https://doi.org/10.17221/119/2024-CJGPB

Agronomic and pod traits in relation to pod shattering in cultivated soybeans

Bingjie Tu[1,3], *Qiuying Zhang*[2], *Xiaobing Liu*[2]*, *Shaopeng Yu*[1,3]*, *Nan Xu*[1,3], *Jia Liu*[1,3], *Changkai Liu*[2]

[1]*College of Geography and Tourism, Harbin University, Heilongjiang Province, Harbin, P.R. China*
[2]*State Key Laboratory of Black Soils Conservation and Utilization, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Harbin, P.R. China*
[3]*Key Laboratory of Heilongjiang Province Cold Region Wetland Ecology and Environment Research, Harbin, P.R. China*

**Corresponding author: liuxb@iga.ac.cn; wetlands1972@126.com*

Citation: Tu B.J., Zhang Q.Y., Liu X.B., Yu S.P., Xu N., Liu J., Liu C.K. (2025): Agronomic and pod traits in relation to pod shattering in cultivated soybeans. Czech. J. Genet. Plant Breed., 61: 67–76.

Abstract: Pod dehiscence or pod shattering from mature soybean (*Glycine max* L.) is one of the most outstanding disadvantages in domesticated cultivars. Pod shattering in relation to 16 quantitative traits and 3 qualitative traits among 140 cultivars of vegetable soybeans, grain soybeans and small-grain soybeans was evaluated over two years. We found the pod shattering percentage is positively correlated with the number of productive branches, pod width, pod length, pod area, 100-seed weight, 1-seeded-pod percentage, 2-seeded-pod percentage and seed protein content, but negatively correlated with the plant height, pod height at the bottom, number of nodes on the main stem, 3-seeded-pod percentage, 4-seeded-pod percentage and seed oil content. The pod shattering percentage in vegetable soybeans is remarkably high, reaching up to 93%, 7.8 times higher than that of grain soybeans. A schematic model of the characteristics for shatter-susceptible and shatter-resistant soybean cultivars is proposed. The pod shattering in vegetable soybeans is related to the "umbrella-shaped" architecture and pod size. It is suggested to select lines with more 2-seeded and 3-seeded pods for vegetable soybeans, but a higher seed oil content and greater node number on the main stem for grain soybeans and small-grain soybeans, to avoid pod shattering in future breeding programmes.

Keywords: breeding; dehiscence; plant type; pod level; quantitative traits

Fruit dehiscence or seed dispersion is essential for the propagation of their progeny and adaptation to varying environmental conditions in wild plants (Nathan & Muller-Landau 2000; Funatsuki et al. 2014). However, this phenomenon presents itself as one of the main limitations in the production of cultivated species (Christiansen et al. 2002; Ballester & Ferrándiz 2017). Pod shattering exists in most Leguminosae, Gramineae, and Brassicaceae crops (Christiansen et al. 2002; Dong et al. 2014, 2017). The soybean is the most significant crop globally in terms of human consumption. However, yield

Supported by the National Key R&D Program of China: Grant No. (2021YFD1201103-03); Youth Doctoral Scientific Research Foundation of Harbin University (HUDF2021111) and Major Program of National Science and Technology of China (2016YFD0100201).

https://doi.org/10.17221/119/2024-CJGPB

loss due to pod shattering in the soybean may range from 34 to 100% depending upon genotype, delayed harvesting after maturity and the environmental conditions during harvesting (Tiwari & Bhatnagar 1991; Agrawal et al. 2002; Bhor et al. 2014). In this regard, eliminating pod shattering is another way to increase the harvested yield (Squires et al. 2003; Raman et al. 2014). Cultivated soybeans can be categorised into two main types: grain soybeans and vegetable soybeans, depending on their intended use. Most common grain soybeans are primarily utilised for oil extraction and the production of various soy-based products, while small-grain soybeans, characterised by a 100-seed weight of less than 12 grams, are specifically used for the production of bean sprouts and natto (Liu et al. 2017). Vegetable soybeans, popularly known as edamame in Japan and mao dou in China, are harvested fresh during the R6 and R7 growth stage, as a leisure or snack food (Gai & Wang 2002; Nair et al. 2023). Therefore, understanding the pod shattering characteristics of soybean cultivars with different uses is of significance for soybean breeding programmes and cultivation practices against pod shattering.

