GENETIC ANALYSES OF POD SHATTERING AND AGRONOMIC TRAITS OF SOYBEAN (*Glycine max* (L.) Merr.) GENOTYPES

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DECLARATION

This thesis is my original work and has not been presented for award of a degree in any other University or institute of higher learning.

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LIST OF ABBREVIATIONS

AGRA - Alliance for a Green Revolution in Africa

AVRDC - Asian Vegetable Research and Development Center

BIDCO - Business and Industrial Development Cooperation Oil

BNF - Biological Nitrogen Fixation

CAN - Calcium Ammonium Nitrate

CAVS - College of Agriculture and Veterinary Sciences

CIAT - International Center for Tropical Agriculture

DAP - Diammonium phosphate

DNA - Deoxyribonucleic acid

DRC - Democratic Republic of Congo

EU – European Union

FAO - Food and Agricultural Organization

FIPs - Farm Input Promotions

GCA - General Combining Ability

GPR - General Predicted Ratio

IITA - International Institute of Tropical Agriculture

ISFM - Integrated Soil Fertility Management

KALRO - Kenya Agricultural and Livestock Research Organization

KEPHIS - Kenya Plant Health Inspectorate Service

LM - Lower midland agro-ecological zone

MAS - Marker Assisted Selection

Masl - meters above sea level

N - Nitrogen

NARS - National Agricultural Research System

NCD - North Carolina Design

NGO - Non-governmental organization

Ppm - parts per million

QTL- Quantitative Trait Locus

REML- Residual Maximum Likelihood

SCA- Specific Combining Ability

SSA - Sub-Sahara Africa

TSBF- Tropical Soil Biology and Fertility

UCG/Bbo - Université Catholique du Graben/Butembo

UM - Upper Midland

UniGom - Université de Goma

USA - United States of America

USDA- United States Department of Agriculture

DEDICATION

This thesis is dedicated to the entire Kataliko's family; my lovely wife Francine Kahindo Munyirungu, my lovely parents Thomas Paluku Kataliko and Adeline Katungu Vagheni, my brothers and my sister.

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ABSTRACT

Pod shattering is an important constraint associated with 34 to 99% loss in productivity of soybean (*Glycine max* (L.) Merr.). Common management strategies such as early harvesting and harvesting when temperature is still low are not very effective. Genetic resistance to shattering is a more effective strategy to reduce losses. The objective of this study was to evaluate soybean genotypes and to determine the combining ability of pod shattering resistance and selected agronomic traits. Twenty soybean genotypes were evaluated during the 2016 long and short rain seasons for resistance to pod shattering and other agronomic traits at KALRO-Embu and Mwea Research Centres. The genotypes included SB lines from IITA and local commercial varieties. The trial was laid out in an alpha-lattice design arranged in a 4 x 5 pattern and replicated three times. Pod shattering was assessed on a scale of 1 to 5 (1=very resistant; 5= highly susceptible). Data was also collected on germination percentage, days to 50% flowering, days to 75% maturity, plant height, biomass, number of pods per plant, number of seeds per pod, grain yield, 100-seed mass and harvest index. F_1 progenies were generated from a half-diallel mating design, involving eight parents. Two of the parental lines were resistant, three moderately resistant, one moderately susceptible and two highly susceptible to pod shattering. The trial design was laid out in an alpha-lattice arranged in a 6 x 6 pattern with three replicates. The 28 F_1 progenies and their parents were evaluated to determine the mode of gene action for pod shattering resistance and other selected traits in soybeans such as days to 50% flowering, days to 75% maturity, plant height and grain yield. Data were subjected to analysis of variance and residual maximum likelihood to test the significance of variation among the genotypes. General and specific combining abilities (GCA and SCA) were calculated following Griffing's Model 1, Method 2. The genotypes varied significantly in pod shattering from resistant to highly susceptible. Ten genotypes were resistant to pod shattering out of which seven were SB lines. Genotypes SB-8, Gazelle, SB-74, SB-4 and Nyala were the most resistant. SB-74 combined resistance to pod shattering and high grain yield. Genotypes SB-90 and SB-25 were highly susceptible while the rest of genotypes were either moderately resistant or susceptible to pod shattering. The high yielding genotypes were 931/5/34 followed by 915/5/12 and SB-154 with grain yields of more than 1800 kg ha^{-1}. Pod shattering resistance had significant negative correlation with number of seed per pod (r=-0.13*), indicating that reduction of seeds in a pod made a significant contribution towards pod shattering resistance. Both general combining ability (GCA) and specific combining ability (SCA) were significant for all the traits measured indicating the

importance of both additive and non-additive gene action in the inheritance of pod shattering and selected traits. The low ratio GCA/SCA (0.00124 to 0.0742) for all the traits studied indicated that non-additive gene action played a more significant role than additive gene action in the inheritance of these traits. Parental lines SB-8 followed by Nyala had the highest negative and significant GCA effects across the environments indicating that they were the best combiners for improving pod shattering resistance. Parental line 835/5/30 was the best combiner for high yield. Only the F_1 progenies of the cross SB-25 x SB-8 had significant negative SCA effects for resistance to pod shattering across the environments. In general early flowering and maturity of progenies did not result in higher grain yield except for some progenies such as 915/5/12 x SB-8. The study identified resistant and moderately resistant genotypes that could be used as sources of resistant genes to develop pod shattering resistant varieties. The results also suggested that genetic improvement for pod shattering resistance and selected agronomic traits in soybeans is possible based on the effective selection of F_2 population generated from all possible combinations and the use of heterosis breeding to allow hybrid offsprings from genetically diverse parents to develop significant improvements. The results suggested selection for pod shattering resistance in late segregating generations may also improve other agronomic traits.

Key words: general combining ability, specific combining ability, pod shattering, soybean.

CHAPTER ONE : INTRODUCTION

1.1. Background information

Soybean is one of the major grain legumes grown worldwide (Boerma and Specht, 2004). In 2005 and 2006, soybean production reached 217.6 million tons. World production of soybeans is predicted to increase by 2.1% annually to 359.7 million tons by 2030 (Masuda and Goldsmith, 2008). Main producers were China (54 million tons), the USA (37 million tons), Argentina (29 million tons), Brazil (27 million tons), and the EU-28 (10 million tons). In Africa, Egypt is still the largest soybean producer with 18 million tons annually (USDA, 2009). Other major producers are Nigeria, South Africa and Uganda, Zimbabwe, Ethiopia and Rwanda (Abate *et al.*, 2011).

Soybean is a small grain with creamy color and few black-seeded varieties. It originated from the Orient, in China (Synder and Kwon, 1987). Important products from this crop are oil (about 20%) and protein (about 40%) with little cholesterol and saturated fat but have high levels of calcium, phosphorous, potassium, thiamine, riboflavin and fiber contents (Myaka *et al*., 2005; BIDCO, 2005). Compared to protein rich foods such as meat, fish or eggs, it has the highest and the cheapest proteins. In terms of oil content, it is the second after groundnut (IITA, 2000). With vitamins A, B, C, D, F and K, soybeans may validly substitute meat, milk and eggs that are lacking in some diets. Michelfelder (2009) stated that 1 kg of soy protein equals to 40 kg of cassava, 13 liters of cow milk, 3 kg of beef and 60 chicken eggs. Soybean is also a major source of minerals such as copper, manganese and molybdenum (Merritt, 2004). These nutritional factors lower risks of severity of some chronic and cardiovascular diseases. Affected by low soil pH and requiring 6.0 to 6.5 of pH value, soybean is one of the widely cultivated legumes where fertilizers are not affordable or available for the small-scale producers (Coulibaly *et al.*, 2009). It improves soil fertility by sequestering atmospheric nitrogen (Kasasa *et al*., 2000). Most varieties fix from 44 to 103 kg N ha^{-1} per year (Sanginga *et al*., 2003). In Africa, particularly in Sub-Saharan region where soils have highly variable fertility gradients and respond differently to an application of inputs (Hossner and Juo, 1999; AGRA, 2007), soybean is still recommended.

1.2. Problem statement

In Sub-Sahara Africa (SSA), the demand outweighs the production, leading to increase in imports of soybean from India, Argentina and Brazil. Imports of soybean in 2011 were estimated at nearly 1.6 million tons. South Africa, Nigeria, and Kenya accounted for nearly

43%, 21%, and 18% of the total import volume. Uganda is the leading producer of soybean in eastern Africa with an increase in production from 158,000 tons in 2005 to 213,300 tons in 2011. Kenya imports about 29,000 tons per year from neighboring countries such as Uganda and Zambia (Abate *et al.,* 2012 cited by Murithi *et al.*, 2015).

Low yields of available soybean varieties make production unattractive to farmers. This has contributed to declining area in soybean in Kenya (FAO, 2011). Annual consumption of all soybean products in Kenya is estimated at 100,000 tons (Jagwe and Owuor, 2004) to 150,000 tons (Tinsley, 2009). Domestic production accounts for a maximum of 4,500 tons (Murithi *et al.*, 2015). Competition from other legumes such as pigeon pea and cowpea in semi-arid areas, and common bean in medium potential agro-ecological zones poses a challenge to increased soybean production. Most of these pulses do not require as much time and effort to prepare. In addition, they command better prices in local markets. For example, a kg of soybean is sold at Kshs 50 compared to Kshs 80 or more for dry beans (Chianu *et al.*, 2008). Pod shattering of soybean is particularly an important challenge that reduces the grain yield by 34 to 100% depending on the environmental conditions, the genotype and the management practices (Tefera *et al.*, 2009; Krisnawati *et al.*, 2015; Krisnawati and Adie, 2016).

1.3. Justification

Among important food crops with net positive characteristics, soybean contributes to livestock and human nutrition, soil health, income of farmers and reduction of poverty in SSA (Kahindi and Karanja, 2009).

Development and release of new cultivars with high yields and resistance or tolerance ability to arrays of constraints such as pod shattering, can contribute to higher soybean yield and stability in the Eastern Africa. The screening of germplasm is the key to develop high quality seeds with farmer preferences and with profitable returns (Lee *et al*., 2011). Research conducted in Kenya by KALRO-Njoro Research Center identified suitable soybean genotypes for diverse agro-ecological environments (Chianu *et al.*, 2008). Five soybean varieties, *Gazelle, Hill, Black Hawk, EAI 3600*, and *Nyala* were consequently released in 2009 by Kenya Plant Health Inspectorate Service (KEPHIS). Thereafter, two dual-purpose promiscuous soybeans, *TG x 1895-33F* and *TG x 1740-2F*, and one grain genotype known as *SCS-1* were released in June 2010 (Emmanuel and Gowda, 2014). Although the new varieties showed a 6.5% yield advantage over the five farmer varieties, they were susceptible to pod

shattering (Chianu *et al.*, 2008). They were medium to late maturing and adapted poorly in varied agro-ecological locations (Emmanuel and Gowda, 2014).

There is a need therefore, to develop improved soybean varieties with better and stable resistance to pod shattering and high yield to ensure economic growth through sustainable production as reported by Chianu *et al.* (2008). Improved varieties could contribute to high local production and provide raw materials for the livestock industry. Improved varieties have proven to be a promising, giving a high grain yield in different ecological locations as well as at research station and farm levels (Chianu *et al.*, 2008). Soybean can improve the diet, livelihoods and incomes of small-scale producers in Southern and Eastern Africa.

Accordingly, soybean improvement is among strategies to fight hunger in SSA and in Kenya particularly. Genetic analysis is the key proof in breeding programs to generate lines that combine traits as required by farmers in any farming system. Information on the mode of inheritance of important agronomic traits is essential for developing effective breeding programs to generate lines that combine farmer and processor preferred traits. However, there is limited work on genetic analyses of agronomic traits such as pod shattering of existing varieties and breeding lines in Eastern Africa. Influence of environments on productivity of soybean is also poorly understood.

1.4. Objectives

The overall objective of the study was to contribute to improved soybean productivity by developing high yielding varieties with resistance to pod shattering and farmer preferred traits.

The specific objectives were:

i. To evaluate soybean varieties for resistance to pod shattering and agronomic traits, yields and yield components across different environments.
ii. To determine the combining ability of resistance of soybean to pod shattering.

1.5. Hypothesis

i. Soybean varieties and breeding lines do not differ in their expression to pod shattering and farmer preferred traits in different agro-ecological zones in Eastern Africa.
ii. There are no differences in general and specific combining ability for pod shattering in soybean genotypes grown in Eastern Africa.

CHAPTER TWO: LITERATURE REVIEW

2.1. Origin and importance of soybean

Soybean (*Glycine max*) originated from China and has been cultivated for more than 3,000 years. Domesticated from the wild soybean (*Glycine soja*) between 1,500-1,100 BC (Pathan and Sleper, 2008), soybean was introduced to European countries between the 16th and 17th centuries from China, Korea and Japan. It was introduced in America in 1765. Soybean was introduced in Africa by Chinese traders along the East coast in the 19th century (Giller and Dashiell, 2006). Today, soybean is grown all over the world, in diverse climates from temperate to tropical and subtropical regions (Tukamuhabwa *et al.*, 2002a).

In Kenya, the British colonists introduced soybean in 1909 for child nutrition (Bulletin of Imperial Institute, 1909). It is cultivated in the maize cropping regions in the upper midland and lower agro-ecological zones. These areas include western Kenya, comprising Homa Bay, Bungoma, Busia, Homa Migori, Kisii, Kakamega, Siaya, Trans-Nzoia, Vihiga, and the Nyamira counties; the central and eastern regions comprising Kirinyaga, Embu, Meru and Tharaka counties, and parts of Rifts Valley (Tinsley, 2009). However, the western region produces more soybean than the central highland regions (Tinsley, 2009). Table 1.1 gives the yield expected by region throughout the country for different soybean varieties.

Table 1.1 : Expected grain yield of soybean varieties in a range of different climatic conditions in Kenya

Climatic description	**Area**	**Variety**	**Expected yield (t ha^{-1})**
Warm temperatures	Homa Bay Mitunguu	Duiker, EAI-3600, Nyala	1.2 to 1.6
Moderate temperatures	Bukura Kakamega Kitale Embu	SCS-1, Duiker, Nyala, Gazelle	1.4 to 1.9
Cool temperatures	Bahati Baraton Njoro Menengai	Sable, SCS-1, Nyala, Gazelle	1.2 to 1.5
Marginal rainfall sites	Matayos Gachoka Makuyu Ol Rongai	Gazelle, EAI-3600, Nyala, Sable	0.6 t 1.0 (to 1.6)

Source: Krause and Wasike, 1998

Soybean is well adapted to soils in western Kenya, where it is higher yielding than beans and more tolerant to diseases, pests and drought (Collombet, 2013). It is an important component of the smallholder small-scale production systems in Western Kenya (Chianu *et al.*, 2008). Recently, it was promoted by Farm Input Promotions (FIPs-Africa), a 'not-for-profit' company incorporated in Kenya whose approach is to assist farmers to gain access to advisory services and local access to the inputs and technologies they need to enhance the productivity of their livestock and crops in a sustainable way (Chianu *et al.*, 2008). FIPs-Africa in collaboration with Kenya Agricultural Livestock Research Organization (KALRO) and the Tropical Soil Biology and Fertility Institute (TSBF) of IITA has been promoting this crop for food security, income and soil improvement (Collombet, 2013).

However, soybean still remains a minor crop largely due to poor adoption and low implementation of new technology, attributed to lack of awareness of procedures related to its processing and uses, low yield estimated at 0.6 t ha^{-1} in East Africa, limited access to market and policy support (USDA, 2009). For instance, soybean demand exceeds 100,000 tons annually in Kenya (Wasike *et al.*, 2009). This is the highest demand in Eastern Africa. However, production has never exceeded 5,000 tons per year (FAO, 2012). This represents a deficit of more than 95% mostly because the adoption of the crop has remained low, unlike countries in the Americas and in the northern hemisphere who have embraced the crop (Wasike *et al*., 2009). This discrepancy is the reason for imports from Uganda, Malawi, Zambia, Zimbabwe and Argentine (Chianu *et al.*, 2008). In Kenya, soybean is mainly cultivated for its seeds that are used for human food, or processed to produce soybean oil and feed for livestock (USAID, 2015).

Soybean is an important source of complete proteins especially for vegetarians. The detection of very small fundamental unique proteins in soybean referred to as peptides increases its values at nutritional level (Bush *et al.*, 2011). These unique peptides include conglycinins, glycinins, defensins, and lunasins and provide health benefits to human, such as regulation of blood pressure, control of blood glucose levels, and improvement of immune function in human bodies (Bush *et al.*, 2011). Soybean is known to have all eight essential amino acids necessary for human body. These amino acids are tryptophan, isoleucine, leucine, phenylalanine, valine, threonine, lysine and methionine (Fukushima, 2001). Vegetable proteins, which lack or have low ratio in one, two or more essential amino acids, are considered "incomplete" proteins. For instance, some grain legumes typically have low concentrations of lysine. Common bean has low concentration of sulfur amino acids such as

cysteine and methionine (Fukushima, 2001). However, soybeans have the highest level of sulfur amino acids compared to other legumes (Anderson and Bush, 2011). Soybean protein is said to be equivalent to animal protein qualitatively (Fukushima, 2001). However, from recent studies, soybean proteins are lower in quantity of certain amino acids compared to animal proteins such as proteins in cow's milk or eggs (Anderson and Bush, 2011).

Soybean also contains isoflavones ('genistein' and 'daidzein') (Messina, 1995) and fiber, that provide health benefits (Ye *et al.*, 2012). It contains about 19% of oil. Its oil consist of about 54% of linoleic (18:2), 22% of oleic (18:1), 10% of linolenic (18:3), of 10% of palmitic (16:0) and 4% of stearic (18:0), acids (Wilson, 2004). It has important amounts of α-linolenic, omega-6 fatty acid. Its proteins reduce cholesterol and are considered useful in high blood pressures reduction (Messina, 1995). Soybean is an important source of mineral nutrients including calcium, iron and vitamins including B3-vitamin also known as niacin, B6-vitamin called pyridoxine, B9-vitamin known as folacin, folic acid or folate and B12-vitamin which is also known as cobalamin (Lampe, 2009 ; Wiersma, 2012).

2.2. Global trends in soybean production

Soybean production worldwide increased by 4.6% per year between 1961 and 2007, with the highest production occurring from 2005 to 2007 (FAO, 2008). The area allocated to soybeans also expanded from about 25 million ha in 1961 to 94.1 million ha in 2005 to 2007, and 100 million ha in 2008. However, the soybean area harvested, in 2005 to 2007, decreased to 29.9 million ha or 31.7% in USA, and 9.2 million ha or 9.8% in China. In contrast, area harvested increased to 15.1 million ha or 16.0% in Argentina, and 21.9 million ha or 23.3% in Brazil. The world average soybean productivity, increased to 2.31 t ha^{-1} $year^{-1}$ in 2005 to 2007 from 1.16 t ha^{-1} $year^{-1}$ in 1961 to 1965 (FAO, 2008). Annual production of soybean averaged 217.6 million tons between 2005 and 2007 (Figure 2.1).

World's soybean production is expected to grow by 2.2% per year and reach 371.3 million tons by 2030 based on an exponential smoothing model with a damped trend (FAO, 2008). An average of 28.6 million tons of soybeans were produced worldwide annually in 1961-1965. The production of 214 million tons in 2005 represents an increase of 4.4 % of the production of 2004 while 217.6 million tons were reached in 2007. Production increased 7.6 times over five decades (FAO, 2007). Five countries accounted for about 90 % of the global output. They are the United States, Brazil, Argentina, China and India as indicated in Table 2.1.

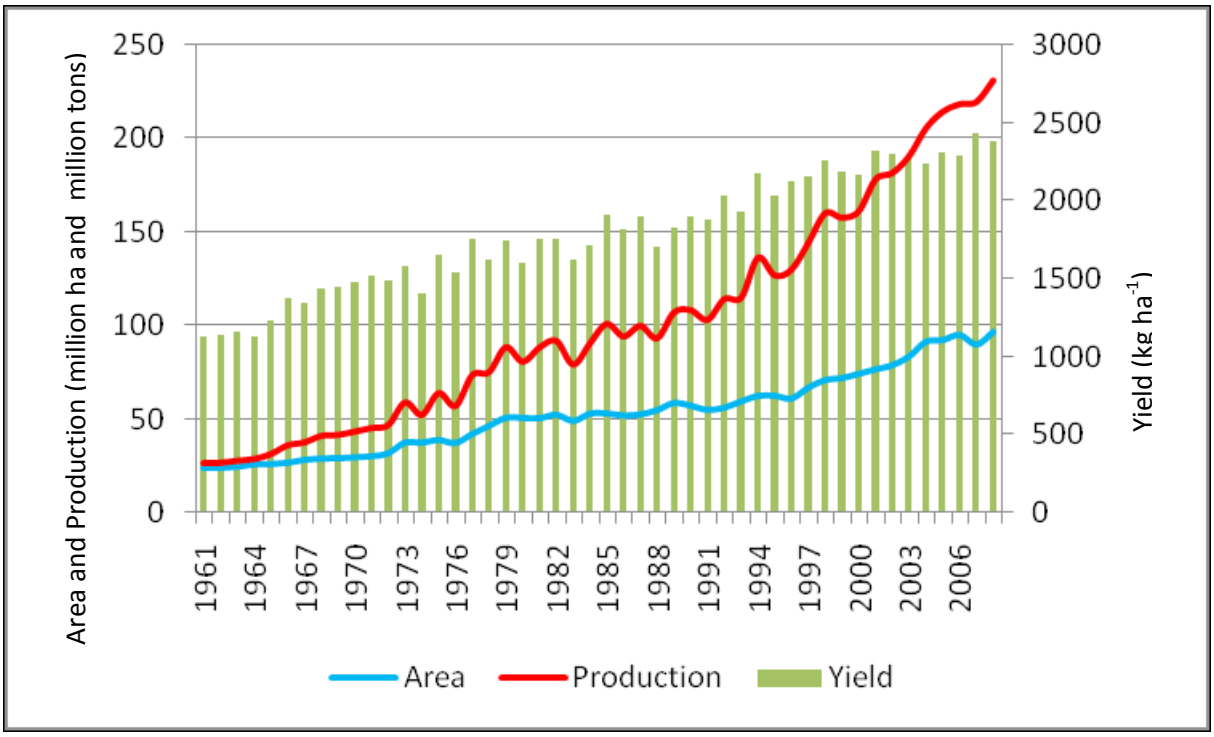


Figure 2.1 : Soybean production world trends (Abate *et al.*, 2011).

Between 2000 and 2010, the annual soybean production in Kenya was 2400 tons from a harvested area of 2700 ha when productivity varied from 913 to about 1000 kg ha^{-1} (Table 2.2). From 2011, yield and production reached the remarkable value of 2.5 t ha^{-1} (FAO, 2011). Recent studies conducted by CIAT-Maseno in 2013 showed that yield potential of improved soybean varieties was 3.5 t ha^{-1} compared to 2.6 t $ha^{-1}$for SB 19 described as TG x 1740-2F (Collombet, 2013). Agnoro (2008) suggested a yield potential of 3 t ha^{-1} in Kenya.

Table 2.1 : Soybean production in top five producer countries and their contribution to world supply

Country	**Production (million tons)**	**World contribution (%)**
United States	91.4	32.8
Brazil	81.7	29.3
Argentina	49.3	17.7
China	11.9	4.2
India	11.9	4.2

Source: FAO, 2016 cited by Weinraub (2017)

Table 2.2 : Soybean yield, production and harvested area in Kenya, 2000-2011

Year	**2000**	**2002**	**2004**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**
Productivity (kg ha^{-1})	913	860	1010	826	840	780	715	950	2500
Production (tons)	2400	2600	3200	2100	2100	2000	2100	1500	4300
Area harvested (ha)	2600	3000	3200	2500	2500	2600	2900	1600	1700

Source: FAO, 2011 cited by Njoroge *et al.*, (2015)

The upward trend in production from 2009 is attributed to improved soybean research by the Government, learning institutions and developmental organizations which resulted in the release of high-yielding varieties with tolerance to different constraints (Murithi *et al.* 2016).

In Kenya, soybean has a short cycle of less than 5 months. Farmers can grow it during the first or second season, or both (Chianu *et al.*, 2008). Although FIPs-Africa in collaboration with the Government of Kenya wants to extend this crop in all the country to fight the malnutrition in rural areas (FAO, 2015), soybean is still not common and its value chain is poorly integrated. The average productivity has stagnated at below 0.8 t ha^{-1} since 1990 (FAO, 2008). Chianu *et al.* (2008) reported a yield of 450 and 560 kg ha^{-1} in western province while the potential yield based on improved varieties and good management practices is 3,000 to 3,600 kg ha^{-1}. Average yields of 790 kg ha^{-1} in Rwanda and 1,113 kg ha^{-1} in Uganda have been reported (FAOSTAT, 2010 cited by Nabintu, 2012). Abate *et al.* (2011) noted the importance of biotic (diseases and pests) and abiotic constraints (drought, rain fed pattern, harvest and post-harvest constraints such as pod shattering), political, socio-economic constraints and lack or few effective breeding strategies to limit this low productivity.

