

GENETICS OF RESISTANCE TO POD SHATTERING IN SOYBEAN

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other University.

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DEDICATION

In memory of my late parents, Samwiri Bitara and Dorokasi Kanshamare Bitara
for their good example and sacrifice in education of their children

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MAY THE LORD'S NAME BE PRAISED.

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ABSTRACT

Hybridization among ten pure breeding lines of soybean was made in 1997 to study the inheritance of pod shattering in soybean. Lines Nam 2, Roan, Duiker, TGx 1448-2E and GC 81090-2E were resistant, AGS 292 and TGm 737P susceptible while Kabanyolo 1, Nam 1 and Samsay 1 were intermediate to pod shattering. Preliminary evaluations for pod shattering among F_2 segregating populations were carried out in oven conditions at 60°C for 12 hours, 80°C for 6 hours and 80°C for 12 hours. Scales of 1 - 5 and 0 -10 were used to group segregating populations into their shattering phenotypes. The 1 - 5 scale was modified into 1 - 3 scale in which 1 was regarded as resistant, 2 intermediate and 3 susceptible. The pods of parental lines, F_1 , F_2 , F_3 and F_4 progenies were assessed for shattering using an oven set at 80°C for 12 hours. A Chi square test was used to determine the departure of the observed frequencies from the expected ones. Maternal influence on the inheritance of pod shattering was determined using crosses of TGm 737P x Duiker, TGm 737P x Roan and AGS 292 x TGx 1448-2E and their reciprocals. The original Castle-Wright's method used by Zeng *et al.* (1990) was used to estimate the number of loci and Bjarco and Line(1987) method was used to determine the number of genes. The half diallel mating design was used to estimate genetic parameters and to detect presence of non allelic interaction of genes affecting pod shattering following analyses by Hayman (1954) and Griffing(1956).

Six lines, Nam 2, TGx 1448-2E, Duiker, Nam 1, TGm 737P and Kabanyolo 1 were grown at three locations during first and second seasons of 1997 and first

season, 1998 to determine amount of seed yield lost in the field due to pod shattering and effect of G X E interactions. Weather parameters were recorded at the locations starting from physiological maturity stage. Basing on the number of shattered and unshattered pods, an extrapolation model was developed and applied to determine the amount of soybean seed yield lost in the field due to pod shattering.

The phenotype of F_1 plants was closer to that of susceptible parents indicating partial dominance and the distribution of F_2 population was not discrete and could not fit Mendelian ratios. Based on a 1 - 3 scale, the distribution best fitted the 1:3:12 genetic model suggesting pod-shattering trait to be conditioned by 2 genes and classical dominant epistasis. The ratios obtained from the single plant progenies advanced to F_3 and F_4 were in agreement with expected ratios of 16:0:0, 0:16:0, 0:0:16, 0:4:12, 4:0:12, 4:12:0 and 1:3:12 for resistant: intermediate: and susceptible phenotypic ratios respectively, confirming dominant epistasis. The improvement made on the oven method to evaluate resistance to pod shattering was effective in terms of reduced time for the experiment to be accomplished and in identification of consistent genetic ratios. There was no significant difference between reciprocal crosses of susceptible and resistant varieties suggesting absence of maternal effects. The parent offspring regression technique indicated that heritability in the narrow sense was 0.73 while estimates from Hayman's and Griffings' diallel was 0.70. The mean number of segregating genes was estimated to be 2.21 at F_2 and 2.24 at F_3 , and the mean number of loci for ten different crosses was 1.65.

Hayman's diallel analysis indicated significant variation of $W_r + V_r$ and $W_r - V_r$ over arrays suggesting epistatic gene action. Similarly results from a joint regression coefficient over replications were significantly ($P < 0.05$) different from unity and zero which further indicated presence of non allelic interaction of genes. The intercept was positive suggesting partial dominance. Varieties AGS 292 and TGm 737P contained more dominant alleles while Nam 2 and Roan contained more recessive alleles than the other parental lines. Both general combining ability (GCA) and specific combining ability (SCA) effects were significant ($P < 0.05$) and the ratio of GCA to SCA was significant ($P < 0.05$) indicating that additive gene effect was important for the shattering trait. Parental lines with high negative GCA effects were Nam 2, Roan and TGx 1448-2E qualifying them as suitable parents for transferring resistance to pod shattering in their progenies and subsequent selected lines.

Yield losses in susceptible and intermediate susceptible varieties ranged from 57 - 175 kg ha⁻¹ and 0 - 186 kg ha⁻¹ respectively depending on genotype, location, season and harvesting date. Delay of harvesting for 14 days from harvesting maturity stage does not lead to significant yield loss due to pod shattering when intermediate varieties are grown as opposed to susceptible ones which start shattering at R8 maturity stage. It was demonstrated that the developed extrapolation method was accurate in estimation of field yield loss due to pod shattering in soybean and produced estimates, which were not significantly different from actual yield loss. The resistant variety did not shatter even when harvested after 21 days. Due to significant influence of genotype, location and

season on pod shattering in soybean, It is recommended that selections for resistance to pod shattering be carried out in different agro- ecological zones over several seasons to cater for the genotype x environment interactions.

1 CHAPTER ONE

1.0 INTRODUCTION

The cultivated soybean *Glycine max* (L.) Merr. ($2n=40$) is a relative of wild soybean *Glycine soja* ($2n=40$) and is ranked the most important grain legume crop in the world (Anon, 1989). It was first domesticated in China some 3000 years ago (Hapgood and Johns, 1987). It occupies a premier position as a world crop because of its high and virtually unrivalled, protein content (40%) and the rich source of high quality edible oil (20%) which makes it a food crop with great potential to improve the diets of millions of people in developing countries (Carrao and Gontijo, 1994)

The global annual production was estimated at 130 in 1996, 143, and 156 million tones from 1997 to 1999 respectively (Anon, 1999), indicating steady increase in world production. By far the largest commercial cultivation of soybeans is in the USA, followed by Brazil. The USA produces more than 60 million tones of soybean worth five billion dollars year⁻¹ and exports half the crop. In the orient, soybeans has been ingeniously transformed into many protein rich products (Hapgood and Johns, 1987) that are consumed as food. This allows China to feed a quarter of World's population on a tenth of its arable land. The Western diet is built on soybean and is a major hope for averting world famine. However, soybean cultivation and utilization in developing countries is still minimal (Singh *et al.* 1987 and Waymark, 1997).

The major areas of soybean production were restricted to temperate regions of the world until the mid 1940's, when the area of production started to spread to tropical and sub-tropical regions. These areas are characterized by warmer and more humid conditions and pose different production problems such as shattering and reduced seed viability (Franca Neto *et al.* 1994). Pod shattering refers to the opening of pods along both the dorsal and ventral sutures. In Africa, the major producing countries are Egypt, Zimbabwe, Nigeria and South Africa (Kollarali *et al.* 1987). While world annual production of soybean grew by 2.19%, Africa registered the highest growth rate of 9.41% followed by Latin America with 5.9% (Anon, 1992). In the same year, the growth rates for the near East and far East were estimated at 3.60% and 3.99%, respectively.

Over the last decade IITA working with other several national research institutes in Nigeria have popularised soybean production and consumption using acceptable recipes for the incorporation of soybean into local dishes. This effort to introduce soybean into the humid tropics have started bearing fruit according to a report by Anon (1998a) where communities producing and using soybeans had more nutritionally normal children and fewer malnourished children than those which didn't. In the Nigerian Guinea savanna, adoption of soybean has had a clear positive impact on household social economic status of rural communities by enhancing better nutritional status of children and income of both men and women (Sanginga, 1999).

In farming systems, soybean has been reported to improve soil properties by enhancing moisture retention and atmospheric nitrogen fixation to the benefit of the following maize and wheat crop in Zimbabwe (Anon, 1988a). In another report, (Anon, 1990) observed that soybean can fix over 100 kg of atmospheric nitrogen hectare⁻¹ year⁻¹, while Carsky (1995) reported 28 - 188kg of nitrogen fixation hectare⁻¹ year⁻¹ depending on variety. When soybean is grown in rotation with maize, wheat or rice their pests as well as those of soybean have been reported to be reduced (Pandey, 1987 and Waymark, 1997). The combination of pest suppression and nitrogen fixation make soybean an ideal crop for rotating with cereals.

In Uganda, soybean is relatively a new crop, but the area under soybean is rapidly increasing (Anon, 1999). Soybean was introduced between 1908 and 1913 ((Rubaihayo and Leakey, 1970; Hittle, 1988). By 1965, the initial germplasm collection was established at Kabanyolo while research was being conducted at both Kawanda and Kabanyolo (Rubaihayo and Leakey, 1970). Interest in soybean production has been in response to three main factors : Recognition of the need for agricultural diversification, interest shown by foreign buyers, and the potential of soybean in improving human nutrition (Leakey and Rubaihayo, 1970).

From 1971 up to 1980, average annual production was estimated at 4900 metric tones harvested from 5,600 hectares (Ddamulira, 1984). In a report by Ngambeki (1992), the major producing areas by national total

percentage in 1989 were: Iganga 29.6%, Kamuli 26.2%, Rakai 10.6%, Jinja 4.74% and Mbale 4.3% . The districts of Lira, Pallisa and Tororo have also adopted soybean production (Tukamuhabwa, 1992). The production of soybeans in Uganda was 71,000 metric tones in 1993 produced from an area of 65,000 hectares (Anon,1993a).

The yield potential of improved varieties range from 2.0 - 3.0 tones hactare ⁻¹ depending on management (Tukamuhabwa, 1992). Currently soybean is one of the non traditional export crops, raw material for some local food processing firms, oil and feed mills (Anon, 1998b). Some of the soybean food products found on Ugandan markets include: soyflour, baked products with soybean as an additive, soy beverages, roasted soybean, animal feeds, and vegetable oil (Tukamuhabwa,1994).

Soybean suffers from many production constraints which include: low seed longevity, pests and diseases, lodging and pod shattering. Seed losses of 50-100% are often associated with pod shattering in susceptible varieties and delayed harvesting after maturity (Anon, 1986), denying farmers time to plan for harvesting before pods start shattering. Shortage of labour and harvesting equipment can postpone harvesting when the farmer is otherwise prepared to harvest, leading to seed yield loss when harvesting is carried out during dry weather conditions. This calls for resistant varieties that can stand relatively longer periods in the field after maturity.

Tiwari and Bhatnagar (1988), observed a considerable genetic variation

among soybean germplasm in their ability to hold seed after reaching maturity. They suggested that development of commercial cultivars resistant to shattering was possible. After screening twenty five varieties, they found two to be very resistant, eight resistant, eight moderately resistant, two moderately susceptible and five highly susceptible. In another study, Tiwari and Bhatnagar (1991) showed that, three of the popular Indian varieties (Punjab-1, JS-2 and Kalitur) were vulnerable to shattering and recommended further studies on this trait under tropical and sub-tropical conditions in order to reduce losses due to shattering.

Ferraz de Toledo *et al.* (1994) reported that shattering in soybean was the most important constraint to soybean production in the tropics. Work at International Institute of Tropical Agriculture (IITA) showed that resistance to shattering was of great economic benefit to farmers in the hot tropics and areas where machines were used for harvesting in terms of reduced yield losses and planning for time and labour (Anon, 1986). If a variety has good resistance to shattering, then farmers can plan flexibly and harvest up to 3-4 weeks after maturity without experiencing significant yield losses (Anon, 1986). Research efforts on shattering in the temperate regions where soybean has been extensively studied and grown are limited because shattering is not perceived as a significant problem under temperate conditions (Caviness, 1969; Dean, 1972; Tsuchiya, 1987 and Anon 1992). This has led to the scarcity of information on genetics of shattering in soybeans (Misra *et al.* 1980 and Bailey

et al. 1997)

A survey conducted in Benue state, Nigeria in 1989 and 1990, found that the most important constraint to soybean production was pod shattering. Based on this survey, resistance to pod shattering is a major priority of IITA's soybean breeding program (Anon, 1992). In another survey by Sanginga *et al.* (1999) in the same region, resistance to pod shattering was found to be a pre-requisite for adoption of any variety by the farming communities.

The area under soybean production in Uganda (Tukamuhabwa, 1992) and in tropical regions (Franca Neto *et al.* 1994), is expanding, thus harvesting within a few days is becoming impossible due to labour shortages. Varieties which are resistant to shattering are therefore highly desirable but some commercial varieties in Uganda are susceptible to shattering; moderately resistant varieties like Nam 1 shatter when they are left to stay in the field for about a week beyond harvesting maturity.

Use of resistant varieties has been recommended as the most cost effective control measure against soybean losses due to shattering (Tiwari and Bhatnagar, 1989). However, in order to initiate an effective shattering resistance breeding program, it is necessary to understand the genetics of the resistance to shattering so that an effective breeding technique is employed. The most efficient breeding procedure to enable selection of superior genotypes in inbred crops like soybean depends on the magnitude of additive genetic variance of that trait (Kearsey and Pooni, 1996).

Heritability (h^2) as described by Caviness (1963), is a statistical tool used to evaluate the genetic control of traits determined by many loci and can be used to effectively plan strategies for incorporating characters into new cultivars. However, only estimates of broad sense heritability (h^2_b) for shattering resistance have been reported in literature (Caviness, 1963; Tsuchiya, 1987; Tiwari and Bhatnagar, 1991). Broad sense heritability estimates include additive, dominance and epistatic sources of genetic variation while narrow sense heritability (h^2_n) is a reflection of additive effects. Thus, h^2_n results in a more reliable genetic parameter on which to base a breeding procedure. Information is therefore necessary to establish h^2_n of pod shattering trait and the number of genes conditioning the expression of shattering to be able to develop more efficient methods for selecting shattering-resistant genotypes of soybean.