The characteristic of pod shattering is influenced by a multitude of factors, including the genetic characteristics of the cultivars, environmental humidity, physiology, and molecular biology (Zhang et al. 2018; Liu et al. 2019; Krisnawati et al. 2020). Key enzymes, endogenous hormones, and anatomical characteristics in the dehiscence zone are crucial factors influencing pod dehiscence (Liu et al. 2022). The marker linked to the transcriptome analysis related to pod shattering can be of value in soybean breeding programmes for the development of pod shattering-resistant cultivars (Kang et al. 2020; Kim et al. 2020). The *Pdh1* gene is the most important gene regulating pod shattering in soybeans, cowpeas, and chickpeas, holding a particular significance in soybeans (Miranda et al. 2019; Aguilar-Benitez et al. 2020; Marsh et al. 2023). The orthologous *Pdh1* genes specifically originated in warm-season legumes, and their loss-of-function alleles have been subsequently selected in parallel during the domestication of these crops (Yong et al. 2023). Artificial selection of mutations in two closely located genes leads to the development of shattering resistance in soybeans (Li et al. 2024).

The pod shattering resistance is mainly considered to be a qualitative trait and described as a syndrome under field conditions in common beans, which is closely related to the pod size and seed weight per pod (Murgia et al. 2017). While in oilseed rape, strong correlations are found between the pod shatter resistance and the weight and length of the valves (Summers et al. 2003). The objective of this study was to explore the relationship between the agronomic traits and pod traits in relation to pod shattering in cultivated soybeans with different uses.

MATERIAL AND METHODS

Plant material. One hundred and forty soybean cultivars were used for the research. Among them, 101 were from Heilongjiang Province, 21 were from Jilin Province, 4 each were from Liaoning and Zhejiang Province, 2 each were from Shandong and Fujian Province, and 1 each was from Beijing and Hebei Province, 2 were from Japan, 1 was from the United States, and 1 was from an unknown source, but was a germplasm. Among the 140 selected materials, 94 were grain soybeans, 30 were vegetable soybeans, and 16 were small-grain soybeans. Figure 1 shows the sources of 140 soybean accessions (A) and classifica-

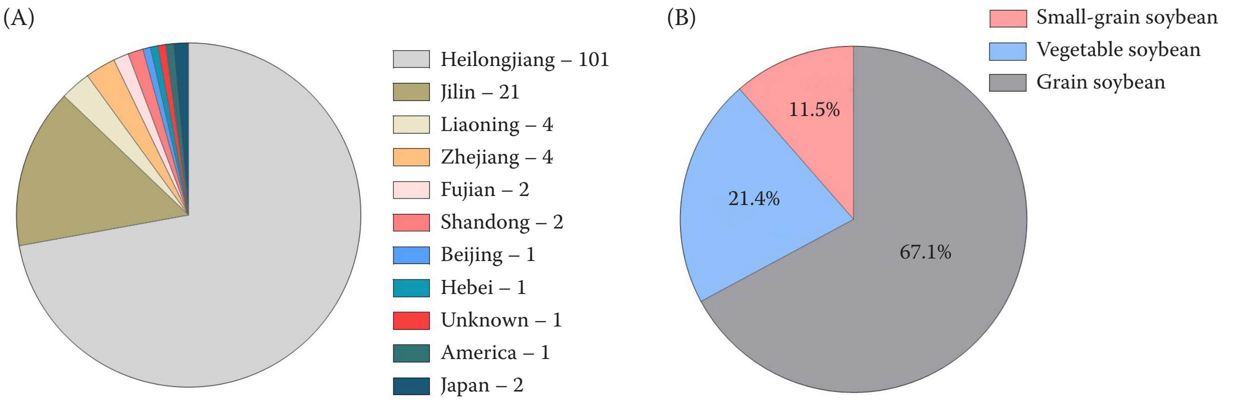

Figure 1. Sources of 140 soybean germplasm resources (A) and classification (B) for the field experiment

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tion (B) for the field experiment. The list of materials and detailed information can be found in Table S1 in the Electronic Supplementary Material (ESM).

