GENETIC ANALYSIS OF RESISTANCE TO POD SHATTERING IN SOYBEAN (*Glycine max*. (L) Merrill).

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A THESIS SUBMITTED TO

THE DEPARTMENT OF CROP AND SOIL SCIENCES, FACULTY OF

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RESOURCES, KWAME NKRUMAH UNIVERSITY OF SCIENCE AND

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(PLANT BREEDING OPTION)

HARUNA MOHAMMED

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DEDICATION

I dedicate the work to Allah, the Most High, and my late father, who left me for eternity during the course of study, my cherished wife and my children (Ilham and Fawzu).

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DECLARATION

I hereby declare that this thesis has not been submitted for degree to any other university and that it is entirely my own work and all help has duly been acknowledged.

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STUDENT

HARUNA MOHAMMED Date

…… ……..

SUPERVISOR

DR. RICHARD AKROMAH Date

…… …….

NYANSAPƆ WƆSANE NO BADWENMA

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ABSTRACT

Genetic analysis of resistance to pod shattering was undertaken on three soybean crosses with reciprocals involving resistant and susceptible varieties to examine broad sense (h^2_{bs}) and narrow sense (h^2_{ns}) heritability, minimum number of genes involved (MNG), mid-parent heterosis (MPH), cytoplasmic inheritance and allelic relationship between shattering and non-shattering. Two sets of experiments were conducted. The first experiment was a non-replicated crossing block in plastic pots to develop F_1 populations at the plant house of the Faculty of Agriculture – Kwame Nkrumah University of Science and Technology, Kumasi (*Latitude 06º 41′ N and longitude 01º 33′ W*). F_1 plants were selfed to produce F_2 generations. The F_1 progenies were backcrossed to both parents to produce BC_1 and BC_2 progenies. The second experiment was a replicated trial laid in a randomized complete block with three replications to determine genetic ratios for levels of pod shattering resistance at F_2 and this was used to determine allelic relationship between shattering and nonshattering genes using chi-square test. Mean h^2_{bs} was 0.30 (range 0.00 – 0.90) and mean h^2_{ns} was 0.92 (range 0.00 – 1.72) indicating the importance of both additive and non additive variances, suggesting that improvement in resistance can be achieved through breeding. Mean MNG was two genes (range 1 – 3) indicating that genes for resistance differed among parental lines. Mean MPH was -3.7% (range -44.1 – 55.7%) indicating that heterosis did not influence the expression of resistance to pod shattering in soybean. There was no difference between the mean of any F_1 population and it‟s reciprocal, indicating lack of maternal influence and that the character could be under nuclear gene control. Observed ratios at F_2 population revealed that, inheritance of

resistance to pod shattering is quantitative and under the influence of either duplicate recessive or dominant and recessive epistasis depending on the parental genotypes used in the cross.

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CHARPTER ONE

1.0 INTRODUCTION

Though a recent introduction into the cropping systems of Ghana, soybean is rapidly expanding partly due to its high nutritional value as food for both humans and livestock and as an important industrial crop. The major areas of soybean production were restricted to temperate regions until the mid-1940s, when the area of production started to expand to tropical and sub-tropical regions (Franca Neto and Henning, 1994). These new production areas are characterised by warmer and more humid conditions, which pose different production problems such as pod shattering and reduced seed viability (Franca Neto and Henning, 1994), pests and diseases.

Pod shattering is the opening of pods along both the dorsal and ventral sutures of the soybean pod. Fully mature pods of soybean are extremely sensitive to opening, resulting in seed loss. This can take place in susceptible varieties prior to harvest due to disturbance of the canopy by wind or during harvesting as the harvesting equipment moves through the crop during dry weather conditions, leading to seed losses of 50-100% (IITA, 1986). Though this trait is important for the adaptation of the wild species to natural environments as a mechanism for seed dispersal, it leads to a significant yield loss in soybean production, if found in cultivated forms. This loss of seed not only has a drastic effect on yield but also results in the emergence of the crop as a weed in the subsequent growing season. In the transition and Guinea Savanna zones of Ghana where the bulk of soybean production takes place, the crop matures at the end of October or early November, for varieties currently in the system. Coincidentally, this is the time that the rains cease and the dry harmattan winds begin

to set in, with the attendant low relative humidity and rising temperatures creating perfect conditions for pod shattering.

Pod shattering is a specific characteristic observed not only in soybean but also in *Brassica species* (Meaken and Roberts, 1990; Child *et al.*, 2003), sesame (Langham and Wiemers, 2002), other pulse crops (Weeden *et al.*, 2002) and birdsfoot trefoil (*Lotus cormiculatus.* L.) (Metcalfe *et al*., 1957. Grant, 1996). Shattering takes place following dehydration of the pod wall and separation of the cells in a dehiscence zone, situated in sutures between the lignified pod wall edge and a replum containing vascular tissue (Picart and Morgan, 1984). The dehiscence zone cells separate along the line of the middle lamella, following degradation of pectin by *polygalacturonase* and subsequent breakdown of the dehiscence zone cell walls (Petersen et al., 1996). The pods open because of the application of external forces supplied by contact with other pods, racemes or harvesting machinery, which pass across the dehiscence zone from pod wall to the replum (Petersen *et al*., 1996).

Pod shattering in soybean can be controlled by several strategies. In Japan, timely planting is done so that, seeds are generally harvested in cool and humid seasons, which have masked the problem of pod dehiscence (Funatsuki *et al.*, 2008). It may be possible to increase the resistance to pod shattering by delaying or stopping the breakdown of the dehiscence layer by manipulating the enzymes responsible (Jenkins et al., 1996). It may also be possible to achieve this by increasing the size or number of vascular strands within the dehiscence zone, increasing the area of the dehiscence zone or modifying pod wall thickness to reduce the mechanical effects of desiccation (Morgan *et al.*, 1998). Among the available control options, genetic improvement, by

introducing resistance genes from related species into susceptible cultivars is usually more effective, less costly, not subject to environmental conditions and easier for growers to implement. However, this is both time consuming and laborious. The hybridisation strategy also has to cope with transferring two or more genes, which are recessive in action into each of the breeding lines. Indeed, different genetic backgrounds have revealed different number of genes to be important in shatter resistance (Caviness, 1963; Carpenter and Fehr, 1986; Tukamuhabwa *et al*, 2000). This has necessitated breeders performing testcrosses at each generation during the attempt to produce elite material since the shattering resistance behaves as a partially recessive trait (Tsuchiya, 1986, 1987, Tukamuhabwa et al, 2002). These difficulties have been compounded by the fact that shattering is a difficult and time-consuming trait to assess in the field because field assessments, based on visual observation and handling, are subjective and depend

greatly on the maturity and moisture state of the crop. (Morgan *et al.*, 1998).

Research work in Ghana on resistance to pod shattering in soybean is scanty. The Savanna Agricultural Research Institute (SARI) in collaboration with the International Institute of Tropical Agriculture (IITA) made advances in this direction by developing two soybean varieties with different levels of resistance to pod shattering (SARI, 2003). This was done through varietal screening without

investigating the genetics of the trait. Information on the inheritance of the trait using locally adapted varieties will contribute to breeding effort aimed at developing resistant varieties that are acceptable to producers. This is important since basically, it

is from the knowledge of its genetic behavior that the breeding procedures for the trait can be devised.

In addition, significant effect of genotype by environment (G X E) interaction on pod shattering in soybean have been reported by Akpan (1988), Bailey *et al*. (1997) and Tukamuhabwa (2000). Thus, varieties which are resistant in other parts of the world may succumb to pod shattering when they are introduced into new areas. Such environmental effects could be the explanation for the prevalence of pod shattering varieties in the tropics. Breeding for shattering resistance in soybean should therefore be carried out in specific production areas since different varieties respond differently depending on location.

1.1 Problem Statement

Pod dehiscence (shattering) is a major production constraint in the soybean production areas of the warm tropics. Seed losses of 50–100% are often associated with pod shattering during dry weather conditions in susceptible varieties when harvesting is delayed after maturity (IITA, 1986). This loss of seed not only has a drastic effect on yield but also results in the emergence of the crop as a weed in the subsequent growing season. In addition, shattering losses diminishes yield potential that has already been achieved.

1.2 Justification

A survey conducted by Sanginga *et al*. (1999) in Benue state, Nigeria, revealed that, resistance to pod shattering was a pre-requisite for adoption of any variety by the farming communities, indicating that resistant varieties that can stand in the field for relatively longer periods after maturity without shattering must be developed. Among the several methods of controlling shattering in soybean, genetic improvement, by introducing genes from within and between related species through hybridisation is the most reliable and environmentally friendly method. Information on the inheritance of the trait using locally adapted varieties will enhance breeding effort aimed at developing resistant varieties that are acceptable to producers. However, due to the highly significant influence of environmental factors reported on the expression of the trait, it is important that, breeding for shattering resistance be carried out in specific production areas since different varieties respond differently depending on location. This research work was therefore, conducted to investigate the genetic basis of resistance to shattering in locally adapted soybean varieties.

1.3 Hypothesis

Hypotheses tested were that, resistance to pod shattering is dominant to susceptibility and that resistance is controlled by polygenes, is under the influence of environmental factors and not easily transferable.

1.4 Objective(s)

The major objective of the study was to investigate the inheritance of resistance to pod shattering in soybean, with the view of establishing its genetic basis.

1.5 Specific Objectives

1. Determine the number of genes controlling shattering resistance in soybean.
2. Determine the allelic relationship between shattering and non-shattering in these varieties.
3. Determine the heritability of shattering resistance in crosses involving these varieties.

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CHARPTER TWO

2.0 LITERATURE REVIEW

2.1 Origin and Systematics of Soybean

The origin of the soybean plant is obscure, but many botanists believe it is derived from *Glycine ussuriensis*, a legume native to Central China (Soybean encyclopedia, 2008). According to the ancient Chinese, in 2853 BC the legendary Emperor Shen Nung of China named five sacred plants – soybeans, rice, wheat, barley, and millet. (History of Soybeans. 2008). According to other sources, the earliest preserved soybeans were unearthed from archaeological sites in Korea (Crawford, 2006). Taxonomically, the soybean is classified in the genus *Glycine* which contains two subgenera; *Glycine* and *Soja*. Seven wild perennial species are grouped in the subgenus *Glycine* whereas two species, a wild annual species (*G. soja*) and a cultivated annual species (*G. max*) are grouped in the subgenus *Soja* (Hymowitz, 1995).The cultivated species (*G. max*) has never been found growing in the wild. It is therefore, believed that it"s most probable progenitor is *G. soja* (Hymowitz and Newel, 1981).

The most commonly reported chromosome number of the genus including that of the cultivated species is 2n=2x=40. (Hymowitz and Newel, 1981). Interspecific hybridization among the species of the genus *Glycine* have been difficult but normal F_1 plants were observed in crosses between the wild annual species *G. soja* and the cultivated annual species *G. max* (Poehlman, 1986).