No work has been reported in literature which has attempted to adequately partition the total genetic variability observed into the different genetic components although this is an important prerequisite to designing an effective breeding program. One of the mating techniques appropriate for self fertilizing crop species is the diallel design (Gumisiriza, 1987; Christie and Shattuck, 1992) with Hayman (1954) analysis being the most satisfactory for a complete set of diallel. In the case of shattering investigation therefore, the diallel cross technique would be the most suitable method.

Observations made by Misra *et al.* (1980) on the relationship between shattering and relative humidity (RH) indicated that high humidity at time of ripening may induce more shattering. Tiwari and Bhatnagar (1989) reported that, shattering was enhanced when rains were followed by dry weather near harvesting time. High humidity and rains during harvest period are common in the humid tropics. Philbrook and Oplinger, (1989) suggested that although shattering was a function of grain and plant moisture content, plant weathering and deterioration made greater contributions to shattering losses when harvesting was delayed longer than 14 days. Tsuchiya (1986) showed that moisture content (MC) of pods decreased gradually as the crop matured in the field with susceptible varieties beginning to shatter at 10-15% MC while resistant cultivars began shattering below 10% MC. Sinclair and Backman, (1989) reported that high temperature and humidity favour development of fungal pathogens in soybeans that induce more shattering.

Several methods have been used to evaluate pod shattering in soybean. Caviness, (1965) used varying humidities (15 – 60%) and alternating wetting and drying of pods to assess pod shattering in soybean. These assays required eight days, which calls for shorter alternative procedures. Caviness (1969) defined shatter resistance as the number of days from plant maturity to the first shattered pod. This method does not have a universal application to all environmental conditions for screening soybean germplasm, such as wet weather conditions when pods cannot shatter. Tsuchiya and Sunada (1980a)

compared field and oven methods for screening soybean germplasm and found the results from the oven method to be more consistent and repeatable. Tsuchiya (1987) also found using a drier for evaluating pod shattering, to give clearer results than field testing under high humid field conditions. Misra *et al.* 1980 observed that genetic study for pod shattering in soybean was very difficult due to lack of discrete distribution at F₂. They further reported that the available literature was inconsistent. Akpan (1988) noted that different methods used to study pod shattering produced different results and called for improvement in the methods used to study pod shattering in soybean.

A ballistic pendulum device was proposed by Hoag (1972) to facilitate measuring soybean shattering in the field and a laboratory based equipment (Ottawa texture meter) was developed to screen mature soybean pods for shattering resistance by Mundel and Mains (1981). The devices however have not been widely used due to high cost and lack of portability. Lamp *et al.* (1962) and Nave *et al.* (1973) made yield loss estimates due to pod shattering focusing on combine header losses. Such losses are different from losses incurred in the tropics where pod shattering is spontaneous due to environmental stress on the pods. Thus, losses incurred in the tropics necessitate methodologies suitable for estimation of specific yield losses experienced under such conditions.

On the basis of information available in literature, there is inadequate knowledge on the genetics and genotype x environment effects of soybean shattering, and there is need for more accurate methods for studying pod shattering in soybean. The magnitude of losses due to soybean shattering under humid tropical conditions have not been quantified. These knowledge gaps formed the main objectives of the studies presented in this thesis.

The specific objectives were to:

- (a) Improve methodology for studying inheritance mechanism of pod shattering in soybeans
- (b) Determine the inheritance mechanism of pod shattering in soybeans
- (c) Estimate narrow sense heritability for pod shattering in soybean
- (d) Develop a methodology for determining yield loss due to soybean shattering in the field
- (e) Quantify yield loss from soybean shattering under different environmental conditions.

2 CHAPTER TWO

2.0 LITERATURE REVIEW

Shattering problem is not restricted to soybean alone but also common in other crops where it reduces harvestible yield, and quality of the produce. Consequently, genetic studies have been carried out to understand the inheritance mechanism in such crops and help plan breeding programme. In pea (*Pisum sativum*), shattering is controlled by a single recessive gene with no maternal effects (Shevchenko, 1980). In a different study Petrick (1985) did not find any shattering individuals among F_1 progenies of *Pisum sativum* suggesting shattering resistance is controlled by dominant genes.

In *Papaver bracteatum* Lindl., a single dominant gene confers resistance to shattering (Arieh, 1985). In guar (*Cyamopsis tetragonoloba* (L.) Taub), a single locus controls pod shattering, while susceptibility, found in the wild species was dominant over resistance in domesticated species (Dabas and Thomas, 1986). Aliboh *et al.* (1996) found that pod shattering in cowpea (*Vigna unguiculata* (L.) Walp was controlled by one dominant gene with an F_2 population ratio of 3 susceptible : 1 resistant, implying shattering trait can easily be manipulated through breeding. Young *et al.* (1991) have also observed transfer of resistance to pod shattering through an interspecific somatic hybrid between birdfoot trefoil (*Lotus corniculatus* L., $2n=4x=24$) which is susceptible to shattering and *Lotus conimbricensis* Brot. wild, ($2n=2x=12$), completely resistant to

shattering. Shattering resistance in birds foot trefoil *Lotus corniculatus* L is, considered to be highly heritable under the control of more than one gene (Grant, 1996).

Current wild rice (*Zizania palustris* L.) has two complementary genes in which complete seed shattering is dominant, but inheritance studies involving older cultivars and wild relatives indicate a trend for major gene control (one to three loci) with intermediate types suggesting existence of modifying genes (Everett and Stucker, 1983). Further studies on rice, found shattering to be controlled by a single recessive gene (Shinya *et al.* 1990). Similarly, Fukuta *et al.* (1994) reported shattering in five mutants of rice to be controlled by a single recessive gene, although the original line, Nan-jing11 had three partial dominant genes controlling the shattering trait.

Young (1990) reported heritability estimates for resistance to seed shattering in Klein grass (*Panicum coloratum* L) to be 0.38 - 0.40 with a large component of G x E interaction, suggesting that improvement for seed shattering resistance will be slow and will require replicated testing in multiple environments per cycle of selection.

A number of techniques have been developed and used to investigate the pod shattering trait in soybean. Through selfing procedure, Ting (1946) observed that segregation for shattering in F₂ generation was very complex due to lack of discrete observations and Misra *et al.* 1980 suggested that this phenomenon in soybean shattering made genetic study of the trait very difficult. Anon (1996) also observed

that when soybean matures in humid conditions, the environment does not favour pod shattering, even for very susceptible varieties. In such cases shattering resistance cannot be assessed. To facilitate selection for resistance to pod shattering, oven drying methods have been developed (Anon, 1986; Jiang *et al.* 1991; Tiwari and Bhatnagar, 1992). The ovens used were set at 30°C, 40°C and 60°C, and the time materials spent in the oven varied. Oven screening results for pod shattering have been found to correlate well with pod shattering results obtained under field conditions (Anon, 1986 and Jiang *et al.* 1991).

By working out the percentage of pods shattered in a plot, different scales have been used to assess soybean shattering: Anon (1979) used 1 - 5 scale to rate soybean shattering in which, 1 = 0% shattering, 2 = 1 - 10%; 3 = 11 - 25% ; 4 = 26 - 50% and 5 = 50% and above shattered. Anon (1993b) recommended another 1 - 5 scale where, 1= 0% shattering; 2 = 1 - 25%; 3 = 26 - 50%; 4 = 51 - 75% and 5 = 76% and above of the plants shattered and recently, Bailey *et al.* (1997) used a 0 - 10 scale, where 0 refers to < 1% shattering, while other levels 1 - 10 correspond to consecutive classes at an interval of 10 in increasing order.

Several genetic studies have been conducted to understand the genetic control of pod shattering in soybeans. Caviness (1969) found no significant variation between crosses involving domesticated cultivars and wild types in terms of shattering, however, Misra *et al.* (1980) observed a wide range of variation for shattering habit after treatment with gamma rays with the treated plants having a higher frequency of plants with

delayed shattering. Tsuchiya (1986) observed no significant differences among sources of resistance from Japan, USA, China and Thailand in conferring resistance to soybean shattering, indicating possibility of a narrow genetic base for the parental lines used. Tiwari and Bhatnagar (1988, 1989) studied 25 varieties of soybeans in India and found a wide range of shattering scores among the cultivars with two varieties rated highly resistant, eight resistant, eight moderate and two susceptible.

Caviness (1969) and Tsuchiya and Sunada (1980b) found susceptibility to soybean pod shattering to be partially dominant. 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. In the same study, significant ($P < 0.05$) combining ability and specific combining ability were observed. However, the additive gene action was predominant in the expression of the trait over dominance effect. They recommended further studies including F_2 progenies since the observations made were based on F_1 hybrids.

Segregation for soybean shattering in F_2 populations was found to be overlapping (Ting, 1946 and Caviness, 1969) suggesting polygenic inheritance. Misra *et al.* (1980) observed difficulty in rating shattering behavior of soybean genotypes and attributed this to the absence of discrete observations in filial generations, leading to further support for multiple genes. In an attempt to describe genetic variation, Griffiths *et al.*

(1997) suggested that if the difference between genotype means is small compared to the environmental variance, even one or two genes can result in continuous variation. Carpenter and Fehr (1986) observed discrete classes for shattering scores in segregating populations from crosses of cultivated soybean with its wild relative *Glycine soja* which is susceptible to shattering. They observed shattering frequency to decrease with each generation of backcrossing to the cultivars and suggested that shattering trait could be completely eliminated by three to four backcrosses suggesting fairly simple inheritance.

Caviness (1963) suggested that four major genes were involved in controlling susceptibility to shattering. Tsuchiya (1986) suggested that depending on the methodology used to rate shattering, a minimum number of genes varied between one and two. Akpan (1988) reported shattering in soybean to be controlled by six to twelve genes and recently Bailey et al. (1997) reported that one major quantitative loci (QTL) and a few minor QTLs interacting epistatically controlled pod shattering in soybean.

Several statistical methods have been proposed for estimating the minimum number of genes contributing to difference in traits between two inbred lines grown in a common environment. Castles -Wrights' method used by Cockerham, 1986; Zeng *et al.* 1990 and Hakiza, 1994 seem to be the simplest and most commonly used. The estimated number of genes is obtained by comparing the phenotypic means and variances of a trait of parental lines , F_1 , and F_2 populations (Lande, 1981).

Average broad sense heritability (h^2_b) estimate of shattering in soybean was put at 90% by Caviness (1969), 93% by Tsuchiya (1987) and 98.84% by Tiwari and Bhatnagar (1991) indicating that the character is highly heritable. However, narrow sense heritability (h^2_n) is the most useful parameter in designing appropriate breeding techniques, because it is a measure of genetic variation that is transferred from one generation to the next unaltered. Heritability in the narrow sense (h^2_n) can be achieved by parent offspring regression if parental values are means of both parents (Falconer, 1989, Kearsey and Pooni, 1996) or from the expected mean squares from ANOVA of the progenies of interest (Brim and Hanson, 1961; Fehr, 1987a). Simmonds (1981), Falconer (1989) and Boss (1993) suggested that heritability determined by the regression coefficient in case of random mating offers a more secure approach to h^2_n than the partition of variance. The h^2_n is of great practical importance to plant breeders since low h^2_n indicates that only a small fraction of trait of interest will be reflected in the next generation. The larger the h^2_n value the more the character will respond to selection (Lavett, 1993). Griffiths *et al.* (1997) reported low h^2_n as a result of small amount of additive variance compared to dominance interaction.

There is no report in literature with adequate information which attempts to partition the total variability observed into different genetic components although this is an important prerequisite to designing an effective breeding program. Kearsey and Pooni, (1996) reported that dominance and additive x dominance variances exist in self

fertilizing crops, but their importance in crop improvement is dependent on the relative magnitude of additive variance.

In order to develop a more efficient breeding procedure for a given trait, there is need to get better understanding of the type of gene action and the magnitude of additive and non additive genetic effects in control of the trait under consideration (Kang, 1994). Estimation of these parameters requires use of an appropriate mating design. One of the designs most commonly used for self fertilizing crop species is the diallel design (Gumisiriza, 1987; Christie and Shattuck, 1992). The advantage of diallel analysis is that it enables predictions to be made at early generations which increases the efficiency of a breeding program (Dickson, 1967). Diallel design has additional benefits in that the analysis applies to all the crosses involved and permits the estimation of parameters for additive, dominance and environmental effects and allows recognition of non allelic interactions (Jinks , 1956; Matther and Jinks, 1982; Christie and Shattuck, 1992). The most satisfactory analysis for a complete set of diallel in view of these aspects is that by Hayman (1954) described by Christie et al. (1988). Gumisiriza (1987) reported that theoretical considerations suggest that the diallel cross technique is a suitable method for the investigation of genetically controlled traits, and Kearsey and Pooni, 1996 reported that $covariance(W_r)/variance(V_r)$ graphical analysis is relevant where the trait in consideration displays non - additive variation).

Hoag, (1972) attributed losses due to shattering at 60% which accounted for over 170m American dollars annually in United States. Anon (1988b) in Turkey, estimated soybean yield losses due to shattering at between 77.5 kg ha⁻¹ and 607.6 kg ha⁻¹ while shattering rates varied between 2.3% and 23.5% depending on genotype. In field trials, Philbrook and Oplinger (1989) observed that shattering was the largest source of field losses in soybean in the South eastern USA, as it contributed 37% of total losses. Additionally, shattering was reduced by moisture at early harvesting but increased when harvesting was delayed. Yield losses due to shattering were estimated at 53 - 310 kg ha⁻¹. Delays from 0 to 14 and 28 to 42 days were not significant. Significant year x cultivar x harvest ($P<0.05$) and cultivar x harvest delay interactions ($P<0.05$) were observed.