Growth conditions. Field experiments were conducted in 2016 and 2017 at the agronomy farm of the Northeast Institute of Geography and Agroecology, Chinese Academy of Science, Harbin, China. The research site (45°73'N; 126°61'E; altitude 128 m) is in the northern temperate zone with a continental monsoon climate (cold and arid in the winter, hot and rainy in the summer). The monthly average temperature (°C) and monthly average relative humidity (%) during the soybean growth across the two years are shown in Table 1. The tested soybean cultivars were grown in the field on May 4, 2016 and May 9, 2017. All the experiments were conducted using a randomised complete design with three replications. Each plot was comprised of five rows having 5 m long and 45 cm row spacing, while the inter-plant distance within the row was 10 cm. Base fertilisers (70 kg/ha diammonium phosphate and 98 kg/ha urea) were applied at seeding and weed control was performed manually.

Evaluation of the pod shattering and agronomic traits. The pod shattering percentage was determined using the oven drying method, where the pods were exposed to a temperature of 60 °C for 7 h in an oven to assess the degree of dehiscence (Romkaew & Umezaki 2006). At full maturity, all the pods from one soybean plant were carefully cut and placed in a nylon bag. After counting the total number of pods, the bags containing the pods were placed in an oven.

The pod shattering percentage was calculated as the percentage of pods that dehisced as:

Pod shattering percentage (%) = the number of shattering pods per plant/the total pods number per plant ×100%

A total of 16 quantitative traits and 3 qualitative traits were recorded. The quantitative traits were: the plant height (cm); pod height at bottom (cm); number of nodes on main stem; productive branch number per plant; pod width (cm); pod length (cm); pod surface area (cm^2); 100-seed weight (g); ratios of 1-seeded pod, 2-seeded pod, 3-seeded pod and 4-seeded pod to total pods per plant (%); maturation period of the soybean (days); pod number per plant; seed protein content (%); and seed oil content (%). The qualitative traits were: the seed coat colour (yellow, other colours);

Table 1. Climate data during the field experiment over two years

	Monthly average			
	temperature (°C)		relative humidity (%)	
	2016	2017	2016	2017
May	16	15	58	49
June	22	20	65	64
July	25	27	70	61
August	24	23	64	74
September	17	16	77	63
October	4	7	59	45

leaf shape (lanceolate, round); flower colour (white, purple). In each replicate, five soybean plants were randomly selected for the assessment of the quantitative traits. The protein and oil content of the seeds were determined through specialised instruments, an Infratec grain analyser (FOSS INFRATEC^{TM}1241 ANALYZER). By placing fully mature seeds into the instrument, the corresponding values can be directly obtained (Patil et al. 2010).

Data analysis. The experimental data were analysed using SPSS statistical software, and figures were created using GraphPad Prism (Ver. 10.1.2) software. The associations between the pod shattering percentage and phenotypic traits were quantified using Pearson's Correlation Coefficient. The analysis of qualitative traits is represented by the F ratio (F) and significance level (P).

RESULTS

Pod shattering and qualitative traits. Figure 2A is the pod shattering percentage at maturity using a 1–5 scale determined according to the classification standard by Asian Vegetable Research and Development Center (AVRDC) (1979). The very resistant (1 = 0%), resistant (2 = 1–10%) and very susceptible (5 ≥ 50%) accounted for 25%, 35.3% and 26.8%, respectively, while the moderately resistant (3 = 11–25%) and moderately susceptible (4 = 26–50%) accounted for 7.9% and 5%, respectively, on average in 2016 and 2017.

