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# FACTORS AFFECTING POD SHATTERING IN SOYBEAN (*Glycine max*)-A REVIEW

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## ABSTRACT

Soybean is an important crop in the world cultivated for its oil and protein content. It is a significant component of the small holder cropping system and has the potential to become a major crop produced in Africa. However, its productivity is hampered by a number of biotic and abiotic factors. Among the important biotic factors affecting the yield of soybean is pod shattering. Pod shattering is the opening of mature pods along the dorsal or ventral sutures (located along the length of the pod) when the crop matures or during harvesting resulting in seed dispersal. It is a quantitative trait that is influenced by one major gene and a few minor genes and is also highly heritable. It can cause yield losses of up to 100%. Apart from causing yield losses, pod shattering may pose a challenge to the crop rotations in the following seasons as seeds from shattered pods tend to emerge as volunteer weeds. There are a number of factors that are linked to pod shattering. An overview of the morphological, anatomical, environmental and genetic aspects associated with pod shattering in soybean is discussed in this review. Understanding all the factors underlying pod shattering in depth is key in breeding soybean varieties that delay to shatter. This can help breeders in knowing which approach to take in breeding for soybeans with pods that delay to shatter. Breeding strategies can focus on manipulating morphological, biochemical and anatomical traits.

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*Keywords: Pod Shattering, ventral suture, dorsal suture, dehiscence zone, quantitative, heritable.*

## 24 **1. INTRODUCTION**

25

26 Soybean is one of the important crops in the world and is grown primarily for its oil and protein.

27 The seeds of soybean are contained in a pod which is made up of a single seed bearing carpel

28 [1, 2, 3]. It is referred to as the 'golden bean' because of its multiple industrial, nutritional and

29 agricultural uses [4,5]. Soybean accounts for 30% and 70 % of the world's oil and oilseed

30 meals production respectively [6,7]. The growing consumption of soybean food supplements

31 has also led to high demand for soybean production [8]. In sub-Saharan Africa, soybean is an

32 important oil crop and constitutes a significant component of the smallholder cropping system

33 [9]. It is a multi-purpose crop that can help solve the problem of poverty and food insecurity

34 particularly in sub-Saharan Africa [10]. Africa is currently the lowest producer of soybean

35 accounting for 1.2% of the total production in the world [11]. Soybean has the potential to

36 become a major crop produced in Africa [4]. However, its productivity is hampered by a

37 number of biotic and abiotic factors. One of the biotic factors affecting the yield of soybean is

38 pod shattering. While pod shattering is a required trait for the purpose of propagation and

39 continuity in wild species, it is undesirable in cultivated soybean as it makes harvesting difficult

40 [12, 5].

41 Pod shattering is the opening of mature pods along the dorsal or ventral sutures (located along

42 the length of the pod) when the crop matures or during harvesting resulting in seed dispersal

43 [13]. Pod shattering can occur when a pod twists (Figure 1). Two types of pod shattering are

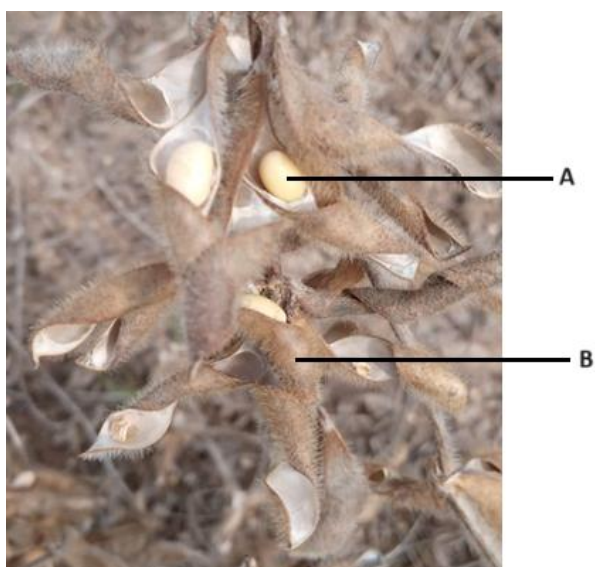
44 known. These are active and passive pod shattering. Active pod shattering occurs when

45 stresses are produced in the drying pods due to an in-built mechanism which usually results

46 in pod shattering with no external disturbance [14]. On the contrary, passive pod shattering

47 does not involve any built-in mechanisms like the development of stresses in the fruit wall. It

48 is as a result of external impact only. Active shattering is common in food legumes.