Tsuchiya (1987) reported low humidity, high temperature, rapid temperature changes, alternating wetting and drying of soybean plants as common factors that induced pod shattering. Tiwari and Bhatnagar (1989) also reported that pod shattering is enhanced when rains are followed by dry weather at time of harvesting. Jiang *et al.* (1991) evaluated 216 soybean varieties and observed that shattering percentage increased with decrease of pod moisture content.

Akpan (1988) observed G x E interactions over season in populations of soybean at two locations in Nigeria. Tiwari and Bhatnagar (1993) tested 9 lines of soybean for stability of shattering across five locations in India and found the resistant genotypes (1.85 – 3.24 %

shattering) stable over the locations, suggesting minimal G x E effects ($P < 0.05$) for resistance to pod shattering. However, susceptible lines ranged between 1.27 – 45.53 % shattering and showed significant G x E effects ($P < 0.05$) on these genotypes suggesting that susceptibility to shattering was unstable. Similarly, significant G x E interactions (0.01) for pod shattering were observed by Bailey et al. (1997) using F_4 populations of soybean grown at two locations over one season in the USA.

In view of the available information on the subject matter, pod shattering is a major production constraint to soybean when susceptible varieties are grown. Several studies have been conducted to investigate the shattering trait and to find possible means of solving the problem. The available broad sense heritability estimates, indicate that the trait is highly heritable. The number of genes estimated is inconsistent and requires further studying, while the methods available to assess the trait need to be standardized for broad application. The amount of soybean yield lost due to pod shattering in the tropics has not been quantified. In regard to the effects of G x E on pod shattering, it is clear that both genotype, environment and harvesting date play a significant role in determining the magnitude of yield lost due to pod shattering in soybean.

3 CHAPTER THREE

3.0 MATERIALS AND METHODS

3.1 EXPERIMENT ONE:

GENETIC ANALYSIS OF POD SHATTERING

Ten parents characterized for their resistance to shattering were used for this study. Resistant genotypes were Nam 2, Roan, Duiker, TGx 1448-2E and GC 81090-48; susceptible genotypes were AGS 292 and TGm 737P, and intermediates were Kabanyolo 1 (Kab1), Samsoy 1 and Nam 1 (Table 1).

Table 1. Origin, pedigree and description of shattering resistance of parental lines

Genotype	Origin	Pedigree	Shattering description
TG x 1448-2E	Nigeria	(TGm 1193 x TGm 618) x (TGm 618 x TGm 7)	Resistant
Nam 2	Nigeria	87D - 668	Resistant
Roan	Zimbabwe	Kudu x 196/6/22	Resistant
Duiker	Zimbabwe	Oribi (15/6/12) x (15/6/22)	Resistant
GC 81090-48	China	Forrest x Shin Shin Tzuzunoko	Resistant
Kab 1	Uganda	Mutant of Clark 63	Intermediate
Samsoy 1	Nigeria	Clemson x Malayan	Intermediate
Nam 1	Colombia	Hales 3 x P1307-861	Intermediate
AGS 292	China	-	Susceptible
TGm 737P	Indonesia	Land-race	Susceptible

3.1.1 Hybridization and evaluation of F_1 and F_2 populations

Crosses were made between Roan x TGm 737P, TGm 737P x Roan, AGS 292 x Nam 2, Duiker x TGm 737P, TGm 737P x Duiker, TGX 1448-2E x AGS 292, AGS 292 x TGX 1448-2E, TGx 1448-2E x TGm 737P, AGS 292 x Roan, GC 81090-48 x AGS 292, and GC 81090-48 x TGm 737P in order to develop and apply a more accurate method for evaluating pod shattering at F_1 , study the segregating population distribution at F_2 , determine the effect of the maternal parent on shattering and estimate the number of genes controlling pod shattering. Emasculation was followed immediately by hand pollination. Before handling a different cross, the forceps and pins used to tease flower buds were sterilised in 70% alcohol to avoid contamination of the new cross with pollen from the previous parental line. The crossing exercise was carried out at 10.00 am and 5.00 pm in calm weather conditions.

F_1 plants were grown at Namulonge, Uganda at a spacing of 60 x 20cm to enhance plant vigour for maximum pod production in non replicated rows, and were harvested as single plants. Progeny advancement was carried out using plant to row technique. Starting from the F_2 generation the spacing was 60 x 5 cm to attain manageable experimental plot size. Care was taken during planting and harvesting to avoid mixing of progenies.

Using F_2 crosses of Roan x TGm 737P, TGm 737P x Roan, AGS 292 x Nam 2, Duiker x TGm 737P, TGm 737P x Duiker, TGX 1448-2E x AGS 292 and AGS 292 x TGX 1448-2E, a preliminary test for pod shattering was carried out.

Twenty pods from each plant were carefully detached at R8 stage (Gazzoni, 1994) when 95 % of pods have attained physiological maturity, put in paper bags (5 x 10 x 20 cm) and allowed to equilibrate to similar moisture content for ten days at room temperature. The pods were oven dried at 60°C for 12 hours, 80°C for 6 hours and 80°C for 12 hours. The oven and technique in which pods were fitted in the oven are illustrated in Plate 1. Since some plants did not raise twenty pods, percentage of pod shattering induced was recorded and determined according to a 0 – 10 scale used by Bailey *et al.* (1997) where 0 < 1% = 0, 1-10% =1, 11-20% = 2, 21-30%=3, 31-40% = 4, 41-50% = 5, 51-60%=6, 61-70%=7, 71-80 = 8, 81-90%=9, 91-100%=10. Shattering was also rated using the 1- 5 scale scale by Anon (1979) in which, 1 = 0% shattering, 2 = 1 - 10%, 3 = 11 - 25%, 4 = 26 - 50% and 5 = 50% and above shattered. The shattering phenotypes on the 1 – 5 scale were described as: 1 is very resistant, 2 is resistant, 3 is moderately resistant, 4 is moderately susceptible and 5 is very susceptible.

The scale suggested by Anon (1979) was modified into a 1 – 3 scale in which 0 - 10 % shattered pods were regarded as resistant, those varying between 11 and 70 % shattering as intermediates , those varying between 71 - 100% as susceptible. The shattering phenotypes on the 1 - 3 scale were described as: 1 is resistant , 2 is intermediate, and 3 is susceptible. A Chi square test to determine the departure of the observed frequencies from the expected frequencies was done basing on critical value of 5.991 for two degrees of freedom on the 0.05 probability level

(a)



Plate 1:

The oven used

in the study

(a) open with paper

bags containing

soybean pods

(b) closed one

side before being

switched on for

drying to start

(b)



3.1.2 Testing accuracy of the 1 - 3 scale

The relative accuracy of the 1-3 scale in determining the frequency distribution at F_2 was determined by carrying out analysis of variance of same data from crosses TGM 737P x Roan, AGS 292 x TGx 1448 -2E and TGM 737P x Duiker. The test was done on eight samples whose size varied from 25 to 150 plants. Separate analysis was done based on the 1 - 3 and 1 - 5 scales and the within(error) source of variation mean square (MS) for the two scales were compared.

All evaluations for pod shattering carried out at this stage and on wards were oven dried at 80°C for 12 hours. Shattering scores were based on percentage of pods dehisced per plant using the 1 – 3 modified scale and tested for significance, following procedures outlined above in this thesis. Further testing for pod shattering was carried out on the progenies of Roan x TGM 737P, TGM 737Px Roan, TGM 737P x TGx 1448-2E, GC 81090-48 x AGS 292 and GC 81090-48 x TGM 737P at F_1 and F_2 generations.

3.1.3 Evaluation of F_3 and F_4 families for pod shattering

120 F_2 single plants from cross AGS 292 x Nam 2 and 103 single plants from cross AGS 292 x Roan were used to examine genetic segregation among families at F_3 in a non replicated plant to row technique at Namulonge. Ten F_3 plants were sampled at random from each progeny row at R8 stage and evaluated for shattering using the oven method. Progenies whose shattering was 0 - 10 %

were regarded as resistant, those varying between 11 and 70 % shattering as intermediates , those varying between 71 - 100% as susceptible and those varying between 0 - 100% as segregating. This was done to test the validity of the expected ratio of 1 resistant : 1 intermediates : 4 susceptible : 10 segregating in order to confirm the dominant epistasis ratio of 1 resistant : 3 intermediates : 12 susceptible observed at F_2 in earlier part of this study. A Chi square test to determine the departure of the observed frequencies from the expected frequencies was performed for significance at ($P = 0.05$) for three degrees of freedom.

F_2 single plants from cross AGS x Nam 2 were selfed to F_3 and F_4 generations to test the validity of the dominant epistasis ratio of 1 resistant: 3 intermediates and : 12 susceptible observed at F_2 in this study, where F_2 and F_3 single plant progenies are expected to produce progenies in the following ratios; 16:0:0, 0:16:0, 0:0:16, 0:4:12, 4:0:12, 4:12:0 and 1:3:12 for resistant , intermediate and susceptible phenotypic ratios respectively. Progenies from each individual plant were harvested separately at R8 growth stage and subjected to oven method for determining pod shattering.

3.1.4 Determination of maternal influence

Maternal influence on the inheritance of soybean pod shattering was determined using crosses of TGM 737P x Duiker, TGM 737P x Roan and AGS 292 x TGx 1448 - 2E and their reciprocals planted at Namulonge and

evaluated for shattering at F_2 and F_3 generations. Mean shattering of the crosses and their respective reciprocal crosses were compared using Z test (Fowler and Cohen, 1990) to determine the difference between the mean of each cross and its respective reciprocal.

3.1.5 Estimation of number of genes

Estimation of the number of genes was carried out following the formulae used by Bjarko and Line, (1988) and Das and Griffey (1994):

$$F_2 \text{ generation: } n = (GR)^2 [1.5 - 2h(1-h)] / 8(VF_2 - (V_{PS} + V_{PR} + 2V_{F1})/4) \quad (1)$$

$$h = (F1_M - P_R) / (P_S - P_R)$$

$$F_3 \text{ generation: } n = (GR)^2 / 5.33 [VF_3 - (V_{PR} + V_{PS})/2] \quad (2)$$

GR = Genotype range, estimated as phenotypic range of segregating populations or difference between the two parents ($P_S - P_R$)

P_R = Mean of resistant parent

P_S = Mean of susceptible parent,

$F1_M$ = Mean of F_1 progenies,

V_{PR}, V_{PS} = Variance of resistant and susceptible parents respectively;

VF_1, VF_2, VF_3 = Variance of F_1, F_2 and F_3 respective generations;

n = The estimated number of segregating genes

Number of loci were also estimated using the original Castle - Wright method, used by Zeng *et al.* 1990 and Hakiza, 1994 as follows:

$$K_{cw} = D^2 / 8VG = D^2 / 8(VF_2 - VE) \quad (3)$$

where; K_{cw} = Number of loci estimated by the original Castle - Wright formula

D = Difference in parental mean ($P_2 - P_1$)

VF_2 = F_2 Phenotypic variance

VE = Environmental variance

The assumptions as per by Lande (1981) and Zeng *et al.* (1990) expect (i) one parent to contain all the the trait increasing alleles and the other all the trait decreasing alleles. (ii) all crosses to occur by mating individuals chosen at random in appropriate populations and (iii) the segregating genes to be unlinked and in random combinations.

3.1.6 Estimation of narrow sense heritability using Parent

Offspring regression

Populations from nine crosses at F_2 were used to determine narrow sense heritability, by regressing F_2 populations on value of their mid parents. The crosses were TGM 737P x Duiker, TGx 1448-2E x TGM 737P, TGx 1448-2E x Samsoy 1, TGx 1448-2E x Duiker, Kab 1 x TGM 737P, Duiker x Kab 1, Kab 1 x Duiker, TGx 1448-2E x Kab 1 and Kab 1 x TGx 1448-2E. The data was subjected to arcsine

transformation and analysed using SAS computer microsoft ware, version 6.12 (Anon, 1988c). A linear regression performance of offsprings on that of parents was based on the following model presented by Vogel, *et al.* (1980).

$$Y_i = a + bX_i + E_i \quad (4)$$

Where: Y_i = Performance of offsprings of i th parent

a = Mean performance of all parents evaluated

b = Linear regression coefficient

X_i = Performance of the i th parent

E_i = Experimental error associated with the measurement of X_i

The use of parent offspring regression was based on the following assumptions: (i) the character of interest is diploid, (ii) the population is random mated, (iii) there is no linkage among loci controlling the trait, (iv) parents are non inbred and (v) there is no environmental correlation between the performance of parents and offsprings (Vogel *et al.* 1980).

3.1.7 Diallel analysis

A half diallel cross was made in seasons 1997B and 1998A (A and B refer to first and second growing seasons respectively) involving ten parental lines (Table 1). The F_1 Plants from the crosses were few varying from two to twelve. The diallel analysis was carried out at F_2 generation when enough seed had been generated following the method presented by Hayman (1954). Griffing's (1956) method was also used according to Bhullar *et al.* (1979) and Patil and

Chopde (1981) using F_2 data. The problem of achieving enough F_1 seed to raise adequate plants for analysis came about due to the unpredictable flowering behaviour of lines TGM 737P, AGS 292 and Duiker whose flower buds would at times self pollinate without opening. This could be due to lack of adaptation to local conditions in view of report by Fehr, (1987b) that flowers of soybean obtained at 12 hour day length self pollinate when they are still too small for artificial manipulation.