The seed coat colour, leaf shape and flower colour traits in the 140 cultivars across two years under different shattering descriptions (1–5 scale) are shown in Figure 2B. The average pod shattering percentage over two years was used to categorise the pod shattering scale in Figure 2B. In the very

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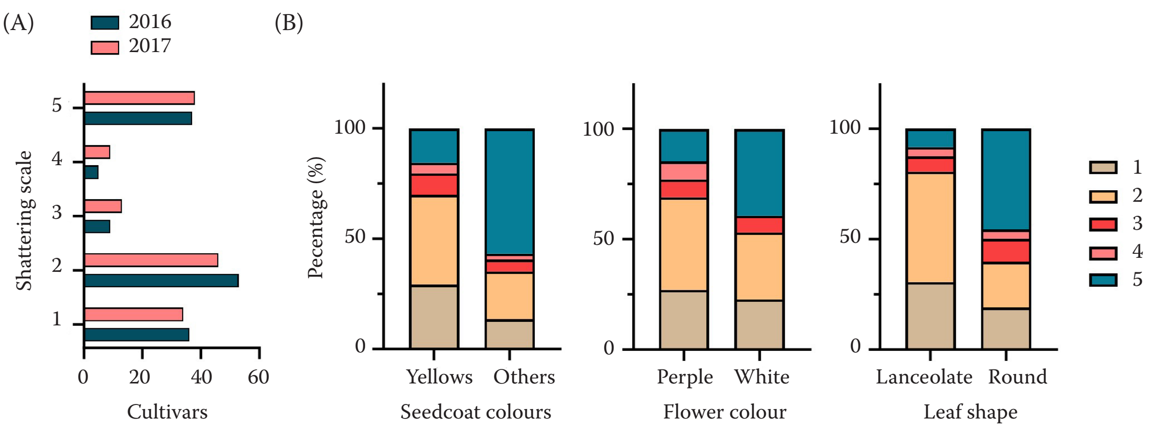

Figure 2. Shattering evaluation and distribution (A) and qualitative traits under a different shattering scale (B) among 140 accessions over two years; pod shattering percentage per plant induced was recorded at maturity using a 1–5 scale 1 = 0% (very resistant); 2 =1–10% (resistant); 3 = 11–25% (moderately resistant); 4 = 26–50% (moderately susceptible); 5 ≥ 50% (very susceptible) (AVRDC 1979)

resistant (1) and resistant (2) scale, the cultivars with a yellow seed coat, lanceolate leaves and purple flowers accounted for 87.2%, 83.9% and 62.8% in 2016, and 71.9%, 57% and 58% in 2017 on average, respectively. While the cultivars in the very susceptible (5) scale with the green and brown seed coat, round leaves and white flowers accounted for 56.1%, 82.7% and 69.3% on average across the two years, respectively.

Pod shattering levels and quantitative traits. Figures 3 and 4 show the correlations between the shattering levels and the 16 quantitative traits, observed among the 140 cultivars in the field conditions over two years. The majority of the shatter-susceptible