In contrast, Vision 2030 identified soybean as one of the crops which could contribute to the economic growth pillar (Chianu *et al.*, 2008). Major production constrains in Kenya include pod shattering, rust and poor agronomic management which jointly lower the yield potential of high yielding varieties. The two first are considered as important threats to soybean productivity in Eastern Africa (Vanlauwe *et al*., 2002, Levy, 2005; Oloka *et al.*, 2008; Dean *et al.*, 2012). Other constraints include high requirement of fuel and time for preparation, conservative attitude towards food types consumed in East Africa, few and rudimentary soybean processing industries (Oniang'o *et al.*, 2003). Perceived negative impacts of soybean products in human nutrition have also contributed to low adoption of soybean as a staple food (Fallon and Enig, 2001). Lack of improved seed and regeneration of quality seed is another important constraint to agricultural growth and a fundamental reason for the slow growth in food production by the small-scale farmers in SSA (De Groote *et al*., 2003).

2.3. Ecology and botany of soybean

Soybean is grown from 0 to 2,200 m above sea level (masl), with the optimum altitude being from 300 to 1,600 masl and a rainfall regime of 300 to 1,400 mm per annum (Mullen, 2003). Water requirement for maximum production of soybean ranges from 450 - 700 mm, well

distributed over the growing season when the temperature must range between 25 and 30°C (FAO, 2002). Optimum pH for soybean growth is 6 to 6.5. Soybean grows best in pure stands. By sequestering atmospheric nitrogen (N), soybean improves the soil fertility (Kasasa *et al*., 2000; Sanginga *et al*., 2003). Annually improved promiscuous varieties fix from 44 to 103 N kg ha^{-1} (Sanginga *et al*., 2003), depending on the soil environment (Gan *et al*., 2002).

Soybean is an annual leguminous that belongs to the Fabaceae family and Papilionoideae sub-family (Singh *et al*., 2007). According to FAO (2002), often, soybean is ranked as an oleaginous rather than a pulse. It has fine brown or grey hairs which cover stems, leaves and pods. It has 3 to 4 leaflets per leaf. Leaves are trifoliolate; leaflets are 2 to 7 cm broad and 6 to 15 cm long (Fig 2.2. A). Just before maturity, leaves fall down. Flowers are purple or pink or white in color and self-fertile, are borne on an axil, which is the junction of a branch or leaf and a stem. Soybean fruit is a pod with hair. It develops in arrays of 3 to 5; one pod being 3 to 8 cm long containing usually 2 to 4 seeds (Infonet-biovision, 2012). It occurs in many dimensions. The hull and seed coat (Fig 2.2. B and C) protect the embryo from infections that may arise from bacteria or fungi before and after planting. The seed coat color varies from black color, blue, brown, yellow, green to mottle. Soybean grows from 60 to 120 cm high and is well adapted to diverse environments. It matures in 3 to 6 months depending on genotype and environmental conditions. The temperature is influenced by the altitude and geographical position and affects the initiation of soybean flowering and duration to maturity. Flowering may not occur at very high altitudes (more than 2,500 m), and the crop remains vegetative. Therefore, soybean needs warm climates to flower and mature and is a suitable crop for medium to low altitudes (Ogema *et al.*, 1988).

Soybean has two important development phases; the vegetative and reproductive phases. Vegetative phase starts at germination when roots are formed and terminates at the time when the first flower appears. The reproductive phase starts when the first flower appears and ends when dry mature grains are ready for harvesting. The development steps such as length of the vegetative growth, days to flowering, and days to maturity are influenced considerably by temperature and photoperiod (Mullen, 2003). Depending on genotypes, geographic locations and ecological conditions the vegetative phase of soybean takes 6 to 8 weeks (Mullen, 2003). Soybean is sensitive to photoperiod. Transition from vegetative to reproductive stages is influenced by day length, altitude and temperature (Howell and Caldwell, 1978; Liu, 1997; Mullen, 2003). In each axil there is a presence of an axillary bud. The development of this bud may give a branch, an inflorescence or may no longer continue depending on

environmental conditions (Mullen, 2003). Flowering begins in the lower part, at the fourth node usually, before reaching the top. Depending on the genotype, soybean petals can be white, pink or purple and are produced in the racemes. Soybean is predominantly a self-pollinated crop. Cross pollination is normally less than one percent. Artificial pollinations are made by plant breeders to develop new cultivars with specific traits (Oplinger, 1980).

Soybean has a complete flower. All the four parts, calyx, corolla, androecium and gynoecium are present in a single flower (Figure 2.3). The five petals including one standard, two wings and two keels enclose the pistil and the 10 stamens. Nine of the ten stamens develop into a tube surrounding the pistil, the tenth remaining free. Pollen grains, the male gametes, from the anthers are shed directly on the top of the stigma. Often, pollen is shed shortly before or immediately after the flower opens. It ensures a high degree of self-pollination and less than 1% natural cross-pollination (Singh *et al.*, 2007). Soybean flower is very small and delicate; it drops even with minor injuries to the pistil. Therefore, during artificial crossing utmost care should be taken not to injure the pistil. Usually during crossing, the anthers are carefully removed from the female parent, process called emasculation, selected for crossing. It is then pollinated with anthers collected from the flowers of a donor parent (Walker *et al.*, 1979). The racemes are short with 2 to 5 flowers. The terminal raceme, however, may have more flowers compared to those that occupy lower positions on the plant (Bernard and Weiss, 1973).

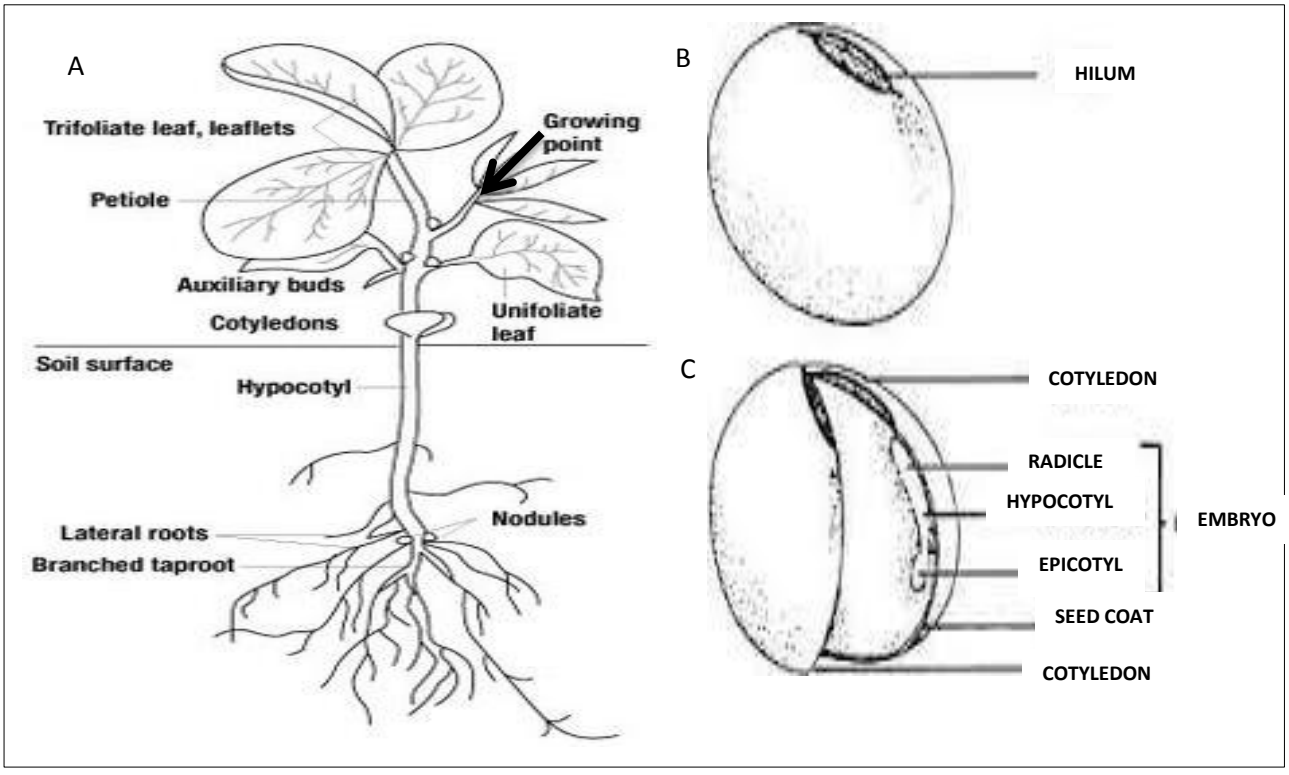
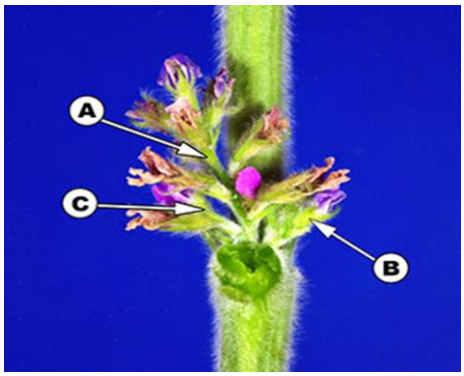


Figure 2.2 : Soybean seed and a soybean seedling structure (Hicks, 1978)

(A) Open soybean flower

(B) Unopened soybean flower with sepals removed; petals cover sexual parts

(C) Sexual parts of an immature flower so stamens have not fully elongated.



(D) Stem node exhibiting three racemes: primary (A), secondary (B), and tertiary (C)

Figure 2.3 : Soybean reproductive organs (Singh *et al.*, 2007)

Soybean requires about 100 to 146 days from germination to plant maturity. However, the actual duration depends on the genotype, growth and environmental conditions (Mullen, 2003). The yields vary from 0.5 t ha^{-1} in low input cropping systems of prevalent in Africa, to 4.5 t ha^{-1} under intensive farming systems. A yield potential of modern varieties is 3 t ha^{-1}(Agnoro, 2008). Immature grains are used to make several recipes, or consumed as a vegetable (TeKrony *et al.*, 1987; Keith and Delouche 1999).

2.4. Constraints in production of soybean

Constraints in soybean production include the biotic stresses which involve the detrimental effects caused by pests and diseases, abiotic stresses and harvest and post-harvest constraints. Soybeans are susceptible to the attack by different pests and diseases during their growing season according to Fuderburk *et al.*, (1999) and Lawrence and McLean (1999). Approximately 100 bacterial, fungal and viral pathogens are known to attack soybeans. Among the fungal diseases brown leafspot, frog eye leafspot, phytophthora root rot, stem canker, purple seed stain and stem blight are of economic important (Bowers and Russin,

1999; and Pratt *et al.*, 2011). Major economic bacterial diseases are bacterial blight, pustule and wildfire (Colyer, 1989). Lastly, main viral diseases include soybean mosaic, bud blight, and bean pot mottle (Hartman *et al.*, 1999).

Main abiotic stresses that constrain the productivity of soybean in Africa include drought, high temperatures associated with climate change, low soil fertility and salinity. Drought is probably the most important threat to soybean production in the world. Recurrent droughts adversely affect yield stability (Dai, 2013; Foyer *et al.*, 2016). Drought also affects symbiotic nitrogen fixation. However, there is little information how different rhizobia and their host genotypes respond to drought stress (Ferguson *et al.*, 2010). The relationship was explained by Kondorosi *et al.* (2013) who reported that plant releases root flavonoids into the rhizosphere under moisture stress conditions. Lopes *et al.* (2011), Tanaka *et al.* (2014), Vadez (2014) and Ali *et al.* (2016) have shown that types of root penetrating the depth of the soil depth to reach a greater "root mass at depth", or roots with large diameters of xylem and/or broader lateral roots with more absorbent hairs contribute to plant adaptation to drought stress. These types of roots tend to be characterized by a larger total surface area, which increases nutrient extraction to stabilize photosynthesis and maximize humidity (Blum, 2011; Lopes *et al.*, 2011; Comas *et al.*, 2013). Identification of soybean cultivars of soybean which have improved root architecture characteristics can be an important selection criterion for drought-tolerance. However, development of varieties with efficient root systems remains a challenge (Ku *et al.*, 2013).

Soil salinity, another abiotic constraint, reduces soybean production and quality significantly (Allakhverdiev *et al.*, 2000). Soybean belongs to salt-sensitive glycophytes. All of its developmental stages are affected adversely by soil salinity (Phang *et al.*, 2008). High levels of salt in soil induce osmotic stress due to a reduction in the amount of water available in the soil and an ionic imbalance in the cytosol of plant cells (Blumwald *et al.*, 2000; Conde *et al.*, 2011). Salinity related stress significantly reduces the height and size of the plant, number of pods and grain yield (Wang *et al.*, 2001; Essa, 2002; Phang *et al.*, 2008). Lu *et al.* (2009) reported that salinity reduces seed quality, protein and chlorophyll concentration. Stress related to soil salinity also significantly affects germination, plant development, biomass and seed yield (Wang and Shannon, 1999; Essa, 2002). The yield of soybean under the soil salinity stress may decrease by up to 40% (Chang *et al.*, 1999).

Tolerant soybean cultivars can reduce the drastic loss of soybean yield in production systems where soil has elevated salt concentrations. Several strategies have reported mechanisms that contribute to salt tolerance in soybean, and which have been exploited to develop tolerant cultivars (Phang *et al.*, 2008). These strategies include maintaining ionic homeostasis by stopping toxic ions from sensitive aerial parts of the plant, regulating the osmotic potential of cells by metabolite accumulation and restoring oxidative equilibrium to avoid other challenges due to a strong accumulation of reactive oxygen species (Phang *et al.*, 2008). For instance, Ren *et al.* (2012) noted that soybean varieties '*WF-7*' bred at Chinese Academy of Agricultural Science, Beijing, China, and '*FT-Abyara*', a Brazilian cultivar have developed stable salt tolerance while '*Union*' from the USDA Soybean Germplasm Collection maintained at the Virginia State University Soybean Breeding Program, is sensitive to salt stress. A recent study carried by Liu *et al.* (2016) in China shown that tolerance to salt toxicity in soybean is associated with a gene named '*GmSALT3'* on chromosome-3 and has the ability to increase the yields in salinized conditions. A good understanding of these mechanisms and the identification of genes capable of controlling this ability would allow breeders to develop sustainable techniques for improving and maintaining salt tolerance.

Development of resistant or tolerant lines against a variety of abiotic impacts is crucial in reducing yield losses. However, developing cultivars with higher levels of tolerance to abiotic constraints is still a challenging task. This is attributed to the multigenic nature of this type of traits (Dai, 2013). Specific DNA markers are needed to locate where these genes are, and to facilitate gene sequencing, cloning and marker assisted breeding (Alberts *et al.*, 2002).

Harvest and post-harvest losses of soybeans occur during threshing, harvesting, winnowing, packaging, storage and transportation, processing and marketing (Mujumdar and Law, 2010)., Particular attention is reported to pod shattering at harvest such that timely harvest at optimum moisture percentage (not more than 14 percent), use of proper method of harvest, avoidance of losses in threshing and winnowing by adopting better mechanical methods are kindly required (Hideyuki *et al.*, 2014).

2.5. Pod shattering in legumes

2.5.1. Mechanisms involved in pod shattering

Pod shattering or pod shattering refers to the dispersal of seeds from mature pods that have opened along the dorsal or ventral sutures (Dong, 2014). The yield loss due to soybean pod shattering may range from 34 to 100 % (Dong, 2014). This depends upon the extent to which

harvesting was delayed after maturity, the genotype and environmental conditions during harvesting (Tiwari and Bhatnagar, 1991 ; Hideyuki *et al.*, 2014). The pattern of pod shattering reveals that the tissues are under tension. Either natural or mechanical condition stimulates the tissue to separate quickly at specific point (Romkaew and Umezaki, 2006). Soybean pod shattering is among the major constraints to mechanical harvest as the production loss increases with seed scattering (Adeyeye *et al.*, 2014). Susceptible genotypes shatter prior due to canopy disturbance caused by wind or during mechanical harvesting particularly under dry weather conditions (IITA, 1986 ; Dong, 2014). Apart from its drastic effect on yield, seed scattered will result in the emergence and development of the crop as a weed in subsequent cropping seasons.

2.5.2. Factors affecting pod shattering in soybean

Several factors that induce or exacerbate pod shattering in soybean include weather conditions, harvest delays, low soil fertility, or severe pod-feeding from grasshoppers and bean leaf beetles (Lindsey, 2012). Late-season spider mite infestations can accelerate soybean senescence and increase pod shattering (Lindsey, 2012). Unfavorable weather conditions particularly drought stress during pod maturation may lead to a weak pod structure. Seams or sutures are along the pods on both sides where they open at maturity (Conley, 2012). If the mature pods are rehydrated by precipitation and dry again, they can open more easily because the attachment of the seams decomposes with the drying and rewet cycles. Occurrence of hail early in the season can lead to empty pods and twisted at harvest (Conley, 2012). Ultimately, pod shattering is more severe at high temperature or in dry weather, low humidity, rapid changes of temperature follow rains (Agrawal *et al.* 2002). Ideally, seeds should be harvested at 13 percent moisture content. Shattering takes important incidence if there is a delay before harvesting (Hellevang, 2013).

2.5.3. Effects of pod shattering on seed yield

Pod shattering is among major factors leading to remarkable yield losses. About 53 to 319 kg ha^{-1} of losses were reported in soybean contributing to 37% of total loss in the south-eastern USA (Philbrook and Oplinger, 1989 ; Tukamuhabwa *et al.*, 2002a). Seed losses of 34 to 99% associated in susceptible varieties and late harvesting are often reported (Tiwari and Bhatnagar, 1991). Tukamuhabwa *et al.* (2002a) reported that yield loss due to shattering was 57 to 175 kg ha^{-1} in susceptible varieties, and 0 to 186 kg ha^{-1} in moderately susceptible

varieties, whereas resistant genotypes are not affected even when harvested 21 days after fully maturity.

Assuming equal yield (weight) per pod for a soybean genotype, and basing on recorded shattered and unshattered pods, actual seed yield lost due to pod shattering may be estimated as follows:

$$\boldsymbol{Y_{ls} = \left(\frac{Y_p}{P_{un}}\right) \times P_{sh}\ ;\ Y_t = \left(\frac{Y_p}{P_{un}}\right) \times (P_{un} + P_{sh})}$$

where Y_t= expected total plot yield (kg ha^{-1}); Y_p= actual plot yield (kg ha^{-1}); Y_{ls}= total yield loss due to shattering (kg ha^{-1}); P_{un}= total number of unshattered pods and P_{sh}= total number of shattered pods (Sokal and Rohlf, 1969).

2.5.4. Methods of assessing pod shattering

Four methods of assessing pod shattering are known. The first is the field-screening method (Helms, 1994; Mohammed, 2010). This method relies on visual observations in the field. Trials are carried out to screen for naturally shatter-resistant lines 2 to 4 weeks after the physiological dry pod maturity. The second is the desiccator method (Metcalfe *et al.*, 1957; Caviness, 1965), where pods that carry 2 to more than 2 seeds each, are kept in a desiccator for 35 days at room temperature. Degree of pod shattering is assessed at 3, 5, 7, 14, 21, 28 and 35 days from the day the samples were placed in the desiccator. The third is the oven-dried method (Tukamuhabwa *et al.*, 2002a) and for which about 30 randomly fully matured pods for each genotype are taken and kept in oven at 30°C for three days, and then elevated up to 40°C for one day, elevated up to 50°C for one day, and lastly elevated up to 60°C for three days. The number of shattered pods are then counted on the 7^{th} day and converted in percentage. This is actually the most frequently used and reliable method because it allows large gene expression for pod shattering under controlled conditions (Krisnawati and muchlish, 2017). The fourth is mechanical cracking method (Kwon *et al.*, 1991; Davies and Bruce, 1997; Morgan *et al.*, 2000; Timothy *et al.*, 2003). This is used in a laboratory to assess individual pods for their resistance to shattering and to note mechanical properties of the pods during shattering.

2.5.5. Management of pod shattering

When prior shattering is a concern, the harvesting must be completed as earlier as possible when plant material is moist (Hanna, 2012). The crop should be harvested when the moisture content is not below 11 % to avoid splits and cracked seed coats (Hanna, 2012). For

mechanized harvesting, slowing down harvesting speed can also reduce shatter and stubble losses. At high harvester speeds, soybean pods can be stripped from the stalk, shatter, and drop to the ground. Reducing speed can help decrease these losses (Hanna, 2012).

Variety selection is another management practice involved in breeding programs. It should be focused on the basis of shattering response when soybean is left for a given time in the field after maturity from one to two weeks (Lee *et al.*, 2014). Breeders and agronomists should select varieties with relative maturities that vary by three days for every week of harvest time required for the operation. If soybean harvest takes two weeks, planting genotypes that vary collectively in maturity by six or more days, is therefore recommended (Agrawal *et al.*, 2000). This process may allow spreading harvest period and reduce the effects of pod shattering due to over mature pods (Schapaugh, 1997 ; Hellevang, 2013).

2.6. Genetics of resistance in pod shattering

Certain studies carried to explain and understand the genetics of soybean pod shattering revealed different findings. Caviness (1963) reported the presence of four major genes governing susceptibility to shattering. Tsuchiya (1986) reported one to two genes governing shattering. Akpan (1988) reported two to 12 genes to be involved in resistance to pod shattering. Bailey *et al* (1997) reported one important quantitative locus and a few minor QTLs controlled soybean pod shattering. Tukamuhabwa *et al.* (2000) indicated that pod shattering is controlled by two genes, partially dominant over resistance.

Inconsistent results have been associated with several inheritance studies of resistance of pod shattering in soybeans. Tiwari and Bhatnagar (1992) revealed contradictory observations from the analysis of F_1 soybean crosses. Some crosses showed susceptibility being dominant, while others revealed partial dominance for resistance. Caviness (1969) found no significant variations between F_1 progenies from wild and domesticated cultivars. Tsuchiya and Sunada (1980) found partial dominance to be associated with susceptibility to pod shattering. Tsuchiya (1986) observed no significant variations among sources of resistance from Japan, USA, China and Thailand in conferring resistance to shattering, indicating that the genetic control is simple and similar in all germplasm. Tiwari and Bhatnagar (1992) found significant ($p<0.05$) general and specific combining ability (GCA and SCA) for shattering resistance. However, they found the pre-dominant importance of the additive gene action over dominance gene action in the expression of pod shattering. They recommended further studies

among the F_2 progenies since the observations made were based on F_1 hybrids. Bailey *et al.* (1997) showed that pod shattering was somewhat influenced by epistasis.

Earlier, Misra *et al.* (1980) stated that absence of discrete phenotypic classes in F_2 generation constitutes the reason why it is difficult to determine with precision the estimates of shattering of soybean genotypes, suggesting therefore the presence of several genes. Carpenter and Fehr (1986) observed discrete reaction types of shattering in segregating populations of soybean involving a susceptible wild relative *Glycine soja* and two resistant varieties and observed a decrease in shattering frequency with each backcrossing generation and suggested the importance of three to four backcrosses to eliminate significantly the effects of pod shattering, because only four genes or less than four genes were involved governing the trait as reported by Caviness (1963) and Tsuchiya (1986). Tiwari and Bhatnagar (1991) reported the high heritability associated with pod shattering. They reported a broad sense heritability (h_b^2) of 98.8%. Caviness (1969) reported a broad sense heritability of 90% while Tsuchiya (1987) reported 93% for the same trait. However, heritability in the broad sense (h_b^2) in self-pollinating crops is not as informative as in the narrow sense (h_n^2), a direct measure of additive variance. Tukamuhabwa *et al.* (2000) found that pod shattering resistance is highly heritable with narrow sense heritability of 79% without being influenced by maternal effects.

This study sought to find additional information on the genetics of pod shattering in order to use such findings to strengthen the soybean breeding program in Kenya. It aims to study the combining ability to provide the basic population and support the effectiveness of selection activities.

2.7. Strategies in breeding soybean

2.7.1. Artificial hybridization in soybean

Forceps with fine tips and a smooth interior are required to manipulate the small flower (Walter, 1980). Plastic tags about 7 × 15 mm and wired a flexible copper strand often are used to identify pollinated flowers. Plastic tags with a snap-on design can be attached quickly to the plant, but can be knocked or blown off more readily than those with a wire attachment (Walter, 1980). Paper tags have been used successfully, but they are more susceptible to weather and insect damage than plastic tags. Some breeders use magnifiers mounted on a headband or a pair of glass frames. A magnification of 2.5× provides satisfactory enlargement of the flower. Petri dishes or envelopes are used to collect male flowers. In some situations,

desiccators containing crystals of calcium chloride serve to dry stamens in order to maximize the pollen shedding (Walter, 1980).