49  
50 Figure 1: Picture showing soybean plant after physiological maturity. A-seed, B-twisted  
51 soybean pod

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53 Pod shattering is a challenge in agriculture and normally leads to significant yield losses [15,3,  
54 16, 18, 19]. It can cause yield losses of up to 100% [20]. [21] reported a maximum yield loss  
55 of up to 186 kg per hectare. Apart from causing yield losses, pod shattering may pose a  
56 challenge to the crop rotations in the following seasons as seeds from shattered pods tend to  
57 emerge as volunteer weeds [1]. This paper reviews the factors affecting pod shattering, giving  
58 an overview of the morphological, anatomical, environmental and genetic aspects associated  
59 with pod shattering in soyabean.

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### 63 **BASICS OF POD SHATTERING**

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65 Pod shattering soybean genotypes when mature burst open along the dorsal and ventral  
66 sutures dispersing off the seed [22, 13]. The pod of soybean is made up of two valves that are  
67 connected by dorsal and ventral sutures [23, 24]. For pod shattering to occur, there has to be  
68 a physical force that triggers the detachment of cells at the separation layer and this involves  
69 weakening of cell adhesion and tensions provided by the surrounding or external factors [25].  
70 If tension exceeds the binding strength of these valves, then pod shattering occurs. There is  
71 a narrow band of valve margin cells between two vascular bundle valves in the ventral sutures  
72 called the dehiscence zone (DZ) [23] while the fibre cap cells are the junction. Pod shattering  
73 resistant varieties possess several layers of thickened fibre cap cells while shattering

74 susceptible genotypes have less [16]. The DZ is a critical area that is connected to pod  
75 shattering. The DZ of soyabean is equivalent to that of crucifers [26]. In fact pod shattering is  
76 as a result of the loss of adhesion between highly active living cells on either side of the  
77 shattering zone, due to the well-coordinated sequence of biochemical events [27]. It is these  
78 biochemical events which cause the cell wall to breakdown in one or two rows of the cell on  
79 either side of the shattering zone. The following subsections discusses detailed aspects or  
80 factors influencing pod shattering

### 81 **POD MORPHOLOGY**

82 The degree to which the pod shatters is also dependant on pod morphological traits such as  
83 pod length, weight, seed size, number of seeds per pod and pod position. A study conducted  
84 by [14] revealed that the length of a pod, its weight as well as the size of the seed contribute  
85 to pod shattering. A long pod increases the chances of pod shattering. It is assumed that long  
86 pods may have thin pod walls causing the pod to open easily. The pods with high weight and  
87 large seed size can also increase shattering. The higher the number of seeds in a pod, the  
88 higher the chances of shattering [28, 14]. [29] observed that plants which possess few seeds  
89 per pod are more tolerant to pod shattering. [13] reported that genotypes that possess small  
90 pods with less weight of the periphery region and width as well as low seed weight do not  
91 usually shatter. [14] also stated that smaller seed numbers in the pod might decrease the  
92 pressure produced by seeds on the pod wall. Therefore, a few seeds in each pod increases  
93 resistance to pod shattering. [30] reported that pod diameter had a negative correlation with  
94 pod shattering.

95 The pod position has also been found to be associated with pod shattering in soybean. It was  
96 revealed by [31] that a high percentage of shattered pods occurred in the lower parts of the  
97 soybean stems, the middle and lastly the upper part. The results of their study showed that  
98 genotypes that were resistant only had shattered pods in the lower parts of the stem.