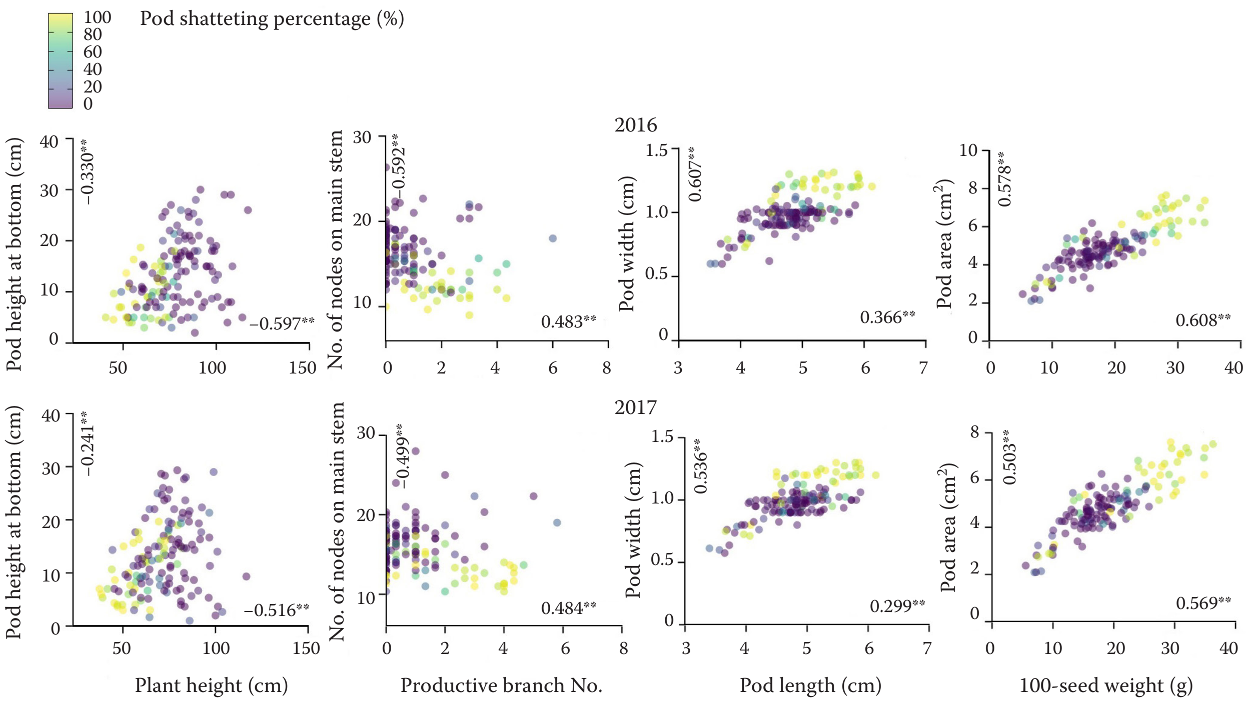

Figure 3. Relationship of the pod shattering percentage with the plant height, pod height at the bottom, number of nodes on the main stem, productive branch number, pod width, pod length, pod area and 100-seed weight over two years **$P < 0.01$

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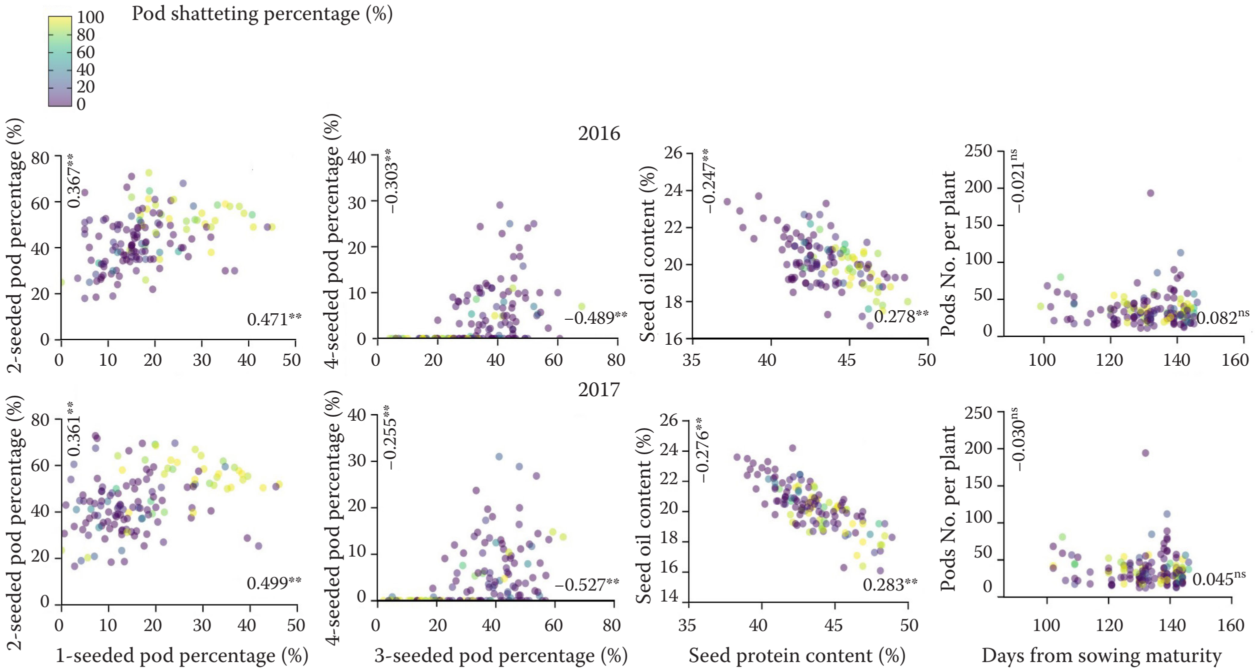