Pollination starts with selection of the female flowers likely to open the next day. Ready female flowers have swollen buds. Three or four buds are prepared on a raceme, while all self-mated flowers or buds that are immature are removed from the plant using forceps. Particular attention is necessary to remove immature buds hiding in stipules at the axil of the leaf. Delicately, the flower is taken using the forefinger and the thumb. The stigma is located by careful examination of the sepals because they are curved and covered by the keel. The stigma usually occupies the opposite side of the flower. The calyx, by grasping a sepal using forceps, should be carefully removed, with all the sepals (Vollmann *et al.*, 1992).

The corolla, on the other hand, is taken out grasping it above the scar of the calyx without injuring the stigma then lifting and wiggling the forceps simultaneously. The anthers are just near the stigma. They form a certain ring are now visible and can be removed, unless they were removed with the petals. If the hooking method is used for pollination, it may be necessary to remove the anthers to allow easier hooking with anthers from the male parent (Walter, 1980).

Immediately after being prepared, the female flower is usually pollinated by hand. Delay of some hours does not affect the efficiency of pollination (Vollmann *et al.*, 1992). The period of pollen shed is primarily a function of temperature. Pollen shed may begin at 0700 hours and end by 0900 hours when early morning temperatures are about 30°C, or might start at 1000 hours and proceed during the day when temperatures are slightly lower. Pollen collected from male flowers is immediately used without any storage (Walter, 1980).

Pollen remains viable for 2 or more days when flowers are kept at 5°C (Walter, 1980). Kuehl (1961) demonstrated that it is possible to store flowers successfully for several weeks in a desiccator at 3°C ; however, cultivars differ in the ratio of pollen that will germinate after a long storage period. He found that flowers stored over calcium chloride for several weeks did not dehisce, but when they were placed over water in a closed container for about 30 min, the anthers would dehisce.

Hand pollination is carried out by carefully removing the stamens from the male flower for which pollens have started to shed with a forceps and kindly the anthers are brushed against the female flower stigma. Ready anthers, brushed on the stigma, break down and then release

important amount of pollens leading to the higher success when crossing and pollens are clearly seen on stigma. It is so important to check the shedding of pollen; breeders often tap the anthers on their thumbnail to confirm pollen shed before brushing the stigma. When conditions are not very favorable, a male with very excellent can be used to pollinate an array of female flowers. Breeders usually prefer to leave the stamens of the male flower hooked over the style of the female. The forceps are cleaned after each pollination by placing the tips in one's mouth or dipping them in 95% ethanol (Walter, 1980).

For a good hybridization, a photoperiod of adequate length is required. A 12-hour photoperiod is used for early flowering and seed production (Wilcox, 1974). Temperature should be maintained at not less than 21°C with 23 to 32°C being most desirable. High relative humidity seems to improve the success of artificial hybridization (Wilcox, 1974). Automatic humidifiers may be used or floors may be kept wet. Multiples planting dates that vary from 7 to 14 days apart are used usually to synchronize the flowering that may happen during different dates (Kiihl *et al.*, 1977).

2.7.2. Factors affecting efficiency of hybridization in soybean

Efficiency of artificial hybridization can be increased when pollen transport and information written on the tag after pollination are minimized (Vollmann *et al.*, 1992). Parental plants should be planted next to another and should be planted at 7-day intervals in rows that are 65 to 100 cm apart to ensure adequate pollen during pollination. Alternatively, delayed flowering of an early maturing parent could be accelerated by artificially creating a short-day mechanism. Flowering of early maturing parent could be artificially delayed by the use of long days delayed planting.

Plants that flower early tend to have small self-pollinated flowers, which may consistently reduce the efficiency of hybridization (Walter, 1980). Grafting is another strategy to accelerate the flowering of late blooming genotypes. A late genotype scion grafted onto a stock that began to bloom will begin to bloom up to 42 days earlier than in the normal situation (generally flowers appear from 21 to 50 days after the grafting) (Kiihl *et al.*, 1997).

2.7.3. Mating designs used in soybean breeding

There are several arrangements and mating designs that plant geneticists and breeders use to develop advanced plant types. Each mating should be made with a definite goal in mind. High yield is generally the foremost goal in any breeding program and goals such as disease and

pest resistance, improved plant architecture, stiff stem, and resistance to shattering are complementary to the goal of higher yield. Other goals may include improved seed quality, oil or protein content, or plant type, and suitable machine harvesting (Hallauer *et al.*, 2010). The identification of suitable parents and mating designs is the key for success in plant breeding schemes to develop superior lines (Acquaah, 2012). Several mating designs have been developed and used to generate populations for genetic analysis (Griffing, 1956; Kearsey and Pooni, 1996 ; Hallauer *et al.*, 2010; and Acquaah, 2012). They include polycross, topcross, line x tester design, bi-parental progenies, North Carolina designs I, III and III, and diallels designs I, II, III and IV. Individuals have to be randomly selected and mated to generate F_1 hybrids, linked each to another as half- or full-sibs. Analysis of variance is used to determine the components of phenotypic variance. The form on analysis of variance depends on the mating design (Hallauer *et al.*, 2010).

Diallel mating design is probably the most frequently used design. In this mating design all the parental combinations are involved (Schlegel, 2010). It may include reciprocals and selfs. However, it is the most laborious design of all mating schemes used to obtain different information on genetic materials (Hallauer *et al.*, 2010). Two analysis models exist, the fixed and the random models (Griffing, 1956). In a random model, parental lines are randomly selected to represent unbiased sample of a population. This model is helpful in estimating the general combining ability (GCA) and specific combination ability (SCA) effects and variances. However, if parents are considered fixed factors, the objective is to assess the GCA effect for the parent and the SCA effect for the offspring generated.

The number of progeny families (pf) generated from (n) parents for each method are different: $pf = n^2$, $pf = ½\ n(n + 1)$, $pf = n(n - 1)$, and $pf = ½\ n(n - 1)$ for methods I, II, III and IV respectively (Acquaah, 2012). The first method (I) or the complete design of the diallel is constituted by the parents, a set of F_1 and its reciprocals. The model ends with n^2 lines (Griffing, 1956). The method II comprises a set of F_1 without the reciprocals but with the parents. This method has been recognized as the most used mating design. This is the method was used in the present study. Method III includes the crosses in one way and their reciprocals. In Method IV (or half diallel without parent inclusion), only one set of F_1 is considered. This method has been recognized as the most common of the diallel coupling systems (Griffing, 1956).

Diallel mating design is also used widely to develop recurrent breeding populations (Acquaah, 2012). Johnson and King (1998) indicated that diallel mating designs were developed to provide maximum chances for managing co-ancestry with selfings and reciprocals. It is the most used and abused of all mating designs in obtaining various genetic informations (Hallauer *et al*., 2010). With this diallel design two models for analysis are developed; fixed and random models (Griffing, 1956). Parents are considered random members of a random population in a random model. This model is helpful in the estimation of GCA and SCA variances. However, in case parents are taken as fixed effects, the aim is to measure the GCA effect for each parent and the SCA effect of each progeny. These effects only apply to the set of parents in the diallel. It is also widely used for developing breeding populations for recurrent selection (Acquaah, 2012). In addition, Johnson and King (1998), reported that diallel mating designs are deployed to provide the maximum opportunity to manage co-ancestry in breeding population and maximize selection differential. However, in practice, a diallel with selfs and reciprocals is neither practical nor useful for several reasons. Selfing does not contribute to the recombination of genes between parents. Furthermore, recombination is achieved by crossing in one direction making reciprocals unnecessary (Acquaah, 2012). Because of the extensive mating patterns, the number of parents that can be mated this way is limited.

Method II includes parents and one set of F_1 without reciprocals. The number of F_1's generated is $\frac{1}{2}n(n+1)$ genotypes, where n is the number of parents.

The mathematical models for combining ability for fixed model is: $Y_{ij} = \mu + g_i + g_j + S_{ij} + \frac{1}{bc}\sum_k \sum_l e_{ijkl}$ where i, j = 1,…, p ; k = 1,…, b ; l = 1,…, c ; μ being the mean of population, g_i, g_j representing the effects of GCA for the i^{th} and j^{th} parents, S_{ij} being the SCA effect of the line from the i^{th} and j^{th} parents such that $S_{ij} = S_{ji}$ and r_{ij} being the reciprocal genotypic effects such that $r_{ij} = r_{ji}$ and, e_{ijkl} being the error for experiment due to the effect of environment associated with the $ijkl^{th}$ observation (Griffing, 1956). Assuming that $\sum_i g_i = 0$, and $\sum_j S_{ij} + S_{ji} = 0$, analysis of variance table is described as follow (Table 2.3).

The following expressions estimate the various effects:

$\hat{\mu} = \frac{2}{p(p+1)}X..$, $\quad \hat{g}_i = \frac{1}{(p+2)}\left[X_{i.} + x_{ii} - \frac{2}{p}X..\right]$, $\quad \hat{s}_{ij} = s_{ij} - \frac{1}{(p+1)}\left[X_{i.} + x_{ii} + X_{j.} + x_{jj}\right] + \frac{2}{(p+1)(p+2)}X..$,

Equations that follow are helpful in effect estimations:

$Var(\hat{\mu}) = \frac{2}{p(p+1)}\hat{\sigma}^2$, $(\widehat{g}_i) = \frac{p-1}{p(p+2)}\hat{\sigma}^2$, $Var(\hat{s}_{ii}) = \frac{p(p-1)}{(p+1)(p+2)}\hat{\sigma}^2$, $Var(\hat{s}_{ij}) = \frac{p^2+p+2}{(p+1)(p+2)}\hat{\sigma}^2$

(Griffing, 1956).

Table 2.3 : Sources of variation and expected mean squares of diallel mating design II

Source	df	SS	MS	Expected mean squares	
				Model I	Model II
GCA	p-1	S_g	M_g	$\sigma^2 + (p-2)(\frac{1}{p-1})\sum g_i^2$	$\sigma^2 + \sigma_s^2 + (p+2)\sigma_g^2$
SCA	p(p-1)/2	S_S	M_s	$\sigma^2 + \frac{2}{p(p-1)}\sum_i\sum_j S_{ij}^2$	$\sigma^2 + \sigma_s^2$
Error	M	S_e	M_e'	σ^2	

(Griffing, 1956)

CHAPTER THREE: RESISTANCE OF SOYBEAN VARIETIES TO POD SHATTERING AND OTHER AGRONOMIC TRAITS

3.1. Abstract

Pod shattering is a serious threat that causes 34 to 99% seed losses. Genetically diverse soybean genotypes differ in their expression of the trait. The objective of this study was to evaluate soybean genotypes for resistance to pod shattering and other agronomic traits. Twenty soybean genotypes were evaluated in two agro-ecological zones in Kenya during the 2016 short and long rain seasons. The trial was laid out in an alpha lattice design arranged in a 4 x 5 pattern and replicated three times. Data was collected on germination percentage, days to 50% flowering, days to 75% maturity, plant height, biomass, number of pods, number of seeds per pod, 100-Seed mass, grain yield, harvest index and pod shattering. The assessment for pod shattering was based on a 1 to 5 AVRDC scale (1=very resistant and 5=highly susceptible genotype). Degree of pod shattering varied from 2.7% to 68.4% in both sites and seasons. None of the genotypes was very resistant, 10 were resistant, 7 moderately resistant, 1 moderately susceptible and 2 highly susceptible to pod shattering. The most resistant materials were from IITA. Genotypes SB-8 followed by Gazelle, SB-74, SB-4, Nyala and SB-20 were the most resistant to pod shattering while SB-90 and SB-25 were the most susceptible. Pod shattering resistance was negatively correlated with number of seeds per pod (r=-0.13*). Plant with few seeds per pod tended to have high resistance to pod shattering. Three varieties (931/5/34, 915/5/12 and SB-154) performed well with grain yields of up to 1800 kg ha^{-1}. Genotypes Black Hawk, 931/5/34 and 915/5/12 had high harvest indexes of up to 0.35. The heavy podding variety, SB-145 with 146.5 pods per plant, had the highest biomass of 209.3 g while 915/5/12 and Black Hawk with 2.5 seeds per pod had the highest biomass. The 100-seed mass of 17.6 g for variety TGM-1420 was the highest. Varieties TGM-1420, SB-25 and SB-151 were the tallest genotypes with 79.8, 78.5 and 73.6 cm. Varieties Nyala and Hill flowered earlier, 56 days after sowing while Black Hawk, SB-19 and Hill were the early maturing genotypes, with less than 100 days to maturity. The study identified resistant and moderately resistant genotypes to pod shattering that can be utilized in breeding programs. Further studies are needed to characterize genes involved in resistance to pod shattering especially among the SB genotypes using molecular makers.

Key worlds: pod shattering, resistance, soybean.

3.2. Introduction

Soybean (*Glycine max* (L.)) is a major source of vegetable oil and high quality protein in the world (Tukamuhabwa *et al.*, 2012 ; Krisnawati *et al.*, 2015). Yield of soybean in the farmers' fields in Kenya is 0.6 t ha^{-1} which is far below the potential yield of 2.5 t ha^{-1} in research managed trials (Chianu *et al.*, 2008). These low yields have been attributed to several constraints including biotic, abiotic and socio economic stresses (Tefera *et al.*, 2009 ; Krisnawati and Adie, 2016). Major biotic factors include pests and diseases especially bacterial blight, rust, brown leafspot, purple seed stain, stem blight, mosaic virus and bean pot (Pratt *et al.*, 2011). The main abiotic stresses are drought, soil salinity and soil acidity. Apart from abiotic and socio-economic stresses, low seed longevity, lodging and pod shattering are considered as important constrains (Foyer *et al.*, 2016). Pod shattering is one of the most important constraints to soybean production in tropical and subtropical regions. Seed losses of 50–100% are often associated with pod shattering in susceptible varieties and delayed harvesting (IITA, 1986; Adeyeye *et al.*, 2014).

With losses of up to 50% of seed losses, pod shattering has been recognized as the most important constraint to soybean production under tropics according to several surveys carried by IITA in Nigeria in 1989 and 1990, by Sanginga *et al.* in 1999 (IITA, 1992 ; Njoroge *et al.* 2015). Therefore, resistance to pod shattering was found to be a pre-requisite for adoption of any variety by the farming communities, indicating that resistant varieties that can stand in the field for relatively longer periods after maturity without shattering must be developed.

The objective of this study was to evaluate soybean genotypes for resistance to pod shattering and other agronomic traits.

3.3. Materials and Methods

3.3.1. Description of experimental sites

Experiments were conducted at Kenya Agricultural and Livestock Research Organization (KALRO) experimental stations at Embu and Mwea between June 2016 to April 2017.
KALRO-Mwea is located in Mwea division, Kirinyaga district, Kirinyaga County in Central Kenya at an altitude of 1159 masl and between latitude 00° 37'S and longitude 37° 20'E. Annual average precipitation at Mwea is 950 mm, with the long rains falling between March and May, while the short rain period is between October and December (Wanderi, 2012). Temperatures range from a maximum of 36.2°C in March to a minimum of 10.2°C in July

with a mean of 23.2°C (King'uyu *et al.*, 2000). The predominant soils in the cultivated areas of Mwea are vertisols with soil pH 5.46 (Sombroek *et al*., 1982). These are characterized by imperfectly drained clays, deep, dark gray to black, firm to very firm, and prone to cracking.

KALRO-Embu is located at 1508 masl in Embu County in eastern Kenya, between latitude 00° 30' S and longitude 37°42' E. The rainfall pattern is bi-modal with two distinct rainy seasons. Long rains occur between March and June while the short rains fall between October and December. Annual average precipitation for Embu is 1,495 mm, with the long rains falling between March and May, while the short rain period is between October and December. Temperatures range from a minimum of 12 °C in July to a maximum of 30 °C in March with a mean of 21 °C. The extensive altitudinal range of Embu County influences temperatures (Appendices 1 and 2). July is usually the coldest month with an average monthly temperature of 15 °C while September is the warmest month with an average monthly temperature rising to 27.1 °C. The predominant soils in the cultivated areas of Embu are nitosols with a pH of 5.97 (Wanderi, 2012).

3.3.2. Description of soybean genotypes

Twenty soybean genotypes were used in this study. Ten were breeding lines, SB varieties, released in 2010 by IITA and the other ten were local commercial varieties released in 2009 by KALRO-Njoro. These materials were released for different traits. Table 3.1 shows the characteristics of the study genotypes.

Table 3.1 : Characteristics of soybean cultivars used in this study

Variety	**Name of Release**	**Year of Release**	**Source of Material**	**Average on-farm yield (kg ha^{-1})**	**Varietal traits selected for**
Nyala	Nyala	2009	KALRO-Njoro	700	Early maturity (80-95 days), large grain size, can be intercropped with other crops; susceptible to rust and nodulates with specific rhizobia strains
Hill	Hill	2009	KALRO-Njoro	850	High yielding, medium maturity (95-115 days), tolerant to aphids
Black Hawk	Black Hawk	2009	KALRO-Njoro	850	High yielding, medium maturity
EAI 3600	EAI 3600	2009	KALRO-Njoro	800	High yielding, early maturity, resistant to major insects
Gazelle	Gazelle	2009	KALRO-Njoro	1100	High yielding, large grain size, attractive

					color
TG x 1740-2F	DPSB 19	2010	IITA	900	Free nodulation, grain and biomass yield, good for monocropping, high pod clearance, good pod load, medium maturity, good for making milk
TG x 1895-33F	DPSB 8	2010	IITA	950	Free nodulation, good for intercropping, grain yield and biomass accumulation, high pod clearance, good pod load, good for making milk, attractive color
SCS-1	Saga	In NPTs	KALRO-Njoro	1,600	High yielding, high oil content, high pod clearance, large seed size, tolerance to soybean rust, good for intercropping
SB 25	DPSB 25	2010	IITA	2000-3000	Many nodules; less resistant to pests and diseases, shatters early in the field, 43% protein, 20% oil, 100-125 as days to maturity,
SB 4	DPSB 4	2010	IITA		Early maturity (<100 days); days to flowering (52)
SB-154	DPSB 154	2009	KALRO-Njoro	2500-3500	Late maturing (>100 days), free nodulation
SB-90	DPSB 90	2010	IITA	1200-2000	Early maturity (82-98 days); 51days to flowering
931/5/34	931/5/34	2009	KALRO-Njoro	1000-1900	Medium maturing, free nodulation
TGM-1420	TGM-1420	2010	IITA	1800-2500	High yielding, large grain size, attractive color, late maturing
SB-74	DPSB 74	2010	IITA	1500-2500	Medium maturing, free nodulation
SB-37	DPSB 37	2010	IITA		Medium maturity
915/5/12	915/5/12	2009	KALRO-Njoro	900-1800	Early maturity (82-98 days); days to flowering (51)
SB-151	DPSB 151	2009	KALRO-Njoro		Late maturing, free nodulation
SB-20	DPSB 20	2010	IITA	1800-2500	Late maturing, high oil content, high pod clearance, large seed size, tolerance to soybean rust, good for intercropping , free nodulation
SB-145	DPSB 145	2010	IITA	2500-3500	Late maturing, free nodulation, good for intercropping

Source: Mahasi *et al.*, (2010)

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3.3.3. Experimental design and crop management

The experiment was carried out during the 2016 long and short rain seasons from May 2016 to April 2017 at Embu and Mwea. Twenty genotypes were planted each in a plot that consisted of five rows of 2 x 2 m each at spacing of 15 cm within rows and 50 cm between rows. The design was an alpha-lattice arranged in a 4 x 5 pattern with three replicates. Two seeds were sown in each hill and thinned to one 21 days after emergence. Diammonium phosphate (18% N and 45% P_2O_5) was applied at planting at 150 kg ha^{-1} (Hundie *et al.*, 2000) and top dressed with calcium ammonium nitrate (26% N), three weeks after emergence at a rate of 100 kg ha^{-1}. Plots were maintained weed free by manual weeding while hand irrigation was done twice a week.

3.3.4. Assessment of agronomic traits

Data was collected on germination percentage, days to 50% flowering and 75% to maturation, plant height, plant biomass, pod shattering, pods per plant, seeds per pod, 100-seed mass, harvest index and grain yield. Germination percentage (%) was taken 2 weeks from the sowing date and was determined by counting the number of plants emerged in a plot, divide by the expected plant number and multiplied by 100. Days to 50% flowering was recorded as number of days from sowing to when approximately 50% of plants in a plot had at least one opened flower. Days to 75% maturity was recorded as the number of days from sowing to when approximately 75% of plants reached at least 95% of maturity. Plant height (cm) was measured at flowering stage on the sample of six different plants as the distance from the ground to the top of the main stem (Wanderi, 2012).

3.3.5. Assessment of pod shattering

Data on pod shattering was assessed using a modified oven-dry method as described by IITA (1986) ; Tsuchiya (1987) ; Krisnawati and Adie (2016). The evaluation was by randomly taking a sample of 50 fully mature three seeded pods of each variety which were placed in khaki envelops and sun-dried for seven days. Ten plants were sampled per plot and five pods harvested from each plant. The number of shattered pods were counted every day and expressed as percentage. Genotypes were then classified into five categories based on their reaction to pod shattering (Table 3.2).

Table 3.2 : Pod shattering scoring scale

Scale	Shattering percentage	Shattering score
1	0	Very resistant (absolutely no shattered pod) (VR)
2	1-10	Resistant (R)
3	11-25	Moderately resistant (MR)
4	26-50	Moderately susceptible (MS)
5	>50	Very susceptible (HS)

Source: AVRDC, 1979 ; IITA 1986 ; Krisnawati and Adie, 2016.

3.3.6. Evaluation of yield and yield components

The yield parameters evaluated at harvesting were plant biomass, pods per plant, seeds per pod, 100-seed mass, harvest index and grain yield. Plant biomass (g) was the average weight of a sample of six randomly selected plants within a plot at maturity. Pods per plant were the average pods collected and counted from a sample of six plants in each plot. Seed per pod was determined by dividing the total number of seeds from those six plants by the total number of pods from six plants. 100-Seed mass (g) was assessed by weighting 100 randomly selected seeds of each genotype. Harvest index (HI) (%) was recorded from a sample of six plants and corresponded to the weight of seeds from a plant (SW) divided by its plant biomass (B) and multiplied by 100 such that $\mathrm{HI} = \frac{\mathrm{SW}}{\mathrm{B}} \times 100$ (Krisnawati *et al.*, 2015). Grain yield was estimated as outlined by Staton (2011). It was measured as the weighing (g) threshed seeds from plants of the middle rows after estimating the surface they occupied (m^2) such that Yield (in bushels/acre)=[(number of plants) x (pods/plant)] ÷60 and then extrapolating the grain yield into kg ha^{-1} for each genotype (Krinawati and Adie, 2016).

3.3.7. Statistical analysis

All data was subjected to a combined analysis of variance using Genstat software (15^{th} edition) (Payne *et al.*, 2009) with locations, seasons, replicates and genotypes as factors and the traits measured as variables. The percentage data on pod shattering was subjected to arcsine-square root transformation before statistical analysis (Singh and Chaudhary, 1979; Mohammed, 2010). Fisher‘s Protected Least significant difference at 5% probability levels was used for mean separation. Pearson’s correlation estimates for pod shattering and agronomic traits was done using Statistix-8 statistical package (Hall, 2015).

3.4. Results

3.4.1. Agronomic traits

Germination percentage differed significantly across the two different agro ecological locations. There was significant interaction between genotypes and seasons (P<0.001). Significant variations were observed among locations and seasons (P<0.001). Germination percentage varied significantly among genotypes (P<0.001) (Table 3.3). Germination percentage was higher in Mwea compared to Embu. Similarly, considering the cropping seasons, the short rain season had the best germination rate compared to the long rain season, in both sites. In general, the study genotypes reached a germination percentage of 61% across sites and seasons. Variety SB-25 among the SB lines, with some commercial varieties from KALRO-Njoro such as Hill, 915/5/12, SCS-1 and Nyala had high germination percentage above 70% while most of other SB lines germinated poorly (Table 3.4).

Days to 50% flowering varied significantly among genotypes (P<0.001). There were significant interactions between genotypes, locations and seasons, genotypes and locations, and genotypes and seasons (P<0.001). Significant variations were observed among locations (P<0.001) (Table 3.3). Genotypes took longer to reach flowering at Embu than at Mwea. In terms of seasons, days to flowering were long during the short rain season than the long rain. Soybeans flowered 65 days after sowing. Nyala, Black Hawk and Hill were genotypes which reached flowering earlier, 56 days from the sowing date. Varieties SB-145, SB-154, SB-20 and TGM took generally more than 70 days to reach flowering, thus were the later flowering varieties (Table 3.4).