F_1 crosses raised enough F_2 seed for a replicated experiment of the forty five progenies and their parental lines, from the diallel cross which were planted in a randomized complete block design experiment with three replications during season 1998B at Namulonge. The plot size was 500 x 120 cm at a spacing of 60 x 5 cm.

The data for diallel analysis was tested for homogeneity of variances using Bartlett's test (Little and Hills, 1978) and subjected to arcsine transformation (Sokal and Rohlf, 1995) to homogenize variance across replications and analyzed using micro computer software developed by (Christie *et al.* 1988). Diallel analysis was done according to Hayman (1954) to generate variances (V_r) and parent-offspring covariances (W_r) of arrays for estimation of genetic parameters and to detect presence of epistasis among the crosses under Hayman's (1954) assumptions of: (i) Presence of diploid segregation, (ii) Presence of homozygous parents (iii) Absence of maternal influence, linkage and multiple alleles.

The variances and covariances used to estimate the genetic parameters are indicated below:

V_p = variance among the parents

V_r = the variance among family means within an array

$\bar{V}_r$ = mean value of V_r over all arrays

$V_{\bar{r}}$ = the variance among the means of the arrays

W_r = the covariance between families within an array and their non recurrent parent

$\bar{W}_r$ = mean value of W_r over all arrays

From these variances and covariances the following five parameters were estimated:

E = Environmental variance

D = $V_p - E$

H_1 = $4\bar{V}_r + V_p - 4\bar{W}_r - (1/n)(3n-2)E$

H_2 = $4\bar{V}_r - 4V_{\bar{r}} - 2(2/n^2)(n^2-1)E$

F = $2V_p - 4\bar{W}_r - (2/n)(n-2)$

Where, E is measure of experimental error, D a measure of additive effects only, while H_1 and H_2 measures dominance effects only. F is a measure of the relative distribution of dominant and recessive alleles among parents.

Further analysis was done using model one and method two of Griffing (1956) to determine the value of general combining ability (GCA) and specific

combining ability (SCA) following the procedures of Patil and Chodpde (1981).

The value of cross $i \times j$ in Griffings's analysis was based on the expression:

$$X_{ij} = \mu + g_i + g_j + s_{ij} \quad (5)$$

Where μ = general mean; g_i, g_j = general combining ability effects of the i th and j th parents, respectively; s_{ij} = specific combining ability effects of the cross $i \times j$.

Using the generated variance components, narrow sense heritability was estimated using the model:

$$h_n^2 = \sigma_A^2 / \sigma_A^2 + \sigma_D^2 + \sigma_E^2 \quad (6)$$

Where: h_n^2 = narrow sense heritability

σ_A^2 = variance due to additive gene effects

σ_D^2 = variance due to dominance gene effects

σ_E^2 = environmental error variance

3.2 EXPERIMENT TWO:

DETERMINATION OF FIELD YIELD LOSS AND EFFECT OF ENVIRONMENT ON POD SHATTERING

The experiment to determine field loss due to pod shattering was planted at three locations; Namulonge, Nakabango and Iki-Iki during 1997A, 1997B and 1998A. Varieties TGx 1448-2E, Nam 1, Duiker, Nam 2, Kab 1 and TGM 737P were used. Variety TGx 1448-2E, Nam 2 and Duiker are resistant to pod shattering, Nam 1 and Kab 1 are intermediate and TGM 737P is susceptible.

Maturity of the varieties was synchronised by planting in a staggered manner (Table 2). Varieties Nam 1, Nam 2, and TGx 1448-2E were planted first, followed by Kab 1 and Duiker after seven days. Genotype TGM 737P was planted 14 days after the first planting date.

Table 2 . The staggered order of planting and days to maturity
of the cultivars used

Genotype	Days first planting	Days to maturity
TGx 1448-2E	0	112
Nam 2	0	112
Nam 1	0	110
Duiker	7	93
Kabanyolo 1	7	95
TGm 737P	14	75

The experiment was arranged in a split plot design with varieties in the main plots (500 x 360 cm) and harvesting dates in sub-plot (500 x 120 cm) in three replications. The subplots were treated as repeated observations (Litte and Hills, 1978).

At physiological maturity a Stephenson screen containing a portable Psycrometer and Maximum and Minimum Thermometer was placed in the trial, one metre above the soil level. A tru-check rain gauge model TRU 202 was

also positioned in the trial at the same time. Temperature and relative humidity(RH) were recorded at 10.00 am, 12.00 noon and 4.00 pm every day until the trial harvesting was completed. Maximum and minimum temperatures were recorded at 10.00am. Rainfall (mm) was also recorded. At physiological maturity, Dursban 5% dust was applied along the rows at ground level to prevent plant damage by termites.

3.2.1 Development of model for determination of field loss due to pod shattering

Seven days after R8 stage, two rows per sub plot were harvested. Harvesting sub plots was carried out at an interval of 7 days after R8 stage until 21 days later. From each subplot, 90 to 130 plants were harvested and used to determine the number of non shattered and shattered pods on each plant. Plot seed from unshattered pods was weighed and its moisture content determined using Steinlite moisture meter (model 400G). Yield was standardized at 12% and converted into kg ha^{-1} . On the assumption of equal yield (weight) per pod in each variety, and basing on recorded shattered and unshattered pods in relation to actual seed yield per plot, models were developed and used to determine expected total seed yield and seed yield lost accruing from pod shattering per plot as follows:

$$Y_t = (Y_p/P_{un}) * (P_{un} + P_{sh}) \quad (7)$$

$$Y_{ls} = (Y_p/P_{un}) * P_{sh} \quad (8)$$

Where, Y_t = expected total plot yield

Y_p = actual plot yield

P_{un} = total number of pods unshattered

P_{sh} = total number of pods shattered

Y_{ls} = total yield loss due to shattering

The data was analyzed to estimate the effect of G x E interactions on genotypes, using general linear model procedure. Possibility of association between soybean pod shattering and temperature, humidity and rainfall was determined using Pearson correlation analysis. Entire data was analysed using SAS computer microsoftware, version 6.12 (Anon,1988c). For stabilization of variance, plot yield loss was recorded as percentage of total yield and then subjected to arcsine transformation prior analysis of Sokal and Rohlf (1995). Varieties TGx 1448-2E, Duiker and Nam 2 did not shatter and were thus eliminated from analysis. Due to the 'elnino' weather conditions in which rainy conditions above normal prevailed most of the time in 1997B, there was no shattering exhibited by any of the varieties except TGM 737P. Since the season presented conditions out of the norm, the results of 199B were also eliminated from the analysis.

3.2.2. Testing accuracy of the extrapolation model used in estimating field yield loss

The accuracy of the model used in estimation of field loss due to pod shattering was verified with 20 plants from the two guard rows per plot that shattered in the field. Varieties TGm 737P, Kab1 and Nam1 were harvested at Namulonge after reaching harvesting maturity, before any pod shattering could occur. The harvested plants were placed in paper bags (30 x 20 x 45 cm) and stapled and oven dried at 80°C for 5 hours.

Each row harvested represented a plot making six replications per genotype. Seeds from shattered pods were trapped in the paper bags, weighed directly to form actual yield loss and actual total yield per plot was determined by adding weights of seed from shattered and unshattered pods. Extrapolation of yield loss and total yield was done using formulae 7 and 8 in section 3.2.1 of this thesis. The accuracy of using yield per pod was checked by extrapolation of total yield, estimated using shattered pods and unshattered pods to form actual field yield 1 and actual field yield 2 respectively.

The accuracy of the extrapolation model in estimation of yield loss and total yield, actual yield loss and actual total yield from observed data set 1 and the corresponding extrapolated yield loss and total yield in observed data set 2 were compared using a T- test to determine the extent to which actual data deviate from extrapolated data. The test was carried out using MSTATC, version 1.42 computer software (Anon, 1988d).

3.2.3 Derivation of Models used in estimation of total yield and total loss of soybean due to pod shattering

$$\text{Actual plot yield} = Y_p$$

$$\text{Total number of pods unshattered} = P_{un}$$

$$\text{Total number of pods shattered} = P_{sh}$$

$$\text{Total number of pods} = P_{un} + P_{sh}$$

$$\text{Yield per pod} = Y_p / P_{un}$$

$$\text{Total expected yield } (Y_t) = (Y_p / P_{un}) * (P_{un} + P_{sh})$$

$$\text{Total yield loss due}$$

$$\text{to shattering } (Y_{ls}) = (Y_p / P_{un}) * P_{sh}$$

Alternative methods:

$$(i) \text{ Total expected yield } (Y_t) = Y_p + (Y_p * P_{sh}) / P_{un}$$

$$= Y_p (1 + P_{sh} / P_{un})$$

$$= Y_p (P_{un} + P_{sh}) / P_{un}$$

$$= (Y_p / P_{un}) * (P_{un} + P_{sh})$$

$$(ii) \text{ Yield loss } (Y_s)$$

$$= (Y_p / P_{un}) * (P_{un} + P_{sh}) - Y_p$$

$$= (Y_p * P_{un} / P_{un}) + (Y_p * P_{sh} / P_{un}) - Y_p$$

$$= Y_p (P_{un} / P_{un} + P_{sh} / P_{un} - 1)$$

$$= Y_p (1 + P_{sh} / P_{un} - 1)$$

$$= Y_p (P_{sh} / P_{un})$$

$$= (Y_p / P_{un}) * P_{sh}$$

4 CHAPTER FOUR

4.0 RESULTS AND DISCUSSION

4.1 EXPERIMENT 1

The results of the shattering scores of F_1 hybrids of susceptible and resistant parents and their parental lines are presented in Table 3. All F_1 plants indicated closer performance to the susceptible parent than the resistant parent, suggesting partial dominance for susceptibility. Similar results were reported by Caviness (1969) and Tsuchiya and Sunada (1980b).

4.1.1 Oven conditions used for evaluating pod shattering in segregating populations

The results of the genetic ratios under different temperature and time conditions are presented in Table 4. The genetic ratios obtained from exposing the pods to oven conditions of 60°C for 12 hours did not fit any genetic ratio. Three out of seven genetic ratios (42.9%) obtained from exposing pods to 80°C for 6 hours were not significantly different from the 1:3:12 genetic ratio while six out of seven ratios (85.7%) of the ratios obtained from exposing the pods to 80°C for 12 hours did not significantly deviate from the 1:3:12 genetic ratio indicating that the latter oven condition was the best for determining soybean shattering for genetic analysis.

Table 3: Shattering percentage and scores of seven parental lines and their F₁ progenies

Genotype	Number of Plants	Mean %	Shattering scores ¹
AGS 292 (S) ²	20	100	5
Duiker (R)	20	10	1
GC 81090-48(R)	20	5	1
Roan (R)	20	0	1
TGm 737P (S)	20	100	5
Nam 2 (R)	20	0	1
Tgx1444-2E (R)	20	5	1
Roan x TGm 737P	5	100	5
AGS 292 x Nam 2	4	100	5
TGm 737P x Duiker	6	100	5
AGS 292 x TGx 1448-2E	19	95	5
TGx 1448-2E x TGm 737P	5	100	5
AGS 292 x Roan	10	100	5
GC 81090-48 x AGS 292	22	95	5
GC 81090-48 x TGm 737P	6	100	5

¹The scores are based on 1 - 5 scale, ² R = Resistant , S = Susceptible

Table 4 . Phenotypic ratios of resistant (R): intermediate (I): susceptible (S) of F₂ populations when fitted on a 1:3:12 genetic model under different oven environments.

Cross	Phenotype	Oven temperature and duration		
		60°C+12 hrs	80°C+6 hrs	80°C+12hrs
Roan	R	23	1	1
x	I	59	9	10
TGm 737P	S	13	40	50
	Total	95	50	61
	χ^2	191.89 *	1.63ns	2.65ns
TGm 737P	R	20	6	7
x	I	109	23	23
Roan	S	41	50	50
	Total	170	80	80
	χ^2	253.57 *	6.20*	6.73*
AGS 292	R	13	5	7
x	I	58	10	10
Nam 2	S	37	36	37
	Total	108	51	54
	χ^2	100.06 *	1.17ns	1.26ns

Table 4 cont.

Cross	Phenotype	Oven temperature and duration		
		60°C+12 hrs	80°C+6 hrs	80°C+12hrs
Duiker	R	22	12	7
x	I	98	37	26
TGm 737P	S	61	86	96
	Total	181	135	129
	χ^2	172.17 *	9.20*	0.28ns
TGm 737P	R	7	14	9
x	I	31	24	25
Duiker	S	35	70	75
	Total	73	108	109
	χ^2	43.42 *	10.51*	1.78ns
TGx 1448-2E	R	42	12	9
x	I	36	18	17
AGS 292	S	47	48	54
	Total	125	78	80
	χ^2	179.71 *	13.06 *	4.07ns
AGS 292	R	25	7	4
x	I	37	12	9
TGx 1448-2E	S	34	38	43
	Total	96	57	57
	χ^2	100.29 *	4.01ns	0.36ns

* = Significant deviation from 1:3:12 ratio ($P < 0.05$); ns = Non significant deviation from 1:3:12 ratio ($P > 0.05$).

These oven conditions could facilitate a study of genetic distributions when studying the inheritance of resistance to soybean pod shattering. The improved method saves time because the period required to accomplish the experiment was eight times shorter than the methods reported in literature (Caviness, 1965, Anon, 1986, Jiang *et al.* 1991). There was improvement on the oven method, therefore, in terms of reduced period requirement for pod shattering assessment and provision for accurate genetic ratios. With short period requirement for the experiment to be conducted, many experimental materials in one day can be handled. The results were also improved by use of the new 1 - 3 scale and controlled temperature leading to minimal experimental error.