Figure 4. Relationship of the pod shattering percentage with the ratios of the 1-seeded pods, 2-seeded pods, 3-seeded pods, and 4-seeded pods to the total pods per plant, seed protein content, seed oil content, pod number per plant and days from sowing to maturity over two years

**$P < 0.01$

soybeans have a shorter plant height, shorter pod height at bottom, wider pod width, longer pod length, larger pod area and larger 100-seed weight. Shatter-susceptible soybeans also have more productive branches per plant, more 1-seeded pods, and more 2-seeded pods, but less 3-seeded pods, 4-seeded pods and node numbers on the main stem per plant. In contrast, there is a reverse trend in the shatter-resistant soybeans. The pod shattering percentage shows a positive correlation with the seed protein content and a negative correlation with the seed oil content. The pod shattering percentage of all the cultivars exhibits a highly significant correlation with these phenotypic traits ($P < 0.01$) over two years. However, there is no significant correlation between the pod numbers per plant, days from sowing to maturity and pod shattering percentage ($P > 0.05$).

Comparison of the pod shattering in soybeans with a different use. Figure 5 shows the average pod shattering percentage of 94 grain soybeans, 30 vegetable soybeans and 16 small-grain soybeans over two years. The average pod shattering percentage for vegetable soybeans reaches an impressive 93%. In comparison, grain soybeans only exhibit an average percentage of 11% for pod shattering, while small-grain soybeans show an average percentage of 29%. Remarkably, the average pod shattering percentage of vegetable soybeans is 7.8 times higher than that of grain soybeans over the two-year period.

Table 2 lists the associations between the levels of pod shattering with a different use and 19 traits. Vegetable soybeans with white flowers show higher

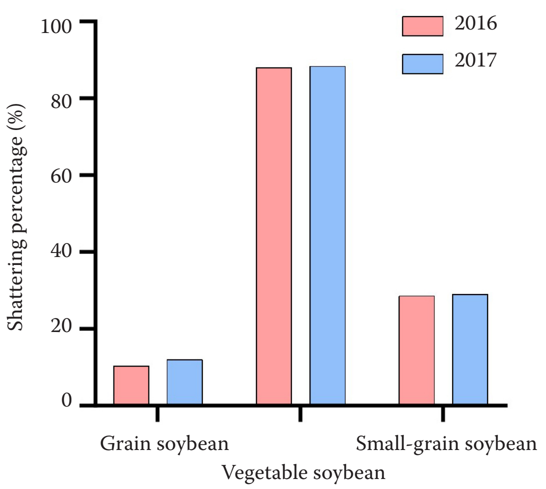

Figure 5. Pod shattering percentage of soybeans with a different use over two years

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Table 2. Correlations between the level of shattering and the traits of vegetable soybeans, grain soybeans, and small-grain soybeans

Traits	grain soybean		vegetable soybean		small-grain soybean	
Quantitative	*P*	*R*	*P*	*R*	*P*	*R*
Plant height (cm)	0.74	–0.185	0.059	–0.348	0.018	**–0.414***
Pod height at bottom (cm)	0.259	–0.118	0.224	–0.229	0.755	0.085
Productive branch number	0.003	**0.298****	0.157	0.265	0.353	–0.170
Number of nodes on the main stem	0.013	**–0.255***	0.657	–0.084	0.001	**–0.570****
Pod length (cm)	0.717	0.038	0.902	–0.024	0.477	–0.130
Pod width (cm)	0.228	0.126	< **10^{-4}**	**0.726****	0.992	0.002
Pod area (cm^2)	0.389	0.090	0.036	**0.384***	0.636	–0.087
100-seed weight (g)	0.922	0.010	0.008	**0.475****	0.627	0.089
The ratio of 1-seeded pods to the total pods per plant (%)	0.112	0.165	0.002	**0.545****	0.237	0.215
The ratio of 2-seeded pods to the total pods per plant (%)	0.646	0.048	0.186	0.248	0.592	–0.098
The ratio of 3-seeded pods to the total pods per plant (%)	0.177	–0.141	< **10^{-4}**	**–0.647****	0.727	–0.064
The ratio of 4-seeded pods to the total pods per plant (%)	0.778	–0.030	< **10^{-4}**	**–0.688****	0.752	–0.058
Seed protein content (%)	0.096	0.180	0.464	0.139	< **10^{-4}**	**0.673****
Seed oil content (%)	0.034	**–0.288***	0.379	–0.167	0.020	**–0.438***
Pod numbers per plant	0.076	0.184	0.393	–0.162	0.163	–0.366
Days from sowing to maturity	0.117	–0.163	0.032	**–0.393***	0.509	0.178
Qualitative	*F*	*P*	*F*	*P*	*F*	*P*
Flower colour	1.885	0.173	18.337	< **10^{-4}**	1.956	0.184
Leaf shape	1.259	0.265	–	–	0.535	0.477
Seed coat colour	0.040	0.842	1.212	0.280	0.582	0.458