Table 3.3 : Mean squares for germination percentage, days to 50% flowering and 75% maturity, plant height, plant biomass and pods plant of soybean genotypes grown at Embu and Mwea Research Centers during the 2016 long and short rain seasons

Source	df	Germination (%)	Days to 50% flowering	Days to 75% maturity	Plant height (cm)	Plant Biomass (g)	Pods plant^{-1}
Replicates	2	153.2	7.176	163.28	324.29	812.1	1882.1
Seasons (S)	1	68514.2*	149.626^{ns}	65488.58*	13262.03*	70022.4*	74269.2*
Error$_1$	2	487	3.864	193.65	8.06	821.6	117.7
Locations (L)	1	22888.2*	3408.834*	550.55*	11392.96^{ns}	143597.1*	90877.4*
L x S	1	867.4^{ns}	1952.251*	4519.68*	4351.21^{ns}	10104*	28527.9*
Error$_2$	4	754	2.586	167.49	188.37	417.2	849.1
Genotypes (G)	19	1115.3*	337.854*	2605.86*	3827*	25824.5*	9938.3*
G x S	19	580.1*	92.898*	920.36*	451.55*	5136*	2100.7*
G x L	19	419.8^{ns}	29.457*	85.88^{ns}	496.27*	12953.9*	5720.9*
G x S x L	19	120.6^{ns}	46.172*	57.6^{ns}	169.51^{ns}	4318.1*	2522.8*
Pooled error	152	167.9	2.15*	37.82	88.88	814.7	473

* Indicates significant difference at P<0.001 and, ns indicates no significant difference

Table 3.4 : Germination percentage and days to flowering of soybean varieties at Embu and Mwea Research Centers during the 2016 long and short rain seasons

Genotype	Germination percentage					Days to 50% flowering				
	Embu		Mwea		Mean	Embu		Mwea		Mean
	Long rain	Short rain	Long rain	Short rain		Long rain	Short rain	Long rain	Short rain	
915/5/12	53.0	65.7	71.2	90.4	70.1	68.7	64.7	54.3	58.3	61.5
931/5/34	11.4	48.5	76.5	93.4	57.4	68.5	68.7	51.7	65.3	63.5
Black Hawk	19.7	71.7	39.4	90.9	55.4	66.3	53.7	52.7	51.7	56.1
EAI-3600	21.2	58.6	52.2	93.9	56.5	68.7	55.3	50.7	75.7	62.6
Gazelle	47.7	79.3	58.3	90.4	68.9	69.0	62.0	57.0	60.3	62.1
Hill	55.4	71.2	64.4	90.4	70.4	65.0	53.7	51.0	55.3	56.3
Nyala	47.7	73.7	67.4	94.9	70.9	68.7	53.3	52.0	49.7	55.9
SB-145	15.9	72.2	8.3	82.3	44.7	78.0	78.3	67.0	76.7	75.0
SB-151	15.9	58.6	16.6	78.8	42.5	81.0	67.3	60.3	65.0	68.4
SB-154	39.4	50.5	55.3	89.4	58.6	80.7	75.3	66.0	65.0	71.8
SB-19	33.3	72.2	36.3	95.9	59.5	68.7	63.7	58.0	61.3	62.9
SB-20	35.6	74.8	43.9	87.4	60.4	71.3	75.3	61.0	74.3	70.5
SB-25	63.6	76.3	69.7	84.8	73.6	71.3	68.7	61.0	68.7	67.4
SB-37	19.7	65.2	28.0	75.3	47.0	69.3	72.3	57.7	70.3	67.4
SB-4	46.9	58.1	60.6	95.5	65.3	69.3	73.0	56.0	68.7	66.8
SB-74	53.0	69.2	61.3	91.4	68.7	69.7	71.0	59.7	71.3	67.9
SB-8	35.6	58.6	52.3	95.9	60.6	68.7	68.0	54.7	67.3	64.7
SB-90	31.8	73.2	56.6	96.9	64.6	68.7	63.0	57.3	52.0	60.3
SCS-1	51.5	85.9	75.7	91.9	76.3	69.3	66.0	52.3	64.3	63.0
TGM-1420	30.3	44.9	49.2	84.8	52.3	70 .0	75.0	65.7	70.3	70.3
MEAN	36.2	66.4	52.1	89.8	61.2	70.5	66.0	57.3	65.0	65.0
$LSD_{0.05}$	25.6	25.9	19.7	10. 9	11.0	2.1	2.5	2.2	2.9	1.2
C.V	42.6	23.6	22.8	7.3	22.3	1.8	2.3	2.3	2.7	2.3

LSD – least significant difference, CV – coefficient of variation

Days to 75% maturity varied significantly among genotypes (P<0.001). There was a significant interaction between genotypes and seasons (P<0.001). Locations and seasons varied significantly (P<0.001) (Table 3.3). Study genotypes took 115 days to mature from the sowing date. Genotypes took longer to mature at Embu than at Mwea. Duration to 75% was much more during the short rain than the long rain. Except SB-19, all the SB genotypes and TGM-1420 matured later than commercial varieties from KALRO-Njoro. In general, Black Hawk, Hill and SB-19 were the early maturing genotypes. They took less than 100 days to mature (Table 3.5).

Plant height varied significantly among genotypes (P<0.001). There were significant interactions between genotypes and locations, and genotypes and seasons (P<0.001). Significant differences were also associated with seasonal effects (P<0.001) (Table 3.3). Plants were significantly taller during the short rain season than the long rain ($l.s.d_{0.05}$=2.4).

Plants were taller at Mwea than at Embu. In general, study genotypes had average plant height of 48.2 cm. Most of SBs were the tallest genotypes with plant height being more than 50 cm, except SB-19, SB-37, SB-90. These SB genotypes and the commercial variety, SCS-1 had medium height (40 and 50 cm). The rest of commercial and local varieties were less than 40 cm tall. TGM-1420, SB-25 and SB-151 were the very tallest genotypes (more than 70 cm). Black Hawk, Hill and Nyala were the shortest (Table 3.5).

Table 3.5 : Days to maturity and plant height of soybean genotypes at Embu and Mwea research centers during the 2016 long and short rain seasons

	Days to 75% maturity					**Plant height (cm)**				
	Embu		**Mwea**		**Mean**	**Embu**		**Mwea**		**Mean**
	Long rain	**Short rain**	**Long rain**	**Short rain**		**Long rain**	**Short rain**	**Long rain**	**Short rain**	
915/5/12	93.7	125.0	88.7	122.7	107.5	29.4	35.0	26.8	36.4	31.9
931/5/34	97.0	124.7	86.0	138.3	111.5	35.8	33.6	24.3	33.4	31.8
Black Hawk	91.0	96.7	82.0	101.7	92.8	19.4	24.2	20.4	34.2	24.5
EAI-3600	113.7	103.3	95.7	104.0	104.2	28.7	24.3	33.9	55.0	35.5
Gazelle	96.3	113.7	90.7	124.7	106.3	31.4	35.1	28.2	38.4	33.3
Hill	111.0	99.3	83.7	101.7	98.9	23.9	25.6	18.7	33.8	25.5
Nyala	95.7	107.3	91.3	114.3	102.2	28.3	22.0	18.3	32.2	25.2
SB-145	129.3	162.7	106.3	167.0	141.3	34.7	53.1	45.5	86.9	55.0
SB-151	111.5	133.7	102.7	150.0	124.5	43.8	69.6	62.8	118.2	73.6
SB-154	124.0	160.7	97.3	161.3	135.8	38. 9	43.9	46.8	106.8	59.1
SB-19	86.3	111.7	81.0	116.0	98.7	34.4	38.5	45.5	60.8	44.8
SB-20	113.3	175.7	99.7	176.3	141.2	49.3	55.5	43.0	85.4	58.3
SB-25	120.7	138.7	103.7	148.3	127.8	69.2	62.7	73.3	108.7	78.5
SB-37	109.3	132.0	99.0	146.7	121.8	31.7	46.2	30.6	61.3	42.4
SB-4	103.3	159.0	96.7	155.7	128.7	38.9	57.5	55.2	72.6	56.0
SB-74	102.3	139.3	96.0	142.0	119.9	33.9	58.8	71.1	86.3	62.5
SB-8	98.7	138.0	93.3	140.3	117.6	53.7	56.0	66.6	81.0	64.3
SB-90	106.7	115.0	92.0	112.0	106.4	37.8	30.8	35.3	44.9	37.2
SCS-1	94.3	126.3	87.0	133.3	110.2	47.8	36.9	44.9	45.0	43.7
TGM-1420	118.3	141.0	109.7	160.3	132.3	50.7	79.3	75.8	113.3	79.8
MEAN	105.8	130.0	94.1	136.0	116.0	38.1	44.4	43.4	66.7	48.2
$LSD_{0.05}$	1.7	17.8	2.6	9.3	5.3	10.2	18.8	9.8	20.4	7.7
C.V	1.0	8.3	1.6	4.2	5.6	16.3	25.6	13.7	18.5	19.7

LSD – least significant difference, CV – coefficient of variation

3.4.2. Resistance of soybean genotypes to pod shattering

There were significant interactions between genotypes, locations and seasons; genotypes and locations and between genotypes and seasons (P<0.001). Pod shattering varied significantly among genotypes (P<0.001) (Table 3.6). Each location had a mean shattering percentage of about 17%. With regard to the cropping seasons, shattering percentage of 18.8% was associated with the short rains while an incidence of 16.6% was observed during the long rains. Study genotypes had an average pod shattering of 17.7%. Considering individual genotypes, most of SB varieties showed better resistance to shattering except SB-90 and SB-25. These two genotypes shattered considerably at the two sites and seasons with combined shattering incidences which exceeded 50%. These materials were confirmed to be susceptible. However, SB lines such as SB-8, SB-74, SB-4 and SB-20 together with Gazelle, Nyala and SCS-1 had less than 10% of shattering and were considered resistant to pod shattering (Table 3.7).

Table 3.6 : Mean squares for seeds per pod, 100-seed mass, harvest index, pod shattering and grain yield of soybean genotypes grown at KALRO-Embu and KALRO-Mwea Research Centers during the 2016 long and short rain seasons

Source	df	Seeds pod^{-1}	100-seed mass (g)	Harvest index	Pod shattering (%)	Grain yield (kg ha^{-1})
Replicates	2	0.00129	1.331	0.00781	42.45	304836
Seasons (S)	1	1.95662*	0.134^{ns}	0.0802^{ns}	287.87^{ns}	268403^{ns}
Error$_1$	2	0.08798	1.501	0.04861	183.26	436961
Locations (L)	1	0.70742*	29.46*	0.73083^{ns}	8.88^{ns}	493207^{ns}
L x S	1	0.00057^{ns}	1^{ns}	0.05204^{ns}	98.2^{ns}	18038^{ns}
Error$_2$	4	0.01698	2.588	0.03872	143.88	401800
Genotypes (G)	19	0.33189*	38.269*	0.14369*	3809.92*	2038572*
G x S	19	0.13921*	1.287^{ns}	0.03048^{ns}	566.48*	76508^{ns}
G x L	19	0.05423^{ns}	1.247^{ns}	0.02825^{ns}	515.55*	63124^{ns}
G x S x L	19	0.03161^{ns}	1.121^{ns}	0.017^{ns}	554.49*	22354^{ns}
Pooled error	152	0.04413	1.456	0.01335	49.07	75900

* Indicates significant difference at P<0.001 and ns indicates no significant difference

Table 3.7 : Pod shattering, scores and reaction type for soybean genotypes grown at Embu and Mwea during the 2016 long rain and the short rain seasons

Site	EMBU			MWEA			Across sites	
Season Genotype	Long rain	Short rain	Score	Long rain	Short rain	Score	Mean score	Combined reaction type
915/5/12	6.7	2.7	2	0.0	52.7	4	3	MR
931/5/34	56.7	79.5	5	51.7	0.7	4	4	MS
Black Hawk	14.6	3.3	2	13.0	21.3	3	3	MR
EAI-3600	4.0	26.9	3	1.3	13.9	2	3	MR
Gazelle	**2. 7**	**1.3**	**2**	**1.3**	**11.3**	**2**	**2**	**R**
Hill	20.2	0.7	2	18.5	49.0	4	3	MR
Nyala	**2.7**	**6.0**	**2**	**1.3**	**14.5**	**2**	**2**	**R**
SB-145	**16.3**	**4.7**	**2**	**16.3**	**6.7**	**3**	**2**	**R**
SB-151	**17.9**	**2.7**	**2**	**17.9**	**4.7**	**3**	**2**	**R**
SB-154	14.6	13.9	3	14.6	12.6	3	3	MR
SB-19	11.3	35.0	3	13.0	12.0	3	3	MR
SB-20	**9.7**	**4.0**	**2**	**8.3**	**6.0**	**2**	**2**	**R**
SB-25	36.0	79.1	5	46.1	55.4	5	5	HS
SB-37	**17.9**	**0.7**	**2**	**20.2**	**2.0**	**3**	**2**	**R**
SB-4	**6.7**	**4.7**	**2**	**5.7**	**6.0**	**2**	**2**	**R**
SB-74	**9.7**	**0.0**	**2**	**9.7**	**2.7**	**2**	**2**	**R**
SB-8	**8.3**	**0. 7**	**2**	**0.0**	**2.0**	**2**	**2**	**R**
SB-90	61.7	83.4	5	46.1	82.6	5	5	HS
SCS-1	**8.3**	**2.0**	**2**	**9.9**	**17.9**	**3**	**2**	**R**
TGM-1420	22.5	15.3	3	20.2	10.7	3	3	MR
Mean	17.4	18.3	-	15.8	19.2	-	-	-
LSD5%	10.5	6.8	-	14.2	13.3	-	-	-
CV	36.6	22.4	-	54.7	41.8	-	-	-

Score of 1=0% shattering, 2=1-10%shattering, 3=11-25% shattering, 4=26-50% and 5=>50% shattering (AVRDC, 1979). Phenotypic description; Score of 1 – very resistant (VR), 2 – resistant (R), 3 – moderately resistant (MR), 4 – moderately susceptible (MS) and a score of 5 – highly susceptible (HS). LSD – least significant difference, CV – coefficient of variation.

3.4.3. Yield and yield components of soybean genotypes

Plant biomass varied significantly among genotypes (P<0.001). Significant interactions between genotypes, locations and seasons, genotypes and locations, genotypes and seasons and even between locations and seasons were observed (P<0.001). Significant differences were also associated with location and seasonal effects (P<0.001) (Table 3.3). Biomass ranged from 22.5 to 209.3 g across sites and seasons with a mean of 73.1 g. Compared to Embu, plant biomass was significantly higher at Mwea (l.s.$d_{0.05}$=7.2). During the long rains, study genotypes had higher biomass than during the short rains. Except SB-19, SB genotypes together with TGM-1420 had high biomass compared to commercial varieties. SB-145 had the highest biomass (209.3 g $plant^{-1}$). Black Hawk had the lowest (22.5 g $plant^{-1}$) (Table 3.8). The difference in biomasses probably was due to genetic make-up of the genotypes.

The number of pods per plant showed significant variations among genotypes (P<0.001). Significant interactions were observed between genotypes, locations and seasons, genotypes

and locations, genotypes and seasons (P<0.001). There were significant differences among locations and seasons (P<0.001) (Table 3.3). The number of pods per plant differed across sites and seasons. At Mwea, the number of pods carried by a plant was almost the double (83.8 pods) that at Embu (44.9 pods). Similarly the long rain had twice as many pods per plant (81.9 pods) the number of pods per plant compared with the short rain season (46.8 pods). Study genotypes had an average of 64.4 pods per plant across sites. In general, SB varieties had more pods per plant compared to commercial varieties. For instance SB-145 had an average of 146.5 pods per plant while Black Hawk had 28.2 pods (Table 3.8).

Seeds per pods varied significantly among genotypes (P<0.001). There were significant interactions between genotypes and seasons. Locations and seasons showed also significant variations (P<0.001). Significant differences were also associated with seasonal effects (P<0.001) (Table 3.6). Genotypes had different number of seeds per pod across locations and seasons. The number was high at Mwea than at Embu ($l.s.d_{0.05}$=0.05) whilst the short rain season resulted with a high seed number compared to the long rain season. In general, study genotypes had 2.29 seeds per pod. Most of commercial varieties had higher number of seeds per pod. For instance genotype 915/5/12 had the highest number followed by Black Hawk, Gazelle and then EAI-3600 with approximately 2.5 seeds per pod. However SB lines such as SB-20, SB-154 and SB-37 with SCS-1 had approximately 2.0 seeds per pod (Table 3.8).

The 100-Seed mass showed significant variations among genotypes (P<0.001). Significant variations were associated with location effects (P<0.001) (Table 3.6). 100-seed mass differed considering the locations ($LSD_{0.05}$=0.3). The test genotypes had a mean 100-seed mass of 14.6 g. Seed mass was higher at Mwea than at Embu. 100-seed mass varied from 11.0 g for Gazelle to 17.6 g for TGM-1420. During the long rain, the average 100-seed mass was the same as during the short rain (14.6 g) (Table 3.9).

Significant variations were observed among genotypes as regard to harvest index (P<0.001) (Table 3.6). Harvest index were greater at Embu compared to Mwea. Considering the separate cropping seasons, harvest index was greater during the short rain season compared to the long rain season. Harvest index was 0.22 in general, but varied considerably among genotypes. Commercial varieties from KALRO-Njoro had greater harvest index compared to SB lines. Black Hawk followed by 931/5/34 and 915/5/12 had the greatest harvest index while SB-25, TGM-1420, SB-145 and SB-37 had the lowest (Table 3.9).

Table 3.8 : Plant biomass, number of pods per plant and number of seeds per pod of soybeans at Embu and Mwea research centers during the 2016 long rain and short rain seasons

	Plant biomass (g)					Number of pods per plant					Number of seeds per pod				
	Embu		Mwea		Mean	Embu		Mwea		Mean	Embu		Mwea		Mean
	Long rain	Short rain	Long rain	Short rain		Long rain	Short rain	Long rain	Short rain		Long rain	Short rain	Long rain	Short rain	
915/5/12	36.8	36.4	54.6	33.1	40.2	38.7	43.9	59.0	48.6	47.5	2.33	2.53	2.67	2.63	2.54
931/5/34	29.4	52.8	41.9	38.5	40.6	29.7	51.4	62.0	47.5	47.7	2.10	2.20	2.57	2.40	2.32
Black Hawk	13.6	18.5	37.4	20.4	22.5	25.0	30.2	36.3	21.2	28.2	2.57	2.47	2.53	2.57	2.53
EAI-3600	34.8	18.6	67.8	37.1	39.6	35.7	25.5	88.0	36.4	46.4	2.30	2.53	2.53	2.60	2.49
Gazelle	41.0	13.8	69.9	21.7	36.6	50.0	22.6	58.7	21.3	38.2	2.30	2.53	2.57	2.57	2.49
Hill	18.6	15.9	44.0	19.1	24.4	31.0	28.5	40.0	24.5	31.0	2.43	2.27	2.47	2.67	2.46
Nyala	35.3	13.5	39.6	26.8	28.8	33.7	20.0	45.7	18.2	29.4	2.33	2.27	2.37	2.80	2.44
SB-145	53.6	56.3	517.2	210.1	209.3	48.5	48.1	362.3	127.2	146.5	2.20	2.2	2.17	2.33	2.23
SB-151	148.6	62.2	164.1	102.8	119.4	108.0	43.9	126.3	75.4	88.4	1.90	2.57	1.97	2.55	2.25
SB-154	106.1	58.2	196.2	99.7	115.0	77.0	38.4	145.0	74.9	83.9	1.70	2.40	1.80	2.45	2.09
SB-19	17.6	16.1	69.0	38.7	35.3	24.0	30.1	113.0	41.5	52.1	2.13	2.27	2.00	2.27	2.17
SB-20	116.4	50.3	113.9	135.2	103.9	35.7	56.7	188.7	76.6	89.4	2.00	2.09	2.03	2.00	2.03
SB-25	132.9	47.2	167.8	103.7	112.9	83.7	47.9	113.7	72.3	79.4	2.23	2.12	2.23	2.18	2.19
SB-37	83.3	29.4	121.1	56.6	72.6	62.7	24.2	110.7	77.1	68.6	1.90	2.18	2.00	2.28	2.09
SB-4	50.5	68.8	121.9	70.9	78.0	76.0	52.7	149.7	56.7	83.8	2.27	2.27	2.27	2.40	2.30
SB-74	28.2	53.5	111.9	134.9	82.1	36.0	49.1	129.3	63.1	69.4	2.17	2.37	2.23	2.52	2.32
SB-8	48.1	49.5	104.0	144.8	86.6	56.0	52.1	147.7	67.2	80.7	2.10	2.67	2.17	2.58	2.38
SB-90	65.3	22.4	130.4	18.9	59.3	64.3	25.6	75.7	19.2	46.2	1.80	2.00	2.30	2.40	2.13
SCS-1	33.3	22.1	77.7	36.5	42.4	36.7	27.5	74.3	46.0	46.1	1.83	2.33	1.90	2.17	2.06
TGM-1420	91.5	55.8	172.7	130.6	112.7	81.0	47.2	121.7	93.1	85.7	2.30	2.32	2.37	2.32	2.33
MEAN	59.3	38.1	121.1	74.0	73.1	51.7	38.3	112.4	55.4	64.4	2.14	2.33	2.26	2.43	2.29
$LSD_{0.05}$	53.8	25.3	57.6	45.3	46.3	25.5	20.9	60.6	20.1	17.6	0.43	0.30	0.37	0.25	0.17
C.V	55.0	40.2	28.8	37.0	39.3	29.9	33.1	32.6	21.9	33.9	12.3	7.8	10.0	6.2	9.2

LSD – least significant difference, CV – coefficient of variation

Table 3.9 : 100-Seed mass, harvest index and grain yield of soybeans at Embu and Mwea research centers during the 2016 long rain and short rain seasons

	100-seed mass (g)					Harvest index					Grain yield (kg ha^{-1})				
	Embu		Mwea		Mean	Embu		Mwea		Mean	Embu		Mwea		Mean
	Long rain	Short rain	Long rain	Short rain		Long rain	Short rain	Long rain	Short rain		Long rain	Short rain	Long rain	Short rain	
915/5/12	15.5	14.1	16.1	16.2	15.5	0.45	0.35	0.31	0.37	0.37	2011.8	1676.3	2121.8	1694.8	1876.2
931/5/34	16.8	15.6	16.1	17.4	16.5	0.56	0.36	0.38	0.28	0.40	2201.1	2086.7	2125.6	1512.6	1981.5
Black Hawk	11.2	10.7	11.6	14.7	12.0	0.65	0.42	0.22	0.38	0.42	1079.3	1043.3	1023.0	1037.0	1045.6
EAI-3600	14.9	14.2	14.8	14.2	14.5	0.42	0.43	0.11	0.25	0.30	972.4	927.8	989.6	1244.4	1033.6
Gazelle	10.8	10.5	11.0	11.8	11.0	0.16	0.40	0.09	0.31	0.24	676.3	694.1	808.1	778.9	739.3
Hill	11.4	10.3	12.1	11.4	11.3	0.28	0.31	0.11	0.25	0.24	696.7	625.6	645.2	696.3	665.9
Nyala	16.6	15.9	17.3	16.3	16.5	0.20	0.38	0.42	0.30	0.32	948.9	648.9	1229.0	1096.3	980.8
SB-145	16	15.8	17.1	17.1	16.5	0.20	0.17	0.02	0.05	0.11	1270.4	1220.2	1207.0	1324.2	1255.5
SB-151	15.0	15.8	15.4	16.0	15.5	0.09	0.21	0.08	0.12	0.12	1540.9	1582.2	1657.0	1580.5	1596.9
SB-154	13.5	13.9	15.9	14.1	14.4	0.16	0.23	0.07	0.15	0.15	1724.7	1823.3	1805.9	1982.1	1834.0
SB-19	11.7	11.2	13.7	13.1	12.4	0.55	0.44	0.11	0.21	0.33	1002.2	899.3	951.1	1022.2	985.4
SB-20	15.3	15.2	15.4	16.0	15.5	0.16	0.25	0.12	0.11	0.16	1571.1	1551.8	1719.8	1659.3	1625.5
SB-25	15.9	15.1	16.2	15.4	15.7	0.05	0.11	0.04	0.06	0.06	808.7	690.4	854.9	761.5	778.8
SB-37	13.3	14.2	13.6	14.7	13.9	0.07	0.20	0.05	0.11	0.11	662.4	731.1	721.8	819.6	733.7
SB-4	15.2	15.0	15.0	14.8	15.0	0.19	0.14	0.08	0.16	0.14	1280.8	1231.8	1377.5	1473.2	1340.8
SB-74	13.7	13.6	14.8	14.5	14.1	0.52	0.23	0.11	0.10	0.24	1470.4	1370.4	1599.5	1738.4	1544.6
SB-8	15.2	15.1	15.7	15.1	15.3	0.25	0.21	0.12	0.09	0.17	146.00	1365.9	1539.3	1486.6	1462.9
SB-90	13.0	14.2	13.9	13.9	13.7	0.18	0.41	0.12	0.42	0.28	1443.4	1102.2	1561.9	1037.0	1286.1
SCS-1	15.0	14.8	15.4	15.7	15.2	0.32	0.30	0.14	0.27	0.26	903.7	837.8	1188.1	1281.5	1052.8
TGM-1420	17.2	18.0	17.3	17.7	17.6	0.07	0.11	0.04	0.05	0.07	802.9	761.5	828.5	804.1	799.2
MEAN	14.3	14.2	14.9	15.0	14.6	0.28	0.28	0.14	0.20	0.22	1227.8	1143.5	1301.1	1251.5	1231.0
$LSD_{0.05}$	1.4	2.2	2.1	2.2	0.9	0.28	0.19	0.16	0.10	0.10	319.9	573.3	266.1	572.5	240.2
C.V	5.7	9.3	8.5	9.0	8.3	60.6	40.2	70.1	28.9	53.6	15.8	30.3	12.4	27.7	24.2

LSD – least significant difference, CV – coefficient of variation

Grain yield showed significant variations among genotypes (P<0.001) (Table 3.4). Mwea had higher yield than Embu. Grain yield ranged from 665.9 for Hill to 1,981.5 kg ha^{-1} for 931/5/34 across sites and seasons. The mean grain yield across seasons and locations was 1,230.9 kg ha^{-1}. SB lines, except SB-37, had higher grain yields compared to commercial varieties. Some varieties were better yielding than others. For instance, variety 931/5/34 followed by 915/5/12 and SB-154 had remarkable grain yields of more than 1,800 kg ha^{-1}. However, varieties Hill, SB-37 and Gazelle had the lowest yields (less than 800 kg ha^{-1}) (Table 3.9).