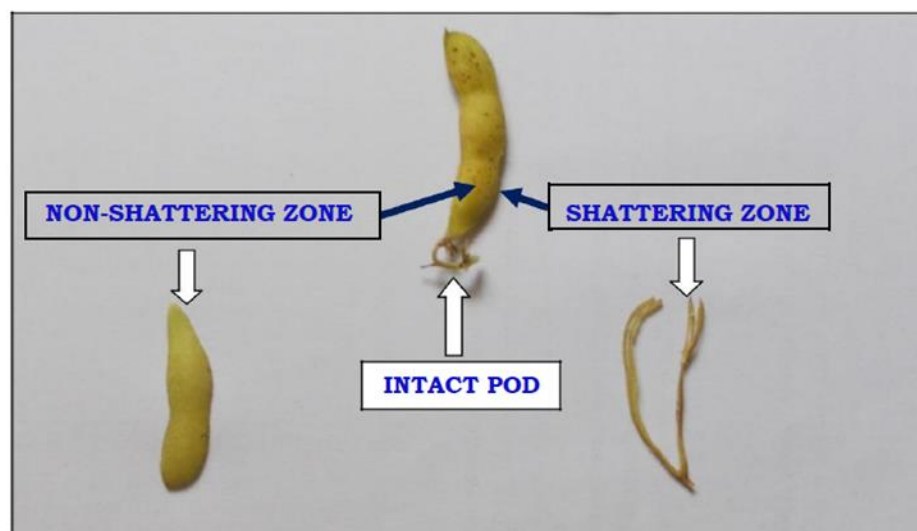
99 Plant height can also have an effect on pod shattering in soybean. [28] reported that taller  
100 plants were likely to be more susceptible to pod shattering than the short plants. This could be  
101 as a result of exposure to environmental factors.

102 It has also been suggested that pod coloration could also be related to pod shattering [49, 50].  
103 Recent research has also revealed that soybean genotypes possessing the *L1* (the classical  
104 locus responsible for black pods in soybean) are more prone to pod shattering. This is due to  
105 the dark pigmentation that increases photothermal efficiency [50]. When exposed to short term  
106 light, the black colored soybean pods undergo a rapid and intense increase in temperature.  
107 This increase in temperature exceeds that of non-black pods when exposed to prolonged light  
108 [50].

### 109 **BIOCHEMICAL FACTORS IN POD SHATTERING**

110 There is a decrease in the pod wall binding strength and the generation of shattering forces  
111 as the pod dries [32]. Before pod shattering occurs, an abscission layer forms at the point  
112 where the pods are attached to the plants [16]. During the shattering process, the entire or a  
113 portion of the cell wall disintegrates due to the biochemical changes. This is as a result of the  
114 elongation of cells in the abscission layer after plasmolysis. Plasmolysis is a typical response  
115 of plant cells exposed to hyperosmotic stress [33]. There is loss of turgor that causes the violet  
116 detachment of the living protoplast from the cell wall. After this, there is a mechanical tearing  
117 of the abscission layer caused by sudden disruption of the cell [16]. Generally, the pods form  
118 abscission layers at the binding sites of its valves thereby accumulating the force to shatter  
119 upon drying, during and after maturation [32]. When this shattering force is more than the  
120 binding strength of the pod walls, the pod shatters and the seed is dispersed. Shattering  
121 usually takes place when the pod walls are dehydrated and the cells in the DZ are separated  
122 [13, 27]. These cells separate along the line of the middle lamella due to the activity of the  
123 enzyme polygalacturonase that degrades the pectin [34]. Polygalacturonases are pectin  
124 depolymerases that hydrolyze alpha-1-4 glycosidic bonds between galacturonic acid residues  
125 of pectin [34].  
126 [26] confirmed the presence of two cell wall carbohydrate hydrolyzing enzymes namely endo-  
127  $\beta$ -1,4-glucanase and endo-PG. At the late stage of maturity, there is a possibility that the  
128 middle lamella disappears due to the build-up of endo-polygalacturonase activity leading to  
129 cell wall modification [26]. It appears as if endo-PG acts jointly with glucanase to make the  
130 primary wall of cells in the DZ weak. The activity of the enzymes decreases when the pods  
131 are approaching senescence most likely due to cell death and proteolytic activities in the DZ.  
132 A study conducted by [27] revealed that the activity of the enzyme polygalacturonase was less  
133 in the non-shattering zone of tolerant varieties and the enzyme activity was found to be vice  
134 versa in susceptible varieties (Figure 2). The increased activity of this enzyme in the shattering  
135 zone of the pod walls for the resistant varieties could be playing a key role in the prevention  
136 of shattering by softening the tissues in the DZ of the pod walls [27].  
137 Another enzyme that is involved in pod shattering is cellulase. In the non-shattering zone of  
138 pod shattering resistant and tolerant varieties, cellulase activities are high while they are low  
139 in the non-shattering zone of susceptible varieties. The activities of cellulase are less in the  
140 shattering zone of the pod walls for pod shattering resistant and tolerant varieties [27]. For the  
141 varieties that are susceptible to pod shattering, the activities of cellulase in the shattering zone  
142 of the pod walls tend to be high. This implies that the increased activity of the enzyme cellulase  
143 in the shattering zone of the varieties that are susceptible to pod shattering could aid in the  
144 breakdown of the tissues in the DZ of the pod wall thereby causing pod shattering [27].

