https://doi.org/10.17221/37/2026-CJGPB

Synergistic effects of low IAA and GA concentrations promote dehiscence-zone separation in vegetable soybean

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Citation: Tu B.J., Liu C.K., Zhang Q.Y., Liu X.B., Xu N. (2026): Synergistic effects of low IAA and GA concentrations promote dehiscence-zone separation in vegetable soybean. Czech J. Genet. Plant Breed., 62: 190–199.

Abstract: Pod dehiscence, also known as pod shattering, is the process by which mature pods open and release their seeds at physiological maturity. In vegetable soybean (*Glycine max* L.), premature seed release from mature pods is a major cause of yield loss during seed production. As pod dehiscence occurs within the dehiscence zone, understanding the physiological mechanisms governing its formation and degradation is essential. To investigate these mechanisms, we compared the activities of pectinase, polygalacturonase (PG), cellulase, indole-3-acetic acid (IAA), gibberellin (GA), abscisic acid (ABA) and zeatin (ZA) in the pod ventral sutures of dehiscent vegetable soybean and indehiscent grain soybeans. The ventral sutures of dehiscent vegetable soybean exhibited significantly higher activities of pectinase, polygalacturonase, and cellulase, but lower concentrations of IAA and GA than those of indehiscent grain soybean. Reduced levels of IAA and GA in the dehiscence zone were associated with increased activities of cellulase, pectinase, and polygalacturonase activities, which may accelerate cell wall degradation and promote lignification, thereby promoting pod dehiscence.

Keywords: dehiscent; enzymes; hormones; pod valves; soybean

Fruit dehiscence, also known as pod shattering, represents a key strategy for the propagation and environmental adaptation of wild plant species (Funatsuki et al. 2014; Dong & Wang 2015). Nevertheless, this trait acts as one of the major limiting factors during the cultivation and production of domesticated crop cultivars (Christiansen et al. 2002; Ballester & Ferrándiz 2017). Pod shattering is a common trait observed across the Leguminosae family. This characteristic has been widely reported in numerous legume crops, including soybean (Dong et al. 2014), common bean (Paker et al. 2020), common vetch (Dong et al. 2017), yard-long bean, cowpea (Suanum et al. 2016), and lima bean (Garcia et al. 2021). Based on their application purposes, cultivated soybeans are generally classified into two groups: grain soybeans (GS) and vegetable soybeans (VS). Vegetable soybeans, known as edamame in Japan and mao dou in China, are harvested at the R6–R7 growth stages and mainly consumed as a snack food (Gai & Wang 2002). Grain soybeans are mainly used for oil extraction, as well as for the manufacturing of a wide range of soybean-derived food and industrial products. Although pod shattering has

Supported by the Heilongjiang Province Natural Science Foundation of China (Grant No. QC2025C027).

https://doi.org/10.17221/37/2026-CJGPB

been gradually mitigated in the course of soybean domestication, significant yield losses still occur. Depending on genotype, delayed harvest after maturity, and environmental conditions during harvest, yield losses caused by pod shattering can range from 34% to 100% (Agrawal et al. 2002a; Bhor et al. 2014). Among soybean production systems, vegetable soybean seed production is especially vulnerable to pod shattering, which can lead to disproportionately high yield losses compared with grain soybeans (Zhang & Kyei-Boahen 2007; Van der Merwe et al. 2024). In this context, reducing or eliminating pod shattering represents an effective strategy to improve the actual harvested yield of soybean (Raman et al. 2014). Consequently, this trait has become a major target and received extensive attention in soybean breeding programs (Bernard 2001; Nair et al. 2023).

Given the severe loss in vegetable seed production, identifying the molecular basis of pod shattering becomes imperative. The *Pdh1* gene, highly expressed in the lignin-rich inner sclerenchyma of pod walls, promotes pod dehiscence by enhancing the torsion of dried pod walls, thereby providing a driving force for dehiscence under low humidity conditions (Funatsuki et al. 2014). The *Pdh1* gene has been recognised as the key gene governing pod shattering in several legume crops, including soybean, cowpea, chickpea, common bean, and mung bean (Miranda et al. 2019; Aguilar-Benitez et al. 2020; Parker et al. 2021; Marsh et al. 2023; Yong et al. 2023; Li et al. 2024a). In the common bean, *PvPdh1* is associated with a selection sweep and contributes to the reduction of pod twisting (Parker et al. 2021). The transition from shattering in wild soybeans to shattering resistance in cultivated soybeans resulted from the selection of mutations within the coding sequences of two nearby genes, *Sh1* and *Pdh1* (Li et al. 2024b). The differences in pod dehiscence mechanisms between vegetable soybean and grain soybean remain unclear.

