	Indehiscent	Epistatic interaction.	Zhang and Singh, (2020)
<i>Sh1</i>	Dehiscent	Reducing thickness of fiber cap cells.	Li <i>et al.</i> (2024)
<i>GmMYB26</i>	Indehiscent	Reducing pod wall fiber abundance.	Takeshima <i>et al.</i> (2025)

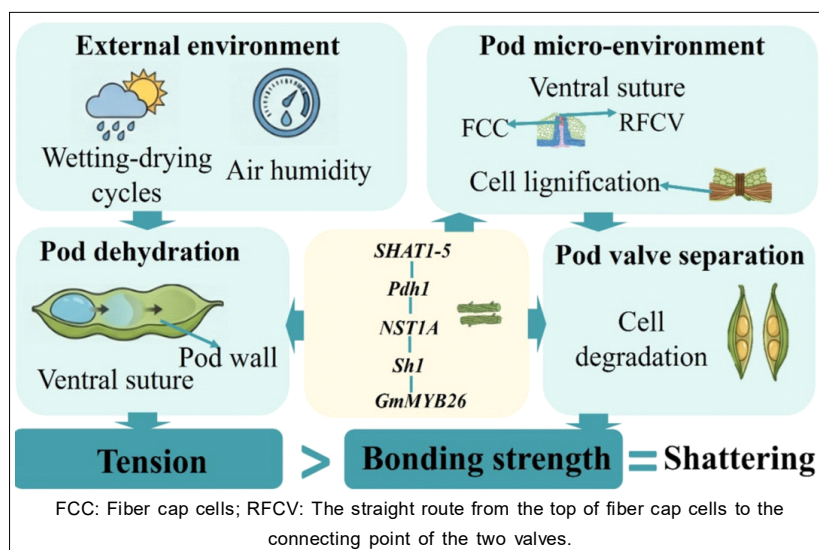


Fig 1: The progression of soybean pod shattering research from environmental induction to anatomical and molecular mechanisms.

endo-polygalacturonase collaboratively break glycosidic linkages in pectin and cellulose, resulting in ventral suture cell wall degradation and enhanced pod shattering tendency (Dong *et al.*, 2017a). In soybean, endogenous 1,4- β -glucanase and polygalacturonase can degrade the middle lamella of the dehiscence zone, weaken intercellular adhesion and ultimately facilitate pod shattering (Tsuchiya, 1986).

Hydrolysis of galacturonic acid chains in pectin by pectinases and degradation of cytoskeletal components in cell walls by cellulases synergistically accelerate middle lamella decomposition (Brs *et al.*, 2011; Hu *et al.*, 2015).

Hormonal regulation may also participate in shattering-related physiology. In model systems, auxin, ethylene, gibberellin and jasmonate pathways can influence abscission zone development, cell wall remodeling and fruit maturation (Berthet *et al.*, 2011; Liu *et al.*, 2019; Maity *et al.*, 2021; María *et al.*, 1990; Oeller *et al.*, 1991). Although the soybean-specific hormonal network remains less completely characterized than that of *Arabidopsis*, it is reasonable to consider that hormone-mediated senescence and cell wall enzyme activity may affect the timing and strength of pod dehiscence. Future studies should connect hormone gradients in the ventral suture with transcriptomic and anatomical changes during pod maturation.

Breeding implications and future research

We deciphered the mechanism underlying pod dehiscence in soybean by examining external environmental signals and the pod internal microenvironment. As illustrated in Fig 1, pod dehiscence occurs when the tension driving pod opening exceeds the bonding strength between the two pod valves. Accordingly, breeding high-quality soybean cultivars resistant to pod dehiscence is of great importance. Breeding for pod shattering resistance should combine

phenotypic evaluation with marker-assisted or genomic selection. Markers linked to *pdh1*, *Sh1*, *SHAT1-5* and *NST1A* can help breeders identify resistant allelic combinations. However, because pod shattering is influenced by many minor loci and environmental conditions, single-gene selection may be insufficient in some backgrounds. Genomic prediction and multi-environment testing may be especially useful for breeding cultivars adapted to diverse humidity and harvest systems. precision editing can remove unfavorable alleles from otherwise valuable cultivars, especially those adapted to humid regions but vulnerable when introduced into drier or mechanized production systems.

Future research should focus on three directions. First, the physiological dynamics of the ventral suture should be studied in more detail, including pectin degradation, cell wall enzyme activity, hormone signaling and dehydration response. Second, biomechanical modeling should be integrated with anatomy, using measurements of pod wall torsion, suture fracture force and tissue-specific shrinkage. Third, molecular studies should move beyond single genes toward regulatory networks that include NAC, MYB, dirigent-like proteins, lignin biosynthesis enzymes, cellulose and hemicellulose synthesis genes and hormone-responsive regulators.

CONCLUSION

Soybean pod shattering is best understood as a multi-scale process. We summarize the progression of soybean pod shattering research from environmental induction to anatomical and molecular mechanisms and propose an integrated model wherein dehydration-generated tensile stress surpasses the bonding strength of pod sutures before pod dehiscence occurs (Fig 1). Environmental humidity determines the drying pressure; pod anatomy determines the mechanical threshold; pod wall tension

provides the driving force; and molecular regulation shapes the tissues that generate or resist that force. A complete understanding of soybean pod shattering therefore requires connecting field ecology, plant biomechanics, anatomy, physiology and molecular genetics. Such an integrated view will help breeders design cultivars that remain resistant across changing climates and modern harvesting systems.

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Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article.

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