145 Cellulase activity is high in the DZ during the maturity period. Cellulase and PG are highly  
 146 responsive to temperature stress [16].



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 148 Figure 2: Partitioning of soybean pod wall in non-shattering zone (central portion) and  
 149 shattering zone (Peripheral portion). Photo credit: [27].

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151 [26] observed that the tonoplast collapses leading to the loss of inner turgor pressure and  
 152 consequently, the deformation of the cell and the primary cell wall. High lignin content of the  
 153 pod walls also leads to pod shattering [27].

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## 156 **ANATOMICAL STRUCTURES OF THE POD**

157 The anatomical structures of the pod also play a critical role in pod shattering. Legume pods  
 158 including soybean develop a thick sclerenchyma with a bilayer structure on the endocarp [35].  
 159 It is this thick sclerenchyma that causes shattering especially under drought conditions. In  
 160 soybean, the ventral suture plays a key role in pod shattering although it is unclear how the  
 161 anatomy of the ventral sutures control pod shattering [23]. The studies conducted by [23]  
 162 revealed that the ventral sutures of susceptible genotypes had a big vascular bundle area and  
 163 bundle area. They also noted that the shape of the bundle cap cells were even and closely  
 164 arranged with less interstitial substance in susceptible genotypes. An analysis of the pod  
 165 ventral sutures by [23] also revealed that susceptible genotypes had a short and straight route  
 166 from the top of FCC to the connecting point of the two valves (RFCV) whereas resistant  
 167 genotypes had a long and curved route. On the other hand, genotypes with a large vascular  
 168 bundle area (VBA) in the ventral suture DZ were more susceptible compared to the resistant

169 ones which exhibited a small VBA [23]. It was further deduced that the thickness of the pod  
170 wall has a negative correlation with pod shattering [36].

171 To break the pod open on the ventral side, a significant force is needed because the ventral  
172 dehiscence zone doesn't span the mesocarp [26]. It is assumed that the differences in the  
173 anatomy of the ventral sutures may be the cause for the separation of valves from the septum,  
174 thereby regulating pod shattering in soybean. A tension which pulls the sutures from both  
175 sides in a plane perpendicular to that of the fiber axis is created by the wall fiber layers, which  
176 are aligned at an oblique angle through the pod [17]. The pod shatters if the tension due to  
177 the contraction of the wall fibers overcomes the load limit of the dehiscence zone (DZ). In  
178 soybean, the DZ is formed by a narrow band of submarginal cells along the ventral and dorsal  
179 sutures of the pod [3]. The DZ is also made up of a separation layer and a lignified layer [34].  
180 There are several forms of weak cells in the medial portions of pod sutures. These include a  
181 non-lignified abscission layer which stretches into the vascular bundle sheath and a DZ with  
182 cells that do not possess secondary cell wall thickening [17].