A soybean pod consists of two valves joined by dorsal and ventral sutures that enclose the developing seeds. Pod dehiscence takes place when the tensile force acting on the pod exceeds the adhesive strength holding the two valves together. Previous studies have indicated that soybean pod dehiscence starts from the dorsal side of the pod more frequently than from the ventral one (Suzuki et al. 2009), whereas other authors believe that the ventral suture is critical to pod shattering in soybean (Agrawal et al. 2002b; Dong et al. 2014). Within the ventral sutures of soybean pods, the dehiscence zone (DZ) emerges as a crucial anatomical feature. This zone is defined as a slender band of valve margin cells that resides between the two vascular bundle valves. Meanwhile, the fibre cap cells serve as the junctional tissue that connects these structures. Overexpression of the *SHAT1-5* gene activates secondary wall biosynthesis and significantly enhances the thickening of fibre cap cells at the ventral suture, thereby leading to marked alterations in pod indehiscence in soybean compared with the wild type (Dong et al. 2014).

In addition to structural genes, phytohormones fine-tune the lignification and cell-separation processes within the DZ. Phytohormones serve as pivotal signalling molecules in the regulation of plant growth and development, orchestrating a myriad of diverse physiological processes that underpin plant responses to both biotic and abiotic stimuli (Davies 1987; Novák et al. 2017). The intricate interplay of key hormones, including gibberellins, abscisic acid, cytokinins, ethylene, and auxins, within the abscission layers exerts a profound influence on the regulation of pod shattering (Liu et al. 2019; Maity et al. 2021). What are the distinctions in key enzyme profiles within the dehiscence zone of the pod ventral suture between dehiscent vegetable soybeans and indehiscent grain soybeans? Moreover, how do endogenous plant hormones function as signalling molecules to modulate this process? It is necessary to identify the potential regulatory mechanism underlying pod shattering in vegetable soybean. Here, we contrast enzyme activities and endogenous hormones in the ventral dehiscence zone between dehiscent vegetable soybeans and indehiscent grain soybeans to uncover why vegetable soybeans' pods are more prone to shattering.

MATERIAL AND METHODS

Experiment site and plant materials. Field experiments were conducted at the Northeast Institute of Geography and Agroecology, Chinese Academy of Science, Harbin, China. The research site (45°41'N; 126°38'E; altitude 128 m) is in the northern temperate zone with a continental monsoon climate, with cold-dry winters and hot-rainy summers. The site has a mean annual precipitation of 500–600 mm, with 65% falling between June and August, and an average annual temperature of 3.5 °C. In our two-year field study (Tu et al. 2019), we evaluated 140 cultivars based on shattering percentage and identified two dehiscent vegetable soybean cultivars (Mao1,

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Table 1. The information of vegetable soybean and grain soybean cultivars used for the experiment

Cultivars	Days to maturity (days)	100-seed weight (g)	Pod shattering percentage (%)	Classification	Shattering groups
T292	120 ± 3	27.0 ± 1.3	90.8 ± 6.7	vegetable soybean	dehiscent
Mao1	120 ± 2	29.2 ± 0.5	92.7 ± 9.2	vegetable soybean	
DS7	120 ± 2	15.7 ± 0.8	0.0	grain soybean	indehiscent
H44	130 ± 1	19.9 ± 1.2	0.0	grain soybean	

T292) and two indehiscent grain soybean cultivars (DS7, H44). The four soybean cultivars were planted in the field on May 4, 2019. Table 1 summarises the characteristics of dehiscent and indehiscent soybeans used in the experiment. Figure 1A presents photographic images of the experimental materials collected at full maturity. Samples were collected at the R6 growth stage, as shown in Figure 1B. The experiment was laid out in a completely randomised design with three replications. Each plot comprised of five rows with 5 m long and 65 cm row spacing, while the inter-plant distance within the row was 10 cm. Base fertilisers (150 kg/ha diammonium phosphate, 20 kg/ha urea and 60 kg/ha potassium sulphate) were applied at seeding, and weed control was done manually.