2.2 The Mechanism of Shattering

Pod shattering refers to the opening of mature pods along the dorsal or ventral sutures and dispersal of seed as the crop reaches maturity, as well as during harvesting. The extent of yield loss due to pod shattering in soybean [Glycine max (L.) Merrill] may range from 34 to 99 percent depending upon delayed harvesting after maturity, the environmental conditions during harvesting and genotype (Tiwari and Bhatnagar, 1991). The development of an ideotype which describes a crop more resistant to seed loss at harvest and maintains high performance agronomically depends upon the identification of many architectural characters (Thurling, 1991). These will include morphological characteristics of the whole plant and raceme as well as those of single pods and how individual characters relate with each other. Within the crop canopy, before and during harvest, much pod shattering occurs because of the natural movement of the canopy which results in pods knocking against each other or against the stems and branches. This problem of mechanical damage is likely to be much affected by other plant attributes such as pod angles, pod length and width (Loof and Jonson, 1970; Thompson and Hughes, 1986). Together with other aspects of plant architecture such as height and stem stiffness, these attributes may affect the laxness of the plant and hence the degree and type of movement made by the canopy and of branches within it (Loof and Jonson, 1970; Thompson and Hughes, 1986). With majority of agriculture operations depending on human labour, the untimely and delayed harvesting result in increased pod

shattering.

Pod shattering is aggravated if there is rain followed by dry weather, low humidity, high temperature, rapid temperature changes, wetting and drying (Agrawal, *et al.*,

2002). Among the causes mentioned above, the genotype of the variety plays an important role on the overall expression of pod shattering.

Shattering takes place following dehydration of the pod wall and separation of the cells in a dehiscence zone which is situated in sutures between the lignified pod wall edge and a replum containing vascular tissue (Picart and Morgan, 1984). The dehiscence zone cells separate along the line of the middle lamella, following degradation of the pectin by polygalacturonase (Petersen *et al.,* 1996) and subsequent breakdown of the dehiscence zone cell walls. The pods open as a result of the application of external forces supplied by contact with other pods, racemes or harvesting machinery which severs the vascular connections which pass across the dehiscence zone from pod wall to the replum.

Agrawal, *et al.* (2003) reported that segregation of pod shattering was highly complex in F_2 generation and showed quantitative response in the cross of susceptible and resistant varieties and concluded that success of any conventional breeding program aimed at pod shattering resistance depends upon the desirable segregates. Increased shatter resistance will promote natural maturing of uniformly ripe seeds with improved oil extraction characteristics. Production costs, efficiency of seed recovery and quality of oil would all be improved by increased shatter resistance (Morgan *et al.*, 1998).

2.3 Various Techniques of Assessing Pod Shattering in Soybean

Assessments by breeders of susceptibility to pod shattering between lines had to rely mainly upon visual observations of the crop in the field or upon hand tests of pods

(Bruce *et al*., 2002). However, a test procedure has been devised that exposes pods to random impacts in a similar manner to those that occur in the crop canopy during harvest (Bruce *et al*., 2002). This random impact test (RIT) enables the rapid comparison of susceptibility to shattering in samples of fully mature pods from individual plants. There are four types of assessing methods for pod shattering.

These are; field-screening method (Caviness 1963, Tiwari and Bhatnagar, 1993; Helmes, 1994) which relies on visual observation in the field, the desiccator method (Metcalfe *et al.*, 1957; Caviness, 1965) where pods are subjected to desiccation inside a desiccator, the oven-dry method (Tsuchiya and Sunada, 1977; Tiwari and Bhatnagar, 1997, Tukamuhabwa *et al*, 2002) where pods are subjected to ovendrying for a specified period and the mechanical cracking method (Kwon *et al.*, 1991; Davies and Bruce , 1997; Morgan *et al.*, 2000; Timothy *et al.*, 2003) is a laboratory procedure used to test individual pods for resistance to shattering and to measure the mechanical properties of the pod during shattering .

2.4 Cultivar Differences in Pod Shattering

Varietal differences in pod shattering was observed by Tiwari and Bhatia (1995), when they studied the pod anatomical structures associated with resistance to pod shattering in sixteen soybean varieties. Varieties susceptible to pod shattering were observed to possess clefts in the tissues above the inner sclerenchyma, especially below the bundles but no such clefts were observed in resistant varieties.

Anatomical structures of the pod, chemical composition of the pod wall and environmental conditions at maturity determine the degree of pod shattering (Gulluoglu *et al.*, 2006). The thickness and length of the bundle cap on the dorsal side

of the pod and thickness of the pod were negatively and significantly correlated with the degree of pod shattering (Tiwari and Bhatia, 1995) and pod thickness was recommended as a selection criterion for shattering resistance in soybean (Tiwari and Bhatia, 1995). Tsuchiya (1986, 1987) demonstrated that three sources of germplasm for pod-shattering resistance are useful for soybean breeding. One is a genetic resource from Thailand, another is an accession from North America and the third originates from China. Bailey, *et al.* (1997) stated that pod dehiscence is relatively uncommon in modern North American soybean cultivars, but is often observed when unimproved germplasm or the wild species, *G. soja* Siebold & Zucc, are used as parents to introgress useful genes or to develop genetically diverse breeding populations.

Morgan *et al.* (1998) studied the genetic variation for pod shatter resistance among lines of oilseed rape developed from synthetic *Brassica napus* and reported that genetic variation among lines of these populations in pod shattering exceeded that found among selections of modern cultivars. This variation was associated with the particular *Brassica* parents used to make the synthetic oilseed rape. They observed significant association between beak length and the force needed to shatter the pod and concluded that, it should be possible to select for resistance to pod shattering independently of other agronomic characters. They also observed that resistance to shattering appears to be linked to a failure of the dehiscence zone‟s cells to degrade and to the presence of extra vascular tissues within the zone.

2.5 Distinction between Shattering and Non-Shattering Regions in Soybean

Soybean pods consist of a single carpel that encloses the central cavity where the seeds are contained. Along the length of the pod are two sutures, the dorsal and ventral,

where the pod opens at maturity (Christiansen *et al.*, 2002). Closer examination of the top of the bundle cap reveals that the two halves of the structure do not meet where the suture begins, but are delimited by two different kinds of cells. Microscopic examination of cross sections of dorsal and ventral sutures of soybean pods at two different stages of maturity revealed that the dehiscence zone of soybean pods is functionally equivalent to the dehiscence zone known from crucifers (Christiansen *et al*., 2002). Enzymatic assays demonstrated the presence of endo-1, 4-β-glucanases and endopolygalacturonase, the activity of which accumulated in the dehiscence zone that peaked during maturation (Christiansen *et al.*, 2002). Analysis of the soybean endopolygalacturonase transcription revealed that the endopolygalacturonase is primarily found in dehiscence-related tissue and is presumably involved in the breakdown of the middle lamella prior to dehiscence (Christiansen *et al*., 2002).

Agrawal *et al.* (2002) reported on the activities of two hydrolytic enzymes (cellulose and polygalacturonase) and two oxidoreductase enzymes (peroxidase and polyphenol oxidase) at the shattering and non-shattering zones of two soybean varieties contrasting in pod shattering. The continuous increase of cellulose activity at the shattering zone of a susceptible variety indicates the involvement and role of this enzyme in the pod shattering process. The shift in the activity from the nonshattering zone to the shattering zone in susceptible variety and vice versa in resistant variety was also observed. Lu *et al.* (1998) also reported that shattering resistant cultivars have high levels of synthesis of Heat Shock Protein (HSP*72-73).* **2.6 Inheritance and Breeding for resistance to pod Shattering in soybean**

Several genetic studies conducted to understand the genetic control of pod shattering in soybeans have generated inconsistent data. Analysis of pod shattering in F_1 populations by Tiwari and Bhatnagar (1992) revealed contradictory observations where some crosses showed susceptibility being dominant while other crosses showed partial dominance for resistance, whilst Caviness (1969) did not find any significant variation between crosses involving domesticated cultivars and wild types in terms of shattering. Misra *et al*. (1980) had difficulty in estimation of shattering trait of soybean genotypes, which they attributed to absence of discrete observations at F_2 generation, suggesting presence of several genes. Carpenter and Fehr (1986) observed discrete classes of shattering scores in segregating populations of soybean involving a susceptible wild relative *Glycine soja* and two resistant cultivars. They observed shattering frequency to decrease with each generation of backcrossing to the cultivars and concluded that the shattering trait could be eliminated by three to four backcrosses, indicating that only a few genes were involved.

Caviness (1963) suggested that four major genes were involved in controlling susceptibility to shattering. On the other hand, Tsuchiya (1986) suggested that depending on methodology, minimum number of genes controlling shattering in soybean varied between one and two, while Akpan (1988) reported six to twelve genes to be involved. Bailey *et al*. (1997) observed that one major quantitative locus, and a few minor QTLs controlled pod shattering in soybean.

Tiwari and Bhatnagar (1991) indicating that the character is highly heritable, put average broad sense heritability (h^2_b) estimate of shattering in soybean at 98.8%, 90% by Caviness (1969) and 93% by Tsuchiya (1987). However, heritability in the broad

sense (h^2_b) in self-pollinating crops is less informative than heritability in the narrow sense (h^2_n) which is a direct measure of additive variance. Tukamuhabwa *et al*. (2000) indicated that pod shattering in soybean is under control of two genes and is partially dominant over resistance and concluded that inheritance of pod shattering is non-allelic resulting in classical dominant epistasis and that the pod shattering trait in soybean is highly heritable with narrow sense heritability of 0.79 and it is not influenced by maternal effects.

This study sought to find additional information on the genetics of pod shattering in order to use such findings to strengthen the soybean breeding program at the Savanna Agricultural Research Institute in Ghana.

CHARPTER THREE

3.0 MATERIALS AND METHODS

3.1 Location

The project consisted of two sets of experiments conducted at two different locations. The fist experiment was conducted at the plant house of the Faculty of Agriculture,

Kwame Nkrumah University of Science and Technology-Kumasi between June and October 2008. The second experiment involving the F_2, BCF_2 populations and the parents in a replicated trial was conducted in June 2009-croping season to observe genetic ratios for levels of pod shattering resistance at F_2 at the Savanna Agricultural Research Institute (SARI) experimental site at Nyankpala in Northern Region of Ghana.

3.2 Climate and Vegetation of Locations

Kumasi is situated in the semi-deciduous forest vegetation zone of Ghana. It is about 356 meters above sea level on latitude 06º 41′ N and longitude 01º 33′ W. The rainfall is bimodal with an average annual rainfall of 1500 mm. The major rainy season starts from mid-May and extends to July, with a dry spell in August, while the minor season extends from September to November. The main dry season is from late November to March. The relative humidity varies from 97% (06 hours GMT) during the major and minor rainy seasons to as low as 20% (15 hours GMT) during the dry season. Annual maximum and minimum temperatures are 34.9ºC and 21.2ºC respectively. The mean daily maximum and minimum temperature during the period of the experiment was 30.4 º C and 21.7ºC respectively. The mean monthly rainfall was 166.5 mm and relative humidity 76.4%. (Agro metrology division, KNUST, 2008). SARI is in the Guinea Savanna vegetation zone of Ghana, located on latitude 9^0, 25′, 41N and longitude 0^0, 58′, 42W and about 183 m above sea level. The rainfall is monomodal with an average annual rainfall of about 1200 mm. The rains begin in early May and ends in October. The cropping season therefore, starts in mid-June to

October with the rest of the year being dry and hazy (Agro metrology section, SARI, 2010).