3.4.4. Correlations between pod shattering and selected agronomic traits of soybeans

There was a significant (P<0.001) negative correlation between pod shattering resistance and the number of seeds per pod. That correlation showed that resistance to pod shattering increased towards reduced seed number within a pod. Pod shattering was not significantly correlated with other selected traits. Furthermore, significant grain yields resulted in late flowering genotypes with heavy plants, larger number of pods and higher 100-seed mass. Late maturing genotypes resulted in late flowering lines with high plant height, larger seed size but low harvest index. High biomass was associated with late flowering materials, tall plants, larger seed size and high grain yield and in reduced number of seeds per plant and harvest index. High number of pods per plant was associated with tall plants, high biomass, larger seed size and high grain yield but reduced number of seeds per pod and harvest index (Table 3.10).

Table 3.10 : Correlation coefficients between pod shattering and selected agronomic traits of soybean at Embu and Mwea Research Centers during the 2016 long rain and the short rain seasons

	DTF	DTM	PH	Biomass	Pods per plant	Seeds per pod	100-seed mass	Yield	HI
DTM	0.5716**								
PH	0.3499**	0.5899**							
Biomass	0.1706**	0.1041	0.3803**						
Pods per plant	0.0342	-0.0552	0.2661**	0.8532**					
Seeds per pod	-0.2924**	0.0179	-0.0351	-0.2398**	-0.2456**				
100-seed wt	0.1904**	0.2785**	0.3337**	0.3230**	0.2861**	-0.0940			
Yield	0.1448*	0.0968	0.1151	0.1567*	0.1554*	-0.0506	0.2872**		
HI	-0.1532*	-0.2221**	-0.4630**	-0.5641**	-0.5054**	0.1368*	-0.2329**	0.1186	
Shatter %	-0.1023	-0.0833	-0.0538	-0.0297	-0.0649	-0.1304*	0.0038	0.0025	0.096

* Indicates significant at P≤0.05 and ** indicates significant at P≤0.01 ; PH = plant height, HI = harvest index ; DTF = days to 50% flowering ; DTM = days to 75% maturity

3.5. Discussion

3.5.1. Agronomic traits of soybean genotypes

Significant differences were found among soybean genotypes across sites and seasons in terms of germination percentage. Findings have shown higher percentage at Mwea compared to Embu with better germination rate during the short rains than the long rains. These observations are in agreement with the research results of Shibles *et al.* (1975). The findings might be attributed to ecological conditions which approximated the requirements of the crop at Mwea than at Embu. Shibles *et al.* (1975) reported that the temperature plays an important role in the soybean emergence process, the ideal temperature for soybean growth being between 25° and 30°C. King'uyu *et al.* (2000) noted an average temperature at Mwea of 23.2°C which approximated the optimal of 25°C. Wanderi (2012) reported that the average temperature at Embu was 21°C, which was less favorable. During the experimental period, 943.7 mm of rainfall and a mean temperature of 23.1°C were recorded at Embu and 839.8 mm and 24.1°C at Mwea (Appendices 1 and 2). Helms *et al.* (1997) added that the emergence and subsequent vegetative events may be significantly delayed by cooler than optimum temperatures. Genotypic differences were also found among the study genotypes. SCS-1 had the highest germination rate followed by SB-25, Nyala, Hill and 915/5/12. Lower records found in general, are consistent to Nafziger (2015) whose findings stated that the seed of soybean is among the most difficult to produce and maintain high and stable quality or maximun germination. He added that germination percentages can be reduced by poor weather conditions. This statement could explain the low germination rate observed for the 2016 long rain crop which was sown in mid-June. Germination percentage was 44.3% during the cooler long rain season compared with 78.1% for the warmer short rain season.

Findings showed that duration to flowering was significantly influenced by seasons, sites and genotypes. Moreover, there were significant interactions among these factors. These observations were consistent with those of Obidiebube *et al.* (2013) and Njoroge *et al.* (2015) who reported that genotypic responses varied with locations and cropping seasons allowing selection of genotypes for specific eco-zones and seasons. The findings might be attributed to genetic differences among the genotypes and different environmental effects. It also indicated that the test genotypes did not respond the same way to environmental influences. Nyala, recognized as the early flowering genotype, took about 56 days to 50% flowering followed by Black Hawk and Hill while SB-145 took 75 days. Study genotypes took an average of 61 days

to 50% flowering at Mwea, compared to 68 days at Embu. These variations are consistent with Petanidou and Smets (1996) ; Saavedra *et al.* (2003) ; Koti *et al.* (2005) who stated that elevated temperatures are known to result in a reduction of duration to flowering, resulting in altered production of flowers. These findings might be attributed to variations of temperatures within the locations. Mwea had about 24.1°C during the study period of experiments while Embu had 23.1°C (Appendices 1 and 2).

Days to maturity showed significant interactions between genotypes and seasons while significant variations were found among locations, seasons and genotypes. These results agreed with Mugendi *et al.* (2011) and Vandamme *et al*. (2013) who found similar variations in western Kenya. Climatic factors such as altitude, temperature, and rainfall pattern might be the core reasons of the observed differences. Indeed, the unreliable and erratic rainfall across sites was observed particularly at Mwea where a severe drought affected negatively the biomass accumulation of late maturing varieties during the short rain season. Mugendi *et al.* (2011) and Vandamme *et al*. (2013) found biomass accumulation being affected by rainfall distribution and initial soil status. Most of SB varieties such as SB-145, SB-151, SB-154, SB-25, TGM-1420 and SB-20 were very late maturing varieties (took more than 115 days to reach 75% maturity) and had generally higher above ground biomass than local or commercial genotypes which varied from early to medium maturing varieties (took 80 to 115 days to full maturity). These results are in agreement with Vanlauwe *et al.* (2003) who reported that high biomass of soybeans is obtainable in late maturing than in the early maturing varieties. Mahasi *et al.* (2010) suggested that the late maturing genotypes are bred for biomass production unlike the earlier and medium maturity types which are bred for grain production. The findings suggested therefore that varieties with longer maturity period produce high amount of biomass. Indeed, with great biomass and generally taller plants, the plants might have used most of the nutrients for biomass accumulation and vegetative growth, a process that takes place before flower initiation and maturity thus delaying the reproductive stage.

Significant interactions were found between genotypes and locations; and genotypes and seasons as regard to plant height. Significant differences were also found among genotypes, locations and seasons. These results were in agreement with research results reported by Giller and Titonell (2013). Their findings demonstrated that crop potential can be intensified by the interaction of factors such as genotype, environmental factors such as location and season and period reserved for management. Significantly, shorter plants were found at Embu

than Mwea across seasons. This is attributed to site variations with regard to germination rate which was higher at Mwea than Embu increasing the plant density and consequently the plant height particularly at Mwea and with respect to rainfall. Wanderi (2012) reported that Embu and Mwea are different micro-ecological zones within Eastern and Central Kenya. The findings are in agreement with Janick (1972) who reported that increasing plant density accelerates the rate of plant growth hence the increased heights in closer spacing. The higher plant population at Mwea may have resulted in increased competition for essential growth factors like nutrients, sunlight, and water. The effect of increasing competition was similar to decreasing the concentration of growth factors as proposed by Janick (1972) and Norman (1992). Average plant height during the long rain season was 40 cm, which was associated with low observed plant density. Plants were generally taller (55.6 cm) during the short rain season, partly associated with a high plant density and high germination capacity. In addition, the amount of rainfall was higher and better distributed during the short rain season (Appendices 1 and 2). Plant density might have played additional role resulting in differences in plant height observed during the two cropping seasons. This is consistent with Amaglo *et al.* (2006) ; Augusto *et al.* (2014) who found that a good rainfall pattern and a closer spacing leads to higher increases in soybean plant height, while wider spacing shows relatively lower increases of plant height. Wycliffe (2015) found that long rain soybean crop in Western Kenya were generally taller compared to those grown during the short rains. Genotypes TGM-1420, SB-25 and SB-151 were the tallest lines across sites and seasons. On the other hand Black Hawk had the shortest plants. Generally, late maturing genotypes were taller than medium or early maturing genotypes. These findings are consistent to Mahasi *et al* (2010) and Ngalamu *et al* (2013) found that late maturing varieties are taller than early maturing varieties due to their genetic composition and longer period to utilize the available resources optimally.

3.5.2. Resistance of soybean genotypes to pod shattering

This study revealed a wide range of resistance to pod shattering with significant differences among soybean genotypes. Locations and seasons interacted significantly with genotypes at $P<0.001$. These findings agreed with Agrawal *et al.* (2002) ; Tukamuhabwa *et al.* (2002a) ; Zhang and Boahen (2010) ; Bhor *et al.* (2014). The findings were attributed to environmental interactions with genetic potential of soybean materials. These observations are consistent to Zhang and Boahen (2010) who started that the degree of soybean pod shattering depends upon the time of harvesting, the locations and the genotypes. Tsuchiya (1987) ; Philbrook and Oplinger (1989) ; Agrawal *et al.* (2002) ; Tukamuhabwa *et al.* (2002a) started before, that

environmental factors such as drought stress during pod maturation has a significant impact on pod shattering. That might be the reason of an increase in pod shattering incidence observed particularly during the short rain season. This season was accompanied with dry weather conditions. Findings were more in agreement with Bhor *et al.* (2014) such that genotypic characteristics played a major role in the overall expression of pod shattering suggesting that these differences could be attributed to differences in genetic information of soybean genotypes and seasonal weather conditions during growth and development.

Nevertheless, the reaction types used in this series of evaluations provided a good basis for classifying genotypes into resistant, moderate resistant, moderately susceptible and highly susceptible categories. SB varieties were the most resistant genotypes particularly SB-8 and SB-4. Varieties Gazelle and Nyala were the resistant among commercial varieties. Results are also consistent with Mahasi *et al.* (2012), whose findings during a study carried in Western Kenya revealed that commercial varieties, Nyala and Gazelle showed some resistance and stability in pod shattering at three locations ; 'Bureti', 'Menengai' and 'Lare' when on the other side Shaahu *et al.* (2013), using most of SB varieties from IITA Ibadan in Nigeria, SB-8, SB-4, SB-20 and SB-74, found these materials to be resistant against pod shattering. They showed an average shattering percentage that varied between 1 to less than 15%. They remained stable throughout different agro-ecological zones. This stability may be due to their genetic package or the genes that control that resistance as mentioned by Carpenter and Fehr (1986). SB varieties might have dominant resistance genes which control their ability of resistance against pod shattering. Susceptible varieties SB-90 and SB-25 may have 6 to 12 genes for susceptibility such that they shatter earlier in the field as reported by FIPs (2009).

3.5.3. Yield and yield components of soybean genotypes

Findings showed significant differences among the study genotypes as regard to biomass accumulation. Significant differences were also found among locations and seasons and all interactions among the main factors. These findings might be attributed to genetic diversity that characterizes soybean genotypes and also environmental effects. Plant biomass at Embu was lower than at Mwea. These differences were attributed to variation in rainfall, temperature and soil conditions of the test sites. Embu had an average annual rainfall of 943.7 mm and an average annual temperature of 23.1°C with a maximum of 26°C while Mwea received about 839.8 mm and an average temperature of 24.1°C with a maximum of 27.2°C, during the experimental period (Appendices 1 and 2). Wanderi (2012) noted the presence of

humic nitosols in Embu station and vertisols in Mwea. The same trend was observed for the two seasons. Biomass was higher during the long rains than during the short rains. Findings showed that biomass was 60.7% higher during the long rain season. These findings were in agreement with findings by Chianu *et al.* (2008) who reported that there is a tendency for many crops to fail during the short rain season but soybean generally survives due to its high drought tolerance but remarkable biomass losses are associated effects. The findings were also in agreement with Okoth *et al*. (2013) whose findings indicated that mid-season drought has detrimental effects on soybean biomass accumulation. During the short rains, there was a severe mid-season drought which adversely affected plant growth and development especially during the reproductive phase as it coincided with pod setting stage. This could also be attributed to more reliable and better distributed rainfall in long rain when compared to short rain (Appendices 1 and 2). About 60% of biomass losses were observed during the short rains. The erratic and unreliable rainfall during the short rain season may have adversely affected vegetative growth, and hence the shoot biomass production.

The findings showed that biomass of SBs, the late maturing genotypes, was three times higher compared to commercial and local lines (94.6 g against 33.2 g). Vanlauwe *et al.* (2003) reported higher biomass accumulation in late maturing than in early maturing soybean varieties. This could be due to the longer period to maturity associated with SB genotypes, which allows plants to accumulate enough nutrients for high biomass production.

Number of pods per plant varied significantly among the study genotypes. Locations and seasons showed also significant influences. Number of pods per plant at Mwea was two times the number observed at Embu. These findings were in agreement with research conducted by Mahasi *et al.* (2010) who reported that soybean characters vary from site to site. During the long rain study genotypes had 68.7% more pods per plant compared to the short rain. These findings might be due to different environmental effects. For instance, FAO (2002) reported a range of 25 to 30°C as the best limit of temperature for a good soybean development and production. Mwea had higher temperature compared to Embu (Appendices 1 and 2). Environmental factors such as rainfall, atmospheric temperature or available soil nutrients strongly influence yield components such as number of pods. Rainfall was erratic and unreliable with severe drought during the short rain season, but was well distributed and reliable during the long rain. Amount and distribution of rainfall was the most probable reason that explains the reduction of pods during the short rains (Appendices 1 and 2). This is in agreement with research conducted by Okoth *et al.* (2013) whose findings indicated that mid-

season drought often encountered during short rains has detrimental effects on yield components of soybean such as pods per plant. The findings of this study were also consistent with those of Wycliffe (2015) who reported that availability of soil moisture especially at critical stages of growth such as pod set and pod filling and other environment factors are the most important factors in determining the number of pods.

Number of pods per plant differed significantly among genotypes. These variations agreed with Wicliffe (2015) who worked on 11 genetically diverse varieties in Western Kenya. They might be attributed to genetic variability that characterizes soybean genotypes. SB varieties and TGM-1420 had the largest number of pods per plant with SB-145 being the best and bearing about 147 pods. Black Hawk had the lowest record (28.2 pods per plant). SBs and TGM-1420 being late maturing varieties might have utilized soil resources more effectively compared to early maturing varieties. The findings of this study were consistent with those of Njoroge *et al.* (2015) ; Wycliffe (2015) who evaluated 11 soybean genotypes with different maturity periods at Njoro, Eldoret, Nakuru and Lanet. They reported that late soybean genotypes had large pod number than early maturing genotypes. The high number of pods could also have been attributed to the genetic make-up of the varieties. Baijukya et *al.* (2013) reported that the high pod load of a genotype originates from its genetic composition. The results are in agreement also with those conducted by Mahasi e*t al.* (2010) in western Kenya whose findings showed a large number of pods being associated with late maturing soybean genotypes.

Locations and seasons significantly affected the number of seeds per pod. At Embu, pods had an average of 2.24 seeds compared with 2.35 seeds per pod at Mwea. The mean number of seeds per pod was 2.20 for the long rain and 2.38 for the short rain. These findings are in agreement with Bodunde (1998) who reported that variations in temperature, rainfall and available nutrients are partly responsible for those environmental differences. The variations might be attributed to environmental effects. Number of seeds per pod was also significantly affected by soybean genotypes. Line 915/5/12 and Black Hawk had the highest number of seeds per pod. On average pods of 915/5/12 had 2.54 seeds, followed by 2.53 for Black Hawk. SB-20 had the lowest number of seeds per pod (2.03). These differences in number of seeds formed were attributed to the genetic and also environmental factors that influence seed filling. The findings are in agreement with Nwofia *et al.* (2016) findings who reported that seeds per pod are associated with genetic make-up. These findings are also in agreement with

the earlier report of RMRDC (2004) in which it was observed that the total output of soybean is dependent on genetic potential of the planting material.

Significant differences were observed only among locations and also among genotypes in terms of 100-seed mass. Seed size was significantly higher at Mwea (4.9% of an increase) compared to Embu. This might be due to reliable temperature for a good soybean development (Appendices 1 and 2). Significant variations among genotypes might be attributed to their different genetic packages. TGM-1420 had the heaviest seeds (17.6 g per 100 seeds) while Gazelle had the lowest seed mass (11 g). These observations are in agreement with Wycliffe (2015) who reported that the size of soybean genotypes depends on their genetic make-up. Akbari *et al*. (2011) found that seed size, generally, may increase under good supply of nitrogen fertilizer but varies particularly with genetic background of the materials.

Only genotypic differences were significant for harvest index ($P<0.001$). This finding is in line with findings of a study carried by Solomon *et al*. (2012) who found that the main source of variation on soybean harvest index was from genotypes but not from neither other factors nor their interactions. This current finding contradicts results reported by Mandal *et al.* (2009) who found no significant differences in soybean harvest index. Harvest index was lower at Mwea compared to Embu. This can be attributed to high plant biomass at Mwea. Commercial varieties had higher harvest index compared to SB lines. Black Hawk followed by 931/5/34 and 915/5/12 had the highest harvest index while SB-25, TGM-1420, SB-145 and SB-37 had the lowest. These differences in harvest index were attributed to effects of plant biomass, 100-seed mass and grain yield.

Findings showed significant variations among soybean genotypes as regard for grain yield. Related observations were made by Njoroge *et al*. (2015) who evaluated soybean genotypes at Njoro, Eldoret and Nakuru for two seasons. These differences could be attributed to genetic influences. No significant differences among locations might suggest that the two locations may have comparable phosphorous concentration. Giller (2001) reported that high available soil phosphorous has been demonstrated to increase productivity and biological nitrogen fixation of legumes. Zingore and Giller (2012) noted a positive correlation between yields of soybean and soil available phosphorous. Commercial varieties 931/5/34, 915/5/12 and SB-154 were well adapted in the two locations and seasons. 931/5/34 with 1981.5 kg ha^{-1} ranked the best and this could be attributed to genetic potential for high stable productivity and

efficient use of fertilizer applied. These research findings were consistent to Alghamdi (1991) ; Vandamme *et al.* (2013) who reported that yield of defined true varieties is more stable across diverse environments and growing periods. The high yield potential of variety 931/5/34 may also be due to contributions of its remarkable yield components such as 100-seed mass which was relatively high and maturity period also as suggested by Lynch (2011). 931/5/34, with 112 days to 75% maturity belonged to medium-maturing genotypes. Lynch (2011) showed that most of medium-maturing genotypes had high grain yields compared to early maturing genotypes. These findings were also consistent to observations during successive 15 years of experimentation carried in central Illinois region by Nafziger (2015) of the University of Illinois. The later author revealed that yields of later-maturing varieties can be higher or lower than those of early-maturing ones depending on the year. However in general cases, on average, mid-maturity varieties tend to yield slightly more than either early or late varieties, and those within a bushel of the top-yielding maturity covered a spread of about one half of a maturity group on either side of the highest-yielding group. 931/5/34 and 915/5/12 were mid-maturing varieties (with the number of days to maturity ranging between 95-115 days). Nafziger (2015) added that it is also clear that yields are much more closely tied to genetic potential than they are to maturity itself. Even though on average varieties with very early or very late maturity tend to yield less, individual varieties within these maturity groups were often as high-yielding as the higher-yielding entries in the mid-maturity group during his observations.

3.5.4. Correlation between pod shattering and selected agronomic traits

In the present study, pod shattering resistance had significant negative correlation with only number of seeds per pod ($r=-0.13^*$) ($P<0.05$). These findings are consistent to Morgan *et al.* (1998) and partly contradictory to those of Ghobnal and Denis (1979) ; Etebom (1987) ; Adeyeye (2014) who found no significant correlation of soybean pod shattering with number of pods per plant, number of seeds per pod and seed mass suggesting that these parameters were not useful as an index for pod shattering selection. The results are also partly contradictory to those of Child *et al.* (2003) whose findings illustrated that pod shattering was significantly and positively correlated with 100-seed mass. The negative correlation with pod shattering resistance suggested that high resistance to pod shattering is associated with low number of seeds per pod. This may be attributed to a good structure and consistency of pods that bear little seeds in number. Metcalfe *et al.* (1957) stated, however, that pod shattering resistance is closely related to its water content.

3.6. Conclusion

This study characterized 20 soybean genotypes for resistance to pod shattering at KALRO-Embu and KALRO-Mwea Research Centers using a 1 to 5 AVRDC scale (1=very resistant and 5=highly susceptible). Resistant varieties included Gazelle, Nyala, SCS-1, SB-145, SB-151, SB-20, SB-37, SB-4, SB-74 and SB-8. Most of these genotypes were SB lines from IITA. The first three genotypes were commercial varieties. Most of SB varieties did well for many of other farmer's traits such as yield or biomass. However they were late maturing. They may be valuable to soybean breeders for the increased genetic diversity that they bring in, and they are likely to provide new, potentially useful sources of resistance that may be introgressed into susceptible local and commercial varieties in Kenya. Thus further studies are needed to characterize the resistance genes present in the most resistant genotypes found under this study, SB-8, SB-74, SB-4 and SB-20 among SB lines and Gazelle, Nyala and SCS-1 among the locals. Moderately resistant genotypes to pod shattering, affected with low incidences may probably carry partial resistance to pod shattering with long term duration. These genotypes included EAI-3600, Black Hawk, SB-154 and 915/5/12. Therefore, they could be used in a breeding program to develop soybean varieties with durable pod shattering resistance, based on partial resistance in Kenya. Pod shattering resistance was negatively correlated with the number of seeds per pod. This implies that resistance to pod shattering is associated with few seeds per pod. Environments had no significant effects on pod shattering. However, there was a significant genotype x environment interactions for days to 50% flowering, days to 75% maturity, plant height, plant biomass and grain yield were influenced by environments. Overall, Mwea had higher plant biomass, grain yield with taller plants compared to Mwea. In addition, genotypes reached days to 50% flowering and 75% maturity earlier at Mwea than at Embu.