Bold – significant associations; *F* – *F* ratio; *R* – Pearson's correlation coefficient; *P* – significance level; *,***P* < 0.05, 0.01

shattering percentage (92.4 ± 7%) than those with purple flowers (70.5 ± 19.8%). A strong positive correlation between the productive branch and pod shattering percentage, but a negative correlation between the number of nodes on main stem and the seed oil content is found in the grain soybean. In vegetable soybeans, pod shattering percentage is positively correlated with the pod width, pod area, 100-seed weight and the ratio of 1-seeded pod, but negatively correlated with the ratios of 3-seeded pod and 4-seeded pod and as well as the days from sowing to maturity. While in small-grain soybeans, the pod shattering percentage is negatively correlated with the plant height, number of the nodes on the main stem, and the seed oil content, but positively correlated with the seed protein content. In general, the shattering percentage is negatively correlated with the number of nodes on the main stem and the seed oil content in both grain soybeans and small-grain soybeans.

DISCUSSION

The pod shattering and plant architecture were domesticated simultaneously (Dong & Wang 2015; Sedivy et al. 2017). The mean values of the plant height and branch number on the main stem in the wild parent are greater than those of the cultivated parent (Li et al. 2017). Studies have found that the plant height is positively correlated with the shattering (Adie et al. 2022). A higher shattering percentage at a lower part of the stem compared to the pods in the middle and upper parts of the plants has been reported (Krisnawati et al. 2021). We observed that the majority of shatter-susceptible soybeans are shorter in plant height and the pod

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height at the bottom, but have a greater number of productive branches per plant and lower number of nodes on the main stem. The combination of these traits develops the plant architecture of pod shatter-susceptible cultivars like an umbrella. Thus, we refer to this plant architecture as the "umbrella-shaped" or "open plant type" and conclude that shatter-resistant soybeans, in general, exhibit a close or compact plant architecture. Based on our two-year results, we propose a schematic model of the characteristics for shatter-susceptible and shatter-resistant soybean cultivars (Figure 6).

The open umbrella-shaped plant structure likely leads to the majority of their pods developing in shaded and enclosed environments frequently, while larger and rounder leaves may increase the crowing and shading of shatter-susceptible soybeans. Shading affects the transport of assimilates in soybean pods and seeds during the growth process (Fraser et al. 1982; Kakiuchi & Kobata 2004). A crowed environment is advantageous to the fibre length and micronaire, but disadvantageous to the fibre strength (Lv et al. 2013), because shading could lead to a reduction in the dry matter accumulation. The partitioning efficiency of dry matter from pod valves to seed is higher in pod shattering resistant cultivars than in pod shattering susceptible cultivars (Agrawal et al. 2002). The fibre content (Suanum et al. 2016) and tenderness (Kongjaimun et al. 2012) of larger-seeded pods are important factors contributing to pod shattering. Thus, the reduction in the pod fibre strength could be one of the reasons for pod shattering in an umbrella-shaped soybean plant. Increased sunlight exposure to the soybean canopy and pods during maturation results in greater dryness, which, in turn, amplifies the tension from the water loss, leading to pod shattering in the umbrella-shaped plant structure.