3.3 Soil Analysis

Ten plastic pots were filled with top soil. The soil was of the Kumasi series type, utisol developed over biotite granite. It is a moderately drained sandy loam. The physico-chemical properties of the soil at the experimental site are presented in Tables 3.1and 3.2.

3.4 Chemical analysis of soil

Soil sample for the first experiment was taken from the plastic pots at a depth of 0-15 cm at the beginning of the experiment. This sample was taken to the laboratory to determine the physical and chemical properties. The sample was dried and sieved using a 2 mm mesh sieve. Soil samples for the second experiment were taken at 0-15 cm deep. The samples were subjected to the same procedure to determine the various soil properties. (The following properties were determined).

Table 3. 1: Chemical properties of soil.

Location	Chemical Properties									
	pH	*C* (%)	*N* (%)	*P* (mg/kg)	K *Cmol/kg*	*Na Cmol/kg*	*Ca Cmol/kg*	*Mg Cmol/kg*	*Al Cmol/kg*	*H Cmol/kg*
Kumasi	5.72	1.19	0.24	12.72	0.24	0.35	11.20	1.00	0.60	2.00
Location	**Chemical Properties**									
	pH	*C* (%)	*N* (%)	*P* (mg/kg)	K (mg/kg)	*Na* (mg/kg)	*Ca* (mg/kg)	*Mg* (mg/kg)	*Al* (mg/kg)	*H* (mg/kg)
Nyankpala	5.11	0.59	0.05	9.05	63.06	22.74	129.96	42.96	-	-

Table 3.2: Physical properties of soil.

Location.	**Particle size (Texture %)**		
	Sand	Clay	Loam
Kumasi	75.8	12.8	11.4
	Soil type: Loamy- Sand		
Location.	**Particle size (Texture %)**		
	Sand	Clay	Loam
Nyankpala	65.8	3.7	30.5
	Soil type: Sandy-Loam		

3.4.1 Organic Carbon

The Walkley-Black wet combustion procedure (Nelson and Sommers, 1982) was used to determine Organic carbon.

3.4.2 Soil pH

This was measured in 1: 2.5 soil to water suspension by the use of a glass Electro calomel electrode (Mclean, 1982) pH metre.

3.4.3 Total Nitrogen

The Macro kjeldahl method described by Bremner and Mulvaney (1982) was used. A 10 g soil sample (< 2 mm in size) was digested with a mixture of 100 g potassium sulphate, 10 g copper sulphate and 1g selenium with 30 mls of concentrated sulfuric acid. This was followed by distillation with 10 ml boric acid (4%) and 4 drops of indicator and 15 mls of 40% NaoH. It was then titrated with Ammonium sulphate solution. Based on the relation that 14 g of nitrogen is contained in one equivalent weight of NH_3, the percentage of nitrogen in the soil was calculated as follows:

Percent Nitrogen

$$\%\text{Nitrogen} = \frac{14x(A - B) \times NX100}{1000 \times 1}$$

Where,

A = Volume of standard acid used in the titration.

B = Normality of the standard acid.

3.4.4 Potassium

The flame photometer method was used to determine the amount of potassium with ammonium acetate as the extractant.

3.4.5 Available Phosphorous

The Bray P 1 method (Jack, 1956) was used for the determination of phosphorus with dilute acid fluoride as the extractant.

3.4.6 Exchangeable Bases (Ca, Mg, K, Na)

The exchangeable base cations were extracted using ammonium acetate

(1.ON NH_4OAc) at pH of 7.0. Calcium and Magnesium were determined using the EDTA titration method (Moss, 1961) while potassium and sodium were determined by the flame photometer.

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3.4.7 Exchangeable Acidity (A1 and H)

Exchangeable acidity (A1 and H) was extracted with 1ml KC1 solution. The extract was then titrated with 0.05N NaOH and 0.05 Hcl and 10 ml NaF solution added. This A1, H was then determined by extracting (A1 + H) (Mclean, 1982)

3.5 Experimental set-up and Design

The first experiment was a non-replicated crossing block whilst the experimental design for the second experiment was a randomized complete block with three replications. Treatments were assigned to four row plots of four meters long and spaced seventy- five centimeters (75 cm) between rows and ten centimeters (10 cm) within rows. Each plot measured 4.0 m x 2.25 m.

3.6 Treatments

Four soybean varieties were used in the crossing block for the first experiment whereas the treatments used to conduct the second experiment were F_2, BCF_2 populations and the four parental varieties.

3.7 Soybean Varieties

The four soybean varieties used in the study, Jenguma (TGX 1448-2E), “Quarshie” (TGX 1445-2E), Salintuya-1 (TGX 297-192C) and Salintuya-2 (TGX 306-036C)) were acquired from the soybean improvement programme of SARI. They have maturity period of 105-120 days with a potential yield of 1.8- 2.5 tonnes per hectare.

These varieties were originally breeding lines developed in IITA and were released as varieties through varietal screening by SARI in 1989 and 2003 in collaboration with IITA based on their stable high yields and resistance to pod shattering.

Table 3.3 Origin, pedigree and characteristics of parental lines.

Parent	Origin	Pedigree	Days to 50% flowering	Days to maturity	Yield (kg/ha)	Shattering description
Jenguma	SARI	TGX 1448-2E	45	112	2.6[Rhy]	Resistant.
"Quarshie"	SARI	TGX 1445-2E	42	105	2.0	Mod. resistant.
Salintuya-1	SARI	TGX 297-192E	43	110	2.0[shy]	Mod. susceptible
Salintuya-2	SARI	TGX 306-036C	52	120	2.5[shy]	Very susceptible

[Rhy] = Resistance to shattering and high yielding. [shy]= Susceptible to shattering but high yielding

3.8 Evaluation of Shattering Resistance

The varieties used in the study were characterized for pod shattering to confirm their level of resistance using field screening and the oven-dry methods (Table 3.3) (Jiang *et al*., 1991). Under the field screening, mature pods were left on the field twelfth days after full maturity (harvest maturity) and shattering score taken every day beginning the twelfth day for three weeks. Under the oven method, twenty fully matured pods of each variety were placed in khaki envelops for two weeks at room temperature for their seed moisture content to equilibrate after which they were subjected to oven drying at 60°C for 12 hours. The percentage pod shattering induced was determined on a 1–5 scale used by Asian Vegetable Research and

Development Centre (AVRDC , 1979) in which, 1 = 0% shattering, 2 = 1–10%, 3 = 11–25%, 4 = 26–50% and 5 ≥ 50%. The shattering phenotypes on the 1–5 scale were described as 1 very resistant, 2 resistant, 3 moderately resistant, 4 moderately susceptible and 5 very susceptible.

3.9 Development of Breeding Populations

Ten plastic pots of diameter 20 cm base, 27 cm top and 27 cm height were planted to each variety. Planting was staggered with the late variety (Salintuya-2) planted a week earlier than the medium maturing ones for synchronous flowering. A total of eleven crosses were made from the four soybean varieties in two sets (Table 3.4). However, for the purpose of this study, only crosses involving the resistant and susceptible varieties were used. Their F_1 progenies were planted and harvested in plastic pots in the plant house of the Faculty of Agriculture of the KNUST, Kumasi. The F_1 progenies were evaluated for pod shattering using the oven-dry method (Tsuchiya and Sunada, 1977; Tiwari and Bhatnagar, 1997, Tukamuhabwa *et al.*, 2002). The number of F_1 plants from the crosses varied from two to eight plants. The F_1 progenies were backcrossed to both parents to produce backcross one (BC_1) and backcross two (BC_2) progenies (Table 3.4). BCF_1 progenies were also planted and harvested in plastic pots in the plant house of the Faculty of Agriculture of the KNUST, Kumasi.

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Table 3.4 Successful F_1 and BC progenies developed.

Nº plants	Cross (F_1)		Number of Cross (BC)	Number of plants
1	$P_1 \times P_2$	f 8	$(P_1 \times P_2) \times P_1$	2
2	$P_1 \times P^1$	f 4	$(P_1 \times P_2) \times P_2$	2
3	$P_1 \times P_4$	f 4	$(P_1 \times P_3) \times P_1$	1
4	$P_2 \times P_1$	f 3	$(P_1 \times P_3) \times P_3$	2
5	$P_2 \times P_3$	f 7	$(P_1 \times P_4) \times P_1$	1
6	$P_2 \times P_4$	f 3	$(P_1 \times P_4) \times P_2$	1
7	$P_3 \times P_1$	f 3	$(P_2 \times P_3) \times P_2$	10
8	$P_3 \times P_2$	s 2	$(P_2 \times P_3) \times P_3$	6
9	$P_3 \times P_4$	s 2	$(P_2 \times P_4) \times P_4$	1
10	$P_4 \times P_1$	s 2		

[1] .9.1 Hybridization Procedure

This included, diallel crossing (crossing in all possible combinations) including reciprocals (n (n-1)), selfing of F_1 progenies and backcrossing to both parents (P_1 x F_1= BC1 and P_2 x F_1= BC2). At flowering, female flowers (fully matured nonopened flowers that were to be pollinated) were emasculated by using a forceps with the aid of an optical visor (magnifying lens). Pollen from male flowers (fully matured opened flowers) was placed on the stigma of emasculated female flower. Each cross was labeled with name and date of crossing till maturity. Crossed seeds were harvested and planted as F_1 in plastic pots.

11 $P_4 \times P_2$ [s] 1

[f] = First set of crosses. [s]= Second set of crosses.

3.10 Response Variables

The response variables measured were

3.10.1 Percentage germination

The number of seeds that germinated from each cross (treatments) was counted seven days after sowing and was expressed as a percentage of the total number of seeds planted.

3.10.2 Number of days to Flowering

This was recorded as date after sowing until 50% of the plants have one or more flowers.

3.10.3 Plant height at flowering and at maturity (cm)

Plant height was taken as the length in centimetres of the main stem at the time of flowering and at maturity.

3.10.4 Number of days to pod maturity

This was taken as days after sowing when 95% of the pods have changed from yellow to tan or grey.

3.10.5 Number of Plants Harvested Per Plot

This was taken as the number of plants in the net plot contributing to the yield sample.

3.10.6 Grain Yield (kg/ha)

Seeds from plants contributing to the yield sample in the net plot were uniformly dried and weighed in grams and transformed to kilograms per hectare.

3.10.7 Number of pods per plant

This was taken as the average pods per plants from five sampled plants within the net plot.

3.10.8 Number of seeds per pod

Number of seeds per pod was taken as the average seeds per pod of the five sampled plants per plot.

3.10.9 100 Seed Weight (gm)

Hundred seeds from the sampled plants were weighed in grams.

3.10.10 Shattering Score

Shattering evaluation was done in the field (field screening) and in the laboratory (oven-dry). On the field, shattering score was taken at one, two and three weeks after full maturity (95% of pods turn tan or grey). 1= No pods shattered , 2= 25% of pods shattered , 3= 50% of pods shattered, 4= 75% of pods shattered and 5= all pods shattered.

3.11 DATA ANALYSIS

3.11.1 Descriptive statistics

The following statistics were estimated by using Microsoft Excel software on the parents, F_1, F_2 and backcross populations for each of the crosses: Variance, standard deviation, standard error and coefficient of variation.