CHAPTER FOUR: COMBINING ABILITY OF POD SHATTERING AND AGRONOMIC TRAITS OF SOYBEAN GENOTYPES

4.1. Abstract

Pod shattering is one of the most constraints in soybean productivity in the tropics and may cause up to 100% seed losses in susceptible soybean varieties. To reduce losses, farmers often have to harvest seeds with high moisture content before pods start shattering. Understanding the genetic control of pod shattering in soybeans is a key determinant and can contribute to the development of effective breeding programs for sustainable management. The objective of this study was to determine the genetic basis of pod shattering and agronomic characters of soybean cultivated in Eastern Africa. Two parental lines resistant to pod shattering (Nyala and SB-8) were crossed to six susceptible parents (SB-25, SB-93, SB-19, 915/5/12, 835/5/30 and SB-98) in a diallel mating scheme to generate 28 F_1 progenies in greenhouse. The F_1 and their parents were evaluated in field experiments at KALRO-Embu and Mwea. The trials were laid out in an alpha-lattice design arranged in a 6 x 6 pattern with three replications. Data was collected on days to 50% flowering, days to 75% maturity, plant height, pod shattering and grain yield. Combined analysis of variance was performed and general and specific combining ability were determined according to Griffing's diallel. General and specific combining ability (GCA and SCA) were significant ($P<0.05$) for all the traits indicating that additive and non-additive gene action were important in the inheritance of pod shattering and other traits. GCA/SCA ratio ranged from 0.00124 to 0.0742. Although the ratio was higher for pod shattering (0.0742) compared to other traits (less than 0.0132), the ratio in general was close to zero. This indicated that non-additive gene action played a more important role over additive in the inheritance of these traits. Parent SB-98 was the best combiner for early flowering. Parents SB-93, SB-19, SB-98, 835/5/30 and Nyala, were the best combiners for early maturity. SB-19, 915/5/12, Nyala, SB-93 and SB-98 contributed significantly towards reduced plant height. Parent 835/5/30 followed by SB-8 were the best combiners for high grain yield. Parents SB-8 and Nyala had the highest negative and significant GCA effects for pod shattering indicating that these lines had favorable gene frequencies for resistance to pod shattering. Progenies of SB-25 x SB-8 were the best combiners for pod shattering resistance across environments. This study found non-additive gene action to be more important over additive and suggested that heterosis breeding and selection of late segregating generations would be effective to improve pod shattering resistance ability and other agronomic traits.

Key words: combining ability, pod shattering and soybean.

4.2. Introduction

Pod shattering is one of the most important constraints to soybean productivity in the tropics. Other important constraints include low yielding cultivars, pests, diseases (Krisnawati and Muchlish, 2017). Seed losses of 50–100% are often associated with pod shattering in susceptible varieties and delayed harvesting (IITA, 1986) impelling farmers to harvest before pods start shattering. However, shortage of labour and harvesting equipment can delay harvesting leading to seed yield losses especially under dry weather conditions. Therefore, several investigators have suggested that breeding strategies for resistance to pod shattering should be prioritized (IITA, 1992; Sanginga *et al.*,1999 ; Krisnawati and Muchlish, 2017).

Understanding the genetic control of pod shattering in soybeans can contribute to the development of efficient and effective breeding programs. However, limits and contradictory information on genetic basis of shattering have been reported. Caviness (1969) did not find any significant variation in shattering resistance in crosses between wild and domesticated cultivars. Misra *et al.* (1980) found variations for shattering irradiated with gamma rays. Treated plants showed a higher frequency of plants with delayed shattering. Tsuchiya (1986) did not find significant variations among resistant genotypes from Japan, USA, China and Thailand suggesting a simple and similar genetic control of pod shattering in soybean. Caviness (1969) and Tsuchiya and Sunada (1980) found that susceptibility to shattering is partially dominant. Tiwari and Bhatnagar (1992) found susceptibility being dominant in some crosses while other crosses showed resistance being partially dominant. However, the non-additive gene action played an important role over additive. Tukamuhabwa *et al.* (2002b) revealed the importance of additive and non-additive gene action in the inheritance of pod shattering. Thus, they recommended further studies including F_1 and F_2 from diverse matings.

In order to understand the type of gene action and the magnitude of additive and non-additive genetic effects in control of the shattering trait, the use of an appropriate mating design is required (Kang, 1994). One of the most commonly used designs for self-fertilizing crop species is the diallel mating design (Gumisiriza, 1987; Christie and Shattuck, 1992) which enables predictions to be made at early generations increasing the efficiency of a breeding program (Dickson, 1967). Diallel mating design has additional benefits in that the analysis applies to all the crosses, and permits the estimation of additive, dominance, and environmental effects and allows detection of non-allelic interactions (Mather and Jinks, 1982; Christie and Shattuck, 1992). Gumisiriza (1987) and Christie *et al*., (1988) reported that

theoretical considerations suggest that the diallel cross technique is a suitable method for the investigation of genetically controlled traits. The objective of this study was to determine the combining ability for pod shattering and other important agronomic traits of soybean genotypes grown in Eastern Africa.

4.3. Materials and Methods

4.3.1. Description of study genotypes

The study materials were two genotypes resistant to pod shattering (SB-8 and Nyala), four moderately resistant (915/5/12, 835/5/30, SB-19 and SB-98) and two highly susceptible genotypes (SB-25 and SB-93). These genotypes were selected for resistance to pod shattering in previous screening trials carried out during the 2016 long and short rains at KALRO-Embu and Mwea Research Centers (Chapter 3). They also differed in maturity, grain yield and other characteristics (Table 4.1).

4.3.2. Generation of crosses

The eight parental lines were planted in crossing blocks in a greenhouse, at Kabete Field Station, College of Agriculture and Veterinary Sciences, University of Nairobi. Seeds of each parent were sown in 10 plastic pots of diameter 40 cm at the base and 60 cm at the top, and 37 cm height. Seeds were sown on five different dates at an interval of one week in order to synchronize different days-to-flowering associated with parents. Growth media was prepared using 3:1:1 ratio of soil, sand and organic manure as recommended by Gavioli *et al.* (2006). Fertilizers were applied at 20 kg N ha^{-1} and 60 kg P_2O_5 ha^{-1} at planting. Before sowing, seeds were treated with thiram and phorate at 10g per plot was applied in the soil to control seed borne fungi and girdle beetle as recommended by Sharma (2004). All recommended agronomic and plant protection practices were followed to raise the healthy crop. Hand irrigation was done twice a day until the soil was flooded to field capacity. At flowering, all possible single crosses, excluding reciprocals, were made in 8 x 8 diallel design, following Griffing's Model 1, Method 2 (Griffing, 1956). Hybridization was achieved by emasculation and hooking methods among the genotypes as described by Walter (1980). Sepals, petals and anthers were gently removed from the unopened flower used as female parent. Male parent, selected from opened flowers, was then hooked to the stigma of the emasculated female flower. Tags were used to identify the crosses. One to two weeks after pollination, success rate of pollination was evaluated by counting young pods developed. Hybridization continued until plants stopped producing flowers.

Table 4.1 : Sources, grain yield and some attributes of parental lines used for genetic studies

Variety	Name of Release	Year of release	Source	Average on-farm yield (kg ha^{-1})	Special attributes
Nyala	Nyala	2009	KALRO -Njoro	700	Early maturity, large grain size; susceptible to rust and nodulates with specific rhizobia strains; Resistant genotype to shattering
TGx1740-2F	DPSB 19	2010	IITA	900	Free nodulation, grain and biomass yield, high pod clearance, good pod load, medium maturity, good for making milk; moderately resistant to shattering
TGx1895-33F	DPSB 8	2010	IITA	950	Free nodulation, grain yield and biomass accumulation, high pod clearance, good pod load, good for making milk, attractive color; resistant to shattering
SB-25	DPSB 25	2010	IITA	2000-3000	Many nodules less resistant to pests and diseases, Shatters early in the field, 43% protein, 20% oil, 100-125 as days to maturity,
915/5/12	915/5/12	2009	KALRO -Njoro	900-1800	Early maturity (82-98 days); days to flowering (51); moderately resistant to shattering
835/5/30	835/5/30	2009	KALRO -Njoro	1500-2000	Medium maturing, nodulation with native rhizobia; moderately resistant to shattering
SB-93	DPSB 93	2010	IITA	600-1300	Susceptible to shattering
SB-98	DPSB 98	2010	IITA	700-1500	Moderately susceptible to pod shattering

Sources: Mahasi *et al*. (2010)

4.3.3. Field evaluation

The 28 F_1 progenies and their parents were evaluated to determine the combining ability for pod shattering under field conditions at KALRO-Embu and KALRO-Mwea between December 2016 and May 2017. The trials were laid out in an alpha-lattice arrangement in a 6 x 6 pattern with three replicates. A plot consisted of three rows of 2 m long. Spacing was 15 cm between plants and 40 cm between rows.

Fields at each trial location were ploughed and harrowed to achieve a moderate tilth seed-bed. Di-ammonium phosphate fertilizer was applied and mixed with soil during sowing at a rate of 150 kg ha^{-1} as recommended by Hundie *et al.* (2000). Plants were top dressed at a rate of 150 kg ha^{-1} at flowering with calcium ammonium nitrate. Field experiments were kept relatively free from weeds throughout the cropping season. Supplemental furrow irrigation was provided at Mwea due to a severe drought during the 2016 short rain season. Weeding and other cultural practices were done manually as recommended for each site.

Days to 50% flowering was recorded as number of days from sowing to when 50% of plants had at least one opened flower within a plot. Days to 75% maturity was recorded as the number of days from sowing to when 75% of plants reached 95% of fully maturity. Plant height (cm) was collected at flowering on a sample of six plants as the distance from the ground to the top of the main stem (Wanderi, 2012). Pod shattering was assessed by randomly sampling 50 fully mature three seeded pods of each variety which were placed in khaki envelops and sun-dried for seven days as described by IITA (1986) ; Tsuchiya (1987) and Krisnawati and Adie (2016). Ten plants were sampled per plot while five pods were taken from each plant. The number of shattered pods were counted every day and expressed as percentage. Genotypes were then classed into five categories from very resistant to highly susceptible genotype (Table 3.2). Grain yield was collected by weighing (g) threshed seeds from plants of the middle rows and then extrapolating into kg ha^{-1} (Wanderi, 2012).

4.3.4. Statistical analysis

Data was subjected to analysis of variance (ANOVA) and residual maximum likelihood (REML) using Genstat statistical package (15^{th} edition) (Payne *et al.*, 2009).
ANOVA model used for this analysis was;

$$Y_{ijk} = \mu + G_i + \beta_j + \varepsilon_k + G\varepsilon_{ik} + E_{ijk}$$

Where:

Y_{ijk} is the observed value of i^{th} genotype (i=1 to 36) in j^{th} replicate (j=1 to 3) for the k^{th} environment (k=1 to 2)

μ is the grand mean

G_i is the treatment effect for the i^{th} genotype

β_j is the block effect for j^{th} block

ε_k is the environmental effect for the k^{th} environment

$G\varepsilon_{ik}$ is the interaction term of i^{th} genotype or family in k^{th} environment, and Eijk is the random error associated with the Yijk experimental unit.

4.3.5. Determination of combining ability

General and specific combining ability, GCA and SCA values, for each trait were calculated following Griffing's Model 1 (with fixed genotype effects), Method 2 (parents and crosses) (Griffing, 1956) using SAS-05 program in SAS 9.2 version (SAS Institute, 2002; Zhang *et al.*, 2005) as follows:

$Y_{ijk} = \mu + g_i + g_j + s_{ij} + \varepsilon_{ijk}$

Where, Y_{ijk} = Observed value of the ij^{th} genotype in the k^{th} environment ; μ = Overall mean ; g_i = the GCA effects of the i^{th} parent ; gj = the GCA effects of the j^{th} parent ; S_{ij} = the SCA effects for the cross between the i^{th} parent and the j^{th} parent ; εijk = experimental error associated with ij^{th} genotype in the k^{th} environment.

The ratio GCA/SCA also known as general predicted ratio (GPR) was used for all the traits to estimate the relative importance of GCA and SCA estimates. This was computed and illustrated by Baker (1978) cited by Wanderi (2012) as follow;

$$\frac{GCA}{SCA} = \frac{2 \times MS_{GCA}}{2 \times MS_{GCA} + MS_{SCA}}$$

Where; MS GCA and MS SCA are the mean squares of GCA and SCA, respectively.

A ratio GCA/SCA close to 1 indicates the preponderance of additive effects in the inheritance of the trait. When that ratio is close to 0, dominance effects are more important.

High-parent heterosis (HP) was calculating using the following formula $HP=(\frac{F_1 - HP}{HP}) \times 100$ where F_1 is the performance of hybrid and HP the performance of best parent (Fehr, 1987).

4.4. Results

4.4.1. Agronomic performance

Days to 50% flowering varied significantly among locations and genotypes (P<0.001). There was significant interactions between genotypes and locations (P<0.001) (Table 4.2). In average, test lines took 64 days to 50% flowering. Among the parents, duration to 50% flowering varied from 49 to 72 days at Embu and 51 to 74 days at Mwea, with parent SB-98 being the earliest to flower across the two environments. The F_1 progenies derived from crosses Nyala x SB-98 and SB-19 x SB-93 were the earliest to reach flowering, while those of SB-25 x SB-8 and 915/5/12 x SB-25 were the latest across the environments (Table 4.3).

Days to 75% maturity showed significant variations among genotypes (P<0.001) (Table 4.2). Study genotypes took 107 days to reach 75% maturity. Among parental lines, duration to 75% maturity ranged from 96 days for parent SB-93 to 127 days for parent SB-25 across the two environments (Table 4.3). None of the F_1 progenies matured earlier than their parents, which matured in 80 to 95 days. Most of the F_1 progenies were medium maturing across locations (between 95 and 115 days). Four of the F_1 progenies were late maturing genotypes (with number of days to maturity beyond 115 days) across environments. They included 915/5/12 x SB-25, 915/5/12 x SB-8, SB-19 x SB-25 and SB-25 x SB-8 (Table 4.3).

Plant height varied significantly among genotypes (P<0.001) (Table 4.2). Test genotypes had an average plant height of 31.7 cm. Among the parental lines, plant height ranged from 22.7 to 50.5 cm, with parent SB-19 being the shortest and parent SB-8 the tallest across environments (Table 4.3). Crosses SB-19 x SB-98 and 915/5/12 x SB-19 had the shortest plants, less than 22.5 cm, while F_1 progenies from the cross SB-25 x SB-8 had the tallest plants with mean height of 47.9 cm (Table 4.3).

Pod shattering varied significantly among the study genotypes at the two locations (P<0.001). There was significant interactions between genotypes and locations (P<0.001) (Table 4.2). Pod shattering varied from 2.8 to 60.4% with a mean of 24.4%. 23.2% and 25.5% were pod shattering percentages observed at Embu and Mwea. Among the parental lines, resistance to pod shattering ranged from 2.8 % (SB-8) to 56.7% (SB-93). Two genotypes were classified as resistant, four intermediate, and two were highly susceptible to pod shattering. Parental genotypes SB-8 and Nyala, consistently had the lowest pod shattering percentage across the two environments. 835/5/30, 915/5/12, SB-19 and SB-98 were moderately resistant. In

contrast, SB-25 and SB-93 were highly susceptible to pod shattering across environments (Table 4.4). Pod shattering score among the F_1 progenies ranged from 9 to 60.4% across the environments (Table 4.4). The F_1 progenies of cross Nyala × SB-8 had the lowest pod shattering while SB-25 × SB-93 progenies had the highest pod shattering percentage. In general, about 43% of the F_1 progenies had moderate pod shattering resistance reactions while 14% expressed resistance reactions. On the other hand, 39% of the F_1 progenies showed moderate susceptibility to shattering, and 4% were highly susceptible (Table 4.4).

Grain yield varied significantly among genotypes (P<0.001) (Table 4.2). The study genotypes had a mean grain yield of 1,064.2 kg ha^{-1}. 835/5/30 performed well with 2,126.1 kg ha^{-1} among all the parental lines followed by 1,663.3 kg ha^{-1} for SB-93. Nyala, the most widely grown commercial variety had the lowest grain yield (605.5 kg ha^{-1}). Parental genotypes had higher yields at Mwea (1,246.8 kg ha^{-1}) compared to Embu (1,222.5 kg ha^{-1}) (Table 4.3). The best yielding F_1 progenies were from the following crosses: SB-25 x SB-8, 915/5/12 x SB-8 and 835/5/30 x 915/5/12 across locations. The progenies of crosses SB-19 x SB-98, Nyala x SB-19 and Nyala x SB-98 were the lowest yielding among F_1 genotypes. F_1 progenies had higher yields at Embu, 1,035.9 kg ha^{-1} compared to 995.06 kg ha^{-1} at Mwea (Table 4.3).

Table 4.2 : Mean squares for days to flowering, maturity, plant height, pod shattering and grain yield of 28 F_1 progenies and their parents grown at Embu and Mwea Research stations during the 2016-2017 short rain season

Source	**Df**	**Days to 50% flowering**	**Days to 75% maturity**	**Plant height (cm)**	**Shattering (%)**	**Grain yield (kg ha^{-1})**
Replicates	2	54.8	47.9	121.8	13.8	541603
Genotypes (G)	35	136.7*	409.7*	342.8*	1311.6*	1170881*
Locations (L)	1	1467.5*	28.2^{ns}	14.4^{ns}	287.1^{ns}	37541^{ns}
G x L	35	37.9*	17.8^{ns}	6.7^{ns}	79.7*	86821^{ns}
Error	142	10.1	11.1	18.3	32	122123

* Indicates significant difference at P<0.001, ns – non significant difference

Table 4.3 : Performance for days to flowering, maturity, plant height and grain yield of 28 F_1 progenies and their parents grown at Embu and Mwea Research stations during the 2016-2017 short rain season

	Days to 50% flowering		Sites	Days to 75% maturity		Sites	Plant height (cm)		Sites	Grain yield (kg ha^{-1})		Sites
Genotype	**Embu**	**Mwea**	**mean**	**Embu**	**Mwea**	**mean**	**Embu**	**Mwea**	**mean**	**Embu**	**Mwea**	**mean**
Parents												
835/5/30	63.0	68.0	65.5	97.0	106.0	101.5	32.5	34.0	33.2	2223.6	2028.7	2126.1
915/5/12	58.0	65.0	61.5	109.0	108.0	108.5	27.8	24.8	26.3	775.5	772.9	774.2
Nyala	49.0	58.0	53.5	101.0	104.0	102.5	27.3	27.7	27.5	584.0	627	605.5
SB-19	61.0	65.0	63.0	99.0	99.0	99.0	20.7	24.7	22.7	1395.1	1034.1	1214.6
SB-25	72.0	74.0	73.0	130.0	125.0	127.5	49.3	49.8	49.5	878.2	1081.2	979.7
SB-8	68.0	70.0	69.0	118.0	124.0	121.0	50.3	50.7	50.5	1483.2	1236.1	1359.6
SB-93	62.0	61.0	61.5	95.0	97.0	96.0	27.0	24.3	25.6	1480.8	1845.8	1663.3
SB-98	52.0	51.0	51.5	103.0	99.0	101.0	29.8	31.3	30.5	959.5	1347.8	1153.6
Parental mean	60.6	64.0	62.3	106.5	107.8	107.1	33.1	33.4	33.2	1222.5	1246.7	1234.6
Progenies												
835/5/30 x 915/5/12	60.0	68.0	64.0	105.0	105.0	105.0	36.2	31.5	33.8	1917.3	1683.3	1800.3
835/5/30 x Nyala	62.0	72.0	67.0	102.0	106.0	104.0	24.7	25.2	24.9	613.5	700.4	656.9
835/5/30 x SB-19	66.0	63.0	64.5	94.0	102.0	98.0	26.0	26.2	26.1	1024.5	953.6	989.0
835/5/30 x SB-25	63.0	59.0	61.0	115.0	114.0	114.5	33.8	38.3	36.0	746.4	768.4	757.4
835/5/30 x SB-8	66.0	65.0	65.5	109.0	113.0	111.0	34.3	36.3	35.3	1425.6	1322	1373.8
835/5/30 x SB-93	60.0	69.0	64.5	96.0	98.0	97.0	30.5	28.0	29.2	862.5	1007.8	935.1
835/5/30 x SB-98	57.0	69.0	63.0	99.0	101.0	100.0	30.3	29.7	30.0	1029.3	1165.8	1097.5
915/5/12 x Nyala	57.0	69.0	63.0	109.0	104.0	106.5	23.0	25.8	24.4	576.4	657.7	617.0
915/5/12 x SB-19	60.0	63.0	61.5	104.0	104.0	104.0	19.0	21.2	20.1	1763.7	1349.6	1556.6
915/5/12 x SB-25	72.0	68.0	70.0	116.0	116.0	116.0	39.3	37.8	38.5	1122.3	1036.7	1079.5
915/5/12 x SB-8	55.0	65.0	60.0	116.0	115.0	115.5	31.5	33.3	32.4	1811.4	2001.9	1906.6
915/5/12 x SB-93	61.0	64.0	62.5	105.0	100.0	102.5	25.3	27.0	26.1	707.3	655.3	681.3
915/5/12 x SB-98	54.0	65.0	59.5	107.0	103.0	105.0	27.5	28.8	28.1	775.2	770.8	773.0
Nyala x SB-19	56.0	70.0	63.0	100.0	103.0	101.5	24.5	24.5	24.5	597.6	559.7	578.6
Nyala x SB-25	68.0	70.0	69.0	114.0	115.0	114.5	43.5	41.8	42.6	631.3	914.6	772.9
Nyala x SB-8	66.0	69.0	67.5	109.0	114.0	111.5	36.0	37.0	36.5	880.9	1379	1129.9
Nyala x SB-93	56.0	61.0	58.5	97.0	101.0	99.0	27.5	26.8	27.1	1397.9	968.5	1183.2
Nyala x SB-98	48.0	64.0	56.0	101.0	101.0	101.0	21.2	24.8	23.0	500.4	590.7	545.5
SB-19 x SB-25	66.0	71.0	68.5	118.0	113.0	115.5	31.3	33.2	32.2	980.7	725.0	852.8
SB-19 x SB-8	64.0	66.0	65.0	111.0	111.0	111.0	33.7	32.2	32.9	798.8	748.1	773.4
SB-19 x SB-93	54.0	62.0	58.0	96.0	97.0	96.5	28.8	26.7	27.7	1277.4	891	1084.2
SB-19 x SB-98	61.0	68.0	64.5	99.0	99.0	99.0	21.5	23.3	22.4	337.9	509.1	423.5
SB-25 x SB-8	70.0	75.0	72.5	128.0	125.0	126.5	46.7	49.2	47.9	2011.7	2217.1	2114.4
SB-25 x SB-93	67.0	71.0	69.0	107.0	112.0	109.5	38.3	37.3	37.8	1460.4	999.9	1230.1
SB-25 x SB-98	64.0	68.0	66.0	114.0	113.0	113.5	39.5	38.5	39.0	1330.8	1106.1	1218.4
SB-8 x SB-93	66.0	70.0	68.0	108.0	111.0	109.5	32.5	34.0	33.2	1048.8	817.8	933.3
SB-8 x SB-98	58.0	69.0	63.5	110.0	112.0	111.0	30.3	33.0	31.6	670.2	552.7	611.4
SB-93 x SB-98	57.0	66.0	61.5	98.0	98.0	98.0	28.8	30.3	29.5	704.5	809.0	756.7
Progenies mean	61.2	67.1	64.2	106.7	107.4	107.0	30.9	31.5	31.2	1035.9	995	1015.4
Mean	61.1	66.4	63.7	106.6	107.4	107.0	31.4	31.9	31.6	1077.3	1050.9	1064.1
$LSD_{0.05}$	4.7	5.4	3.6	5.3	5.7	3.8	8.4	5.2	4.8	675.6	434.6	398.8
CV (%)	4.7	5.0	5.0	3.0	3.2	3.1	16.5	10.0	13.5	38.5	25.4	32.8

LSD – least significant difference, CV – coefficient of variation

Table 4.4 : Pod shattering of 28 F_1 progenies and their parents grown at Embu and Mwea Research stations during the 2016-2017 short rain season

Site	Embu			Mwea			Sites mean		
Genotype	**Pod shattering (%)**	**Score**	**Reaction type**	**Pod shattering (%)**	**Score**	**Reaction type**	**Shattering (%)**	**Shattering Score**	**Reaction type**
Parents									
835/5/30	15.1	3	MR	15.9	3	MR	15.5	3	MR
915/5/12	6.7	2	R	26.6	4	MS	16.6	3	MR
Nyala	**4.3**	**2**	**R**	**14.5**	**3**	**MR**	**9.4**	**2**	**R**
SB-19	23.4	3	MR	11.8	3	MR	17.6	3	MR
SB-25	59.8	5	HS	51.1	5	HS	55.4	5	HS
SB-8	**4.5**	**2**	**R**	**1**	**2**	**R**	**2.8**	**2**	**R**
SB-93	52.9	5	HS	60.4	5	HS	56.7	5	HS
SB-98	19	3	MR	16.4	3	MR	17.7	3	MR
Parental mean	23.2	3	MR	24.7	3	MR	23.9	3	MR
Progenies									
835/5/30 x 915/5/12	10.6	2	R	22.1	3	MR	16.4	3	MR
835/5/30 x Nyala	**9.5**	**2**	**R**	**12.3**	**3**	**MR**	**10.9**	**2**	**R**
835/5/30 x SB-19	19.	3	MR	14.2	3	MR	16.6	3	MR
835/5/30 x SB-25	38.4	4	MS	34.5	4	MS	36.5	4	MS
835/5/30 x SB-8	**12.5**	**3**	**MR**	**8.2**	**2**	**R**	**10.4**	**2**	**R**
835/5/30 x SB-93	32.9	4	MS	39.8	4	MS	36.4	4	MS
835/5/30 x SB-98	18.5	3	MR	16.5	3	MR	17.5	3	MR
915/5/12 x Nyala	**3.3**	**2**	**R**	**17.9**	**3**	**MR**	**10.6**	**2**	**R**
915/5/12 x SB-19	17	3	MR	19.8	3	MR	18.4	3	MR
915/5/12 x SB-25	34.7	4	MS	39.8	4	MS	37.3	4	MS
915/5/12 x SB-8	10.6	2	R	11.5	3	MR	11	3	MR
915/5/12 x SB-93	30.7	4	MS	50.3	5	HS	40.5	4	MS
915/5/12 x SB-98	12.9	3	MR	18.7	3	MR	15.8	3	MR
Nyala x SB-19	16.3	3	MR	9.9	2	R	13.1	3	MR
Nyala x SB-25	33.6	4	MS	35.7	4	MS	34.6	4	MS
Nyala x SB-8	**7.7**	**2**	**R**	**10.3**	**2**	**R**	**9**	**2**	**R**
Nyala x SB-93	29.6	4	MS	35.8	4	MS	32.7	4	MS
Nyala x SB-98	11.7	3	MR	16.8	3	MR	14.2	3	MR
SB-19 x SB-25	42.5	4	MS	37.8	4	MS	40.2	4	MS
SB-19 x SB-8	9.8	2	R	15.6	3	MR	12.7	3	MR
SB-19 x SB-93	36.1	4	MS	37.6	4	MS	36.8	4	MS
SB-19 x SB-98	21.2	3	MR	16.9	3	MR	19.1	3	MR
SB-25 x SB-8	20.7	3	MR	23.1	3	MR	21.9	3	MR
SB-25 x SB-93	56.5	5	HS	64.4	5	HS	60.4	5	HS
SB-25 x SB-98	37.4	4	MS	34.5	4	MS	35.9	4	MS
SB-8 x SB-93	29.7	4	MS	29.3	4	MS	29.5	4	MS
SB-8 x SB-98	14.5	3	MR	8.7	2	R	11.6	3	MR
SB-93 x SB-98	32.7	4	MS	39.7	4	MS	36.2	4	MS
Progenies mean	23.2	3	MR	25.7	3	MR	24.5	3	MR
Mean	23.23	-	-	25.54	-	-	24.38	-	-
$LSD_{0.05}$	7.104	-	-	10.62	-	-	6.461	-	-
CV	18.8	-	-	25.5	-	-	23.2	-	-

LSD – least significant difference, CV – coefficient of variation

Score of 1=0% shattering, 2=1-10%shattering, 3=11-25% shattering, 4=26-50% and 5=>50% shattering (AVRDC, 1979). Phenotypic description; Reaction type of score 1=very resistant (VR), 2=resistant (R), 3=moderately resistant (MR), 4=moderately susceptible (MS) and 5=highly susceptible (HS).

