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A Review of Factors Affecting Pod Shattering in Soybean (*Glycine max*)

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Authors' contributions

This work was carried out in collaboration among all authors. Author VN Conceptualized the study and prepared the original draft. Author LT reviewed and edited the manuscript. Author GC supervised the study and proof read the manuscript. Author MOA supervised the study. All authors read and approved the final manuscript.

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Review Article

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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

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cause yield losses of up to100%. 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.

Keywords: Dehiscence zone; dorsal suture; heritable; pod shattering; quantitative; ventral suture.

1. INTRODUCTION

Soybean is one of the important crops in the world and is grown primarily for its oil and protein. The seeds of soybean are contained in a pod which is made up of a single seed bearing carpel [1-3]. It is referred to as the ‘golden bean’ because of its multiple industrial, nutritional and agricultural uses [4,5]. Soybean accounts for 30% and 70 % of the world’s oil and oilseed meals production respectively [6,7]. The growing consumption of soybean food supplements has also led to high demand for soybean production [8]. In sub-Saharan Africa, soybean is an important oil crop and constitutes a significant component of the smallholder cropping system [9]. It is a multi-purpose crop that can help solve the problem of poverty and food insecurity particularly in sub-Saharan Africa [10]. The top five soybean producing countries are Brazil, United States, Argentina, China and India with each producing at-least 12 metric tonnes per hectare [11]. Africa is currently the lowest producer of soybean accounting for 1.2% of the total production in the world [12]. Soybean has the potential to become a major crop produced in Africa [4]. However, its productivity is hampered by a number of biotic and abiotic factors. One of the biotic factors affecting the yield of soybean is pod shattering. While pod shattering is a required trait for the purpose of propagation and continuity in wild species, it is undesirable in cultivated soybean as it makes harvesting difficult [13,5].

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 [14]. Pod shattering can occur when a pod twists (Fig. 1). Two types of pod shattering are known. These are active and passive pod shattering. Active pod shattering occurs when stresses are produced in the drying pods due to an in-built mechanism which usually results in pod shattering with no external disturbance [15]. On the contrary, passive pod shattering does not involve any built-in mechanisms like the development of stresses in the fruit wall. It is as a result of external impact only. Active shattering is common in food legumes.

Fig. 1. Image of a soybean plant after physiological maturity: A depicts a mature seed, B depicts a twisted pod

Pod shattering is a challenge in agriculture and normally leads to significant yield losses [16,3,17, 18-20]. It can cause yield losses of up to 100% [21]. [22] reported a maximum yield loss of up to 186 kg per hectare. 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 [1]. This paper reviews the factors affecting pod shattering, giving an overview of the morphological, anatomical, environmental and genetic aspects associated with pod shattering in soyabean.

2. BASICS OF POD SHATTERING

Pod shattering soybean genotypes when mature burst open along the dorsal and ventral sutures dispersing off the seed [23,14]. The pod of soybean is made up of two valves that are connected by dorsal and ventral sutures [24,25]. For pod shattering to occur, there has to be a physical force that triggers the detachment of cells at the separation layer and this involves weakening of cell adhesion and tensions provided by the surrounding or external factors [26]. If tension exceeds the binding strength of these valves, then pod shattering occurs. There is a narrow band of valve margin cells between two vascular bundle valves in the ventral sutures called the dehiscence zone (DZ) [24] while the fibre cap cells are the junction. Pod shattering resistant varieties possess several layers of thickened fibre cap cells while shattering susceptible genotypes have less [17]. The DZ is a critical area that is connected to pod shattering. The DZ of soybean is equivalent to that of crucifers [27]. In fact, pod shattering is as a result of the loss of adhesion between highly active living cells on either side of the shattering zone, due to the well-coordinated sequence of biochemical events [28]. It is these biochemical events which cause the cell wall to breakdown in one or two rows of the cell on either side of the shattering zone. The following subsections discusses detailed aspects or factors influencing pod shattering.