4.1.2 Accuracy of the 1 - 3 scale

The results of tests for homogeneity of within mean squares (WMS) of 1 - 3 and 1 - 5 scales among scale groups are presented in Table 5. Out of the eight samples tested, seven samples indicated lower WMS for the 1 - 3 scale suggesting that the 1 -3 scale accounts for most of variation statistically than the 1 - 5 scale and is dependable for analysing phenotypic differences in populations segregating for pod shattering in soybean.

Table 5: The analysis of variance for 1- 3 scale and 1-5 data sets

Sample no. and size(n)	Source of Variation	1 - 3 scale		1 - 5 scale	
		DF	MS	DF	MS
1 (25)	Between	2	8059.7*	4	4315.6*
	Within	22	152.2	20	110.3
	Cv(%)		24.6		29.0
2 (25)	Between	2	12058.9*	4	6013.0*
	Within	22	108.9	20	123.1
	Cv(%)		17.7		18.7
3 (50)	Between	2	17862.3*	4	8724.9*
	Within	47	105.9	45	128.9
	Cv(%)		15.5		17.1
4 (50)	Between	2	11495.8*	4	6174.4*
	Within	47	144.6	45	113.0
	Cv(%)		21.9		19.3
5 (75)	Between	2	24811.8*	4	12291.1*
	Within	72	155.2	70	166.1
	Cv(%)		22.3		23.1
6 (75)	Between	2	20808.1*	4	10182.1*
	Within	72	125.2	70	153.9
	Cv(%)		17.4		19.3
7 (100)	Between	2	27852.2*	4	13959.2*
	Within	97	149.9	95	151.7
	Cv(%)		21.5		21.7
8 (150)	Between	2	10355.3*	4	22953.1*
	Within	147	139.3	145	153.7
	Cv(%)		19.6		20.6

* = Significant at $P < 0.05$

The results imply that the reduced number of groups in the 1-3 scale do not lead to loss of details in the 1-5 scale but lead to improved accuracy of the results reflected in defined genetic ratios (Table 4) and higher frequency of low WMS values (Table 5).

4.1.3 Application of the method in other F_2 populations

Further genetic ratios for levels of pod shattering resistance at F_2 are presented in Table 6. A Chi square test on the ratios obtained in three out of four crosses did not significantly deviate from the 1: 3 : 12 , suggesting dominant epistasis and presence of two genes. These results are different from Akpan's (1988) that the number of genes controlling pod shattering in soybean varied from 6 to 12, and Fukuta *et al.* (1994) who found 3 partially dominant genes for the same trait.

The frequency distributions of F_2 populations are shown in Figure 1 for the 0 - 10 and 1 - 5 respective scales. Contrary to observations made by Ting (1946) and Caviness (1969) the frequency distribution of F_2 was not overlapping in a normal distribution manner but presented a skewed distribution with a wide range of susceptible to resistant scores similar to a distribution in which dominant epistasis plays a major role (Fehr, 1987a and Griffiths *et al.* 1997). Qualitatively inherited traits usually display discrete frequency distribution at F_2 , however epistasis is responsible for the complex distribution observed in Figures 1 and 2.

Table 6 : Phenotypic ratios of resistant (R) : intermediate (I): susceptible
(S) of F₂ populations when fitted on a 1:3:12 genetic model

Cross	Phenotype	Observed	Expected	χ^2
TGx 1448-2E	R	31	20.00	6.05
x	I	56	60.00	0.27
TGm 737P	S	233	240.00	0.20
	Total	320	320.00	6.54*
AGS 292	R	7	7.81	0.08
x	I	23	3.44	0.00
Roan	S	95	93.75	0.01
	Total	125	125.00	0.02ns
GC 81090-48	R	5	3.69	0.47
x	I	12	11.06	0.08
AGS 292	S	42	44.25	0.11
	Total	59	59	0.66ns
GC 81090-48	R	14	9.06	2.69
x	I	21	20.63	0.00
TGm 737P	S	110	108.75	0.01
	Total	145	145.00	2.70ns

* = Significant deviation from 1:3:12 ratio ($P < 0.05$); ns = Non significant deviation from 1:3:12 ratio
($P > 0.05$);

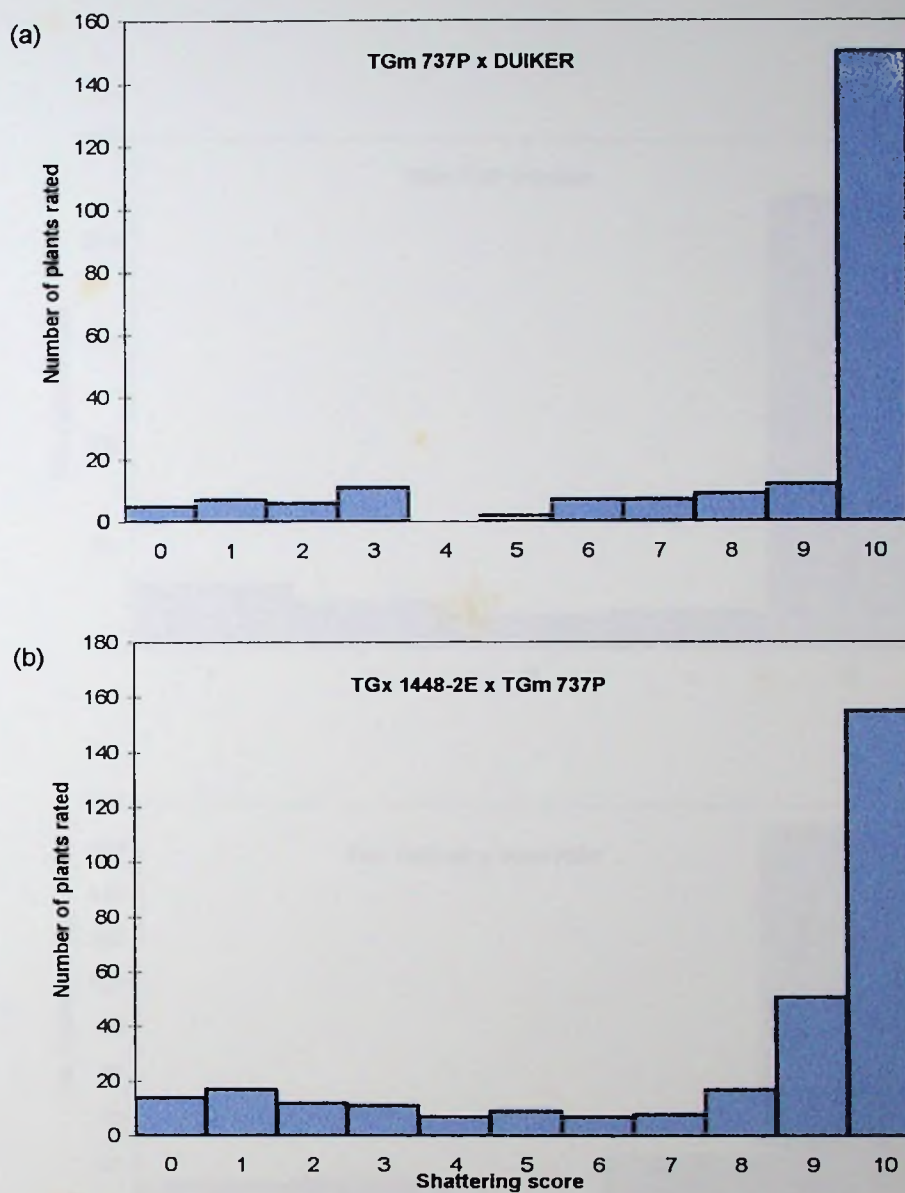


Figure 1. Frequency distribution of shattering scores in (a) TGm 737P x Duiker and (b) TGx 1448-2E x TGm 737P soybeans crosses at F₂ generation using a 0-10 scale

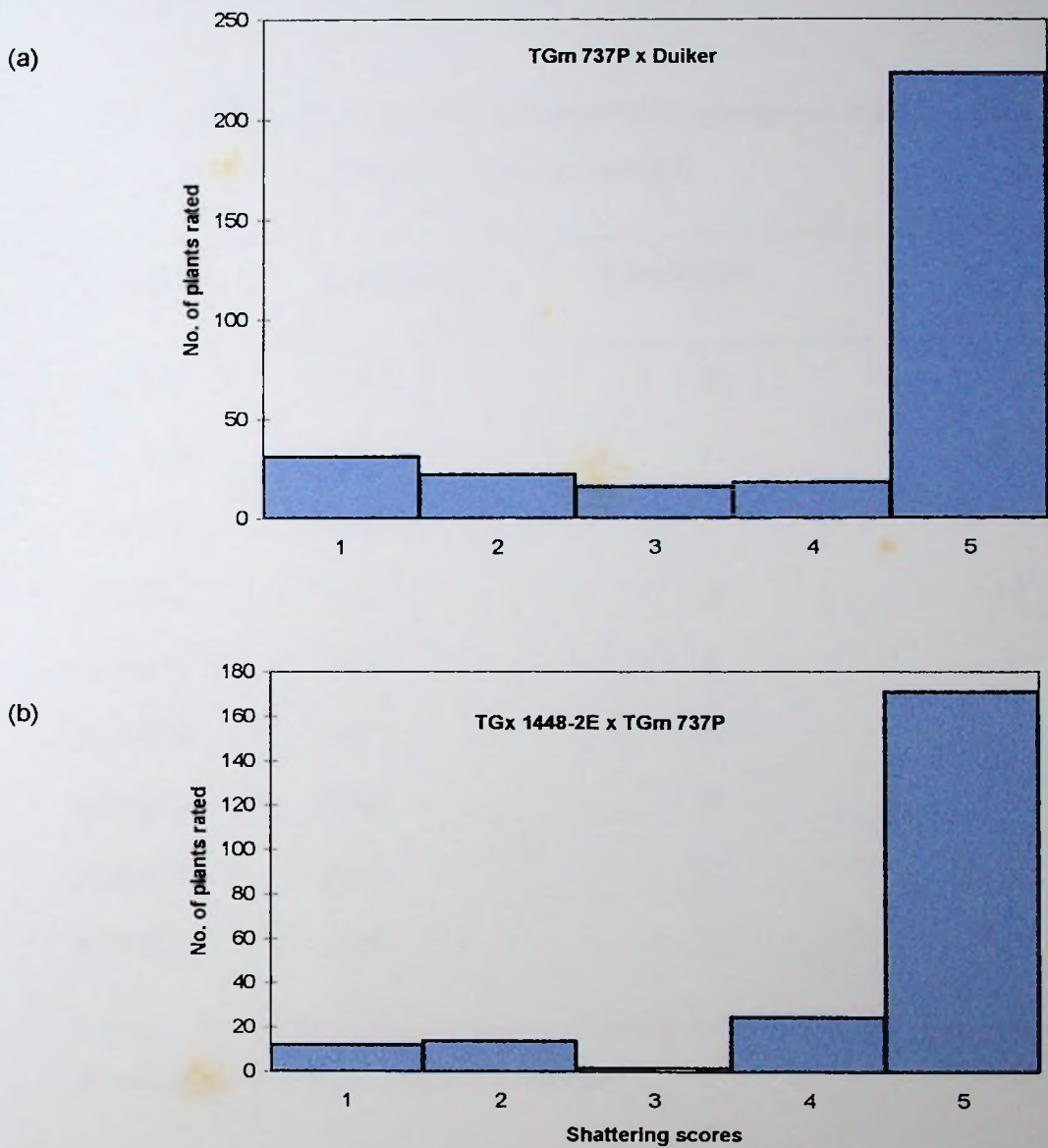


Figure 2. Frequency distribution of shattering scores of (a) TGm 737P x Duiker and (b) TGx1448-2E x TGm 737P F_2 crosses of soybean using 1 - 5 scale

The results suggested a classical model for the two gene control mechanism of pod shattering in soybean presented in Table 7.

Table 7. Relationship between genotype and phenotype in an F_2 population showing classical dominant epistasis

Genotype	Frequency	Phenotype	Ratio
$A^-A^-B^-B^-$	1/16	R	1
$A^-A^-B^+B^+$	1/16	I	3
$A^-A^-B^+B^-$	2/16	I	
$A^+A^+B^+B^+$	1/16	S	12
$A^+A^+B^+B^-$	2/16	S	
$A^+A^+B^-B^-$	1/16	S	
$A^+A^-B^+B^+$	2/16	S	
$A^+A^-B^+B^-$	4/16	S	
$A^+A^-B^-B^-$	2/16	S	

S = Susceptible; I = Intermediate; R = Resistant

This model suggests that genes at same locus interact resulting in susceptibility alleles being dominant over alleles for resistance plus non allelic interaction (epistasis). On basis of a two gene model, genotypes $A^+A^+B^+B^+$ and $A^-A^-B^-B^-$ are attributed to homozygous dominant and homozygous recessive parental lines

respectively for pod shattering. The observed ratio of 1:3:12 in which the presence of at least one dominant allele (A^+) at one locus masks the expression of both alleles present in a genotype, resulting in the dominant phenotype while the presence, of (B^+) in absence of (A^+) results in an intermediate phenotype. The final distribution is a reflection of classical dominant epistasis which causes modification of 9:3:3:1 Mendelian ratio (Kearsey and Pooni, 1996) and agree with Bailey *et al.* (1997) that epistasis influences soybean pod shattering.