4.4.2. General and specific combining ability

General combining ability effects (GCA) were significant for days to 50 % flowering. No significant interactions between GCA and environments (P<0.01) were observed (Table 4.5). Parents with significant negative GCA effects can be used to improve early flowering. Among the parental genotypes, only SB-98 exhibited highly significant (P<0.01) negative GCA effects for days to flowering in both environments. Line 915/5/12 and Nyala had inconsistent GCA effects in the two environments. They had significant negative GCA effects at Embu but not significant at Mwea. SB-25 followed by SB-8 had the relative positive GCA effects in both environments (Table 4.6). Significant variations were also observed for SCA effects (P<0.01). There were significant interactions between SCA estimates and environments (P<0.05) (Table 4.5). Desirable F_1 progenies had negative significant SCA estimates and can be used for heterosis breeding for early flowering. Among F_1 progenies, only the cross 835/5/30 x SB-25 had significant negative SCA effects in both environments. Crosses 835/5/30 x SB-19, 835/5/30 x SB-8 and Nyala x SB-98 had inconsistent SCA effects. They had negative significant SCA effects in one location but positive SCA effect in another. Crosses 835/5/30 x Nyala and SB-19 x SB-8 had significant positive SCA effects (Table 4.7). There were significant interactions between SCA and environments (P<0.01) (Table 4.5). GCA/SCA ratio for duration to flowering was low and close to zero (Table 4.5).

General combining ability effects were highly significant for 75% maturity among genotypes (P<0.01). There were significant interactions between GCA and environments (P<0.01) (Table 4.5). Desirable parental lines were associated with significant negative GCA effects of days to maturity as they can be used to improve early maturity. Among parental genotypes, SB-93, SB-19, SB-98, 835/5/30 and Nyala exhibited significant negative GCA effects in both environments. SB-25 followed by SB-8 had the relative positive GCA estimates in each of environments (Table 4.6). There were significant variations in terms of SCA effects (P<0.01) (Table 4.5). Significant interactions between SCA and environments were also observed (P<0.01) (Table 4.5). Crosses with significant negative SCA estimates were desirable because they represent early maturing genotypes. Among F_1 progenies, none of crosses had significant SCA effects at Mwea. In contrast, 835/5/30 x SB-98, 915/5/12 x SB-25 and SB-19 x SB-93 had negative SCA effects in both sites but significant only at Embu but insignificant at Mwea. Progenies SB-19 x SB-25 and SB-25 x SB-8 had significant positive SCA effects at Embu (Table 4.7). GCA/SCA ratio was close to zero (Table 4.5).

Table 4.5 : General and specific combining ability mean squares for flowering, maturity, plant height, pod shattering and grain yield at Embu and Mwea Research stations

Source	Df	Days to 50% flowering	Days to 75% maturity	Plant height (cm)	Pod shattering (%)	Grain yield (kg ha^{-1})
GCA	7	130.7**	309.85**	251.25**	1124.6**	335323.8**
SCA	28	88920.9**	250168.9**	21830.1**	12909.1**	24725198.6**
GCA x Environments	7	1.276^{ns}	161.78**	250.88**	1073.84**	318529.51**
SCA x Environments	28	85429.8**	239466.6**	21826.3**	12882.81*	24712432.0**
Error	142	1.68	1.86	3.04	5.34	20353.8
GCA/SCA ratio	-	0.00147	0.00124	0.01125	0.0742	0.0132

***Significant at P<0.001, **Significant at P<0.01, *Significant at P<0.05 and ns is not significant

There were significant GCA effects for plant height (P<0.01). Interactions between GCA estimates and environments were also significant (P<0.01) (Table 4.5). Parental lines with significant negative GCA values were the desirable as they represent alleles that contribute to reduced plant height and therefore shorter plants. All the parental lines exhibited significant negative GCA effects for plant height at both sites except SB-25 and SB-8 which had significant positive GCA estimates (P<0.001) (Table 4.6). Plant height showed significant variations among SCA effects (P<0.01). Significant interactions were observed between SCA and environments (P<0.01) (Table 4.5). Hybrids with negative significant SCA effects were the desirable as they contributed towards reduced plant height. Only a few F_1 progenies had significant SCA effects in both sites. Crosses Nyala x SB-98 and SB-8 x SB-98 exhibited significant negative SCA effects (P<0.05). The cross 835/5/30 x SB-25 exhibited negative SCA effects across sites, the effect being significant only at KALRO-Embu (P<0.05). Crosses 835/5/30 x 915/5/12 and Nyala x SB-25 had significant positive SCA effects (P<0.05) (Table 4.7). GCA/SCA ratio was low and close to zero (Table 4.5).

General combining ability effects for pod shattering were highly significant (P<0.01). Significant interactions were observed between GCA and environments (P<0.05) (Table 4.5). Based on the AVRDC scale used in this study, high, positive values for the GCA effect imply that the genotype would enhance shattering when used in breeding program, while negative significant GCA values were desirable for pod shattering. GCA effects for pod shattering ranged from -10.79 to 16.64 across environments. Among parents, SB-8 and Nyala exhibited highly significant (P<0.05) negative GCA effects for pod shattering across both environments. Therefore, they can be used to improve resistance to pod shattering. Parents 915/5/12, SB-19, 835/5/30 and SB-98 also had negative GCA values but they were not

significant across environments. Parents SB-93 and SB-25 on the other hand, had significant positive GCA values across environments. However some other genotypes had inconsistent GCA values in the two environments. For instance, genotype 915/5/12 had significant and negative GCA effects for pod shattering at Embu while the effects were positive at Mwea. Similarly, genotype SB-19 had positive GCA estimates at Embu and negative GCA values at Mwea (Table 4.8). SCA effects for pod shattering were highly significant ($P<0.01$). Interactions between SCA effects and environments were also significant ($P<0.01$) (Table 4.5). SCA effects for pod shattering ranged from -7.54 to 3.6 across environments. Generally, only a few F_1 progenies had significant SCA effects in both sites. Only the F_1 progenies of the cross SB-25 x SB-8 had significant negative SCA effects across environments. At Mwea none of the crosses had significant negative SCA effects (Table 4.9). At Embu, F_1 progenies of crosses SB-25 x SB-8, SB-19 x SB-8 and 915/5/12 x Nyala had significant negative SCA effects and can be used in heterosis breeding for reduced shattering. In contrast, progenies of crosses SB-8 x SB-98, Nyala x SB-8, 835/5/30 x SB-8, Nyala x SB-19, SB-19 x SB-25 and Nyala x SB-25 had significant positive SCA effects (Table 4.9). GCA/SCA ratio was less than 1 and close to zero (Table 4.5).

There were significant GCA effects for grain yield at $P<0.01$. Significant interactions between GCA and environments were observed ($P<0.01$) (Table 4.5). Positive significant GCA estimates were desirable for improving grain yield. Among parental lines, only genotype 835/5/30 exhibited significant positive GCA effects in both sites ($P<0.05$). Therefore, this genotype can be used in a breeding program to improve soybean grain yield. However, SB-8 had inconsistent GCA effect for this trait at $P<0.05$. It had positive significant GCA effects at Mwea, but not significant at Embu. Parent Nyala, the commercial local genotype and SB-98 had significant negative GCA effects in both sites ($P<0.05$) (Table 4.6). Significant variations were also observed among SCA effects ($P<0.01$) (Table 4.5). There were significant interactions between SCA and environments ($P<0.01$) (Table 4.5). Desirable F_1 crosses had positive significant SCA estimates as they contributed towards increased grain yield. Among F_1 progenies, crosses 915/5/12 x SB-19, 835/5/30 x 915/5/12, 915/5/12 x SB-8 and SB-25 x SB-8 exhibited significant positive SCA effects ($P<0.05$) in both sites. In contrast, Nyala x SB-8 had inconsistent results. SCA effect was significant and positive at Mwea ($P<0.05$) while at Embu it was significant but negative (Table 4.7). Crosses Nyala x SB-93 and SB-25 x SB-98 had significant positive SCA effects ($P<0.05$) at Embu but not significant at Mwea. However, 835/5/30 x SB-93, 915/5/12 x SB-93, SB-19 x SB-8 and SB-19 x SB-98 exhibited

significant negative SCA effects in both environments (P<0.05) (Table 4.7). GCA/SCA ratio was close to zero (Table 4.5).

Table 4.6 : General combining ability effects for flowering, maturity, plant height and grain yield of eight parents grown at Embu and Mwea Research stations during the 2016-2017 short rain season

	Days to 50% flowering		Days to 75% maturity		Plant height		Grain yield	
Parents	**Embu**	**Mwea**	**Embu**	**Mwea**	**Embu**	**Mwea**	**Embu**	**Mwea**
835/5/30	0.97*	0.38	-4.63***	-1.58*	-0.18	-0.41	237.01*	219.98***
915/5/12	-1.43**	-0.23	1.97**	-0.38	-2.51*	-3.23***	52.86	24.22
Nyala	-3.93***	-0.63	-2.63**	-1.48*	-2.76**	-2.59***	-333.01*	-243.4***
SB-19	-0.13	-0.43	-4.03***	-3.98***	-5.64***	-5.07***	-12.54	-165.46***
SB-25	6.37***	3.28**	11.17***	9.12***	8.85***	8.86***	34.39	47.16
SB-8	3.17***	2.28***	6.67***	8.22***	6.3***	6.9***	191.76	205.19***
SB-93	-0.53	-1.23	-6.33***	-5.58***	-1.68*	-2.84***	72.4	38.21
SB-98	-4.73***	-2.63**	-2.63**	-4.18***	-2.39*	-1.61*	-242.89*	-125.89*

***Significant at P<0.001, **Significant at P<0.01, and *Significant at P<0.05

Table 4.7 : Specific combining ability effects for flowering, maturity, plant height and grain yield of 28 F_1 progenies grown at Embu and Mwea Research stations during the 2016-2017 short rain season

	Days to 50% flowering		Days to 75% maturity		Plant height		Grain yield	
Crosses	**Embu**	**Mwea**	**Embu**	**Mwea**	**Embu**	**Mwea**	**Embu**	**Mwea**
835/5/30 x 915/5/12	-0.68	1.49	0.96	-0.46	7.46**	3.23*	550.12**	388.12**
835/5/30 x Nyala	3.82**	5.82**	2.56	1.64	-3.79	-3.75*	-367.89	-327.13*
835/5/30 x SB-19	4.02**	-3.31*	-4.04*	0.14	0.42	-0.27	-277.34	-151.96
835/5/30 x SB-25	-5.48***	-11.01***	1.76	-0.96	-6.25*	-2.04	-602.3**	-549.7***
835/5/30 x SB-8	0.72	-4.01*	0.26	-1.06	-3.19	-2.08	-80.5	-154.17
835/5/30 x SB-93	-1.58	3.49*	0.26	-2.26	0.95	-0.66	-524.28*	-301.41*
835/5/30 x SB-98	-0.38	4.49**	-0.44**	-0.66	1.49	-0.23	-42.17	20.73
915/5/12 x Nyala	1.22	3.49*	2.96*	-1.56	-3.13	-0.26	-220.76	-174.1
915/5/12 x SB-19	0.42	-2.71	-0.64	0.94	-4.24	-2.44	646.00**	439.82**
915/5/12 x SB-25	5.92***	-1.41	-3.84*	-0.16	1.58	0.29	-42.29	-85.63
915/5/12 x SB-8	-6.88***	-2.41	0.66	-0.26	-3.68	-2.33	489.56*	721.49***
915/5/12 x SB-93	1.82	-0.9	2.66	-1.46	-1.88	1.16	-495.29*	-458.14**
915/5/12 x SB-98	-0.98	1.49	0.96	0.14	0.99	1.76	-112.13	-178.46
Nyala x SB-19	-1.08	4.68**	-0.04	1.04	1.5	0.25	-134.16	-82.46
Nyala x SB-25	4.42**	0.99	-1.24	-0.06	6.0*	3.65*	-147.48	59.9
Nyala x SB-8	5.62***	0.99	-1.74	-0.16	1.06	0.77	-55.27*	366.25**
Nyala x SB-93	-0.68	-3.51*	-0.74	0.64	0.54	0.35	581.16**	122.75
Nyala x SB-98	-4.48**	0.89	-0.74	-0.76	-5.08*	-2.88*	-1.08	-90.94
SB-19 x SB-25	-1.38	1.79	4.16*	0.44	-3.28	-2.53	-118.52	-207.65
SB-19 x SB-8	-0.18	-2.21	1.66	-0.66	1.61	-1.57	-457.72*	-342.62*
SB-19 x SB-93	-6.48***	-2.71	-0.34*	-0.86	4.75*	2.67	140.16	-32.7
SB-19 x SB-98	4.72**	4.69**	-1.04	-0.26	-1.87	-1.9	-483.99*	-250.56*
SB-25 x SB-8	-0.68	3.09*	3.46*	0.24	0.12	1.49	708.18**	913.8***
SB-25 x SB-93	0.02	2.59	-4.54**	1.04	-0.25	-0.6	276.27	-136.42
SB-25 x SB-98	1.22	0.99	-1.24	0.64	1.63	-0.66	461.95*	133.89
SB-8 x SB-93	2.22	2.59	0.96	0.94	-3.52	-1.97	-292.74	-476.6***
SB-8 x SB-98	-1.58	2.99*	-0.74	0.54	-5.06*	-4.21**	-356.05	-577.6***
SB-93 x SB-98	1.12	3.49*	0.26	0.34	1.49	2.87*	-202.4	-154.3

***Significant at P<0.001, **Significant at P<0.01, and *Significant at P<0.05

Table 4.8 : General combining ability effects for pod shattering of eight parents grown at Embu and Mwea Research stations during the 2016-2017 short rain season

Parents	Embu	Mwea	Across environments
835/5/30	-3.74***	-5.03**	-4.38
915/5/12	-7.59***	0.35	-3.62
Nyala	-8.87***	-6.23***	-7.55*
SB-19	0.02	-5.44***	-2.71
SB-25	17.41***	14.22***	15.81**
SB-8	-9.46***	-12.13***	-10.79*
SB-93	14.50***	18.79***	16.64**
SB-98	-2.23*	-4.52**	-3.38

***Significant at P<0.001, **Significant at P<0.01, and *Significant at P<0.05

Table 4.9 : Specific combining ability effects for pod shattering of 28 F_1 progenies grown at Embu and Mwea Research stations during the 2016-2017 short rain season

Crosses	Cross type	KALRO-Embu	KALRO-Mwea	Across Env.
835/5/30 x 915/5/12	MR X MR	-1.26	1.29	0.02
835/5/30 x Nyala	MR X MR	-1.14	-1.98	-1.56
835/5/30 x SB-19	MR X MR	-0.44	-0.86	-0.65
835/5/30 x SB-25	MR X HS	1.48	-0.19	0.65
835/5/30 x SB-8	MR X R	2.50**	-0.22	1.14
835/5/30 x SB-93	MR X HS	-1.06	0.52	-0.27
835/5/30 x SB-98	MR X MR	1.21	0.53	0.87
915/5/12 x Nyala	MR X MR	-3.51***	-1.77	-2.64
915/5/12 x SB-19	MR X MR	1.43	-0.66	0.39
915/5/12 x SB-25	MR X HS	1.63	-0.27	0.68
915/5/12 x SB-8	MR X R	4.42***	-2.28	1.07
915/5/12 x SB-93	MR X HS	0.58	5.67	3.13
915/5/12 x SB-98	MR X MR	-0.53	-2.70	-1.62
Nyala x SB-19	MR X MR	1.97*	-3.96	-0.99
Nyala x SB-25	MR X HS	1.81*	2.18	1.99
Nyala x SB-8	MR X R	2.82**	3.13	2.98
Nyala x SB-93	MR X MR	0.76	-2.30	-0.77
Nyala x SB-98	MR X MR	-0.41	1.98	0.79
SB-19 x SB-25	MR X HS	1.88*	3.53	2.71
SB-19 x SB-8	MR X R	-3.94***	7.60*	1.83
SB-19 x SB-93	MR X HS	-1.60	-1.29	-1.45
SB-19 x SB-98	MR X MR	0.23	1.34	0.79
SB-25 x SB-8	HS X MR	-10.51***	-4.56	-7.54**
SB-25 x SB-93	HS X HS	1.31	5.83*	3.60
SB-25 x SB-98	HS X MR	-1.04	-0.75	-0.90
SB-8 x SB-93	R X HS	1.43	-2.95	-0.76
SB-8 x SB-98	R X MR	2.91**	-0.15	1.38
SB-93 x SB-98	HS X MR	-2.81	-0.11	-1.46

***Significant at P<0.001, **Significant at P<0.01, and *Significant at P<0.05

Table 4. 10 : High-parent heterosis (%) of days to 50% flowering, days to 75% maturity, plant height, pod shattering and grain yield of 28 F_1 progenies grown at Embu and Mwea Research stations during the 2016-2017 short rain season

Crosses	Days to 50% flowering	Days to 750 maturity	Plant height	Pod shattering	Grain yield
835/5/30 x 915/5/12	-2.3	-3.2	0.3	-1.2	-15.3
835/5/30 x Nyala	2.3	1.4	-25.0	-34.3	-69.1
835/5/30 x SB-19	-1.5	-3.4	-21.4	-5.7	-53.5
835/5/30 x SB-25	-16.4	-10.2	-27.2	-34.1	-64.3
835/5/30 x SB-8	-5.0	-8.2	-29.7	-32.9	-35.4
835/5/30 x SB-93	-1.5	-4.4	-12.0	-35.8	-56.0
835/5/30 x SB-98	-3.8	-1.5	-9.6	-1.1	-48.3
915/5/12 x Nyala	-2.4	-1.8	-11.2	-36.1	-20.3
915/5/12 x SB-19	-2.3	-4.1	-23.5	4.5	28.1
915/5/12 x SB-25	-4.1	-8.6	-22.2	-32.6	10.2
915/5/12 x SB-8	-13.0	-4.5	-35.8	-33.7	40.2
915/5/12 x SB-93	1.6	-5.5	-0.7	-28.5	-59.0
915/5/12 x SB-98	-3.2	-3.2	-7.8	-10.7	-33.0
Nyala x SB-19	0.0	-0.7	-10.9	-25.5	-52.3
Nyala x SB-25	-5.4	-10.2	-13.9	-37.5	-21.1
Nyala x SB-8	-2.1	-7.8	-27.7	-4.2	-16.8
Nyala x SB-93	-4.1	-3.4	-1.4	-42.3	-28.8
Nyala x SB-98	4.6	-1.4	-24.6	-19.7	-52.7
SB-19 x SB-25	-6.1	-9.8	-34.9	-27.4	-29.8
SB-19 x SB-8	-5.8	-8.2	-34.8	-27.8	-43.1
SB-19 x SB-93	-7.9	-2.7	8.2	-35.1	-34.8
SB-19 x SB-98	2.4	-1.9	-26.5	7.9	-65.1
SB-25 x SB-8	-0.9	-0.8	-5.1	-60.4	-55.5
SB-25 x SB-93	-5.4	-14.1	-23.6	6.5	-26.0
SB-25 x SB-98	-9.5	-10.9	-21.2	-35.2	-5.6
SB-8 x SB-93	-1.4	-9.5	-34.2	-47.9	-43.9
SB-8 x SB-98	0.0	-8.2	-37.4	-34.4	-55.0
SB-93 x SB-98	-4.3	-2.9	-3.2	-36.1	-54.5
Mean	-3.5	-5.3	-18.4	-25.0	-34.3

4.5. Discussion

4.5.1. Performance of study genotypes

Significant variations were found among locations and among genotypes in terms of days to 50% flowering. These findings suggested the influence of genetic and environmental factors in expression of days to flowering. Genetic variability for duration to flowering in soybean genotypes has been reported by several authors. Painkra (2014) ; Maphosa *et al.* (2012) reported genetic variability in the genotypes they studied. However, Sharma (2004) found no variability among his test genotypes for duration to flowering. In the present study, duration to flowering varied between parents and their F_1 progenies. On average, the parental lines

flowered two days earlier than F_1 progenies. Parental genotypes took about 62 days to reach 50% flowering while F_1 genotypes took 64 days. The results are in agreement with Mohammed (2010) who also found that parental lines flowered earlier than their F_1 progenies. However, Sharma (2004) reported that F_1 and F_2 progenies had shorter duration to flowering compared to their parents. These observations suggest that duration to flowering of progenies depends on whether parents transmitted genes that conferred earliness or lateness.

Days to 75% maturity varied significantly among genotypes suggesting that parents and F_1 progenies were genetically diverse. Parental lines, matured from the 96^{th} day from the sowing to the 127^{th} day while most of progenies were the medium maturing (between 100 and 115 days) and some were late maturing (beyond 115 days). These results were in agreement with those reported by Painkra (2014), but contradictory to those of Wanderi (2012) who found no significant differences among genotypes. Mohammed (2010) also found no difference for number of days to 75% maturity between parents and their F_1 progenies. These differences might be due to specific genetic make-up of genotypes. In contrast, Sharma (2004) reported that the F_1 progenies had shorter duration to maturity compared to their parents. This could be attributed to the vigor associated with progenies that combine alleles for earliness from their parents.

Plant height varied significantly among genotypes suggesting genetic diversity of parents and progenies. Parental genotypes were generally taller (33.3 cm) compared to their F_1 progenies (31.2 cm). These findings were in agreement with Sharma (2004); Wanderi (2012); Karyawati *et al.* (2015) but were not in agreement with Gavioli *et al.* (2006) who found progenies to be more taller than parents. Genes that control the plant height in parents could be recessive. The findings were also in agreement with Mohammed (2010), but were not consistent to those of Sharma and Sharma (1988) who showed that F_1 and F_2 genotypes were taller than their parents. This could be due to a good genetic combination of alleles in progenies.