2.1 Pod Morphology

The degree to which the pod shatters is also dependent on pod morphological traits such as pod length, weight, seed size, number of seeds per pod and pod position. A study conducted by Krisnawati et al. [15] revealed that the length of a pod, its weight as well as the size of the seed contribute to pod shattering. A long pod increases the chances of pod shattering. It is assumed that long pods may have thin pod walls causing the pod to open easily. The pods with high weight and large seed size can also increase shattering. The higher the number of seeds in a pod, the higher the chances of shattering [29,15]. Kataliko et al. [30] observed that plants which possess few seeds per pod are more tolerant to pod shattering. Bara et al. [14] reported that genotypes that possess small pods with less weight of the periphery region and width as well as low seed weight do not usually shatter. Krisnawati et al. [15] also stated that smaller seed numbers in the pod might decrease the pressure produced by seeds on the pod wall. Therefore, a few seeds in each pod increases resistance to pod shattering. Adeyeye et al. [31] reported that pod diameter had a negative correlation with pod shattering.

The pod position has also been found to be associated with pod shattering in soybean. It was revealed by Krisnawati et al. [32] that a high percentage of shattered pods occurred in the lower parts of the soybean stems, the middle and lastly the upper part. The results of their study showed that genotypes that were resistant only had shattered pods in the lower parts of the stem. Plant height can also have an effect on pod shattering in soybean. Fatima et al. [29] reported that taller plants were likely to be more susceptible to pod shattering than the short plants. This could be as a result of exposure to environmental factors.

It has also been suggested that pod coloration could also be related to pod shattering [33,34]. Recent research has also revealed that soybean genotypes possessing the *L1* (the classical locus responsible for black pods in soybean) are more prone to pod shattering. This is due to the dark pigmentation that increases photothermal efficiency [34]. When exposed to short term light, the black colored soybean pods undergo a rapid and intense increase in temperature. This increase in temperature exceeds that of non-black pods when exposed to prolonged light [34].

2.2 Biochemical Factors in Pod Shattering

There is a decrease in the pod wall binding strength and the generation of shattering forces as the pod dries [35]. Before pod shattering occurs, an abscission layer forms at the point where the pods are attached to the plants

[17]. During the shattering process, the entire or a portion of the cell wall disintegrates due to the biochemical changes. This is as a result of the elongation of cells in the abscission layer after plasmolysis. Plasmolysis is a typical response of plant cells exposed to hyperosmotic stress [36]. There is loss of turgor that causes the violet detachment of the living protoplast from the cell wall. After this, there is a mechanical tearing of the abscission layer caused by sudden disruption of the cell [17]. Generally, the pods form abscission layers at the binding sites of its valves thereby accumulating the force to shatter upon drying, during and after maturation [35]. When this shattering force is more than the binding strength of the pod walls, the pod shatters and the seed is dispersed. Shattering usually takes place when the pod walls are dehydrated and the cells in the DZ are separated [14,28]. These cells separate along the line of the middle lamella due to the activity of the enzyme polygalacturonase that degrades the pectin [37]. Polygalacturonases are pectin depolymerases that hydrolyze alpha-1-4 glycosidic bonds between galacturonic acid residues of pectin [37].

Christiansen et al. [27] confirmed the presence of two cell wall carbohydrate hydrolyzing enzymes namely endo- β-1,4-glucanase and endo-PG. At the late stage of maturity, there is a possibility that the middle lamella disappears due to the build-up of endo-polygalacturonase activity leading to cell wall modification [27]. It appears as if endo-PG acts jointly with glucanase to make the primary wall of cells in the DZ weak. The activity of the enzymes decreases when the pods are approaching senescence most likely due to cell death and proteolytic activities in the DZ. A study conducted by Gaikwad et al. [28] revealed that the activity of the enzyme polygalacturonase was less in the non-shattering zone of tolerant varieties and the enzyme activity was found to be vice versa in susceptible varieties (Fig. 2). The increased activity of this enzyme in the shattering zone of the pod walls for the resistant varieties could be playing a key role in the prevention of shattering by softening the tissues in the DZ of the pod walls [28].