3.11.2 Estimation of additive and dominance gene effects

Additive and dominance gene effects were estimated according to methods by Mather and Jinks (1971) as follows:

$$VF_2 = \frac{1}{2}A + \frac{1}{4}D + E \quad (1)$$

$$E = \frac{Vp1 + Vp2 + VF1}{3} \quad (2)$$

$$V(BC_{1)} + V(BC_2) = \frac{1}{2}A + \frac{1}{2}D + 2E \quad (3)$$

where,

$V(F_2)$ = variance for F_2 generation.

$V(BC_1)$ and $V(BC_2)$ = variances for the two backcross generations, respectively.

E = environmental effects

Vp_1, Vp_2 and V_{F1}= variances for parent 1, parent 2 and the F_1 generations, respectively.

A = the contribution to additive genetic variance

D = the contribution to dominance variance

Additive and dominance genetic variances were obtained by solving the two simultaneous equations (1) and (3).

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3.11.3 Broadsense heritability

Broadsense heritability was calculated as follows (Strickberger, 1976)

$$h^2_{broadsense} = \frac{V(G)}{V(F2)} = \frac{VA + VD}{V(F2)} \quad (4)$$

Where,

V(G) = total genetic variance

V_A = additive variance

V_D = dominance variance

$V(F_2)$ = phenotypic variance = $\frac{VP1 + VP2 + VF1}{3}$

3.11.4 Narrowsense heritability ($h^2_{narrowsense}$)

Narrowsense heritability was estimated by the methods of genetic components of variance and regression analysis.

The genetic component of variance method was as follows (Strickberger, 1976)

$$h^2_{narrowsense} = \frac{VA}{V(F2)} \quad (5)$$

The regression analysis method was performed by regressing the offspring phenotypes on those of the parents (mid-parent values) to obtain the following relationship (Poehlman, 1986).

$h^2_{ns} = b \times 100$ (6)

where, b is the regression coefficient.

3.11.5 Nonallelic gene interaction

The chi-square test of significance was used to investigate epistatic gene interactions for the F_2 generations.

3.11.6 Number of genes controlling shattering

Number of genes controlling shattering was estimated by using the formula according to Bjarko and Line (1987). This formula was based on the assumption that the genes have equal effects in size and direction, no dominance, no epistasis and no linkage. The following was therefore applied:

$n = (GR)^2[1.5-2h(1-h) / 8 [(VF_2) - (Vp_1+Vp_2+2VF_1) / 4)]$

Where,

n= the estimated number of genes. GR=Genotypic range ($P_S - P_R$)

$h = F_1 - \left(\frac{PR}{PR - PS}\right)$

VF_1, VF_2, Vp_1 and Vp_2 = Variances of F_1, F_2, parent one and parent two respectively.

P_S and P_R = Susceptible parent and resistant parent respectively.

3.11.7 Estimation of epistatic interaction

The following epistatic effects were estimated by using analysis of variance and generation mean analysis of the parents, F_1, F_2 and the backcross populations:

I. Additive x additive effect

II. Additive x dominance effect

III. Dominance x dominance effect

The SAS computer statistical software was used for the analysis (SAS Institute, 1998).

3.11.8 Mid-parent heterosis

Mid-parent heterosis was estimated as the percentage deviation of the mean F_1 value from the mid-parent value using the formula (Wright, 1969):

$$\text{Heterosis} = \frac{(F1 - MP)}{MP} \times 100$$

Where,

MP = Mid-parent value (average value of the two parents involved in a particular cross).

3.11.9 Estimation of number of loci

Number of loci was estimated using the following (Zeng et al., 1990).

$$Kcw = \frac{D2}{8}VG = \frac{D2}{8}(VF_2\text{-}VE)$$

Where;

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Kcw = estimated number of loci

D = difference in parental mean ($P_R - P_1$)

VF_2 = phenotype variance and VE = environmental variance.

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4.0 RESULTS AND DISCUSSION

4.1 Shattering evaluation

The shattering resistance scores for F_1 hybrids and their parental lines are presented in Table 4.1. The mean shattering percentage of F_1 progenies in all crosses and their reciprocals was equal to or higher than the average of the parents but closer to the susceptible parents than the resistant parent, suggesting that genes for susceptibility are showing some dominance over resistance. Among the parental varieties,

Salintuya-2 had the highest percentage shattering (90%) followed by *salintuya-1*, *Quarshie* and *Jenguma* respectively. The cross between the resistant parent and the susceptible parent (*Jenguma / salintuya-2*) gave shattering percentage (63%) higher than crosses involving the resistant parent and intermediate parents and this gave further reasoning that susceptibility is dominant. This result is in agreement with results reported by Caviness (1969) and Tukamuhabwa *el al.* (2000). In a selfpollinated crop such as soybean, the F_1 mean value is expected to be exactly intermediate or equal to the average of its parents if the genetic effects are additive, a departure from this mid-parent value would indicate the effect of dominance. The results from this study show that the F_1 plants exhibited partial dominance for susceptibility.

Table 4.1 Shattering scores of parental lines and F_1 progenies.

Genotypes/Cross	Number of plants	Mean shattering (%)	Shattering scores
Jenguma (R)	20	8	2
„Quarshie" (I)	20	25	3
Salintuya-1(I)	20	30	4
Salintuya-2(S)	20	90	5
Jenguma x „Quarshie"	8	16	3
Jenguma x Salintuya-1	4	38	4
Jenguma x Salintuya-2	4	63	5
„Quarshie" x Jenguma	3	23	3
Salintuya-1 x Jenguma	3	53	5
Salintuya-2 x Jenguma	2	45	4

R = Resistant. I=Intermediate. S= susceptible. Score of 1=0% shattering, 2=1-10%shattering, 3=11-25% shattering, 4=26-50% and 5=>50% shattering (AVRD, 1979). Phenotypic description; Score of 1=Very resistant, 2=Resistant, 3/ 4=Intermediate and a score of 5=Susceptible

4.2. Mean scores, variances and coefficient of variation for shattering resistance in three soybean crosses

Means, variances (S^2) and coefficient of variation (CV) for shattering resistance were estimated for three crosses (Table 4.2). Among the parents, *Jenguma* had a significantly higher ($p \leq 0.05$) mean resistance score (5) whilst *Salintuya-2* had the lowest score (3.33). The means for the reciprocals were not different from their respective crosses and were therefore pooled. Failure to detect reciprocal differences

in the F_1 generation for shattering resistance score in these crosses may have been due to the smaller number of plants evaluated (Table 4.1). The F_1 mean score for shattering resistance in all three crosses was lower than the mean of their parents but closer to the susceptible parent (Table 4.2) suggesting an incomplete or partial dominance for susceptibility. This observation disagrees with Tiwari & Bhatnagar (1992) who reported contradictory observations in F_1 populations where some crosses showed susceptibility being dominant while other crosses showed partial dominance for resistance. The F_2 generation had mean resistance scores higher than the F_1 generations. There were no significant differences ($p \geq 0.05$) between the means and variances of BC_1 and BC_2 in the resistance/susceptible cross (J*enguma x Salintuya-2*) suggesting that in a backcrossing programme to improve resistance to pod shattering in soybean the choice of a recurrent parent is not important. The mean resistance score of the backcrosses was also not significantly different ($p \geq 0.05$) from the resistant parent (Table 4.2). This suggests that the genes for resistance introgress at each backcross. This agrees with Carpenter and Fehr (1986) who observed shattering frequency to decrease with each generation of backcrossing and concluded that the shattering trait could be eliminated by three to four backcrosses. *Salintuya-1* and *Salintuya-2* showed the highest coefficient of variation (CV) and this could mean that they have great genetic divert.

Table 4.2 Mean shattering resistance score, variance and coefficient of variation for parents F_1, F_2, BC1 and BC_2 generations of three crosses.

Generation	*Jenguma x 'Quarshie'*			*Jenguma x Salintuya-1*			*Jenguma x Salintuya-2*		
	Mean*	S^2	CV (%)	Mean	S^2	CV (%)	Mean	S^2	CV (%)
P_1	5 a	0	0	5a	0	0	5a	0	0
P_2	3.67b	0.33	15.7	3.67bc	1.33	34.6	3.33bc	0.33	34.6
F_1	3.33bc	0.33	17.3	2.33c	0.33	24.7	2.67c	0.33	12.4
F_2	3.67b	2.33	41.7	4.00ab	0	0	5.00a	0.33	17.3
BC_1	2.33c	0.33	24.7	2.67c	0	0	4.00ab	0.33	17.3
BC_2	3.33bc	0.33	17.3	4.00ab	0.33	12.4	4.67a	0.33	24.7
MP	4.34			4.34			4.17		

MP = Mid-parent value. S^2 = Variance SE = Standard error *Mean resistance score of 1-2= Resistant. 3-4= Intermediates and 5= Susceptible.

4.3 Evaluation of shattering resistance, yield and yield components in three soybean crosses

Grain yield was significantly different ($p \leq 0.05$) among the generations in all three crosses (Table 4.3). Mean grain yield ranged from 880 to 2240 kilograms per hectare with the backcrosses recording the greatest grain yield (2239 kg/ha). Among the parental, Jenguma had an average grain yield greater than the three other varieties (*„Quarshie", Salintuya-1* and *Salintuya-2*). The F_2 population had the lowest grain yield (718 kg/ha) and this could be attributed to segregation (independent assortment) of the genes into various genotypes including recombinants with low yield potential. There was no significant difference ($p \geq 0.05$) between the crosses in all parameters studied except for number of primary branches (Table 4.3). The *Jenguma/„Quarshie"* cross gave the highest number of primary branches per plant.

There was significant difference ($p \leq 0.05$) between the generations for shattering resistance with *Jenguma* (resistant parent) recording the highest resistance score.

The results suggest that the backcross method is a useful breeding tool for the improvement of shattering resistance in soybean because both backcross one (BC_1) and backcross two (BC_2) had resistance scores higher than the susceptible variety indicating a reduction in shattering in each backcross.

Cross/Generation	Parameters									
Contrast between crosses.	**DFF**	**Maturity**	**Canopy spread**	**Primary branch**	**Pods /plant**	**Seeds/ pod**	**Pod length (mm)**	**100 Seed wt.gm**	**Grain yield Kg/ha.**	**Shattering score**
Jeng. x "Q"	47	116	66	7	166	1.9	33	12.4	1305.8	3.37
Jeng. X sal-1	48	116	61	6	175	2.0	35	12.7	1511.3	3.93
Jeng. X sal-2	50	119	66	6	178	1.9	35	11.8	1272.3	3.27
Mean	48.3^{ns}	117 ^{ns}	64.3 ^{ns}	6.3*	173 ^{ns}	1.93 ^{ns}	34.3 ^{ns}	12.3 ^{ns}	1363.13^{ns}	3.52 ^{ns}
SE ±	0.88	1	1.67	0.33	3.6	0.03	0.67	0.26	74.7	0.21
Contrast between generations.										
P1	48	109	57	5	102	1.9	29	13.6	1026.3	4.9
P2	50	113	58	6	106	1.9	29	12.2	879.6	2.63
F1	39	112	71	7	159	2.1	41	12.4	1369.6	3.23
F2	52	110	59	6	85	1.9	30	13.1	718.1	4.07
BC1	50	128	72	7	259	1.9	37	11.2	1945.9	3.0
BC2	51	129	69	7	325	1.9	36	11.1	2239.2	3.3
Mean	48.3**	116.8**	64.3**	6.3**	172.7*	1.93 ^{ns}	33.7*	12.3*	1362.5**	3.52*
SE ±	1.94	3.74	2.87	0.33	39.99	0.33	2.06	0.40	249.2	0.34

Table 4.3. Mean shattering resistance scores, yield and yield components in three crosses involving shattering resistant by susceptible soybean varieties.