183 There are also possibilities that pod shattering resistance could be related to leaf hairness. A  
184 study conducted by [28] suggested that genotypes with leaf pubescence are resistant to pod  
185 shattering while those with glabrous leaf are susceptible. The relationship between leaf hair and  
186 shattering is not clearly understood.

#### 187 **ENVIRONMENTAL FACTORS AFFECTING POD SHATTERING**

188 Environmental conditions under which plants are grown also play a key role in pod shattering  
189 especially after the pod has matured. Previous studies have demonstrated that temperature,  
190 relative humidity (RH) and the moisture content of the pod are highly correlated with pod  
191 shattering [37, 3, 16]. High temperature triggers pod shattering in soybeans. Furthermore, [38]  
192 found that low RH results in severe yield losses when the crop is harvested mechanically. Low  
193 humidity and high precipitation increases pod shattering in soybean [22]. A low RH during  
194 harvesting may lead to a decrease in the moisture content of the pods, this in turn causes high  
195 shattering [14]. It was also reported that low RH, high temperature, rapid temperature changes  
196 coupled with wetting and drying can reduce the pod moisture and may also induce pod  
197 shattering in soybean [22]. The differences in moisture content when the pods are drying  
198 causes contraction between pod wall layers [17]. The moisture equilibrium between the pods  
199 and the atmosphere at a particular RH is the main factor that causes the pod to split [3]. When  
200 RH is low (less than 25%), mature soybean pod shatter.

201 The moisture content of the pod plays a key role in pod shattering [39]. As pods mature, their  
202 moisture content gradually decrease. In soybean, the frequency of shattering tends to increase  
203 as pods lose moisture [40, 3]. Susceptible varieties usually shatter at a moisture content of  
204 10% [37].

205 [17] also pointed out that environmental dryness aggravates pod shattering. Yield losses can  
206 be from 50 – 100% in soybean under arid conditions. Climate change models have predicted  
207 that there will be an increase in aridity. This entails that losses due to pod shattering will  
208 increase especially in dry areas [41]. [42] also reported that shattering susceptibility increases  
209 as the environment gets drier in legumes. Under such conditions, the pod walls tend to shrink  
210 and curl in a vertical plane that is perpendicular to the axis of fibre direction [32]. This curling  
211 causes twisting or spiral coiling of pod walls after shattering because the fibre and pod axes  
212 cross at an angle. [13] found that high temperatures influenced pod shattering at the time of  
213 maturity. Such temperatures enhance the dehydration of the pod wall and the division of the  
214 DZ leading to pod shattering [43]. Drought conditions during pod development can also  
215 increase the risk of pod shattering [44]. Drought during pod development causes weak pod  
216 sutures which are prone to separating especially when the plant is re-wet by rainfall after  
217 maturity.