In self pollinated plants like soybean, epistasis is more important than dominance which lasts for a short time with progressive selfing, but non allelic interaction can generate different phenotypes some of which represent real genetic advance over their parents (Allard ,1960). Hallauer and Miranda (1988) recommended identification of loci with favourable epistatic combinations for improvement of economically important traits in crops. Kearsey (1993) suggested that non allelic interactions posed limitations when predicting response to selection, by preventing identification of the most promising crosses at an early stage in the breeding program.

Kearsey and Pooni (1996) reported that the effect of epistasis is more profound on means as opposed to variances and epistatic effects of generation means are more amenable to analysis than those of variances. Where epistasis is important, recurrent selection and reciprocal recurrent selection have been recommended as efficient techniques for selecting favourable epistatic gene combinations (Allard ,1960; Moreno-Gonzalez and Cubero, 1993).

4.1.4 Genetic ratios of F₃ progeny rows and effect of maternal influence on pod shattering.

The distribution of genotypes within progeny rows at F₃ is presented in Table 8 and non segregating pure lines and segregating families are illustrated in Plates 2 and 3. The χ^2 of crosses AGS 292 x Nam 2, and AGS 292 x Roan revealed no significant deviation from the expected ratio of 1:1:4:10 for resistant: intermediates: susceptible: and segregating families respectively confirming the 1:3:12 dominant epistasis phenomenon earlier observed at F₂.

Table 8. Phenotypic ratios of resistant(R): intermediates (I) :susceptible(S) : segregating(G) families of F₃ populations fitted on a 1 : 1 : 4 : 10 genetic ratio.

Cross	Phenotype	Observed	Expected	χ^2
AGS 292 x Nam 2	R	6	7.50	0.30
	I	4	7.50	1.63
	S	25	30.00	0.83
	G	85	75.00	1.33
	Total	120	120	4.09ns
AGS 292 x Roan	R	7	6.44	0.05
	I	7	6.44	0.05
	S	24	25.75	0.12
	G	65	64.38	0.01
	Total	103	103	0.23ns

* = Significant deviation from 1:1:4:10 ($P < 0.05$); ns = Non significant deviation from 1:1:4:10 ($P > 0.05$)

(a)



(b)



Plate 3: Soybean families at F_3 of cross AGS 292 x Nam 2 showing

(a) segregating family and (b) resistant non segregating family.

The ratios obtained from the single plant progenies advanced to F_3 and F_4 through selfing are presented in Table 9.

Table 9: Families fitted on expected classical genetic ratios of resistant:
Intermediate: susceptible at F_3 and F_4 generations of cross
AGS 292 x Nam 2

Expected genetic ratio	Filial generation			
	F3		F4	
	Number of familes tested	Number of families fitting expected ratios	Number of families tested	Number of families fitting expected ratios
16:0:0	5	5	13	13
0:16:0	5	3	9	7
0:0:16	18	18	31	31
0:4:12	16	10	10	10
4:0;12	5	4	6	3
4:12:0	4	4	4	1
1:3:12	13	11	15	8
Total	66	55	88	73

At F_3 , 55 (83%) families out of 66 crosses were in agreement with expected ratios 16:0:0, 0:16:0, 0:0:16, 0:4:12, 4:0:12, 4:12:0 and 1:3:12 for resistant : intermediate : susceptible phenotypic ratios respectively confirming dominant epistasis. At F_4 73 (83.0%) families out of 88 crosses showed ratios which did not significantly ($P < 0.05$) differ from the expected ratios at F_3 generation indicating that a few number of genes control the trait. In view of the two gene model with dominant epistasis, the ratios of 1:3:12, 0:4:12, 4:0:12 and 4:12:0 represented a proportion of progenies still segregating and formed 43.9% of total population at F_3 and 25% at F_4 implying that effective selection for resistance to shattering can be easily achieved at these stages since 39.4% and 58.0% at the respective generations were already genetically fixed for the shattering trait.

The results of the maternal influence are shown in Table 10. There was no significant difference between the crosses and their reciprocals, indicating absence of maternal influence on pod shattering in soybean. Thus there will not be any variation in efficiency related to genetic gain among segregating populations whether either susceptible or resistant parental line is made female during hybridization program for incorporating pod shattering resistance into susceptible cultivars.

Table 10. Maternal influence on soybean shattering in F₂ and F₃ populations of three crosses and their reciprocals

Cross	Filial Generation			
	F ₂		F ₃	
	Number	Mean	Number	Mean
	of plants(n)	shatter score $\pm$ s.e	of plants(n)	shatter score $\pm$ s.e
TGm 737P x Duiker	100	4.20 $\pm$ 0.15ns	100	3.47 $\pm$ 0.71ns
Duiker x TGm 737P	100	4.5	100	4.48
TGm 737P x Roan	80	4.09 $\pm$ 0.25*	70	4.27 $\pm$ 0.16ns
Roan x TGm 737P	80	4.58	70	4.49
AGS 292 x TGx x 1448-2E	80	4.44 $\pm$ 0.14ns	140	4.19 $\pm$ 0.01ns
TGx 1448-2E x AGS 292	80	4.16	140	4.21

* Significant, ns = non significant at P < 0.05

4.1.5 Number of genes conferring resistance to pod shattering in soybean

The results of estimated number of genes controlling shattering are presented in Table 11.

Table 11: Estimated number of genes determining soybean shattering
in ten crosses of soybean at F_2 and F_3 generations.

Cross	Number of plants in a cross	Filial generation		
		F_2^w	F_2^j	F_3^j
Roan x TGm 737P	50	2.33	3.01	2.46
TGm 737P x Roan	81	1.48	2.02	2.32
AGS 292 x Nam 2	53	1.35	3.07	2.36
Duiker x TGm 737P	128	2.00	2.50	2.72
TGm 737P x Duiker	111	1.45	1.90	1.60
TGx 1448-2E x AGS 292	80	1.45	1.97	2.01
TGx 1448-2E x TGm 737P	310	2.11	2.19	2.20
AGS 292 x Roan	58	1.74	2.33	2.28
GC 81090-48 x AGS 292	58	1.34	1.63	1.93
GC 81090-48 x TGm 737P	140	1.14	1.42	2.62
Mean	102	1.65	2.21	2.24

^wEstimates by the original Castle - Wright's method used by Zeng *et al.* (1990) and

^j by Bjarko and Line, (1987)

Using F_2 and F_3 progenies, estimates of genes ranged from 1.4 to 3.0 following method used by Bjarko and Lines' (1987). At F_2 generation, six crosses out of ten suggested two genes, three crosses for three genes and one cross indicated that one gene controlled shattering. At F_3 , eight crosses out of ten stipulated two genes while two crosses showed three genes to be responsible for controlling shattering trait in soybean. The results showed a mean of 2.21 genes at F_2 and 2.24 at F_3 suggesting two genes being involved in controlling pod shattering. However the number of loci varied between one and two using the original method of Castle and Wright, used by Zeng *et al.* 1990 and Hakiza, 1994 where seven out of ten crosses showed estimate of two loci while the other three crosses suggested one loci with a mean of 1.65 loci for the ten crosses. Zeng *et al.* (1990) observed that this method underestimates the number of loci. These results are in agreement with the observed phenotypic ratio of 1:3:12 at F_2 (Table 6). Similar results were reported by Tsuchiya, (1986). Contrary estimates however, were made by Caviness (1963) who indicated four major genes and Akpan (1988) who reported 6 to 12 genes to be responsible for shattering in the crop. Further, diverging results were presented by Bailey *et al.*, (1997) who showed pod shattering in soybean to be conditioned by one major gene and a few minor ones.

4.1.6 Results from parent - offspring regression

The results of mid-parent offspring regression analysis are presented in Table 12. The results showed a regression coefficient b of 0.73 which is a measure of

heritability in the narrow sense (h^2_n), indicating that shattering is highly heritable.

Table 12. Analysis of variance for mid-parent regression on F_2 progenies for pod shattering

SOURCE	DF	SS	MS	F
Model	1	121.733	121.733	67.041*
Error	8	14.527	1.816	
Total	9	136.260		

$$cv (\%) = 3.7; \quad r^2 = 0.89; \quad b = 0.73 = h^2_n$$

*Significant at $P < 0.05$

Heritability estimates obtained from regressing offsprings on their mid-parent values is a direct estimate of heritability in the narrow sense (Vogel *et al.* 1980., Simmonds, 1981., Falconer, 1989., Kearsley and Pooni, 1996; Griffiths *et al.* 1997). This explains why this estimate is lower than the broad sense heritability estimates reported by Caviness, (1963); Tsuchiya, (1987); Tiwari and Bhatnagar (1991). The estimates of h^2_n still portray shattering trait as highly heritable and might have been inflated by the presence of epistasis (Ferdnandez and Miller, 1985).

4.1.7 Observations from diallel analysis

Results of the Bartlett's test of homogeneity of variances are presented in Table 13. The results showed that data variances were heterogeneous and consequently the arcsine transformation was made to fulfill the condition of constant variance for variance analysis.

Table 13. Results of Bartlett's test for homogeneity of variance of F_2 scores for pod shattering in soybean

Aspect	Non transformed data	Transformed data
Total degrees of freedom	110.00	110.00
Total variance	923.46	8490.82
Mean variance	16.79	154.38
Log of mean	2.82	5.04
Un adjusted X^2	37.74*	10.99
Bartlett's correction factor	1.17	1.17
Adjusted X^2	32.26*	9.40

* Significant at $P < 0.05$

The results of variation among the crosses is presented in Table 14. The variation was significant, thus giving justification for further analysis. The differences over the arrays for the $(W_r - V_r)$ was significant as opposed to the

expected constant values suggesting presence of non allelic interaction of genes. Similarly, the values of parental order of dominance ($W_r + V_r$) were significantly different along the arrays confirming presence of non allelic interaction.

Table 14. Analysis of variance for crosses, variances and covariances of arrays of parental lines

	Source	DF	SS	MS	F
(a) Crosses	Blocks	2	3.586	1.793	8.019*
	Crosses	54	780.129	14.447	64.616*
	Error	108	24.146	0.224	
	Total	164	807.861		
(b) $W_r - V_r$	Blocks	2	1.024	0.512	0.545ns
	$W_r - V_r$	9	359.899	39.989	42.597*
	Error	18	16.898	0.939	
	Total	29	377.822		
(c) $W_r + V_r$	Blocks	2	0.584	0.292	3.369ns
	$W_r + V_r$	9	7.413	0.824	9.502*
	Error	18	1.560	0.939	
	Total	29	9.558		

*=Significant at ($P < 0.05$); ns = Not significant

If gene action fits the additive - dominance genetic model then the values of $(W_r - V_r)$ and $(W_r + V_r)$ will be constant over the arrays and significant differences is evidence of epistatic gene action (Mather and Jinks 1982, Christie and Shattuck, 1992). The values of variances and covariances of arrays are presented in Table 15.

Table 15. Arcsine mean of array variances, covariances and parental lines over replicates for pod shattering

Array	W_r	V_r	$W_r - V_r$	$W_r + V_r$	Parent mean	Array mean
TGx 1448-2E	4.20	4.54	-0.34	8.74	6.45	8.89
Roan	4.80	5.12	-0.33	9.92	6.62	8.78
Kab 1	2.77	2.69	0.08	5.46	8.52	9.87
Samsoy 1	1.49	1.47	0.15	2.96	10.03	10.92
Duiker	4.16	4.41	-0.25	8.57	7.41	9.74
GC81090-48	4.42	4.42	0.01	8.84	7.92	9.25
AGS 292	0.97	0.35	0.62	1.33	12.92	12.14
Nam 2	5.11	6.36	-1.25	11.46	6.11	8.48
TGm 737P	0.85	0.39	0.46	1.24	12.92	12.31
Nam 1	3.87	3.58	0.29	7.46	10.19	9.61

The results indicated varieties AGS 292 and TGm 737P to possess highest shattering intensity followed by Nam 1 and Samsoy 1. These lines were characterised by low variances (V_r) and covariances(W_r) suggesting predominance of dominant genes for the shattering trait at every loci (Kearsey and Pooni, 1996). On the other hand, varieties Nam 2, TGx 1448-2E, Roan

and Duiker had relatively low parental and array means for pod shattering as well as negative $W_r - V_r$ values but high $W_r + V_r$ values portraying resistance to pod shattering in these parents and suggesting predominance of recessive alleles at all loci.

The array means were higher than the parental means over the 10 arrays suggesting that the genes for enhancement of pod shattering were dominant over genes for resistance to pod shattering (Chrstitie *et al.* 1988). This is in agreement with observations made at F_1 and F_2 which are presented in Tables 1 and 3.

The results from a joint regression over the three replications of W_r on V_r are presented in Table 16. The regression coefficient ($b=0.78$) was significantly ($P<0.05$) different from unity indicating presence of epistasis (Jana, 1975; Chrstitie *et al.*, 1988).

