



Original Research Article

Combining ability of resistance to pod shattering and selected agronomic traits of soybean

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Eight parents Nyala and SB-8, SB-25, SB-93, SB-19, 915/5/12, 835/5/30 and SB-98 were crossed in a diallel mating scheme to generate 28 F₁ progenies in a greenhouse at Kabete, University of Nairobi. The F₁ and their parents were evaluated at KALRO-Embu and Mwea Research Centers between December 2016 and May 2017. The trials were laid out in an alpha-lattice design arranged in a 6 × 6 pattern with 3 replicates. Data was collected on maturity, plant height, grain yield and pod shattering. General and specific combining ability were determined according to Griffing's diallel, Method 2. 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 varied 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 gene action in the inheritance of these traits. 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 significantly contributed towards reduced plant height. Parent 835/5/30 followed by SB-8 had the higher GCA gene action thus 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 of 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 in soybeans.

Key words: combining ability, pod shattering and soybean.

INTRODUCTION

Pod shattering is one of the most important constraints to soybean productivity in the tropics. Seed losses of 50–100% are often associated with pod dehiscence in susceptible varieties and delayed harvesting (IITA, 1986). The loss of seeds associated with pod shattering results in reduced yield and also in the emergence of the crop as a weed in subsequent growing season (Mohammed, 2010). 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).

The screening of germplasm is the key element to develop high quality seeds with farmer preferences and with profitable returns (Lee et al., 2011). Research conducted in 2009 in Kenya by Kenya Agricultural and Livestock Research Organization, KALRO-Njoro Research Center, identified five suitable soybean varieties, *Gazelle*, *Hill*, *Black Hawk*, *EAI 3600*, and *Nyala*. Thereafter, two dual-

purpose promiscuous soybeans, *TG x 1895-33F* and *TG x 1740-2F*, and one grain genotype, *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). So there is a need to understand the mode of gene action that control pod shattering to develop high yielding genotypes with high resistance to pod shattering.

Understanding the genetic control of pod dehiscence 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 soybean 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 dehiscence in soybean. Caviness (1969); 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 effect while Tukamuhabwa et al. (2002) 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. Therefore this study aims to determine the combining ability of resistance of soybean to pod shattering of F_1 progenies generated from a half diallel mating.

MATERIALS AND METHODS

Experimental sites

This study was carried in two locations, KARLO-Embu and KARLO-Mwea Research Centres in Eastern and Central highlands of Kenya (Table 1).

Soybean materials and hybridization

The study materials were two resistant genotypes 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) (Table 2).

Parental lines were planted in crossing blocks in a greenhouse where each parental genotype was sown in 10 plastic pots at five different dates at an interval of one week in order to synchronize flowering. The growth media was prepared using 3:1:1 ratio of soil, sand and organic manure. Fertilizers were applied at 20 kg N ha⁻¹ and 60 kg P₂O₅ 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 half diallel mating design, following Griffing (1956) Model 1, Method 2. Hybridization was achieved by emasculation and hooking methods among the genotypes as described by Walter (1980).

Field evaluation of soybean genotypes

The 28 F_1 progenies and their parents were evaluated to determine the combining ability for pod shattering under field conditions at KARLO-Embu and KARLO-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 where each plot consisted of three rows of 2 M long at an inter-row and intra-row spacing of 40 cm and 15 cm, respectively. Di-ammonium phosphate (18% N and 45% P₂O₅) 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 (26% N). Field experiments were kept relatively free from weeds throughout the cropping seasons. Supplemental furrow irrigation was provided at Mwea due to a severe drought during the 2016 short rain season. Data was assessed on days to 75% maturity, plant height, pod shattering and grain yield.

Assessment of agronomic traits and pod shattering

Days to 75% maturity was recorded as the number of days from sowing to when approximately 75% of plants reached 95% of fully maturity. Plant height (cm) was measured on six plants at reproductive stage as the distance from the ground to the top of the main stem. Pod shattering was collected using a modified oven-dry method as described by IITA (1986); Tsuchiya (1987); Krisnawati and Adie (2016). A random sample of fifty fully mature three seeded pods of each variety which were sun-dried in khaki envelopes for seven days. The number of shattered pods were counted daily and expressed as percentage. Genotypes were then classified into five categories based on their reaction to pod shattering (Table 3). Grain yield was collected by weighting (g) threshed seeds from plants of the middle rows and then extrapolating from g m⁻² into kg ha⁻¹ (Wanderi, 2012).