Sampling was performed at the full seed stage (R6). Pods from the middle and upper canopy were excised with scissors and immediately placed into an ice box. In the laboratory, pod walls were dissected along the ventral suture on a pre-cooled ice block (Electronic Supplementary Material). Dissected tissues were wrapped in aluminium foil, flash-frozen in liquid nitrogen for 30 min, and stored at –80 °C for subsequent analyses of enzyme activity and endogenous hormones.

Determination of hydrolytic enzymes' activities. Activities of cellulase, pectinase and polygalacturonase (PG) were determined according to the methods described by Wu et al. (2008) and Agrawal et al. (2002b), with minor modifications. Approximately 0.1 g of fresh soybean pods was weighed and homogenised in 1 mL of extraction buffer on ice. The homogenate was then centrifuged at 4 °C for 10 min, and the supernatant was collected for subsequent analysis. Pectinase and polygalacturonase (PG) activities were determined using the 3,5-dinitrosalicylic acid (DNS) colourimetric method, while cellulase activity was measured using the anthrone colourimetric method. One unit of pectinase activity was defined as the amount of enzyme that liberates 1 mg of galacturonic acid from pectin per gram of sample per hour at 50 °C and pH 3.5. One unit (U) of PG activity was defined as the amount of enzyme that liberates 1 mg of galacturonic acid from polygalacturonic acid per gram of sample per hour at 40 °C and pH 6.0. One unit (U) of cellulase activity was defined as the

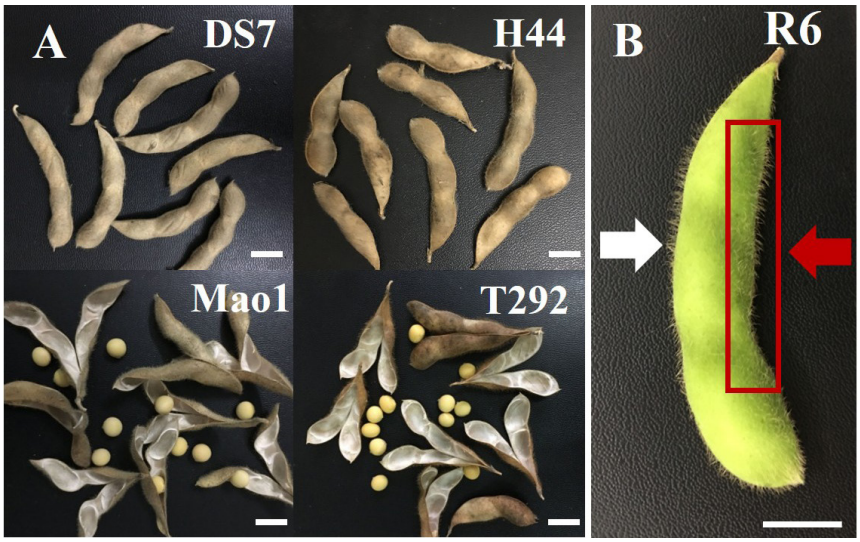

Figure 1. Images of experimental materials at full maturity (R8) (A), red arrows indicate the ventral suture; white arrows indicate the dorsal suture (B)
Scale bar = 1 cm

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amount of enzyme that catalyses the production of 1 μg of glucose per gram of tissue per minute.

Determination of endogenous plant hormones. The determination of plant hormones was performed using high-performance liquid chromatography (HPLC) according to Pan et al. (2010) and Chauvaux et al. (1997), with minor modifications. The identified and quantified phytohormones included indole-3-acetic acid (IAA) as the main auxin, gibberellic acid A3 (GA_3) as the representative gibberellin, abscisic acid (ABA) as the representative abscisic acid, and zeatin (ZA) as the representative cytokinin. Only the free forms of these hormones were determined; conjugated forms were not analysed in this study.

Briefly, approximately 0.2 g of frozen pod samples was ground into powder in liquid nitrogen and extracted in 5 mL of 80% methanol (v/v) containing 20 mg/L butylated hydroxytoluene (BHT) as an antioxidant. The homogenate was incubated at 4 °C for 12 h in the dark, then centrifuged at 12 000 × g for 15 min at 4 °C. The supernatant was collected and evaporated to dryness under nitrogen gas, and the residue was dissolved in 1 mL of methanol, filtered through a 0.22 μm organic filter before HPLC analysis. The analysis was carried out on a Rigol L3000 high-performance liquid chromatography system equipped with a Kromasil C18 reversed-phase column (250 mm × 4.6 mm, 5 μm). The mobile phase consisted of methanol : 1% acetic acid aqueous solution = 2 : 3 (v/v). Standard compounds, including IAA, GA_3, ZA and ABA, were purchased from Sigma-Aldrich (St. Louis, MO, USA) and used to generate standard curves for quantification. The detection wavelength was 254 nm.