****= Significant at 1%. *= Significant at 5%. ^{ns}= Not significant. DFF= Days to 50% flowering**

4.4 Determination of allelic relationship between shattering and non- shattering

Genetic ratios for levels of pod resistance at F_2 are presented in (Table 4.4). The following phenotypic ratios: 3:1, 12:3:1, 9:7 and 13:3 were used to test for goodness of fit of observed segregation at F_2 using the Chi-square test. Observed ratios at F_2 varied in all six crosses. Two crosses: the *Jenguma x „Quarshie"* cross and *Jenguma x Salintuya-1* cross fitted the 9:7 model, whilst *Jenguma x Salintuya-2* cross fitted the 13:3 model, suggesting a classical duplicate recessive epistasis and dominance and recessive epistasis respectively. There are six types of epistatic ratios commonly recognized, three of which have three phenotypes (dominance epistasis; 12 : 3 : 1, recessive epistasis; 9 : 3 : 4 and duplicate epistasis with cumulative effect; 9 : 6 : 1) and the other three having only two phenotypes (duplicate dominant epistasis; 15 : 1, duplicate recessive epistasis; 9 : 7 and dominant and recessive epistasis; 13 : 3) (Williams, 1988). Results in this study according to the chi-square test fitted the two phenotypic classes because the intermediates were behaving as susceptible phenotypes. There were no differences between the crosses and their reciprocals in terms of segregation pattern. The observed ratios suggest that inheritance of pod shattering resistance in soybean is qualitative and influenced by dominance and recessive epistasis or duplicate recessive epistasis. These observations agrees with Carpenter and Fehr (1986) who observed discrete classes of shattering scores in segregating populations of soybean involving a susceptible wild relative *Glycine soja*

and two resistant cultivars. The results also agrees with Caviness (1963), Akpan (1988) and Tukamuhabwa *et al.* (2000) who indicated that pod shattering in soybean is under control of two genes and is partially dominant over resistance. They concluded that inheritance of pod shattering is non-allelic resulting in classical dominant epistasis. In a self-pollinated plant like soybean, epistasis is more important than dominance and can generate different phenotypes some of which represent real genetic advance over their parents (Allard, 1960). No difference was observed between the ratios obtained from the F_2s and their respective reciprocals

(Table 4.4). Crosses involving the resistant parent, *Jenguma* and the intermediates („*Quarshie" and Salintuya-1*) showed similar segregation patterns but the *Jenguma x Salintuya-1* cross segregated with more resistant plants than susceptible plants suggesting that the genes for resistance in these intermediate varieties are at different loci. There was transgressive segregation with some F_2 plants shattering earlier than the susceptible parent and others showing delayed shattering. With transgressive segregation, each parent makes a contribution to the gene pool of the progeny and both superior and inferior segregates are generated (Poehlman, 1987). Two forms of gene interactions were therefore observed in the current study and depended on the parental genotypes used in the cross.

Table 4.4 Phenotypic ratios at F_2 populations

Cross	Phenotype	Observed	Expected	X^2	Fit ratio
	R	120	129.94	0.76	
Jenguma x „Quarshie"	I	150			
P_1 x P_2	S	27	167.06	0.59	
	R	54	59.5	0.51	
„Quarshie" x Jenguma	I	74			
P_2x P_1	S	8	76.5	0.40	
	Total	136	136.0	0.91***	9(I+S):7(R)
	R	85	89.44	0.22	
Jenguma x Salintuya-1	I	73			
P_1 x P_3	S	1	69.56	0.28	
	Total	159	159.0	0.50***	9(R): 7(I+S)
	R	99	104.63	0.30	
Salintuya-1 x Jenguma	I	85			
P_3 x P_1	S	2	81.37	0.39	
	Total	186	186.0	0.69***	9(R):7(I+S)
	R	30	35.44	0.84	
Jenguma x Salintuya-2	I	114			
P_1 x P_4	S	45	153.56	0.19	
	Total	189	189.0	1.03***	13(I+S):3(R)
	R	23	27	0.59	
Salintuya-2 x Jenguma	I	87			
P_4 x P_1	S	34	117	0.14	

	Total	144	144	0.73***	13(I+S): 3(R)
	Total	297	297.00		1.35***9(I+S):7(R)

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R= resistant I= intermediate. S= susceptible. Significant goodness of fit. ***p≤0.10

4.5 Relationship between pod shattering and other agronomic attributes in soybean

Multi-regression analysis between shattering scores (dependent variable) and six agronomic characters (independent variables) were carried out. The correlation matrix is presented in (Table 4.5). Pod shattering score showed negative correlation with all

the characters measured but there was a significant negative correlation between resistance score and number of primary branches, maturity and pod length showing that these characters affect pod shattering in soybean. There was however, a weak negative correlation between pod shattering and plant height, pods per plant and grain yield. The results suggest that, it is possible to breed a low shattering variety with medium to late maturity, higher number of pods/plant and increased yield. In general, it can be taken that resistance to pod shattering is related to characters such as, number of primary branches per plant, pods per plant, maturity and grain yield. This conforms to reports by Thurling, (1991), Loof and Johnson, (1970) and Thompson and Hughes, (1986) that, seed loss at harvest was related to many architectural and morphological characters of both the whole plant and racemes in oilseed rape. They also observed that, the problem of mechanical damage was affected much by plant attributes such as height, pod angles, pod width and stem stiffness. These attributes could affect the laxness of the plant and hence, the degree and type of movement made by the canopy and branches within it which may accentuate shattering. The coefficient of determination (r^2) for the multi-regression analysis was 0.62. The r^2 is a measure of variability of the dependent variable (shattering score) as explained by the independent variables (Plant height, maturity, number of primary branches, number of pod/plant, pod length and grain yield). This indicates that 62% of the variability in the dependent variable is explained by the independent variables. The intercept of 19.89 (Table 4.5) indicates that for each unit change in the independent variables there is an approximate 20 units change in the dependent variables. This result agree with reports by Tiwari and Bhatnagar, (1991) that pod shattering showed a significant negative correlation

with 100 seed weight, days to maturity and seed yield. Morgan, *et al* (1998) also reported negative correlation between the force needed to break pod („force") with beak length, silique length and number of seeds per pod among oilseed rape lines developed from synthetic *Brassica napus*.

Table 4.5. Correlation matrix between shattering resistance score as dependent variable and some agronomic characters as independent variables.

Parameter	Plant height. (cm)	Days to Maturity	Number of Primary branches	Pods per plant	Pod length (mm)	Grain yield (kg/ha)	Shatter score
Plant height(cm)	….						
Maturity	-0.821	……					
Number of Primary branches	0.623	-0.503	…..				
Number of Pods/plant	0.062	-0.415	-0.318	……			
Pod length(mm)	0.383	-0.309	-0.177	0.183	……		
Grain yield (kg/ha)	0.259	-0.056	0.521	0.817	-0.202	……	
Shattering score	-0.069	-0.415	-0.623	0.209	-0.341	-0.035	…….

Intercept = 19.89 R-Square = 0.63 *Significance = 0.05

4.6 Frequency distribution of F_2 generation in three soybean crosses

The frequency distribution of shattering resistance of F_2 populations in three crosses (*Jenguma x „Quarshie"*), (*Jenguma x Sal-1*) and (*Jenguma x Sal-2*) using a 0-10 scale is shown in (Appendix 4, 5 and 6 and figures 4.1a, 4.1b and 4.1c) respectively. The frequency distribution of F_2 generation of crosses involving the resistant parent,

(*Jenguma*) and the intermediates *(„Quarshie" and Salintuya-1*) were skewed towards the resistant parent suggesting that the F_2 generation segregated more for resistance than susceptibility in these crosses (Figure 4.1a and 4.1b) whilst the frequency distribution in the *Jenguma/salintuya-2* cross was bimodal suggesting the absence of dominance of any character (Figure 4.1c). The contribution of both additive and non-additive gene effects could be apparent in the cross. This conforms to reports by Tiwari & Bhatnagar (1992) which revealed contradictory observations where some crosses showed susceptibility being dominant while other crosses showed partial dominance for resistance. It is also in agreement with reports by Ting (1946) and Caviness (1969) who stated that the frequency distribution in F_2 was overlapping in a normal distribution manner. The complex distribution observed in F_2 progenies of a self-pollinated crop can be attributed to epistasis which causes deviation from the expected normal distribution (Poehlman, 1986). This suggests that, there are various types of gene interactions, including the activities of complementary genes, modifiers and genes with pleiotropic effects in which a single gene affects both susceptibility and resistance to the trait (Paul and Todd, 2001).

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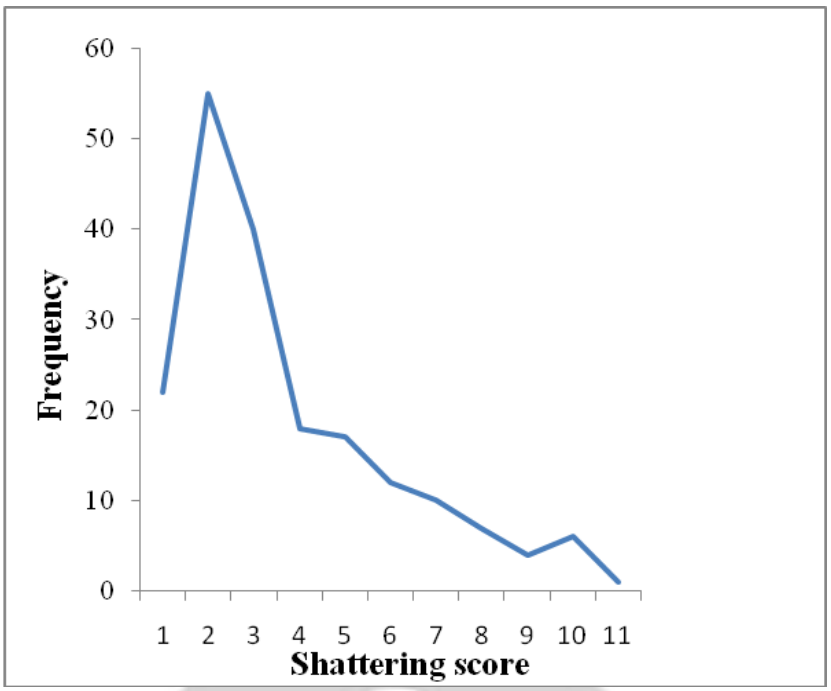

Figure. 4.1a Frequency distribution of shattering in F_2 generation for *Jenguma x 'Quarshie'* cross