Table 16. Analysis of variance for joint regression of W_r on V_r over three replications

Source	DF	SS	MS	F
Joint regression	1	71.638	71.638	578*
Heterogeneity	2	0.226	0.113	0.911
Error	24	2.984	0.124	

*Significant at $P<0.05$

The results of W_r/V_r graph demonstrating the distribution of dominant and recessive alleles among ten soybean varieties used in the diallel cross is presented in Figure 3. The graph has a slope of 0.78 indicating failure of the additive dominance genetic model for the shattering trait. The intercept is positive which suggests partial dominance which is in agreement with the observations made at F_1 generation (Table 3)

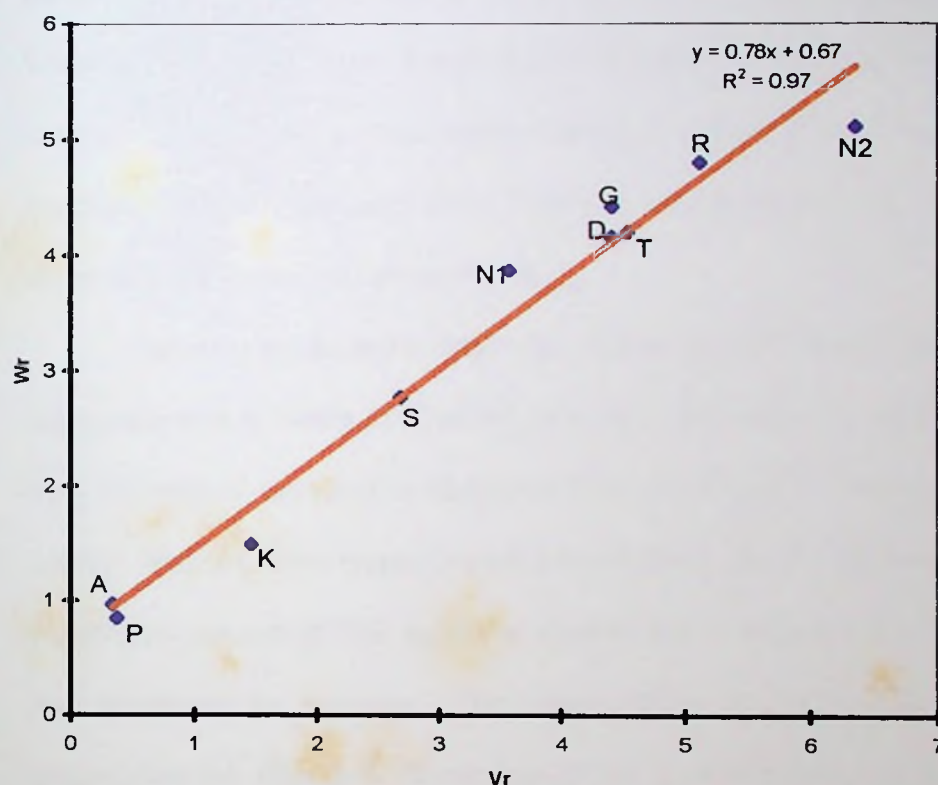


Figure 3. The relative number of dominant and recessive alleles in the ten varieties making up the parents of the diallel cross

A = AGS 292, P = TGm 737P, K = Kabanyolo 1, S = Samsoy 1, N1 = Nam 1, D = Duiker, T = TGx 1448 - 2E, G = GC 81090-48E, R = Roan, N2 = Nam 2

Those varieties near the origin (AGS 292 and TGm 737P) contain the most dominant alleles and they are susceptible while varieties Nam 2, Roan, TGx 1448-2E, Duiker and GC 81090-48 have the most recessive alleles respectively, and are resistant (Kearsey and Pooni, 1996). This confirms the results presented in Table 3 suggesting that susceptibility is dominant over resistance. The results are also in agreement with the description given to the parental lines on the basis of their resistance to pod shattering in Table 1. Varieties Samsoy 1, Nam 1 and Kab 1 are presumed to have about the same number of dominant and recessive alleles as they are presented in the middle position of the regression line. These varieties responded as intermediate when assessed for shattering (Table 1).

Genetic parameters affecting shattering trait using Hayman's method are presented in Table 17. The h^2_b was 0.96 and was not significantly different from estimates reported in literature (Tsuchiya, 1987; Tiwari and Bhatnagar, 1991). Results from Hayman's (1954) analysis show that the value of D was significant indicating that additive effects play a major role in the genetics of pod shattering in soybean. The values of H1 and H2 were also significant suggesting the effects of dominance to be significant at $P < 0.05$ (Table 16). H1 value was greater than H2 value indicating that alleles increasing mean pod shattering (dominant alleles) were more frequent among the parents than the recessive alleles. The average degree of dominance ($H1/D$) was less than 1 confirming partial dominance reported in Table 3.

Table 17. Genetic parameters affecting soybean shattering
estimated with Hayman's (1954) method

Parameter	Value $\pm$ s.e
Error (E)	0.22 $\pm$ 0.06*
Additive effects (D)	6.21 $\pm$ 0.20*
Dominance effects(H1)	6.10 $\pm$ 0.37*
Dominance effects(H2)	5.47 $\pm$ 0.37*
Direction of gene distribution (F)	-0.54 $\pm$ 0.47ns
Average degree of dominance(H1/D)	0.98
Broad sense heritability (h^2_b)	0.97
Narrow sense heritability (h^2_n)	0.70

* = Significant at $P < 0.05$

Genetic parameters affecting pod shattering in soybean following method by Griffing (1956) are presented in Table 18. The h^2_n value was (0.69) indicating further that the shattering trait is highly heritable. A similar value of 0.70 was obtained using Hayman's method (Table 15). However, the values are likely to be over estimated due to the presence of epistasis. The variation of these two h^2_n estimates from diallel analysis and the value of 0.73 obtained from parent-offspring regression using different populations grown at different time was minimal, suggesting that analyses were accurate and the values estimated are true estimates for the h^2_n . Nevertheless all the estimates demonstrate h^2_n as highly heritable which means that selection for resistance to

pod shattering can be readily achieved during the conventional breeding process.

Table 18. Variance components and narrow sense heritability estimated by Griffing's (1956) method

Source	Df	SS	MS	F
General combining ability	9	191.826	21.314	285.993*
Specific combining ability	45	68.218	1.516	20.341*
Error	108	8.049	0.075	

Additive variance (s^2_A)	= 3.30			
Dominance variance (s^2_D)	= 1.44			
Narrow sense heritability (h^2_n)	= 0.69			
s^2_A (% of total variance)	= 69.60			

* = Significant difference ($P < 0.05$)

Both general combining ability (GCA) and specific combining ability (SCA) effects were observed to be significant ($P < 0.05$) with GCA predominant over SCA which was reflected in the value of additive variance occupying 69.6% of the total variance (Table 18). This indicated predominance of additive effects, which is similar to the observations made by Tiwari and Bhatnagar, (1992). The ratio of GCA mean squares was 14 times that of SCA which indicates presence of epistasis. Bhullar *et al.* (1979) reported that when the ratio of GCA mean squares is several times the one of SCA, then considerable

magnitude of additive x additive components of epistatic variance is indicted. Consequently, effective selection should be possible within such a population at F₂ generation(Patil and Chopde, 1981).

The estimates of GCA effects for each parent and SCA for each cross are presented in Table 19.

Table. 19. GCA effects of parental lines (diagonal and underlined) and SCA for effects of crosses for resistance to pod shattering

Parent	T	R	K	S	D	G	A	N2	P	N1
T	<u>-1.13</u>	1.42	0.86	0.34	0.71	0.04	0.74	1.35	1.17	1.45
R		<u>-1.20</u>	0.11	-0.11	-1.99	-2.16	0.96	0.27	1.15	2.09
K			<u>-0.14</u>	-1.32	1.87	0.51	0.82	0.06	0.04	-0.09
S				<u>0.86</u>	1.16	1.33	-0.78	2.52	-0.28	0.34
D					<u>-0.34</u>	1.17	0.33	0.06	0.70	-0.39
G						<u>-0.71</u>	0.02	-0.83	0.61	0.51
A							<u>2.12</u>	1.64	-1.36	0.07
N2								<u>-1.50</u>	1.03	-1.81
P									<u>2.26</u>	-0.07
N1										<u>-2.22</u>

A = AGS 292, P = TGm 737P, G = GC 81090-48E, K = Kabanyolo 1, S = Samsoy 1, N2= Nam 2, D = Duiker, T= TGx 1448-2E, R = Roan, N1 = Nam 1.

The parents with highest positive GCA ability were TGm 737P and AGS 292 indicating that these parents lead to increased pod shattering among their progenies, and are not useful as parents for deployment in the breeding process focussed on reduced pod shattering (Sprague and Tatum, 1942; Mushi and Slumpa, 1995).

Parental lines with high negative GCA effects were Nam 1, Nam 2, Roan and TGx 1448-2E indicating that these parents are most suited for transferring resistance to pod shattering in their progenies and subsequent selected lines (Ayele, 1993). Varieties GC 81090-48E, Duiker, and Kab 1 showed low negative GCA suggesting they can be used as parents for intermediate resistance to shattering.

Crosses Roan x GC 81090-48E, Roan x Duiker, Nam 2 x Nam 1 and TGm 737P x Nam1 had the highest negative SCA, indicating that they possess several plants which are resistant to pod shattering, an indication that the parents involved in these crosses are good combiners for resistance to pod shattering. On the other hand crosses of Samsoy 1 x Nam 2, Roan x Nam 1, Kab 1 x Duiker, AGS 292 x Nam 2 and TGx1448-2E x Roan had highest positive values of SCA effects suggesting predominance of susceptible plants in their progenies.

4.2 EXPERIMENT TWO:

4.2.1 Verification of accuracy of the model used to determine yield loss due to pod shattering

The results of actual and extrapolated yield and yield loss due to pod shattering means are presented in Table 20.

Table 20. Yield loss from pod shattering and expected total seed yield kg ha⁻¹ of three varieties using actual plot yields and extrapolated yields

Genotype	Parameter [#]	Yield kg ha ⁻¹	
		Actual field yield	Extrapolated yield $\pm$ s.e
TGm 737P	Yield loss	1650	1636 $\pm$ 116 ns
	Total yield1	1869	1922 $\pm$ 84 ns
	Total yield2	1869	1856 $\pm$ 16 ns
Kab1	Yield loss	1197	1138 $\pm$ 70 ns
	Total yield1	2181	2239 $\pm$ 76 ns
	Total yield2	2181	2117 $\pm$ 131 ns
Nam1	Yield loss	775	597 $\pm$ 72 ns
	Total yield1	2414	3011 $\pm$ 207 *
	Total yield2	2414	2239 $\pm$ 73 ns

* = Significant at (P<0.05); ns = Non significant at (P<0.05); [#] Total yield1 is determined from shattered pods; Total yield2 is determined from unshattered pods.

Based on T-tests (Sokal and Rohlf, 1995) the results indicated that the two methods were not significantly different from each other. There was no significant difference between yield determined using extrapolation models and the actual field yield determined directly. Out of the nine comparisons made between the results obtained using the model and those weighed directly, eight were not significantly different. Only one case showed a significant difference, thus confirming the extrapolation model used in the study as dependable in estimation of total seed yield and total seed yield loss due to pod shattering in the field. The main limitation of the model is the need to have unshattered pods remaining on some plants where pod shattering has taken place. The method however can be used when the shattered seed on the ground is not available or has been picked by birds as was the case at Namulonge Research Institute. This method is cost effective in that it does not require any special equipment.

4.2.2 Field loss due to pod shattering and effect of genotype

x environment interactions

The results of variation of seed yield loss among genotypes, locations and seasons are presented in Table 21.

Table 21. Combined analysis of variance for total yield loss due to pod shattering at Namulonge , Nakabango and Iki-Iki over 1997A and 1998A.

Source of variation [#]	Degrees of freedom	Mean squares	Probability
S	1	9350	0.001
L	2	1950	0.001
R(L)	6	25	0.249
G	2	5500	0.001
HD	2	3819	0.001
L x G	4	745	0.001
L x HD	4	283	0.001
G x HD	4	59	0.019
G x S	2	3298	0.001
G x S x HD	4	631	0.001
G x L x HD	8	113	0.001
G x S x L x HD	18	231	0.001
Error	102	19	
CV (%)		22.46	

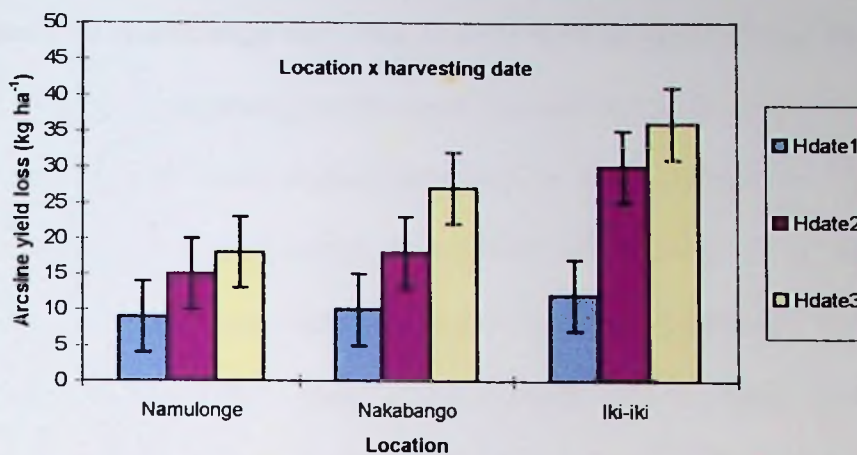
S[#] = Season, L = Location, R = Replication, G = Genotype, HD = Harvesting date

Findings showed highly significant ($P < 0.001$) genotype x location, genotype x season, genotype x harvesting date, location x genotype x harvesting date and genotype x season x harvesting date interactions

indicating significant influence of locations, seasons and harvesting dates on genotypes' shattering. The results confirm Akpans' (1988) observation that selection for resistance to pod shattering in a breeding program should be carried out in locations where production is to be carried out since different varieties respond differently to specific locations. Similar observations were made by Philbrook and Oplinger (1989), Young (1990) and Bailey *et al.*, (1997). Thus for effective selection for resistance to pod shattering in soybean, it is recommended that testing and evaluation be carried out in several locations over a number of seasons.