Another enzyme that is involved in pod shattering is cellulase. In the non-shattering zone of pod shattering resistant and tolerant varieties, cellulase activities are high while they are low in the non-shattering zone of susceptible varieties. The activities of cellulase are less in the shattering zone of the pod walls for pod shattering resistant and tolerant varieties [28]. For the varieties that are susceptible to pod shattering, the activities of cellulase in the shattering zone of the pod walls tend to be high. This implies that the increased activity of the enzyme cellulase in the shattering zone of the varieties that are susceptible to pod shattering could aid in the breakdown of the tissues in the DZ of the pod wall thereby causing pod shattering [28]. Cellulase activity is high in the DZ during the maturity period. Cellulase and PG are highly responsive to temperature stress [17].

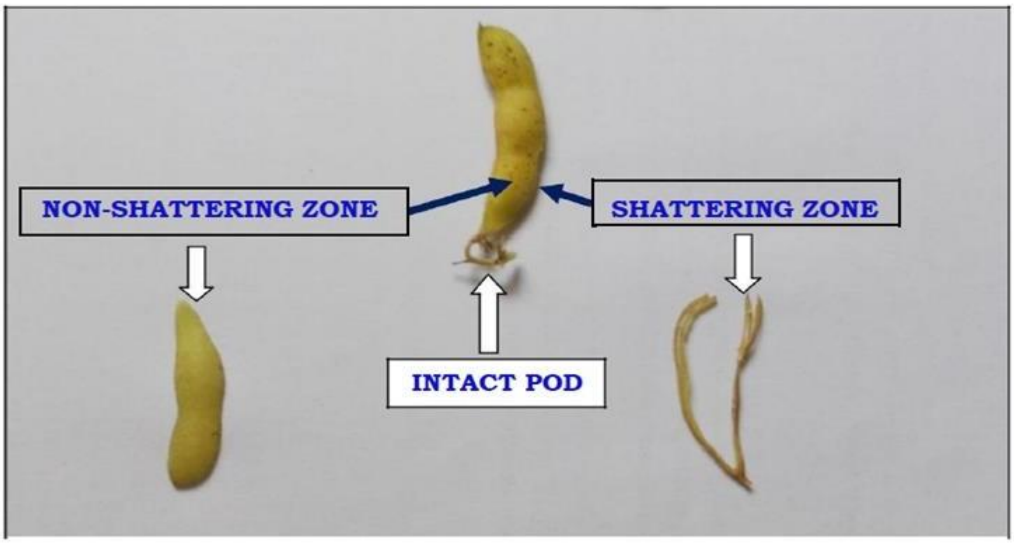

Fig. 2. Image of soybean pod showing non-shattering zone (central portion) and shattering zone (Peripheral portion). Photo credit: [27]

Christiansen et al. [27] observed that the tonoplast collapses leading to the loss of inner turgor pressure and consequently, the deformation of the cell and the primary cell wall. High lignin content of the pod walls also leads to pod shattering [28]. This mechanism is also common in other legumes such as common vetch [28 Dong].

2.3 Anatomical Structures of the Pod

The anatomical structures of the pod also play a critical role in pod shattering. Legume pods including soybean develop a thick sclerenchyma with a bilayer structure on the endocarp [38]. It is this thick sclerenchyma that causes shattering especially under drought conditions. In soybean, the ventral suture plays a key role in pod shattering although it is unclear how the anatomy of the ventral sutures control pod shattering [24]. The studies conducted by Tu et al. [24] revealed that the ventral sutures of susceptible genotypes had a big vascular bundle area and bundle area. They also noted that the shape of the bundle cap cells were even and closely arranged with less interstitial substance in susceptible genotypes. An analysis of the pod ventral sutures by Tu et al. [24] also revealed that susceptible genotypes had a short and straight route from the top of FCC to the connecting point of the two valves (RFCV) whereas resistant genotypes had a long and curved route. On the other hand, genotypes with a large vascular bundle area (VBA) in the ventral suture DZ were more susceptible compared to the resistant ones which exhibited a small VBA [24]. It was further deduced that the thickness of the pod wall has a negative correlation with pod shattering [39].