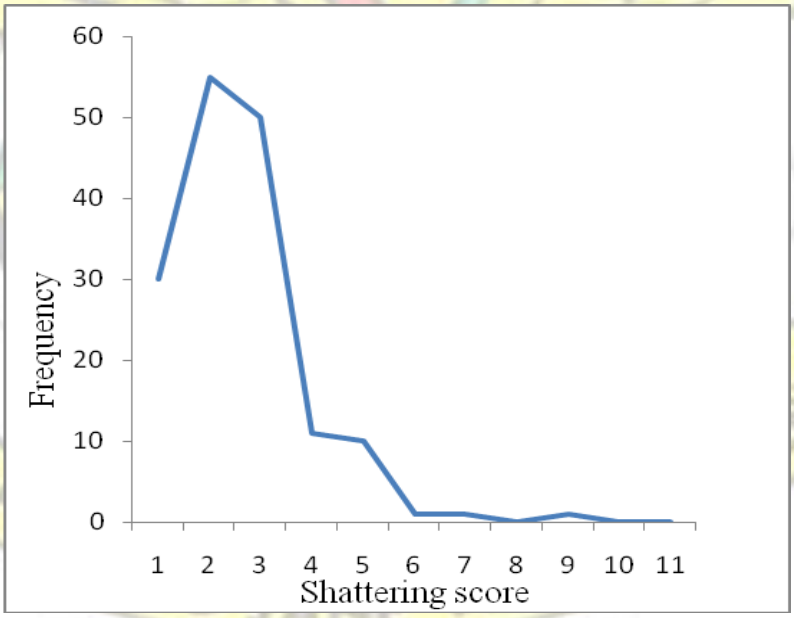

Figure. 4.1b Frequency distribution of shattering in F_2 generation for *Jenguma x Sal-1* cross

Fig.4.1c. Frequency distribution of shattering in F_2 generation for *Jenguma x Sal-2* Cross

4.7 Genotypic and Phenotypic relationship in F_2 populations of shattering resistant by susceptible crosses

To demonstrate the genetic control mechanism of pod shattering resistance in soybean, a hypothetical model is presented in (Table 4.7) and (Table 4.8). This assumption is based on the two gene model where genotypes are represented by $S^+S^+R^+R^+$ and $S^-S^-R^-R^-$ for homozygous dominance and homozygous recessive parental lines respectively. The observed ratio of 13:3 is a classical dominance and recessive epistasis, where at least one dominant allele at a locus ($S^+\_$) and the recessive allele at another locus ($S^-S^-R^-R^-$) produce the same phenotypic effect. Thus, $S^+\_\ R^+$, $S^+R^-R^-$ and $S^-S^-R^-R^-$ produces one phenotype and $S^-S^-R^+R\_$ produce another in the ratio of 13:3 (Williams, 1988). In the case of duplicate recessive epistasis identical phenotypes are produced by both homozygous recessive genotypes. The genotypes $S^-S^-R^+R\_$, $S^+\_R^-$

R^- and $S^-S^-R^-R^-$ produce one phenotype. Both dominant alleles when present together complement each other and produce the same phenotype (Williams, 1988). The presence of (R^+) in the absence of (S^+) results in an intermediate phenotype. These observed distributions are classical example of epistasis which cause modification of the Mendelian dihybrid ratio of 9:3:3:1 and fits the suggestion that epistasis influences soybean pod shattering (Bailey *et al*, 1997). Checkerboard demonstrating the various gene combinations in a dihybrid genotype is represented in (Table 4.6).

Table 4.6 Checkerboard showing gene combination

	¼ R^+R^+	½ R^+R^-	¼ R^-R^-
¼ S^+S^+	1/16 S^+S^+ R^+R^+	2/16 S^+S^+ R^+R^-	1/16 S^+S^+ R^-R^-
½ S^+S^-	2/16 S^+S^- R^+R^+	4/16 $S^+S^-R^+R^-$	2/16 $S^+S^-R^-R^-$
¼ S^-S^-	1/16 S^-S^- R^+R^+	2/16 S^-S^- R^+R^-	1/16 $S^-S^-R^-R^-$

Table 4.7 Relationship between genotype and phenotype in an F_2 population showing classical dominance and recessive epistasis.

Genotype	Frequency	Phenotype	Ratio
$S^+S^+R^+R^+$	1/16	S	
$S^+S^+R^+R^-$	2/16	S	
$S^+S^+R^-R^-$	1/16	S	
$S^+S^-R^+R^+$	2/16	S	…… 13
$S^+S^-R^+R^-$	4/16	I	
$S^+S^-R^-R^-$	2/16	I	
$S^-S^-R^-R^-$	1/16	S	
$S^-S^-R^+R^+$	1/16	R	
$S^-S^-R^+R^-$	2/16	R	……... 3

Table 4.8 Relationship between genotype and phenotype in an F_2 population showing classical duplicate recessive epistasis.

Genotype	Frequency	Phenotype	Ratio
$S^+S^+R^+R^+$	1/16	S	
$S^+S^+R^+R^-$	2/16	S	
$S^+S^-R^+R^+$	2/16	I	……..9
$S^+S^-R^+R^-$	4/16	I	
$S^+S^+R^-R^-$	1/16	R	
$S^+S^-R^-R^-$	2/16	R	
$S^-S^-R^-R^-$	1/16	R	
$S^-S^-R^+R^+$	1/16	R	……..7
$S^-S^-R^+R^-$	2/16	R	

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4.8 Variance components and heritability estimates for shattering scores in three crosses.

4.8.1 Variance components:

Estimates of variance components varied considerably between crosses. Calculation was done using the formula developed by Mather and Jinks, (1971)

Additive variance ranged from -0.67 to 4.0 and dominance variance ranged from -1.89 to 0.67 (Table 4.9). The environmental component of variance was larger than additive or dominance variance for shattering scores in the *Jenguma x Salintuya-1* cross which negatively affected narrow sense heritability estimate. Additive variance was larger in the *Jenguma x „Quarshie"* cross resulting in a higher estimates for both broad sense and narrow sense heritability. Estimate of dominance variance was negative in crosses involving the resistant variety and the two intermediate varieties (*Jenguma x „Quarshie" and Jenguma x Salintuya-1*) indicating that the dominance effects contributed more to resistance in these crosses in contrast with significant

estimates of negative additive variance (-0.67) in the cross between the resistant and the susceptible variety (*Jenguma x Salintuya-2*), indicating the contribution of additive effect in the cross. Similar observations were reported by Tiwari & Bhatnagar (1992). The environmental variance was relatively higher in two of the crosses suggesting that the environment had influence on the expression of the shattering trait therefore, breeding methodologies that control environmental variation well may help improve the rate of gain of resistance to shattering. The results show that total variability in the F_2 generation of these crosses was due to both additive and dominance gene effects.

4.8.2 Heritability:

Heritability varied considerably between the three crosses (Table 4.9). Negative estimates were assumed to be zero (Robinson, *et al.*, 1955) but had to be reported as recommended by Dudley and Moll (1969) for future comparisons and were used for variance component estimates (Appendix 7). Mean broad sense heritability (h^2_b) in all three crosses was 0.30 whilst the mean narrow sense heritability (h^2_n) was 0.92.

The negative dominance variance drastically reduced the broad sense heritability. However, heritability in the broad sense (h^2_b) in a self-pollinating crop is less informative than heritability in the narrow sense (h^2_n) which is a direct measure of additive variance (Caviness, 1969; Tsuchiya, 1987). Narrow sense heritability estimate in the *Jenguma x „Quarshie"* cross was larger than the broad sense heritability due to additive variance being larger than the phenotypic variance. The generally low estimates of broad sense heritability indicated that the environment in which the plants were evaluated had a large effect on shattering.

4.8.3 Genetic gain:

Genetic gain (G_s) per cycle for selection at the 10% level was calculated as;

$G_s = i\sqrt{Vph}\ h^2$ where G_s is genetic gain, (i) is the 10% level of selection which is a constant (1.76), $\sqrt{Vph}$, square root of phenotypic variance and h^2 is narrow sense heritability estimate (Poehlman, 1986). Genetic gain ranged from -0.61 to 1.26 in the three crosses (Table 4.8). The average genetic gain was 0.28 and this meant that if 10 plants with highest shattering resistance score were selected at F_2, their progenies were predicted to have an average shattering resistance score that would be 28% higher in shattering resistance than the progeny of an unselected F_2 assuming similar environmental influence. No cross exhibited complete dominance or distinct bimodal distribution, suggesting that no single gene of a major effect controlled resistance to shattering in the crosses.

Table 4.9 Estimates of additive (V_A), dominance (V_D) and environmental (V_E) variances, broad (h^2_b) and narrow (h^2_n) sense heritability and genetic gain through selection (G_s) for shattering resistance in three resistance by susceptible soybean crosses.

Variables	Crosses		
	Jenguma x'Quarshie'	***Jenguma xSalintuya-1***	***Jenguma x Salintuya-2***	**Mean**
V_A	4.0	0.34	-0.67	1.22
V_D	-1.89	-0.56	0.67	-0.59
V_E	0.22	0.55	0.33	0.37
h_{2b}	0.90	0.0n	0.00	0.30
h_{2n}	$1.72(1.94)^R$	$1.03(1.00)^R$	$0.0n(0.0)^R$	$0.92(0.98)^R$
Gs	1.26	0.20	-0.61	0.28

n = negative heritability. ^{R} Estimate using parent offspring regression

4.9 Maternal influence on resistance to pod shattering at F_2 generation in three soybean crosses

The results of maternal influence on resistance to pod shattering in soybean are presented in (Table 4.10). There were no significant differences ($p \geq 0.05$) between the crosses and their reciprocals for shattering resistance, indicating absence of maternal influence on pod shattering in soybean. The character could therefore be attributed to nuclear gene control. This suggests that choice of maternal parent is not important in hybridization programme that focuses on the improvement of soybean for resistance to pod shattering. This result is in agreement with the findings of Tukamuhabwa, *et al*. (200). Maternal effects arise from egg cytoplasm which has been modified by chromosomally transmitted genes (Strickberger, 1976). Its distinguishing characteristic is the difference in the results of reciprocal crosses, so that cytoplasm produced by a particular genotype acts differently on a developing zygote than cytoplasm produced by a different genotype; that is, there is a difference in the phenotypes of offspring A♂ x a♀ and a♀ x A♂ (Strickberger, 1976). Sex linkage may also produce differences in the results of reciprocal crosses, but in those cases the phenotype can be predicted from the sex of the parents and offspring (Strickberger, 1976). In the maternal effect, phenotypic changes appear because of differences in sex chromosomes and often affect both male and female offspring equally (Strickberger, 1976).

Table 4.10. Maternal influence on resistance to shattering at F_2 population in soybean.

Cross	Number of observations	Mean shatter score	Standard Error
Jenguma x "Quarshie"	192	3.98	± 0.13
"Quarshie" x Jenguma	136	3.67	
Jenguma x Salintuya-1	159	3.42	±0.15
Salintuya-1 x Jenguma	186	3.77	
Jenguma x Salintuya-2	189	4.32	±0.29
Salintuya-2 x Jenguma	144	4.16	

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4.10 Estimated minimum number of genes contributing to shattering resistance in F_2 progenies

Using the F_2 progenies, estimated minimum number of genes contributing to shattering resistance range from 1.37 to 3.18 and mean of 2 genes according to Bjarko and Lines" (1987) suggesting two genes being involved in the control of resistance to pod shattering in soybean (Table 4.11). However, this formula has the following assumptions;

(1) Genes have equal effects in size and direction.

(2) No dominance (3) No epistatsis and

(4) No linkage.