The results of interactions between specific location and genotypes in relation to harvesting date are presented in Figure 4. Location $\times$ harvesting date was significant for the location at Nakabango and Iki-Iki for first and third harvesting dates (Fig.4a) with significant ($P < 0.05$) differences between first and second harvesting dates being observed only at Iki-iki. Similarly, significant yield loss in the three varieties was experienced between the first and third harvesting dates (Fig. 4b) indicating that a delay of 14 days before harvesting would not lead to significant ($P < 0.05$) seed yield loss through pod shattering. Variation among genotypes was significant ($P < 0.05$) between Kab 1, Nam 1 and TGM 737P suggesting different shattering responses of different cultivars to delayed harvesting and the importance of timeliness of harvesting in controlling pod shattering in susceptible varieties. Similar results were reported by Philbrook and Oplinger, (1989).

(a)



(b)

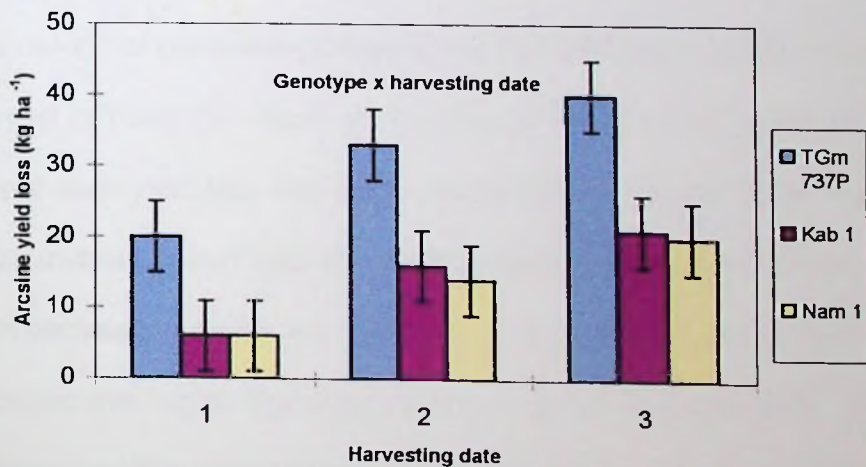


Figure.4: Response in yield loss (kg ha⁻¹) indicating (a) Location x harvesting date interaction over three locations and (b) Genotype x harvesting date interactions among three varieties.

The results of yield loss associated with shattering on specific locations and seasons is presented in Figure 5. Maximum yield loss was experienced at Iki-Iki followed by Nakabango and least experienced at Namulonge for variety TGm 737P (Fig.5a) suggesting conditions at Nakabango to be more conducive for pod shattering and those at Namulonge to be least conducive. The yield loss in 1998A was lower than losses recorded in 1997A (Figure 5b) indicating that the weather factors were more favourable for pod shattering in 1997A. Unlike variety TGm 737P, yield loss between intermediate susceptible varieties, Kab 1 and Nam 1 were not significantly different across the locations and seasons which is in agreement with observations by Tiwari and Bhatnagar, (1993).

The results of correlation between weather components and yield loss are presented in Table 22. Positively significant ($P < 0.05$) correlations were observed between yield loss and daily mean temperature and maximum daily temperature indicating that high temperature enhances shattering intensity. Correlation between humidity and yield loss was negatively significant ($P < 0.05$) indicating that higher humidity leads to reduced pod shattering. The effect of these weather components account for the G x E interactions observed in terms of different temperatures and humidity at different locations and seasons.

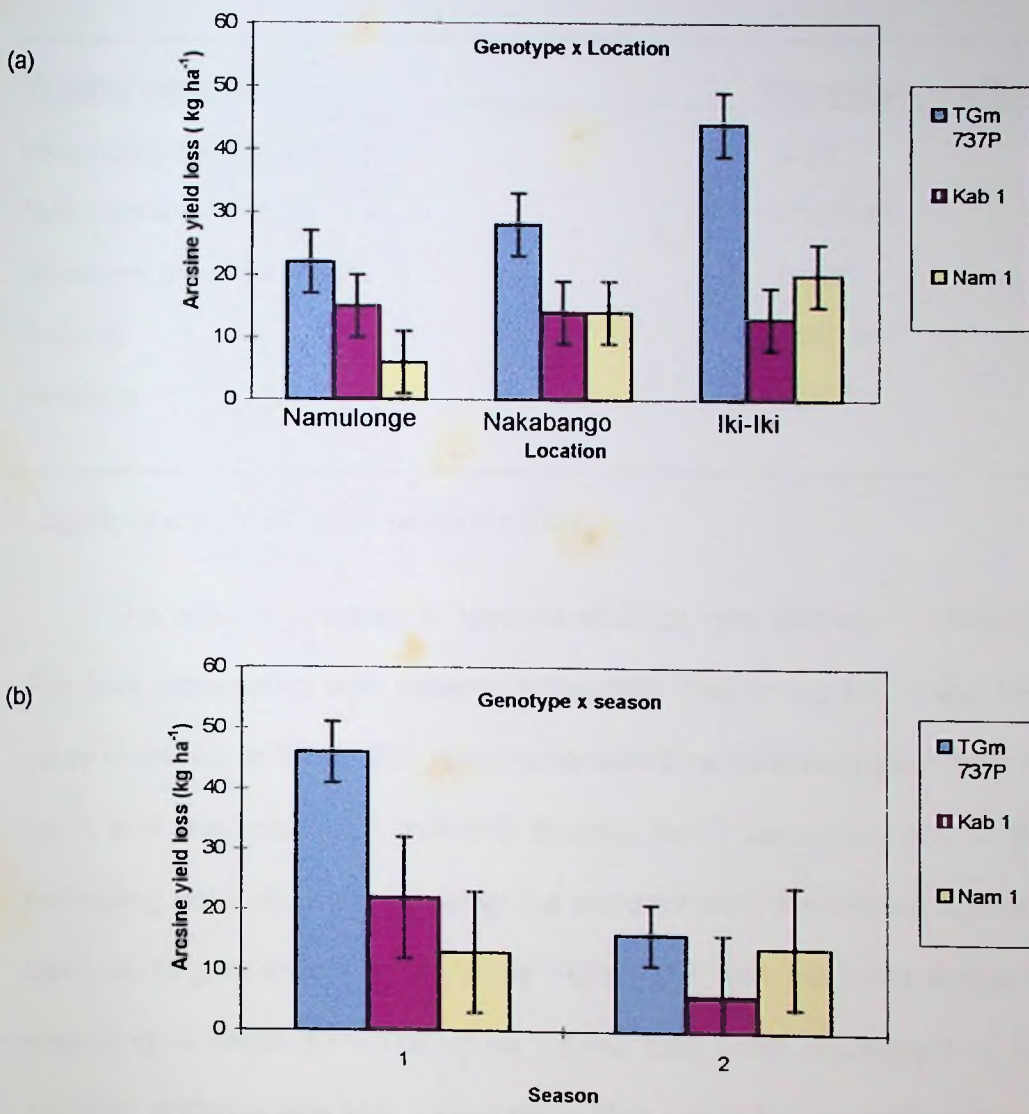


Figure. 5: Response in yield loss (kg ha^{-1}) showing (a) Genotype x location interactions and (b) Genotype x season interactions based on data from three varieties

Table 22. Correlation coefficient of yield loss due to shattering and weather components over three locations in two seasons

Weather component	Correlation coefficient
Mean daily temperature	0.29*
Minimum temperature	-0.13 ns
Maximum temperature	0.48*
Rainfall	0.08 ns
Humidity	-0.21 *

* Significant at $P < 0.05$; *significant at $P < 0.01$

The cost of soybean in Uganda shillings was 800 kg $^{-1}$ (Anon, 2000). The loss associated with delayed harvesting date in kg ha $^{-1}$ and monetary value is shown in Table 22. Results showed that maximum yield loss (186 kg ha $^{-1}$) and financial loss (148,800 shillings ha $^{-1}$) were recorded at the third harvesting date, thus emphasising the need for early harvesting to avoid such loss due to pod shattering. Variety TGm 737P was the most susceptible to shattering in which 57 - 175 kg ha $^{-1}$ of the total yield, equivalent to 45,600 - 140,000 shillings was lost. Genotypes Kab 1 and Nam 1 exhibited maximum losses of 24% and 10% equivalent to 148,800 and 71,200 shillings respectively. Similar results were reported by Hoag,(1972).

Table 23 Mean Yield loss in kg ha⁻¹ and its equivalent in monetary value over 3 locations in three genotypes across 1997A and 1998A

Genotype	Harvesting date	Total yield ha ⁻¹	Yield loss ha ⁻¹	% yield loss ha ⁻¹	Monetary value (Ug shs ³)	Monetary value (US \$)
TGm 737P	1	581	57	10	45,600	30
	2	712	145	20	116,000	77
	3	615	175	28	140,000	93
KAB1	1	775	0	0	0	0
	2	943	69	7	55,200	37
	3	777	186	24	148,800	99
NAM1	1	903	0	0	0	0
	2	983	92	9	73,600	49
	3	888	89	10	71,200	47

³(1 US Dollar = 1500 Uganda Shillings)

Results by Anon (1988b) were similar to ones observed for the susceptible variety, TGm 737P. Genotypes TGx 1448-2E, Duiker and Nam 2 did not show any loss over the three weeks harvesting period which demonstrated high level of shattering resistance that effectively controlled yield loss due to pod

shattering in conditions similar to those where the experiment was conducted. These varieties are thus recommended sources of resistance to be used in incorporation of shattering resistance into elite soybean lines which are susceptible to pod shattering. The results clearly suggest that cultivation of susceptible varieties should be avoided since they start shattering on commencement of maturity.

Philbrook and Oplinger (1989) observed relatively lower yield loss in the USA due to shattering than reported in this study due to milder weather conditions, which might be the explanation why little research on soybean shattering has been done in North America. Bailey et al. (1997) reported that North American varieties are resistant to pod shattering, however, the case may be different when they are grown in tropical environment where weather conditions are more conducive for shattering. Yield loss estimates, observed in Turkey (Anon, 1988b) were higher compared to the results obtained in this study suggesting more severe weather conditions and or more susceptible cultivars used.

5 CHAPTER FIVE

5.1 CONCLUSIONS AND RECOMMENDATIONS

The oven method modified in this study for evaluating pod shattering takes a shorter time, and results in consistent defined genetic ratios which is a reflection of an improved method. The new 1 - 3 scale used to determine frequency distribution of F_2 soybean populations segregating for pod shattering was more effective and accounted for the observed variation between scale groups than the 1 - 5 scale and resulted in consistent genetic ratios of 1 resistant : 3 intermediate : 12 susceptible indicating that the shattering trait is influenced by non allelic interactions resulting in classical dominant epistasis. Pod shattering in soybean is under control of two genes and is partially dominant over resistance. Pod shattering is not influenced by maternal effects.

The diallel analysis techniques detected non allelic interaction for pod shattering among the crosses used. Both GCA and SCA effects on pod shattering were significant with GCA predominant over SCA.

The pod shattering trait in soybean is highly heritable with narrow sense heritability (h_n^2) ranging from 0.70 to 0.73. The estimates of h_n^2 , additive and dominance effects obtained using Hayman's approach were the same as those obtained using Griffing's method and the h_n^2 estimate obtained by parent - offspring regression was very close to the estimates generated by the diallel analysis techniques.

None of the methods used to analyze the progenies for pod shattering, seemed to correct for failures in the test of the additive - dominance genetic

model. Epistasis was consistently detected in all the genetic analyses done suggesting that epistasis was a general feature in the crosses under consideration and or that the basic assumptions outlined for diallel analysis were not being fulfilled.

Resistance to pod shattering in soybean production is controlled by recessive alleles hence the backcross breeding technique alternating with progeny testing is the best method for increasing the frequency of lines resistant to pod shattering.

The extrapolation model developed for estimating yield loss in the field was effective and efficient . It produced results which were similar to those derived from the actual seed lost due to pod shattering.

Delay of harvesting for 14 days from harvesting maturity stage did not lead to significant yield loss due to pod shattering when intermediate susceptible varieties were grown as opposed to susceptible varieties which started shattering at R8 maturity stage. Resistant varieties did not shatter, even when delayed for 21 days to be harvested.

Basing on the yield potential of genotypes used in this study, significant yield loss due pod shattering ranging between 0 - 186 kg ha⁻¹ occurred in field and was significantly influenced by genotype, location, season, temperature and humidity.

Due to the significant influence of genotype, location and season on pod shattering in soybean, it is recommended that selection for resistance to pod shattering be carried out in several locations in different agro ecological zones

over several seasons to cater for genotype x environment interactions.

The significant non additive variance observed in the study was made up of combined dominance and epistatic effects. It is therefore recommended that further study be undertaken to partition this non additive genetic variance into components attributable to dominance and epistasis.

The extrapolation model is recommended for use in farming systems where pod shattering is spontaneous due to stress from environmental factors. It does not apply to loss caused by header of the combine during harvesting. It is proposed that studies in controlled environment be conducted to determine threshold levels of temperature and humidity on pod shattering in soybean genotypes in order to develop a more comprehensive model to be applied in determining yield loss due to pod shattering in defined environments. Such a model will be a useful tool in breeding and production of soybeans in such environments.

These results show that resistant varieties should be used to minimise yield loss due to pod shattering in the field or, harvesting should be timely which is approximately one week after the crop has reached physiological maturity.

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