Data analysis and calculation of combining ability

Data was subjected to analysis of variance (ANOVA) with locations, replicates and genotypes as factors and the traits measured as variables using Genstat statistical package (15th edition) (Payne et al., 2009). General and specific combining abilities, GCA and SCA values, for each trait

Table 1. Description of KALRO-Embu, KALRO-Mwea and Kabete Research Centers

Characteristics	Embu	Mwea	Kabete Field Station
Latitude	00°30' S	00° 37' S	1° 15' S
Longitude	37°42' E	37° 20' E	36° 44' E
Elevation (meters above sea level)	1508	1159	1737
Annual rainfall(mm)	1200-1495	850	1000
Annual maximum temperature (°C)	25	28.6	24.3
Annual minimum temperatures (°C)	14.1	15.6	13.7
Soil type	Humic nitosol	Vertisols	Nitosols
Soil PH	5.46	5.97	5.60

(Source : Wanderi, 2012 ; Njau, 2016)

Table 2. 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

Source: Mahasi et al. (2010)

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:

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

Where, Y_{ijk} = Observed value of the i^{th} genotype in the k^{th} environment ; μ = Overall mean ; g_i = the GCA effects of the i^{th} parent ; g_j = 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 ; ϵ_{ijk} = experimental error associated with ij^{th} genotype in the k^{th} environment.

GCA/SCA ratio known as general predicted ratio (GPR) was used for all the traits to estimate the relative

importance of GCA and SCA gene action and was computed as illustrated by Baker (1978) 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 for GCA and SCA.

A ratio GCA/SCA close to 1 indicates the importance of additive effects in the inheritance of the trait. When that ratio is close to 0, dominance effects are more important. The percentage data on pod shattering was subjected to arcsine-square root transformation before statistical analysis.

Table 3. 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)

(AVRDC, 1979 ; IITA 1986 ; Krisnawati and Adie, 2016)

Table 4. Mean sum of squares studied characters at Embu and Mwea Research stations during the 2016-2017 short rain season

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

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

RESULTS

Agronomic traits

Days to 75% maturity showed significant variations among genotypes (P<0.001) (Table 4). 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 5). Most of the F₁ progenies were medium maturing across locations (between 95 and 115 days). Four of the F₁ 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 6).

There were significant GCA effects among genotypes (P<0.01). There were significant interactions between GCA and environments (P<0.01) (Table 7). Desirable parental lines were associated with significant negative GCA estimates of days to maturity as they represent early maturing genotypes. 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 both environments (Table 8). There were significant variations in terms of SCA effects (P<0.01). Significant interactions between SCA and environments were also observed (P<0.01). Crosses with significant negative SCA estimates were desirable because they represent early maturing genotypes. Among F₁ 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. Progenies

SB-19 x SB-25 and SB-25 x SB-8 had significant positive SCA effects at Embu (Table 9). GCA/SCA ratio was close to zero (Table 7).

Plant height varied significantly among genotypes (P<0.001) (Table 4). 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. Crosses SB-19 x SB-98 and 915/5/12 x SB-19 had the shortest plants, less than 22.5 cm, while F₁ progenies from the cross SB-25 x SB-8 had the tallest plants with mean height of 47.9 cm (Table 5).

There were significant GCA effects for plant height (P<0.01). Interactions between GCA estimates and environments were also significant (P<0.01) (Table 7). 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 at P<0.001 (Table 8). Plant height showed significant variations among SCA effects (P<0.01). Significant interactions were observed between SCA and environments (P<0.01) (Table 7). Hybrids with negative significant SCA effects were the desirable as they contributed towards reduced plant height. Only a few F₁ 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 9). GCA/SCA ratio was low and close to zero (Table 7).

Table 5 : Performance of 28 F₁ progenies and their parents grown at Embu and Mwea Research stations during the 2016-2017 short rain season