With crosses for breeding purposes, it is usually impractical to try to estimate the number of genes contributing to a quantitative character (Poehlman, 1986) since these

assumptions would seldom hold. The actual number of genes is usually higher than estimated. Often the best the breeder can do is to estimate if the quantitative character is governed by a relatively large or a relatively small number of genes (Poehlman, 1986). A gene might have a major effect on one character and a minor effect on another character (Poehlman, 1986). Then there are the modifying genes, which have no major function other than modifying the functions of other genes.

Also only those genes in which the parents differ would be detected (Poehlman, 1986). Dominance and most types of epistasis will bias the estimates of minimum number of genes downward (Wright, 1968). It is likely that estimates of number of genes were highly biased (reduced) by the failure to meet the analysis assumptions of no epistasis and no dominance, because some dominance and epistasis effects were present in these crosses as presented in (Table 4.9).

Table 4.11. Estimated number of genes contributing to pod shattering resistance in soybean.

		Estimated number of genes.
Cross	Number of progenies	F_2J
Jenguma x "Quarshie"	192	3
Jenguma x Salintuya-1	159	2
Jenguma x Salintuya-2	189	1
Mean	180	2

J estimate according to Bjarko and Line (1987) method.

4.11 Estimates of minimum number of loci contributing to shattering resistance in F_2 progenies

The average number of loci was two using the formula established by Castle and Wright"s (1968). However, this formula was observed by Zeng *et al*. (1990) to underestimate the number of loci. These results are in agreement with the observed phenotypic ratios of 13:3 and 9:7 at F_2 (Table4.4). Similar results were reported by Tsuchiya (1986) who suggested that depending on the method, minimum number of genes controlling shattering in soybean varied between one and two while contrary observations were given by Akpan (1988) who reported six to twelve genes to be responsible for pod shattering in soybean. Other diverging results were reported by Bailey *et al*, (1997) who observed shattering to be conditioned by one major gene and few modifiers.

Table 4.12 Estimated number of Loci at F_2 generation in three crosses.

Cross	No of progenies	Number of Loci at F_2^W
Jenguma x "Quarshie"	192	1
Jenguma x Salintuya-1	159	2
Jenguma x Salintuya-2	189	3
Mean	180	2

^{W} Estimate by Wright"s (1968) method.

4.12 Heterosis

Results of mid-parent heterosis for shattering resistance and other agronomic characters varied in the three crosses (Table 4.13). Mid-parent heterosis was calculated

as the performance of the F_1 compared with the mean performance of its parents; $\frac{(F1 - MP)}{MP}$ x 100 (Fehr, 1991). The F_1 shattering score was below the average of both parents in the *Jenguma/,,Quarshie"* and *Jenguma/Salintuya-1* crosses but it was higher than the average of parents in the *Jenguma/Salintuya-2* cross indicating that some degree of heterosis existed in that cross (Table 4.13). Among the agronomic characters measured, pod per plant gave the highest mean mid-parent heterosis value of 54.6% followed by heterosis values of 26.1% and 23.7% for primary branches and canopy spread respectively (Table 4.13). Mean heterosis for shattering resistance score was -3.7% with a range of -44.1% to 55.7% (Table 4.13). Heterosis was therefore, not a major factor in the expression of resistance to pod shattering in this study. These results indicate that, there is no difference between alleles that cause a heterotic effect at a locus or that there is a low level of dominance among these alleles in the F_1 generation confirming the dominance hypothesis by Fehr (1997). Similar results were reported by Roger, *et al.* (2007) when they examined heterosis in pea (*Pisum sativum*.L.) for resistance to Mycosphaerella blight. To the Plant Breeder, heterosis will generally mean a luxuriant, unfixable superiority of the hybrid as compared to its parents in any of the economic traits (Janossy and Lupton, 1976). It is usually evaluated in plant breeding to detect hybrid vigor for the production of hybrids. In such cases, the performance of the F_1 is either compared to the mean performance of its parents or the better parent.

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Table 4.13. Estimates of mid-parent heterosis on shattering and other agronomic characters.

	% heterosis			
Character	***Jenguma x 'Quarshie'***	***Jenguma x Salintuya-1***	***Jenguma x Salintuya-2***	**Mean**
DFF	-17.9	-18.8	-22.9	-19.9
Plant height	-23.2	-13.8	-34.4	-23.8
Maturity	1.5	1.5	-0.9	0.7
Primary branches	23.5	37.3	17.6	26.1
Canopy spread (cm)	25.2	13.9	32.0	23.7
Pods/plant	5.8	50.5	107.4	54.6
Seeds/pod	9.2	17.3	-1.0	8.5
Shattering	-23.3	-44.1	55.67	-3.9

4.13 Gene effect in *Jenguma x Quarshie* cross

Gene effects were estimated using non-weighted least square mean method (Hayman, 1958) and are listed in (Table 4.14). The mid-parent (*M*) value for shattering resistance was 3.67 and was highly significant. Additive (*d*) gene effect was negative (towards the susceptible parent) but dominance (d), additive x additive (*aa*) and additive x dominance effects were negative (towards the resistant parent). Dominance x dominance was significant and positive (towards the resistant parent) and had the greatest magnitude of any single effect. However, positive *j* effect was reduced by negative *d* effects. These results indicate that epistasis was involved in the inheritance of resistance to pod shattering in the cross and both additive x dominance and dominance x dominance gene effects contributed significantly to the inheritance of resistance to pod shattering in soybean.

Table 4.14. Estimates of gene effects for pod shattering resistance in (*Jenguma x „Quarshie"*).

Parameter	Estimate	SE-means	t-value	Probability
M	3.67**	0.42	8.79	< 0.0001
d	-1.00	0.59	-1.69	0.12
h	-4.33	2.11	-2.06	0.07
l	-3.33	2.04	-1.63	0.13
i	-3.33*	1.33	-2.53	0.03
J	7.33*	3.07	2.39	0.04

M= mean of F2 d= sum of additive effect h= sum of dominance effect l= sum of additive x additive effect i= sum of additive x dominance effect J= sum of dominance x dominance effect

4.14 Gene effect in *Jenguma x Salintuya-1* cross

The mid-parent value of 5.00 was significant ($p<0.01$). Dominance effect was significant ($p< 0.05$) and negative (-4.5) towards the resistant parent. Additive x dominance was the only form of epistasis that was significant and negative (towards the resistant parent). Dominance appeared to be the most important factor contributing to the genetic control of resistance to shattering and was enough to explain the genetic control in the cross (Table 4.15)

Table 4.15 Estimates of gene effects for pod shattering resistance in (*Jenguma x Salintuya-1*) cross.

Parameter	Estimate	SE-means	t-value	Probability
M	5.00**	0.3	13.89	< 0.0001
d	-0.67	0.51	-1.31	0.22
h	-4.5*	1.82	-2.48	0.03
l	-2.67	1.76	-1.51	0.16
i	-3.00*	1.14	-2.63	0.03
J	-1.67	2.65	-0.63	0.54

M= mean of F2 d= sum of additive effect h= sum of dominance effect l= sum of additive x additive effect i= sum of additive x dominance effect J= sum of dominance x dominance effect

4.15 Gene effect in *Jenguma x Salintuya-2* cross

The mid-parent value was 3.33 (Table 4.16). Additive effect was positive towards the susceptible parent. Dominance, additive x additive and additive x dominance effects were negative towards the susceptible parent. The dominance x dominance effect appeared to be the only gene effect that was significant ($p< 0.05$) and was positive towards the resistance parent. These results indicate that epistasis was involved in the inheritance of resistance to pod shattering in this cross and dominance x dominance gene effects contributed significantly to the inheritance of resistance to pod shattering.

Table 4.16. Estimates of gene effects for pod shattering resistance in (*Jenguma x Salintuya-2*) cross.

Parameter	Estimate	SE-means	t-value	Probability
M	3.33**	0.33	10.17	<0.0001

d	1.00	0.46	2.16	0.06
h	-0.67	1.65	-0.40	0.70
l	-2.00	1.61	-1.25	0.24
i	-1.33	1.04	-1.29	0.23
J	6.67*	2.41	2.77	0.02

M= mean of F_2 d= sum of additive effect h= sum of dominance effect
l= sum of additive x additive effect i= sum of additive x dominance effect
J= sum of dominance x dominance effect.

4.16 Gene effect for resistance to pod shattering in three soybean crosses

Generation mean analysis used to test the six-parameter model to explain the genetic control of resistance to pod shattering in three soybean crosses involving a resistant parent and three parents with different levels of susceptibility to shattering are listed in (Table 4.17). The midparent point ranged from 3.33 to 5.00 for all three crosses. Dominance *(h),* additive x additive *(l)* and additive x dominance (*i*) were negative and (towards the resistant parent). Additive effect was negative in *Jenguma x „Quarshie"* and *Jenguma x Salintuya-1* crosses (towards the susceptible parent). Dominance x dominance effects (*j*), where significant, was always positive (towards the resistant parent) and had the greatest effect. In the Jenguma x Salintuya1 cross the dominance effect was enough to explain the genetic control of resistance to shattering. There were epistasis effects in the *Jenguma x „Quarshie"* and *Jenguma x salintuya2* crosses. In these crosses, the dominance x dominance was always significant ($p<0.05$) and positive (towards the resistant parent). The negative sign attached to the additive effects was not important and had no significant meaning. It was only a result of which parent was chosen as P_1. The sign of *h,* (dominance) effects was a function of the F_1 mean value in relation to the mid-parent value and indicated which parent was contributing to the dominance

effect. Dominance effects in the *Jenguma/,,Quarshie"* and *Jenguma/ Salintuya-1* crosses were contributed by the genes differing in the *Jenguma* (resistant) parent while in the Jenguma/salintuya-2 cross the dominance effects were contributed by the *Salintuya-2* (susceptible) parent. These results show that in the development of resistance to pod shattering in soybean, the dominance effect depends on the level of resistance of both parents involved in the cross.

Table 4.17. Estimates of gene effects for resistance to pod shattering in three crosses.

Parameter	Estimates		
	Jenguma x 'Quarshie'	***Jenguma x Salintuya-1***	***Jenguma x Salintuya-1***
M	3.67±0.42**	5.00±0.36**	3.33±0.33**
d	-1.00 ±0.59	-0.67 ±0.51	1.00 ±0.46
h	-4.33±2.11	-4.5 ±1.82*	-0.67±1.65
l	-3.33±2.04	-2.67±1.76	-2.00 ±1.61
i	-3.33±1.33*	-3.00 ±1.14*	-1.33 ±1.04
j	7.33 ±3.07*	-1.67 ±2.65	6.67 ±2.41*

M= mean of F_2 d= sum of additive effect h= sum of dominance effect l=sum of additive x additive effect i= sum of additive x dominance effect J= sum of dominance x dominance effect.