Statistical analysis. Experimental data were analysed by SPSS statistical software (Ver. 26), and figures were created with GraphPad Prism (Ver. 10.1.2) and OriginPro2026. Two-sample *t*-tests were performed to test the differences between dehiscent vegetable soybean and indehiscent grain soybean cultivars for cellulase, pectinase, and PG activities and endogenous plant hormones (IAA, GA, ZR, ABA). One-way ANOVA was used to examine the level in different soybean cultivars. The correlations between enzymes, endogenous hormones in the pod ventral suture, and pod shattering were analysed using Pearson's correlation coefficient.

RESULTS

Hydrolytic enzymes activity. The cellulase content in the pod ventral suture of dehiscent vegetable soybeans was significantly higher than that of indehiscent grain soybeans (*t*-test, $P < 0.05$), with an average increase of 4% (Figure 2). Among the four cultivars, Mao1 exhibited the highest cellulase activity (1 426 ± 23), whereas DS7 showed the lowest (1 359 ± 10). The activity of PG and pectinase in the ventral suture of dehiscent vegetable soybeans also surpassed those in indehiscent grain soybeans,

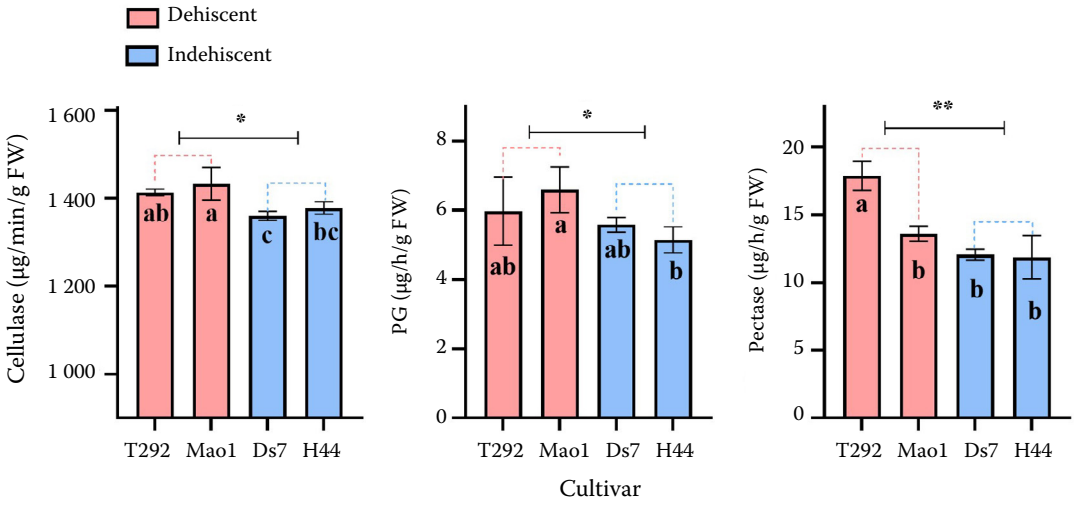

Figure 2. Pectinase, cellulase and polygalacturonase (PG) activities in the pod ventral sutures of dehiscent vegetable soybean and indehiscent grain soybean cultivars

Bars not sharing the same letter are significantly different (ANOVA, $P < 0.05$); *,**significant difference (*t*-test, $P < 0.05, 0.01$); error bars represent SD