Our study observed that the shatter-susceptible soybeans exhibit a longer pod length, wider pod width, larger pod area, and higher 100-seed weight. In addition, higher ratios of the 1-seeded pod and 2-seeded pod percentage are also found in the shatter-susceptible soybean cultivars. The positive correlation of the seed size with pod shattering has been reported in soybeans (Adie et al. 2022). The QTL for seed size and pod shattering mainly cluster in two areas of the LGs 1 and 10 in the cowpea (Andargie et al. 2011). RNA-seq data revealed that 4275 differentially expressed genes are related to pod dehiscence and seed development in Lima beans (Garcia et al. 2021). Therefore, pod shattering is genetically related to the seed size. The findings of positive correlation of the pod shattering percentage with the seed protein content, but negative correlation with the seed oil content in present study is an interesting phenomenon, which deserves an in-depth investigation. Besides, the level of shattering in present study is based on a 0–5 scale outlined by AVRDC, without considering the twisting trait. A 0–9 scale classification for shattering has been proposed in common beans (Murgia et al. 2017) and cowpeas (Bijarniya et al. 2024) with twisting involved. Since a very small percentage of twisting pods was found in our study, any future classification for soybean shattering could consider this trait.

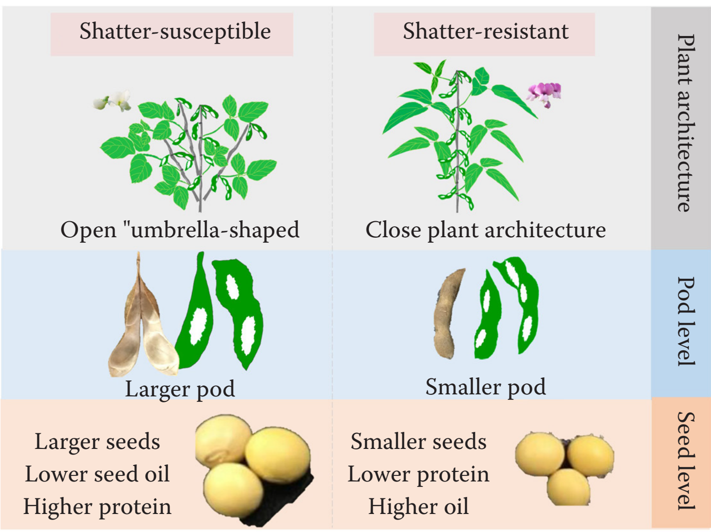

Figure 6. Schematic model of the characteristics of shatter-susceptible and shatter-resistance soybean accessions

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Though no consistent trend of variation in pod shattering was observed among vegetable soybeans, grain soybeans, and small-grain soybeans, we found that the average pod shattering percentage of vegetable soybeans is 7.8 times higher than that of grain soybeans. Therefore, more attention should be paid to pod shattering in vegetable soybeans (Bernard 2001; Nair et al. 2023) rather than grain soybeans and small-grain soybeans. Based on the current results, we suggest that, in order to avoid pod shattering, it is better to select lines with more 2-seeded and 3-seeded pods for vegetable soybeans, while for grain soybeans and small-grain soybeans, the seed oil content and node number on the main stem should be given priority. The resolution of pod shattering could definitely warrant potential seed production, and save the costs.

CONCLUSION

The pod shattering percentage is positively correlated with the productive branches, pod width, pod length, pod area, 100-seed weight, 1-seeded-pod percentage, 2-seeded-pod percentage and seed protein content, but negatively correlated with the plant height, pod height at the bottom, number of nodes on the main stem, 3-seeded-pod percentage, 4-seeded-pod percentage and seed oil content. The pod shattering percentage in vegetable soybeans is 7.8 times higher than that of grain soybeans. The prevalence of pod shattering in vegetable soybeans is related to the "umbrella-shaped" architecture and pod size. More 2-seeded and 3-seeded pods are preferred for vegetable soybeans, while the seed oil content and node number on the main stem should be given priority for grain soybeans and small-grain soybeans, to avoid pod shattering in the future breeding programmes.

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Received September 29, 2024
Accepted January 16, 2025
Published online: February 3, 2025