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5.0 CONCLUSION AND RECOMMENDATION

5.1 Conclusions

From the results of the study the following conclusions can be drawn:

1. The study detected non allelic interaction for pod shattering resistance among the crosses used and showed shattering trait to be partially dominant over resistance and under the control of two genes.
2. Inheritance of resistance to pod shattering in soybean is qualitative and influenced by duplicate recessive epistasis or dominant and recessive epistasis depending on the parental genotypes used in the cross.
3. Inheritance of resistance to pod shattering in soybean is not influenced by maternal effects, suggesting that choice of maternal parent is not important in hybridization programme that focus on the improvement of soybean for resistance to pod shattering.
4. High narrow sense heritability (h^2_{ns}) estimates (0.92) indicate that it is possible to transfer the resistant genes to a susceptible variety in a relatively short period. This agrees with conclusion of Carpenter and Fehr (1986) that the shattering trait could be eliminated by three to four backcrosses.
5. Both additive and non additive gene effects were significant in the expression of resistance to pod shattering in the four varieties. Additive x dominance (*i*) and

6. dominance x dominance (*j*) were the epistasis forms that were of great importance in the expression of the trait, indicating that breeding procedures that make good use of these gene interactions can be employed to improve soybean for resistance to pod shattering

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5.2 Recommendations.

From the conclusion the following recommendations can be considered;

1. Since both additive and non additive gene effects were of great importance in expression of the trait, it is recommended that breeding methods, which make the best use of additive effects such as recurrent selection or diallel selection mating (DSM) (Asante et al, 2007) and the pedigree method are applied to develop lines with resistance to pod shattering in soybean. Selection for resistance can be made in an early generation segregation population because of the high genetic gain for selection at F_2 population.
2. It is recommended that stability of resistance to pod shattering in soybean be investigated.
3. Biotechnology techniques such as, molecular markers (MAS) or genetic mapping for identification of quantitative trait loci (QTL) that condition resistance to shattering should be considered to reduce the drudgery associated with the conventional method and also improve on the accuracy of results.
4. It is also important to investigate the biochemical mechanism of shattering.

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APPENDICES

SUMMARY OF ANOVA

Appendix 1. Genetic analysis of resistance to shattering in Jenguma x „Quarshie‟ cross.

Source	Degree of freedom	Sum of Squares	Mean sum of squares	F-value	P > F
Replication	2	1144.4	572.2	2.39	0.142

Generation	5	12863.6	2572.7	10.7	0.0009**
Model	7	14008.1	2001.2		
Error	10	2395.6	239.6		
Corrected Total	17	16403.6			

Grand mean= 41.7 Coefficient of variation= 37.1% Standard error of means=15.5

**Significant at 0.01

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Appendix 2. Genetic analysis of resistance to shattering in Jenguma x Salintuya-1cross.

Source	Degree of freedom	Sum of Squares	Mean sum of squares	F-value	P > F
Replication	2	13.4	6.7	0.07	0.94
Generation	5	16017.8	3203.6	31.95	<0.001**
Model	7	16031.2	2290.2	22.84	<0.0001**
Error	10	1002.6	100.3		
Corrected Total	17	17033.8			

Grand mean= 57.1 Coefficient of variation= 17.5% Standard error of means= 10.0

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Appendix 3. Genetic analysis of resistance to shattering in Jenguma x „Quarshie" cross.

Source	Degree of freedom	Sum of Squares	Mean sum of squares	F-value	P > F
Replication	2	34.8	17.4	0.12	0.89
Generation	5	18214.9	3642.9	25.11	<0.0001**
Model	7	18249.7	2607.1		

Error	10	1450.6	145.0
Corrected Total	17	19700.3	

Grand mean= 37.4 Coefficient of variation= 32.2% Standard error of means= 12.0

Appendix 4. Frequency distribution of shattering resistance in F_2 generation of *Jenguma x „Quarshie"* cross.

x	f	fx	$(x- \mu)^2$	$f(x- \mu)^2$
0	22	0	7.40	162.76
1	55	55	2.96	162.71
2	40	80	0.52	20.74
3	18	54	0.08	1.41
4	17	68	1.64	27.85
5	12	60	5.20	62.38
6	10	60	10.76	107.58
7	7	49	18.32	128.23
8	4	32	27.88	111.51
9	6	54	39.44	236.63
10	1	10	53.00	53.00
	Σ f 192	Σ fx 522	$\Sigma(x- \mu)^2$ 167.2	$\Sigma f(x- \mu)^2$ 1074.8

n=192 μ= fx/ f = 522/192= 2.72 $S^2= \Sigma f(x- \mu)^2/n-1$= 1074.8/191=5.63 S= 2.3

Appendix 5. Frequency distribution of shattering resistance in F_2 generation of *Jenguma x Salintuya-1* cross.

	f			$f(x- \mu)^2$ x
fx $(x- \mu)$ 0 30 0 2.40 72				
1	55	55	0.30	16.5
2	50	100	0.20	10
3	11	33	2.10	23.1

4	10	40	6.00	60
5	1	5	11.90	11.9
6	1	6	19.80	19.8
7	0	0	29.70	0
8	1	8	41.60	41.6
9	0	0	55.50	0
10	0		0 0	71.40
	Σ f 159	Σ fx 247	Σ f(x-	Σ(x- μ)^{2}240.9 μ)^2 255.0

n=159 μ= fx/ f =247/159=1.55 S^2= Σ f(x- μ)^2/n-1=255.0/158=1.61 S=1.26

Appendix 6. Frequency distribution of shattering resistance in F_2 generation of *Jenguma x Salintuya-2* cross.

x	f	fx	(x- μ)^2	f(x- μ)^2
0	8	8	25.3	202.41
1	22	22	16.24	357.28
2	25	50	9.18	229.52
3	13	39	4.12	53.57
4	12	48	1.06	12.73
5	12	60	0.0009	0.01
6	22	132	0.94	20.69
7	30	210	3.88	116.43
8	20	160	8.82	176.42
9	20	180	15.76	315.2
10	5	50	24.7	123.5
	Σ f 189	Σ fx 959	Σ(x- μ)^2 110	Σ f(x- μ)^2 1607.76

n=189 μ= fx/ f =959/189= 5.07 S^2= Σ f(x- μ)^2/n-1= 1607.76/188= 8.55 S= 8.55

Appendix 7. Determination of variance components for shattering resistance using Mather and Jinks (1971) formula.

Vp_1= 0

Vp_2 = 0.33

VF_1 = 0.33

VF_2 = 2.33

VBC_1 = 0.33

VBC_2 = 0.33

$$VF_2 = \frac{1}{2}A + \frac{1}{4}D + E$$

but $E = \frac{Vp1 + Vp2 + VF1}{3}$

E= 0+0.33+0.33/3 = 0.22

E = 0.22

$\frac{1}{2}A + \frac{1}{4}D + 0.22$ 2.33 =

$\frac{1}{2}A + \frac{1}{4}D$ 2.33- 0.22 =

$\frac{1}{2}A + \frac{1}{4}D$ 2.11=

VBC + $VBC_2 = \frac{1}{2}A + \frac{1}{2}D + 2E$ 1

0.33 + 0.33 = $\frac{1}{2}A + \frac{1}{2}D$ + 2(0.22)

0.66-0.44 = $\frac{1}{2}A + \frac{1}{2}D$

0.22 $\frac{1}{2}A + \frac{1}{2}D$ =

$\frac{1}{2}A$ + $\frac{1}{4}D$ 2.11 = (solving two equations simultaneously)

- $\frac{1}{4}D$ = V_D 1.89 =

D = -7.56

$\frac{1}{2}A$ 2.11 = + -1.89 (Substituting 1/4D with -1.89)

2.11 + 1.89 = $\frac{1}{2}A$

$\frac{1}{2}A$ = V_A

4 =

A = 8

Appendix 8. Estimation of broad sense (h^2_{bs}) and narrow sense (h^2_{ns}) using the variancecomponent method.

Using data from appendix 4 above $h^2_{bs} = \frac{VG}{VPh}$

But $V_G = V_A + V_D$

= 4 + -1.89

V_G = 2.11

$Vph = V_A + V_D + E \quad = 4 + -1.89 + 0.22$

$Vph = 2.33$

$h^2_{bs} = \frac{2.11}{2.33} = 0.90$

$h^2_{bs} = 0.90$

Narrow sense heritability (h^2_{ns}) = $\frac{VA}{VPh}$

$h^2_{ns} = \frac{4}{2.33} = 1.72$

$h^2_{ns} = 1.72$

Appendix 9: Estimation of narrow sense heritability (h^2_{ns}) on resistance to shattering using Parent - offspring regression.

	Rep	X (mid-parent)	Y (F_1, Offspring)	XY	X^2
1	4.5	3	13.5	20.25	
2	4.5	3	13.5	20.25	
3	4.0	4	16.0	16.0	
	$\sum X = 13.0$	$\sum Y = 10$	$\sum XY = 43$	$\sum X^2 = 56.5$	

$$B = \frac{\sum XY - \frac{\sum X \sum Y}{N}}{\sum X^2 - \frac{(\sum X)2}{N}} \quad \frac{43 - \frac{13x10}{3}}{56.5 - \frac{(13)2}{3}} =$$

$$= \frac{43 - 43.33}{56.5 - 56.332} \quad = \frac{-0.33}{4.17} \quad = -0.08$$

b = -0.08

h^2_{ns} = -0.08 or 0.00

Appendix 10. Estimating number of genes contributing to shattering resistance according to Bjarko and Line (1986) formula.

$$N = (GR)^2 \left([1.5 - 2h(1-h)]/8\right) \times \left[(VF_2) - \left(\frac{[Vps + VpR + 2VF1]}{4}\right) \right]$$

$$h = \frac{F1m - PR}{PR - PS}$$

Where;

N = estimated number of genes.

F1m = mean of F_1

P_{Rm} = mean of resistant parent

P_{Sm} = mean of susceptible parent

GR = difference between susceptible and resistant parents (P_S -P_R)

VF_1, VF_2, V_{pR} and V_{ps} are variance of F_1, F_2, resistant and susceptible parents respectively.

P_{Rm} = 5.0 V_{pR} = 0

P_{Sm} = 3.67 V_{ps} = 0.33

F_{1m} = 3.33 VF_1 = 0.33

F_{2m} = 3.67 VF_2 = 2.33

$$h = \frac{F1m - PR}{PR - PS} = \frac{3.33 - 5.0}{3.67 - 5.0} = \frac{-1.67}{-1.33} = 1.26$$

h= 1.26

$(GR)^2 = (P_S - P_R)^2 = (3.67\text{-}5.0)^2 = 1.8$

$$\frac{[1.5 - 2h(1-h)]}{8}$$

$$= \frac{[1.5 - 2(1.26)(-0.26)]}{8} = \frac{2.1552}{8} = 0.27$$

$$= (GR)^2 \frac{[1.5 - 2h(1-h)]}{8} = 1.8 \times 0.27 = 0.49$$

$$= \left[(VF_2) - \left(\frac{[Vps + VpR + 2VF1]}{4}\right) \right]$$

$$= 2.33 - \frac{[0.33 + 0 + 2(0.33)]}{4} = 2.33 - 0.25 = 2.08$$

$n = (GR)^2 [1.5\text{-}2h (1\text{-}h)]/8 \times (VF_2\text{-}(V_{ps}+V_{pR}+2VF_1)/4)$

$n = (1.8) \times (0.27) \times (2.08) = 1.01$

Estimated number of genes =

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Plates showing developmental stages of the study

Plate 1: Artificial pollination in progress.

Plate 2: F_1 progenies growing in pots

Plate 3: Backcross progenies at pod formation.

Plate 4: F_2 progenies at harvest maturity.