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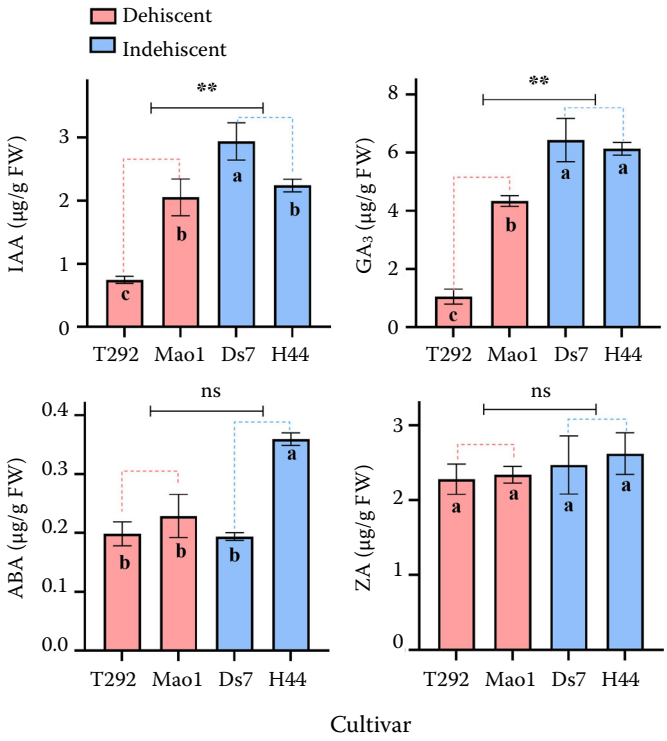

Figure 3. Contents of indole-3-acetic acid (IAA), gibberellic acid A3 (GA_3), abscisic acid (ABA) and zeatin (ZA) in the pod ventral sutures of dehiscent vegetable soybean and indehiscent grain soybean cultivars

Bars not sharing the same letter are significantly different (ANOVA, $P < 0.05$); **significant difference (t-test, $P < 0.01$), ns indicates no significant difference; error bars represent SD

with the differences attaining significance (t-test, $P < 0.05$) and high significance (t-test, $P < 0.01$), respectively. Specifically, the activities of PG and pectinase in vegetable soybeans were, on average, 17.1% and 31.6% greater than those in grain soybeans. Mao1 exhibited the highest polygalacturonase activity (6.6 ± 0.6), while H44 showed the lowest (5.1 ± 0.4). For pectinase activity, T292 had the highest value (17.8 ± 1.1), and H44 had the lowest (11.8 ± 1.6).

Endogenous hormones contents. The levels of IAA and GA in vegetable soybeans were significantly lower than those in grain soybeans, averaging a 46% and 57% reduction, respectively (Figure 3). In contrast, the levels of ZA and ABA did not significantly differ between vegetable soybeans and grain soybeans. Correlations between soybean pod shattering percentage, key enzymes and endogenous hormones of the pod in the dehiscence zone are presented in Figure 4 as a network diagram. Soybean pod shattering percentage was significantly positively correlated with the contents of cellulase and pectinase in the ventral suture of pod valve ($r = 0.81$, $r = 0.73$, Pearson's correlation, $P < 0.01$), positively correlated with polygalacturonase content ($r = 0.63$, Pearson's correlation, $P < 0.05$), and significantly negatively correlated with the contents of endogenous IAA and GA ($r = -0.73$, $r = -0.82$, Pearson's correlation, $P < 0.01$). The pectinase content was significantly negatively correlated with IAA and GA contents ($r = -0.86$, $r = -0.92$, Pearson's correlation, $P < 0.001$), and the contents of auxin and gibberellin were significantly positively correlated with each other ($r = 0.9$, Pearson's correlation, $P < 0.001$).

DISCUSSION

The separation of all cells from one another is a process involving the degradation of intercellular adhesion substances and the degeneration of cell walls (Lewis et al. 2006). The degeneration of the dehiscence zone facilitates the development of the non-shattering pod trait. The present study found that vegetable soybeans have a higher cellulase, PG and pectinase activity in the pod ventral suture than grain soybean. The degradation in the dehiscence zone of the pod is dependent on hydrolytic enzymes such as cellulase, pectinase, and PG (Petersen et al. 1996). In particular, endogenous 1,4-β-glucanase and PG may disrupt the middle lamella of the separation layer, thereby reducing intercellular adhesion and promoting pod shattering (Tsuchiya 1986). The increased activities of pectinase and cellulase in the pod ventral suture are essential for the autolysis of abscission layer (AL) cells in shatter-susceptible *Medicago ruthenica* (Guo et al. 2022). The hydrolysis of galacturonan chains within pectin by pectinase

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and the degradation of cytoskeletal elements in the cell wall by cellulase collectively facilitate the breakdown of the middle lamella (Brás et al. 2011; Hu et al. 2015). A common ~8 kb deletion present in the domesticated common bean population removes the promoter and transcription start site (TSS), resulting in significantly reduced expression of *PvMYB26*. This leads to decreased lignin deposition in the pod fibre layer, softer tissue, and reduced torsion force, ultimately decreasing pod shattering (Celebioglu et al. 2026).