To break the pod open on the ventral side, a significant force is needed because the ventral dehiscence zone doesn’t scan the mesocarp [27]. It is assumed that the differences in the anatomy of the ventral sutures may be the cause for the separation of valves from the septum, thereby regulating pod shattering in soybean. A tension which pulls the sutures from both sides in a plane perpendicular to that of the fiber axis is created by the wall fiber layers, which are aligned at an oblique angle through the pod [18]. The pod shatters if the tension due to the contraction of the wall fibers overcomes the load limit of the dehiscence zone (DZ). In soybean, the DZ is formed by a narrow band of submarginal cells along the ventral and dorsal sutures of the pod [3]. The DZ is also made up of a separation layer and a lignified layer [37]. There are several forms of weak cells in the medial portions of pod sutures. These include a non-lignified abscission layer which stretches into the vascular bundle sheath and a DZ with cells that do not possess secondary cell wall thickening [18].

There are also possibilities that pod shattering resistance could be related to leaf hairness. A study conducted by Fatima et al. [29] suggested that genotypes with leaf pubsence are resistant to pod shattering while those with glarous leaf are susceptible. The relationship between leaf hair and shattering is not clearly understood.

2.4 Environmental Factors Affecting Pod Shattering

Environmental conditions under which plants are grown also play a key role in pod shattering especially after the pod has matured. Previous studies have demonstrated that temperature, relative humidity (RH) and the moisture content of the pod are highly correlated with pod shattering [40,3,17]. High temperature triggers pod shattering in soybeans. Furthermore, [41] found that low RH results in severe yield losses when the crop is harvested mechanically. Low humidity and high precipitation increases pod shattering in soybean [23]. A low RH during harvesting may lead to a decrease in the moisture content of the pods, this in turn causes high shattering [15]. It was also reported that low RH, high temperature, rapid temperature changes coupled with wetting and drying can reduce the pod moisture and may also induce pod shattering in soybean [23]. The differences in moisture content when the pods are drying causes contraction between pod wall layers [18]. The moisture equilibrium between the pods and the atmosphere at a particular RH is the main factor that causes the pod to split [3]. When RH is low (less than 25%), mature soybean pod shatter.

The moisture content of the pod plays a key role in pod shattering [42]. As pods mature, their moisture content gradually decrease. In soybean, the frequency of shattering tends to increase as pods lose moisture [43,3]. Susceptible varieties usually shatter at a moisture content of 10% [40].

Parker et al. [18,44] also pointed out that environmental dryness aggravates pod shattering. Yield losses can be from 50 – 100% in soybean under arid conditions. Climate change models have predicted that there will be an increase in aridity. This entails that losses due to pod shattering will increase especially in dry areas [45,]. [46] also reported that shattering susceptibility increases as the environment gets drier in legumes. Under such conditions, the pod walls tend to shrink and curl in a vertical plane that is perpendicular to the axis of fibre direction [35]. This curling causes twisting or spiral coiling of pod walls after shattering because the fibre and pod axes cross at an angle. [14] found that high temperatures influenced pod shattering at the time of maturity. Such temperatures enhance the dehydration of the pod wall and the division of the DZ leading to pod shattering [47]. Drought conditions during pod development can also increase the risk of pod shattering [48]. Drought during pod development causes weak pod sutures which are prone to separating especially when the plant is re-wet by rainfall after maturity.

2.5 Genes Involved in Pod Shattering

Pod shattering is highly heritable and is conditioned by one major gene and a few minor genes Liu et al. [49]. A complex network of genes and their interactions are known to regulate pod shattering [13]. A gene known as the *SHAT1-5* in soybean, homologous to *NST1/2* in *Arabidopsis thaliana*, promotes pod wall binding strength [35,46] and is located on chromosome 16. The expression of the *SHAT1-5* is localized in the developing FCCs [50]. It is responsible for activating secondary cell wall biosynthesis and encourages the thickening of fiber cap cells in pod sutures which are the shattering sites in the pods of soybean [35]. A study conducted by Dong et al. [51] found that the lignified fibre cap cells (FCC) gives soybean a pod shattering phenotype and are promoted by the NAC gene *SHAT*1-5. NAC gene is a gene family name derived from 3 transcription factors: NAM (no apical meristem, Petunia), ATAF1-2 (*Arabidopsis thaliana* activing factor) and CUC2 (cup-shaped cotyledon, Arabidopsis) that share the same DNA binding domain [52]. The *NAC* genes are found in a wide range of plants. The fibre cap cells in the ventral suture of the pod are involved in pod shattering. The excessive secondary wall thickening in the FCC could be due to the over expression of the *SHAT1-5* gene which promotes the excessive deposition of secondary cell walls [51]. Another study conducted by Tu et al. [24] showed that genotypes that had a short FCC length in soybean were susceptible while those which had a long FFC were resistant. It was observed that FCC were extremely thickened in soybean genotypes that showed resistance to pod shattering. Thin FCC only lead to a weak cohesive force that connects the two valves which may trigger the separation of the two valves resulting in pod shattering [24] Apart from SHAT1- 5, *PDH1* is another gene involved in pod shattering.