### 218 **GENES INVOLVED IN POD SHATTERING**

219 Pod shattering is highly heritable and is conditioned by one major gene and a few minor genes  
220 [45]. A complex network of genes and their interactions are known to regulate pod shattering  
221 [12]. A gene known as the *SHAT1-5* in soybean, homologous to *NST1/2* in *Arabidopsis*  
222 *thaliana*, promotes pod wall binding strength [32, 42] and is located on chromosome 16. The  
223 expression of the *SHAT1-5* is localized in the developing FCCs [46]. It is responsible for  
224 activating secondary cell wall biosynthesis and encourages the thickening of fiber cap cells in  
225 pod sutures which are the shattering sites in the pods of soybean [32]. A study conducted by  
226 [47] found that the lignified fibre cap cells (FCC) gives soybean a pod shattering phenotype  
227 and are promoted by the NAC gene *SHAT1-5*. NAC gene is a gene family name derived from  
228 3 transcription factors: NAM (no apical meristem, *Petunia*), ATAF1-2 (*Arabidopsis thaliana*  
229 activating factor) and CUC2 (cup-shaped cotyledon, *Arabidopsis*) that share the same DNA  
230 binding domain [48]. The NAC genes are found in a wide range of plants. The fibre cap cells  
231 in the ventral suture of the pod are involved in pod shattering. The excessive secondary wall  
232 thickening in the FCC could be due to the over expression of the *SHAT1-5* gene which  
233 promotes the excessive deposition of secondary cell walls [47]. Another study conducted by  
234 [23] showed that genotypes that had a short FCC length in soybean were susceptible while  
235 those which had a long FCC were resistant. It was observed that FCC were extremely  
236 thickened in soybean genotypes that showed resistance to pod shattering. Thin FCC only lead  
237 to a weak cohesive force that connects the two valves which may trigger the separation of the  
238 two valves resulting in pod shattering [23] Apart from *SHAT1-5*, *PDH1* is another gene  
239 involved in pod shattering.

240 *PDH1* is a major qualitative trait loci (QTL) responsible for the reduction of pod shattering in  
241 soybean [7, 17] explained that there is a likely wood that *PDH1* and its orthologs have an  
242 indirect role in pod shattering. *PDH1* is known to have an effect on molecular chirality during  
243 lignin synthesis. It is also known that the two valves of a pod consist of opposite chirality, and  
244 that the protein product of *PDH1* guides the production of only one chiral isomer. This makes  
245 it difficult to explain the role of *PDH1* in directly creating both chiralities [17] A study conducted  
246 by [7] found that the *PDH1* gene is strongly associated with temperature and precipitation.  
247 When humidity is low *PDH1* serves as a driving force for pod shattering by causing pod walls  
248 of mature soybeans to coil [32]. *PDH1* is also thought to encourage pod shattering by  
249 influencing the physical properties of the inner sclerenchyma [32]. It is also expressed in the  
250 pod endocarp layer. A study conducted by [32] found that there was an abundance of the  
251 *Pdh1* gene in the pod walls. They found none in the leaves, stems and root tissues and only  
252 traces in the flowers and immature seeds.

253 In this write up, we have so far reviewed that resistance to pod shattering in soybeans is  
254 influenced by *PDH1*, *NST1* and *SHAT1-5*. However, it has been suggested that there are  
255 interactions among *PDH1*, *NST1* and *SHAT1-5* more especially between *PDH1* and *NST1* loci  
256 [12]. It has been suggested that there are epistatic interactions among the three loci controlling  
257 pod shattering especially *PDH1* and *NST1* [34]. *PDH1* and *NST1* homologs are closely related  
258 to each other. A premature stop codon in *NST1* associated with non-shattering was identified  
259 and it is similar to *PDH1*. For *PDH1*, the premature stop codon leading to its malfunction is  
260 near the N terminal of the protein while the *NST1* is close to the C terminal [12]. The premature  
261 stop codon in *NST1* leads to the loss of 47 amino acids out of 446. The conserved NAC domain  
262 at the N terminal remains intact.

263 [19] also identified another QTL *qPS-DS16-1* (*Glyma.16g076600*) which is thought to play a  
264 role in pod shattering basing on its expression pattern. It is a member of the CYP707A family  
265 and could be involved in the catabolism of ABA. This ABA is a hormone that is involved in  
266 several physiological functions among which is pod shattering [19].

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## 269 **CONCLUSION**

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271 Although pod shattering is genetically controlled, it is also influenced by other factors such as  
272 morphological, anatomical, biochemical and environmental. The morphological traits of a plant  
273 such as pod structure, vascular bundle size and structure can influence pod shattering.  
274 Understanding all the factors underlying pod shattering in depth is key in breeding soybean  
275 varieties that delay to shatter. This can help breeders in knowing which approach to take in

276 breeding for soybeans with pods that delay to shatter. Breeding Programs can focus on  
277 manipulating morphological, biochemical and anatomical traits.  
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