In our study, an intriguing finding was observed: vegetable soybeans exhibited significantly lower levels of IAA and GA in the pod ventral suture compared to grain soybeans. IAA is a class of essential hormones that regulate plant growth and development. Research both domestically and internationally has demonstrated that auxin plays a crucial role in modulating apical dominance, tissue differentiation, organogenesis, and morphogenesis in plants (Larsson et al. 2017; Li et al. 2017; Park et al. 2017). The response to auxin and the expression of auxin-regulated genes are orchestrated by a complex interplay among auxin receptors (F-box proteins), repressors (Aux/IAAs), and auxin response factors (ARFs). Under conditions of low auxin concentration, the formation of Aux/IAA heterodimers results in the suppression of target ARF transcription factors (Tiwari et al. 2001). GAs are bioactive diterpenoid compounds that regulate diverse developmental processes, including seed germination, stem elongation, leaf expansion, trichome development, and flower and fruit development (Olszewski & Gubler 2002). The synergistic action of IAA and GA can jointly regulate root growth, citrus fruit set, and internode growth in decapitated dwarf bean plants (Kigel 1981; Tanimoto 2005; Bermejo et al. 2017).

Our results suggest that synergistic effects of low concentrations of IAA and GA in the ventral suture dehiscence zone contribute to pod shattering in vegetable soybeans. We have elucidated two mechanisms by which IAA and GA mediate cell wall degradation in the dehiscence zone (Figure 5). Firstly, low concentrations of IAA and GA can stimulate the activities of cellulase, pectinase, and polygalacturonase in the dehiscence zone, thereby accelerating the dissolution of cell walls in this region, enhancing the degree of cell lignification, and ultimately promoting the occurrence of pod dehiscence. Phytohormones, particularly ethylene and IAA, have been reported to be associated with pod dehiscence through their involvement in the regulation of cellulase enzyme activity (Tucker et al. 1988; Oeller et al. 1991; Maity et al. 2021).

Furthermore, the role of *Bna.WAG2*-mediated IAA transport in alleviating cell wall loosening, reducing PG activity, and enhancing pod shattering

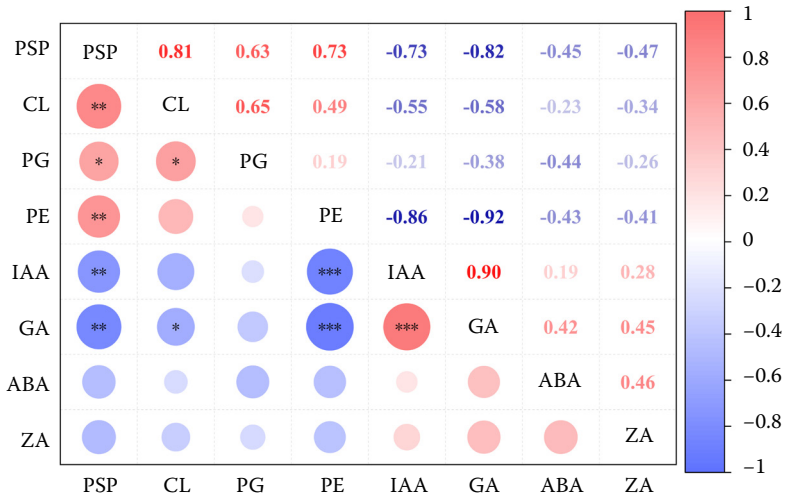

Figure 4. Network diagram of correlations between enzymes, endogenous hormones in the pod ventral suture and pod shattering percentage across all soybean cultivars

PSP – pod shattering percentage; CL – cellulase; PG – polygalacturonase; PE – pectinase; IAA – indole-3-acetic acid; GA – gibberellic acid; ABA – abscisic acid; ZA – trans-zeatin; circle size reflects the magnitude of Pearson's *r*, and the sign of correlations is indicated by the direction in the matrix (positive vs. negative); *,**,***denote significance (Pearson's correlation, $P < 0.05, 0.01, 0.001$)