PDH1 is a major qualitative trait loci (QTL) responsible for the reduction of pod shattering in soybean [7,18] explained that there is a likely wood that *PDH1* and its orthologs have an indirect role in pod shattering. *PDH1* is known to have an effect on molecular chirality during lignin synthesis. It is also known that the two valves of a pod consist of opposite chirality, and that the protein product of *PDH1* guides the production of only one chiral isomer. This makes it difficult to explain the role of *PDH1* in directly creating both chiralities [18]. A study conducted by Bandillo et al. [7] found that the *PDH1* gene is strongly associated with temperature and precipitation. When humidity is low *PDH1* serves as a driving force for pod shattering by causing pod walls of mature soybeans to coil [35]. *PDH1* is also thought to encourage pod shattering by influencing the physical properties of the inner sclerenchyma [35]. It is also expressed in the pod endocarp layer. A study conducted by Funatsuki et al. [35] found that there was an abundance of the *Pdh1* gene in the pod walls. They found none in the leaves, stems and root tissues and only traces in the flowers and immature seeds.

In this write up, we have so far reviewed that resistance to pod shattering in soybeans is influenced by *PDH1, NST1* and *SHAT1-5*. However, it has been suggested that there are interactions among *PDH1, NST1* and *SHAT1-5* more especially between *PDH1* and *NST1* loci [13]. It has been suggested that there are epistatic interactions among the three loci controlling pod shattering especially *PDH1* and *NST1* [37]. *PDH1* and *NST1* homologs are closely related to each other. A premature stop codon in *NST1* associated with non-shattering was identified and it is similar to *PDH1*. For *PDH1*, the premature stop codon leading to its malfunction is near the N terminal of the protein while the *NST1* is close to the C terminal [13]. The premature stop codon in *NST1* leads to the loss of 47 amino acids out of 446. The conserved NAC domain at the N terminal remains intact.

Seo et al. [20] also identified another QTL *qPS-DS16-1* (*Glyma.16g076600*) which is thought to play a role in pod shattering basing on its expression pattern. It is a member of the CYP707A family and could be involved in the catabolism of ABA. This ABA is a hormone that is involved in several physiological functions among which is pod shattering [20].

3. CONCLUSION

Pod shattering is highly heritable and is conditioned by one major gene and a few minor genes. It is genetically controlled and this influences morphological, anatomical and biochemical factors. In addition to genetics, environmental factors also play a role. The morphological traits of a plant such as pod structure, vascular bundle size and structure can influence pod shattering. In addition, pod morphological traits such as pod length, weight, seed size, number of seeds per pod and pod position can have an effect on the degree to which the pod shatters. The anatomical structures of the pod also play a critical role in pod shattering. In soybean, the ventral suture plays a key role in pod shattering although it is unclear how the anatomy of the ventral sutures control pod shattering. Environmental conditions under which plants are grown also play a key role in pod shattering especially after the pod has matured. Temperature, relative humidity (RH) and the moisture content of the pod are highly correlated with pod shattering. A low RH during harvesting may lead to a decrease in the moisture content of the pods, this in turn causes high shattering. The moisture equilibrium between the pods and the atmosphere at a particular RH is the main factor that causes the pod to split. When RH is low (less than 25%), mature soybean pods shatter. 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 Programs can focus on manipulating morphological, biochemical and anatomical traits.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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