Significant differences found among genotypes for pod shattering suggested the presence of genetic variability for this trait. Furthermore, there were significant differences in pod shattering between parents and F_1 progenies. Among parental genotypes, pod shattering varied from 2.8% with parent SB-8 to 56.7% with SB-93 with a mean of 24%. Among progenies it ranged from 9% with cross Nyala x SB-8 to 60.4% with SB-25 x SB-93 with a mean of 24.5%. This variability indicated the possibility of developing varieties that are more resistant to pod shattering. These findings are consistent with those of Tsuchiya (1987) ;

Mohammed (2010). They showed that the mean percentage of shattering of F_1 progenies in all crosses was equal to or higher than the mean of the parents and closer to the susceptible parents than the resistant, suggesting that genes for susceptibility are showing some dominance over resistance. Caviness (1969) and Tukamuhabwa *el al.* (2000) suggested that the average pod shattering in F_1 progeny of a self-pollinated crop such as soybean is expected to equal or intermediate exactly the average of its parents. In contrast, Tiwari and Bhatnagar (1992) found that in some crosses susceptibility to pod shattering was dominant, while in others it showed partial dominance.

Grain yield varied significantly among genotypes suggesting a significant genetic variability among the parents and their progenies. The grain yield of the parents was higher and varied from 605.5 kg ha^{-1} with Nyala to 2,126.1 kg ha^{-1} with 835/5/30 with an average of 1,234.6 kg ha^{-1}. In contrast, the grain yield of F_1 progenies varied from 423.5 kg ha^{-1} with cross SB-19 x SB-98 to 1,906.7 kg ha^{-1} with cross 915/5/12 x SB-8 with a mean of 1,015.5 kg ha^{-1}. These findings are consistent to Wanderi (2012) who found that parental genotypes performed better than progenies across locations, KALRO-Embu and KALRO-Mwea during her experiments carried during the 2012 long rain cropping season using eight parents and F_2 population generated from 28 F_1 progenies. Contradictory results were supported by Sharma (2004) and Mohamed (2010) who found no significant variations for grain yield among genotypes. Grain yield of soybean varies with genotypes, production environment and crop management as reported by Wycliffe (2015).

4.5.2. General and specific combining ability

Significant GCA and SCA effects found in number of days to 50% flowering indicated that both additive and non-additive gene action were important determinants of duration to flowering in soybean genotypes studied. These results were in agreement with Agrawal *et al.* (2005) whose reported significant GCA and SCA effects on 5 soybean parents and 10 single crosses at University of Agricultural Sciences, Oharwad (Karnataka). The results were also in agreement with Wanderi (2012) who found importance of additive and non-additive gene action controlling flowering during the 2012 long rain evaluation under field conditions of 8 parents and F_2 population from 28 F_1 progenies generated from a half diallel at KALRO-Embu and KALRO-Mwea. Additive gene action for days to 50% flowering in soybeans also was reported by Tawar *et al.* (1989) and Halvankar and Patil (1993) while non-additive gene action was suggested by Bernard (1972) and Sneller, *et al.* (2005).

GCA/SCA ratio was found close to zero indicating the preponderance of non-additive over additive gene action. These results were consistent with those of Srivastava and Jain (1994), Choukan (1996), Bonato and Vello (1999), Sharma (2004), Sher, *et al.* (2012) and Karyawati *et al.* (2015) who also reported that non-additive gene effects were more important in control of duration to flowering in soybean and partly contradictory to those found by Agrawal *et al.* (2005), Gavioli *et al.* (2006), Shiv *et al.* (2011) and Wanderi (2012). Higher magnitude of additive effects was particularly noted by Cruz *et al.* (1987), Toledo *et al.* (1994) and Rahangdale and Raut (2002). Moro (1993) cited by Toledo *et al.* (1994) also reported that additive effects were more important for duration to flowering but there was no dominance or utmost some slight partial dominance influencing this trait. The highly significant SCA x environment mean squares suggested significant levels of interactions and instability of non-additive effects across the environments.

Ludlow and Muchow (1990) suggested that short duration varieties ensure better and stable yields under rain fed conditions. Based on this consideration Bhatnagar (1994) recognized the value of incorporating early flowering in tropical soybean varieties. Parent SB-98 was found the best general combiner for early flowering. In general, early flowering did not result in significant high yield increase as suggested by Ludlow and Muchow (1990) except for some progenies such as 915/5/12 x SB-8. Progeny from SB-19 X SB-93 and 835/5/30 X SB-98 showed inconsistent trends. These results are consistent to those of Wang *et al.* (2001) who showed that earliness may adversely affect podding or seed development and bring down yield levels by limiting dry matter production. However, this drawback in early maturing genotypes could overcome to some extent in soybean by increasing seed filling duration and selecting for relatively high grain yield.

Significant environmental interactions with GCA and SCA in terms of days to 75% maturity indicated lack of stability of additive or non-additive gene action making selection for early maturation difficult throughout a range of environments as reported by Tukamuhabwa *et al*. (2002b). The highly significant GCA and SCA for duration to 75 % maturity suggested that both the additive and non-additive gene action was important in determination of this trait. Similar results were reported by Srivastava *et al.* (1978) ; Limproongratna and Maneephong (1979) ; Agrawal *et al.* (2005) ; Gavioli *et al.* (2006) ; Tukamuhabwa *et al.* (2002b) and Sher *et al.* (2012). GCA/SCA ratio close to zero suggested that non-additive gene action played a bigger role than additive gene action. These results are in line with those found by Gadag *et al.* (1999), Sharma (2004) ; Sher, *et al.* (2012). In contrast, Wanderi (2012) found that only

the additive gene effects were important in the inheritance of the trait. Rahangdale and Raut (2002) and Gravioli *et al.* (2006) also noted the preponderance of additive over dominance gene effects.

Ludlow and Muchow (1990) reported that varieties with short term maturation compared to long term maturation ensure better and stable yields under a range of environments through avoidance of drought or low water available. These genotypes are easy to adapt in diverse cropping systems. Bhatnagar (1994) recognized the importance of incorporating early maturity in tropical soybean varieties. Parental genotypes 835/5/30 and SB-93 were the best combiners for early maturity. This indicated the superiority of these parents in transmitting desirable genes for early maturity. However, early maturity did not result in significant high yield increase among the F_1 progenies. These findings are in line with those found by Wang *et al.* (2001) ; Nafziger (2015) whose findings showed that yields of medium maturing genotypes tend to yield slightly more than either early or late maturing lines.

Significant GCA and SCA effects for plant height suggested that both additive and non-additive gene action controlled the inheritance of the trait. Sharma (2004), Agrawal *et al.* (2005), Gravioli *et al.* (2006) and Wanderi (2012) also reported that both additive and dominance effects played an important role in determination of plant height. GCA/SCA ratio which was close to zero indicated that non-additive gene action was more important than additive gene action. These results are in agreement with Sharma (2004) and Karyawati *et al.* (2015), but contradicted those of Agrawal *at al.* (2005) ; Gravioli *et al.* (2006) ; Shiv *et al.* (2011) and Wanderi (2012) whose findings showed the preponderance of additive gene action over non-additive gene action.

Significant environmental interactions with GCA and SCA effects suggested that additive and non-additive gene effects were not stable across environments. These results are in line with Cruz *et al.* (1987) who found significant interactions between environments and GCA and SCA effects. This makes selection for superior parents or crosses more difficult as reported by Tukamuhabwa *et al.* (2002b).

Findings showed that parental lines SB-19, 915/5/12, Nyala, SB-93 and SB-98 had significant negative GCA effects suggesting their contribution towards reduced plant height. F_1 progenies 835/5/30 x Nyala and Nyala x SB-98 had significant negative SCA effects indicating that they can be used in a breeding program to reduce plant height.

Highly significant environmental interactions with GCA and SCA as regard to pod shattering suggested instability of additive or non-additive gene effects across environments. Therefore

selection for low pod shattering resistance from parents or crosses widely adapted across a full range of environments may be difficult. The findings agreed with Tukamuhabwa *et al.* (2002b) who reported significant GCA x environment and SCA x environment interactions. Therefore, parents and their respective crosses need to be evaluated in several environments to obtain reliable genetic information for appropriate selection and breeding procedures during the improvement of resistance to soybean pod shattering. The findings also showed highly significant GCA and SCA effects. Cruz *et al.* (1987) and Tukamuhabwa (2002b) also found highly significant GCA and SCA effects for resistance to pod shattering. Findings suggested that additive and non-additive effects were important determinants of resistance to pod shattering. Additive gene action represents the fixable genetic component of variation in conditioning inheritance of pod shattering. The GCA values are important for breeders who work with autogamous plants due to the additive variance. SCA effects were also significant indicating the contribution of non-additive genetic effects controlling pod shattering. These findings were in agreement with Saxe *et al.* (1996) ; Bailey *et al.* (1997) who reported the importance of non-additive gene action governing the inheritance of resistance to pod shattering in soybean. The observed SCA values showed that there were crosses that presented a different performance from what would be expected if only the additive effects were of influence. Baker (1978) reported that additive effects explain between 45% and 93% of the observed variability. It is therefore possible to predict the future generations for some traits, by the underlying mean F_1 population values.

GCA/SCA ratio of pod shattering was close to zero. This indicated that non-additive gene action (epistatic or dominance effect) played a more important role than additive gene action in the inheritance of pod shattering. These results are in agreement with Tukamuhabwa *et al.* (2000) who reported that inheritance of pod shattering was due to dominant epistasis. Application of selection pressure to the segregating genotypes from the best parental combinations should provide more significant genetic gains and improved expression of desirable traits in the population under development. These variations are to be expected, depending on the genetic background of soybean genotypes used and the environmental conditions under which the studies were carried.

Breeding of soybean hybrids has not yet been fully developed. This is the reason why the exploitation of dominant gene actions is still limited. Another difficulty is to generate sufficient hybrids from crossing. This is because of the cleistogamous condition that characterizes soybean flowers, poor rate of crossing when hand pollinating, low seed set of crosses, and the lack of cytoplasmic male sterility reported by Singh and Hymowitz (1999).

Breeding methods, which make the best use of non-additive gene action such as heterosis breeding, can contribute to improved productivity and reduced shattering in soybeans (Asante *et al*., 2007). Use of male gametocytes to induce male sterility has been suggested as an alternative to manual cross-pollination in soybeans (Lai *et al.*, 2004).

Hybridization followed by selection is usually more successfully when breeders rely on the mean performance and respective GCA effects of the parents for diverse traits that may easily be fixed for a self-pollinated crop such as soybean. Parents SB-8 and Nyala had significant negative GCA effects, indicating highly favorable gene frequencies for pod shattering resistance and their ability to transfer the resistance genes to their progenies. Significant and negative GCA effects associated with SB-8 and Nyala also indicated that they were good sources of resistance genes, and that they were the best general combiners for pod shattering resistance. Moderately resistant parents such as 835/5/30, 915/5/12, SB-19 and SB-98 had partly negative GCA effects, indicating few favorable gene frequencies for resistance to pod shattering and the ability to transmit this resistance from a generation to another as reported by Bhatnagar (1994). Thus based on various estimates such as mean performance and combining ability, the best soybean parents identified for pod shattering and seed yield and its important component traits were SB-8 and 835/5/30. Besides high GCA effects, these genotypes also showed high performance for most of the other agronomic traits. Hence, it appeared that favorable genes might have accumulated in these parents and could be gainfully utilized in soybean breeding programs as suggested by Jenson (1970) and Gadag *et al.* (1999).

Significant environmental interactions with GCA and SCA in terms of grain yield indicated no stability of additive or non-additive gene action for inheritance of high yield potential making selection uneasy throughout a range of environments. These findings are in agreement with those reported by Tukamuhabwa *et al*. (2002b) and Sharma (2004) who found significant environmental interactions with GCA and SCA estimates. Similar findings were also reported by Kimani and Derera (2009) and Iqbal *et al.* (2010) in beans. Consequently, parents and crosses should be selected and recommended for specific locations. GCA/SCA ratio was close to zero indicating the preponderance of non-additive gene action over additive in the inheritance of grain yield. In contrast, Sharma and Sharma (1988) reported the importance of additive gene action. The involvement of non-additive gene action in the inheritance of grain yields has been reported by Gadag *et al.* (1999), Sharma, (2004), Kiryowa *et al.* (2009) and Wanderi (2012). In contrast, Cho and Scott (2000) ; De Almeida Lopes *et al.* (2008) and Shiv *et al.* (2011) reported the predominance of additive gene action over non-additive and

suggesting that selection for grain yield in soybeans may be more effective in the F_2 and later generations.

It was found that parent 835/5/30 followed closely by SB-8 had significant GCA effects and were the best combiners towards high grain yield. F_1 hybrids 835/5/30 x 915/5/12, 915/5/12 x SB-19, 915/5/12 x SB-8 and SB-25 x SB-8 were significantly the best for high grain yields in the two sites. High significant SCA effects for seed yield might be due to contribution of some important characters that may arise from heterosis and biological yield or seed mass across locations. These findings are consistent to Kapila *et al.* (1994) who noted that SCA effects for seed yield were due to the genetic ability transferred from parental lines to their progenies and biological yield and 100-seed mass. Cho and Scott (2000) suggested that selection should be effective at later generations if SCA is predominant.

4.6. Conclusion

The aim of this study was genetic analyses of pod shattering and selected agronomic traits of eight soybean parental lines and their F_1 progenies using the diallel mating design, Model 1 (with fixed genotype effects), Method 2 (parents and crosses). Genetic analyses were based on SAS-05 program, version SAS 9.2. Significant differences were observed for both GCA and SCA. These differences suggest an important role that played additive and non-additive gene effects in controlling pod shattering resistance and other selected agronomic traits in soybeans. GCA/SCA ratio was close to zero for all the traits indicating the preponderance of non-additive gene action over additive gene action. This implied that selection at later generations should be the best approach to improve pod shattering resistance ability and other selected agronomic trait including grain yield.

Parents SB-8 and Nyala were the best combiners for improving resistance to pod shattering. Parent SB-98 had a remarkable contribution towards early flowering, followed slightly by Nyala and 915/5/12 while parents 835/5/30 and SB-93 were the best combiners for early maturity. Parents SB-19, 915/5/12, Nyala, SB-93 and SB-98 significantly contributed towards reduced plant height. Finally, parent 835/5/30 significantly was the best combiner for high grain yield, slightly followed by SB-8.

None of the F_1 progenies at KALRO-Mwea had a significant negative SCA effect for pod shattering. However at KALRO-Embu, SB-25 x SB-8 had the highest significant negative SCA effects for pod shattering, followed by SB-19 x SB-8 and 915/5/12 x Nyala suggesting that they would produce the most promising shattering resistant progenies. The Progeny

835/5/30 x SB-25 was the best significantly for early flowering throughout the two site, slightly followed by SB-19 x SB-93, 915/5/12 x SB-8 and Nyala x SB-93. None was significantly the best for early maturity throughout the two sites while 835/5/30 x Nyala and Nyala x SB-98 were significantly the best throughout the two sites for reduced plant height. Significant interaction of the genotype, GCA and SCA with the environment could be a major problem in the development of stable soybean pod shattering resistance varieties with other preferred attributes. It is therefore recommended that parents, together with their respective crosses, should be evaluated in a range of environments to obtain reliable genetic information necessary for effectiveness of selection and other breeding procedures.

High-parent heterosis values were mostly negative for all the traits. They varied from -16.4% for 835/5/30 x SB-25 to 4.6% for Nyala x SB-98 for days to 50% flowering, -14.1% for SB-25 x SB-93 to 1.4% for 835/5/30 x Nyala for days 75% maturity, from -37.4% for SB-8 x SB-98 to 8.2% for SB-19 x SB-93 for plant height. Pod shattering had high-parent heterosis values that varied from -60.4% for SB-25 x SB-93 to 7.9% for SB-19 x SB-98 and from -69.1% for 835/5/30 x Nyala to 40.2% for 915/5/12 x SB-8 for grain yield. It was therefore suggested to identify late segregates with better heterosis for development of progenies with high potential for different traits.

CHAPTER FIVE: GENERAL DISCUSSIONS, CONCLUSIONS AND RECOMMENDATIONS

5.1. General discussions

Significant differences were found among the 20 genotypes evaluated for pod shattering and other agronomic traits studied. These findings agreed with Mohammed (2010) ; Wanderi (2012) ; Vandamme *et al.* (2013) ; Nafziger (2015) ; Wycliffe (2015) ; Kang *et al.* (2017). These significant variations might be attributed to genetic diversity associated with these materials. Findings are in agreement with Njoroge *et al.* (2015) who used fifteen soybean genotypes. Significant environmental interactions with genotypes for duration to flowering, plant biomass, pods per plant and pod shattering suggested that genotypes responded differently to environments allowing selection of genotypes for specific zones. The findings agreed with Njoroge *et al.* (2015). However, no significant environmental interactions with genotypes found for grain yield, harvest index, seeds per pod, seed size, duration to maturation and plant height suggested how difficult selection is when genotypes are selected for specific zones. Findings agreed with Pfeiffer *et al.* (1995) who did not find significant interactions in terms of grain yield and seeds per pod. The study revealed a wide range of resistance to pod shattering from resistant to highly susceptible genotypes. These findings agreed with Krisnawati and Adie (2017) who found a broad range of shattering from 0 to 100% when class studying 150 soybean genotypes in Indonesia. Significant variations could be attributed to genetic diversity associated with the materials. Most of the SB genotypes were resistant to pod shattering particularly SB-8 and SB-4 except SB-90 and SB-25. Among local varieties, Nyala and Gazelle were the most resistant. Findings agreed with Mahasi *et al.* (2012) and Shaahu *et al.* (2013) who carried independently trials in Western Kenya and in Nigeria. They found Nyala and Gazelle among the commercial varieties in Kenya and SB-8, SB-4 with SB-20 and SB-74 among the SBs to be resistant and stable to pod shattering across environments. This variability might be attributed to the genetic ability for resistance to pod shattering associated with these materials.

Significant GCA and SCA effects were found among genotypes for all the traits studied. These results were in agreement with Agrawal *et al.* (2005) who found significant GCA and SCA effects for duration to flowering, maturity, plant height and grain yield when using diallel set of soybean crosses evaluated along with their parents at University of Agricultural Sciences at Dharwad. These findings were partly in satisfactory with Wanderi (2012) who found no significant GCA effects for grain yield and no significant SCA effects for duration

to maturation when evaluating F_2 population along with their parents at Embu and Mwea from April to August 2012. The ratio GCA/SCA was close to zero for all the traits studied indicating the importance of non-additive over additive gene action. Findings agreed with Sharma (2004) who found that non-additive gene effects governed flowering, maturation, plant height and grain yield when evaluating the F_1, F_2 and F_3 along with their parents. Srivastava and Jain (1994) ; Choukan (1996) ; Gadag *et al.* (1999) found similar observations. On contrary, the importance of additive gene action for flowering, maturation and plant height was reported by Harer and Desmukkh (1991) ; Rahangdale and Raut (2002) ; Wanderi (2012). Cruz *et al.* (1987) also reported the importance of dominance effects for plant height in diallel analysis in soybean. Findings showed the importance of non-additive gene action controlling the grain yield. These findings agreed with Sharma (2004) who found the estimation of variance components of SCA being predominant over GCA for grain yield. Findings agreed also with Gadag *et al.* (1999) and Wanderi (2012). GCA/SCA ratio of pod shattering was close to zero. This finding was in agreement with Tukamuhabwa *et al.* (2000) who reported that inheritance of pod shattering was due to dominant epistasis.

5.2. Conclusions

The 20 soybean genotypes evaluated at two locations for two seasons were genetically diverse for all the agronomic traits including pod shattering. Based on 1 to 5 AVRDC scale (1=very resistant, 5 highly susceptible), three commercial varieties, Gazelle, Nyala and SCS-1 and most of SB varieties, SB-145, SB-151, SB-20, SB-37, SB-4, SB-74 and SB-8 showed stability and resistance to pod shattering across seasons and locations. Two genotypes SB-25 and SB-90 were very susceptible to pod shattering. Results showed that two commercial varieties, 931/5/34 and 915/5/12 were the best yielding. In general, most of SB varieties had high yields with better farmer's key traits compared to commercial varieties but flowered and matured late. Five of the SB lines (SB-20, SB-154, SB-151, SB-74 and SB-8) showed high yield stability and were resistant to pod shattering. They may be more valuable to breeders for the increased genetic diversity and they are likely to provide potentially, new useful sources of resistance that may be introgressed into highly susceptible local and commercial varieties. Future work on genetic characterization of resistance in SB-8, SB-74, SB-4 and SB-20 among the SB lines and Gazelle, Nyala and SCS-1 among the local varieties is needed. Four genotypes, EAI-3600, Black Hawk, SB-154 and 915/5/12 showed partial resistance to pod shattering that may be durable. Therefore, these genotypes could be useful in breeding programs to develop soybean varieties with durable pod shattering resistance.

Analysis of variance showed that there were significant genotypic differences among parents and their F_1 progenies for all the traits studied suggesting a remarkable genetic diversity. Genetic analyses revealed significant GCA and SCA suggesting the importance of additive and non-additive gene action in inheritance of pod shattering resistance and selected traits in soybeans. The GCA/SCA ratio varied from 0.00124 to 0.0742 suggesting the dominance of non-additive gene action in the inheritance of these traits. Parents SB-8 and Nyala exhibited high negative and significant GCA effects for pod shattering across the environment indicating that they were the best general combiners for pod shattering resistance improvement and this suggests their ability to transfer resistant genes to their progenies. Parent SB-98 was the best combiner for early flowering while SB-93, SB-19, SB-98, 835/5/30 and Nyala were the most promising parental lines for early maturity. Parents SB-19, 915/5/12, Nyala, SB-93 and SB-98 were the best combiners towards reduced plant height while finally, the parent 835/5/30 showed its better ability to combine towards high yield across different environments. With regard to SCA estimates, crosses between SB-25 x SB-8, SB-19 x SB-8 and 915/5/12 x Nyala showed remarkable specific combining ability for resistance to pod shattering at KALRO-Embu and can be used for heterosis breeding.

5.3. Recommendations

i. SB lines, particularly SB-20, SB-151 and SB-74 are recommended as they showed resistance to pod shattering and had a yield potential of more than 1,500 kg ha^{-1}.

ii. Further studies are needed to characterize the resistance genes present in SB genotypes and other local soybean varieties. This information would be useful in developing an effective and efficient soybean program.

iii. Breeding methods such as heterosis breeding should be applied to develop lines with resistance to pod shattering in soybean. Selection for resistance can be made in late generation of segregating population because of the low progenies generated from crosses and high genetic gain for selection at F_2 population.

iv. Stability of resistance to pod shattering in soybean to be further investigated across several agro ecological conditions and diverse seasons.

v. Biotechnology techniques such as molecular markers (MAS) or genetic mapping for identification of quantitative trait loci (QTL) that condition resistance to shattering should be considered to reduce the drudgery associated with the conventional method and also improve the accuracy of results.

vi. It is also important to investigate the biochemical basis of shattering resistance.

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APPENDICES

Appendix 1. Mean monthly of rainfall and temperature at KALRO-Embu and KALRO-Mwea/Kirogo farm during the 2016 long rain season

Month	KALRO-Embu		KALRO-Mwea/Kirogo	
	Rainfall (mm)	**Temperature (°C)**	**Rainfall (mm)**	**Temperature (°C)**
May 2016	96.8	22.9	100.7	23.7
June 2016	57	22	59.3	22.8
July 2016	49.6	19.5	51.6	20.3
August 2016	62.4	23	64.9	23.8
September 2016	67.4	24	70.1	24.8
October 2016	107	23	111.3	23.8
Total	**440.2**	**134.4**	**457.9**	**139.2**
Mean	**73.36**	**22.4**	**76.3**	**23.2**

Appendix 2. Mean monthly of rainfall and temperature at KALRO-Embu and KALRO-Mwea/Kirogo farm during the 2016 short rain season

Month	KALRO-Embu		KALRO-Mwea/Kirogo	
	Rainfall (mm)	**Temperature (°C)**	**Rainfall (mm)**	**Temperature (°C)**
November 2016	138.2	21.7	102	22.6
December 2016	19.5	22.6	15.1	23.7
January 2017	39.2	24	27.3	25.1
February 2017	27.4	24.5	21.2	25.7
March 2017	87.8	26	68	27.2
April 2017	191.4	24	148.3	25.2
Total	**503.5**	**142.8**	**381.9**	**149.5**
Mean	**83.91**	**23.8**	**63.65**	**24.9**