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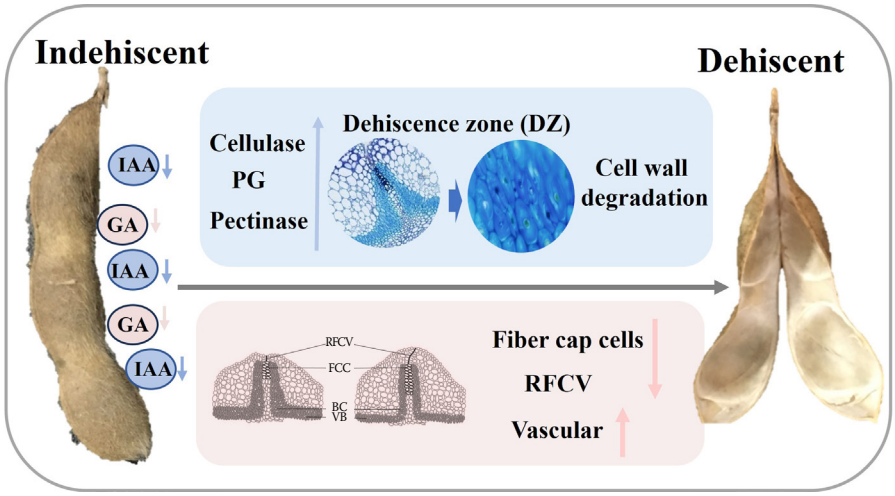

Figure 5. Physiological mechanisms of pod shattering in vegetable soybeans
IAA – indole-3-acetic acid; GA – gibberellic acid; PG – polygalacturonase; RFCV – the route from the top of fibre cap cells to the connecting point of the two valves; FCC – fiber cap cells; BC – bundle cap; VB – vascular bundle; the blue box indicates the first mechanism, and the pink box represents the second mechanism; all anatomical diagrams of the dehiscence zone of ventral suture in this figure are cited from our previous study (Tu et al. 2019)

resistance was observed, which may be associated with increased lignin synthesis and accumulation (Mahmood et al. 2023). Accumulating evidence has demonstrated that peroxidases play a crucial role in the polymerisation of lignin precursors (Berthet et al. 2011). Cell wall peroxidases are capable of oxidising the lignin precursor coniferyl alcohol, while higher concentrations of IAA exhibit an inhibitory effect (Ferrer et al. 1990).

Secondly, IAA and GA also influence the anatomical structure of the dehiscence zone, such as the thinner fibrous cap cells, shorter RFCV (the route from the top of fibre cap cells to the connecting point of the two valves), and larger vascular bundle area, thereby contributing to the characteristics associated with pod dehiscence. Our previously published study confirmed that there are significant differences in the anatomical structure of the dehiscence zone between vegetable soybeans and grain soybeans (Tu et al. 2019). Anatomical analyses revealed that IAA-treated siliquae exhibited thick-walled cells in the dehiscence zone, an enlarged cross-sectional area of the main vascular bundle (MVB), and increased siliqua wall thickness in *Brassica napus* L. (Kaur et al. 2018).

Although auxin and gibberellin are closely associated with the activities of key enzymes in the dehiscence zone, the regulatory relationship between pod dehiscence formation and related genes in vegetable soybean remains to be further elucidated. In future studies, near-isogenic lines (NILs) with well-defined genetic backgrounds will be employed for validation to further confirm the genetic and molecular mechanisms underlying pod resistance. Indeed, such NILs are currently under construction in our laboratory. To mitigate pod shattering during seed production in vegetable soybeans, elevating the concentrations of IAA and GA in the dehiscence zone emerges as a promising strategy. In forthcoming field trials, we intend to apply appropriate growth regulators to the pods to effectively control and suppress pod dehiscence during the seed production process in vegetable soybean. Concurrently, we will delve into the molecular mechanisms governing the synergistic regulation of dehiscence zone separation by IAA and GA.

CONCLUSION

The activities of cellulase, pectinase, and polygalacturonase in the dehiscence zone of the pod ventral suture in dehiscence vegetable soybeans are higher than those in indehiscence grain soybeans. Relatively low content of IAA and GA is observed in the pod ventral suture of vegetable soybeans than that of grain soybeans. The synergistic action of IAA and GA activates hydrolase activity, promotes cell wall degradation in the dehiscence

https://doi.org/10.17221/37/2026-CJGPB

zone of the ventral suture, and alters the anatomical structure of this region, thereby inducing pod shattering in vegetable soybeans.

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Received: March 18, 2026
Accepted: May 12, 2026
Published online: June 8, 2026