Genotype	Days to 75% maturity		Plant height (cm)		Grain yield (kg ha ⁻¹)	
	Embu	Mwea	Embu	Mwea	Embu	Mwea
Parents						
835/5/30	97	106	32.5	34	2223.6	2028.7
915/5/12	109	108	27.8	24.8	775.5	772.9
Nyala	101	104	27.3	27.7	584	627
SB-19	99	99	20.7	24.7	1395.1	1034.1
SB-25	130	125	49.3	49.8	878.2	1081.2
SB-8	118	124	50.3	50.7	1483.2	1236.1
SB-93	95	97	27	24.3	1480.8	1845.8
SB-98	103	99	29.8	31.3	959.5	1347.8
Parental mean	106.5	107.8	33.1	33.4	1222.5	1246.7
Progenies						
835/5/30 x 915/5/12	105	105	36.2	31.5	1917.3	1683.3
835/5/30 x Nyala	102	106	24.7	25.2	613.5	700.4
835/5/30 x SB-19	94	102	26	26.2	1024.5	953.6
835/5/30 x SB-25	115	114	33.8	38.3	746.4	768.4
835/5/30 x SB-8	109	113	34.3	36.3	1425.6	1322
835/5/30 x SB-93	96	98	30.5	28	862.5	1007.8
835/5/30 x SB-98	99	101	30.3	29.7	1029.3	1165.8
915/5/12 x Nyala	109	104	23	25.8	576.4	657.7
915/5/12 x SB-19	104	104	19	21.2	1763.7	1349.6
915/5/12 x SB-25	116	116	39.3	37.8	1122.3	1036.7
915/5/12 x SB-8	116	115	31.5	33.3	1811.4	2001.9
915/5/12 x SB-93	105	100	25.3	27	707.3	655.3
915/5/12 x SB-98	107	103	27.5	28.8	775.2	770.8
Nyala x SB-19	100	103	24.5	24.5	597.6	559.7
Nyala x SB-25	114	115	43.5	41.8	631.3	914.6
Nyala x SB-8	109	114	36	37	880.9	1379
Nyala x SB-93	97	101	27.5	26.8	1397.9	968.5
Nyala x SB-98	101	101	21.2	24.8	500.4	590.7
SB-19 x SB-25	118	113	31.3	33.2	980.7	725
SB-19 x SB-8	111	111	33.7	32.2	798.8	748.1
SB-19 x SB-93	96	97	28.8	26.7	1277.4	891
SB-19 x SB-98	99	99	21.5	23.3	337.9	509.1
SB-25 x SB-8	128	125	46.7	49.2	2011.7	2217.1
SB-25 x SB-93	107	112	38.3	37.3	1460.4	999.9
SB-25 x SB-98	114	113	39.5	38.5	1330.8	1106.1
SB-8 x SB-93	108	111	32.5	34	1048.8	817.8
SB-8 x SB-98	110	112	30.3	33	670.2	552.7
SB-93 x SB-98	98	98	28.8	30.3	704.5	809
Progenies mean	106.7	107.4	30.9	31.5	1035.9	995
Mean	106.6	107.4	31.4	31.9	1077.35	1050.98
LSD _{0.05}	5.3	5.7	8.42	5.2	675.67	434.65
CV (%)	3	3.2	16.5	10	38.5	25.4

LSD – least significant difference, CV – coefficient of variation

Grain yield varied significantly among genotypes ($P < 0.001$) (Table 4). 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 5). The best yielding F₁ 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 F₁ genotypes. F₁ progenies had higher yields at Embu, 1,035.9 kg ha⁻¹ compared to 995.06 kg ha⁻¹ at Mwea (Table 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 7). Positive

Table 6 . Pod shattering of 28 F₁ progenies and their parents grown at Embu and Mwea Research stations during the 2016-2017 short rain season

Site Genotype	Embu			Mwea			Sites mean		
	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).

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 positive significant GCA effects at Mwea,

but insignificant at Embu. Parent Nyala, the commercial local genotype and SB-98 had significant negative GCA effects in both sites (P<0.05) (Table 8). Significant variations were also observed among SCA effects (P<0.01). There were significant interactions between SCA and environments (P<0.01) (Table 7). Desirable F₁ progenies

Table 7. GCA and SCA mean sum of squares of studied characters at Embu and Mwea Research stations

Source	Df	Days to 75% maturity	Plant height (cm)	Shattering %	Grain yield (kg ha ⁻¹)
GCA	7	309.85**	251.25**	1124.6**	335323.8**
SCA	28	250168.9**	21830.1**	12909.1**	24725198.6**
GCA x Envir.	7	161.78**	250.88**	1073.84**	318529.51**
SCA x Envir.	28	239466.6**	21826.3**	12882.81*	24712432.0**
Error	142	1.86	3.04	5.34	20353.8
GCA/SCA ratio	-	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 non-significant

Table 8. GCA effects of studied characters of eight parents grown at Embu and Mwea Research stations during the 2016-2017 short rain season.

Parents	Days to 75% maturity		Plant height		Grain yield		Pod shattering		
	Embu	Mwea	Embu	Mwea	Embu	Mwea	Embu	Mwea	Accross env.
835/5/30	-4.63***	-1.58*	-0.18	-0.41	237.01*	219.98***	-3.74***	-5.03**	-4.38
915/5/12	1.97**	-0.38	-2.51*	-3.23***	52.86	24.22	-7.59***	0.35	-3.62
Nyala	-2.63**	-1.48*	-2.76**	-2.59***	-333.01*	-243.4***	-8.87***	-6.23***	-7.55*
SB-19	-4.03***	-3.98***	-5.64***	-5.07***	-12.54	-165.46***	0.02	-5.44***	-2.71
SB-25	11.17***	9.12***	8.85***	8.86***	34.39	47.16	17.41***	14.22***	15.81**
SB-8	6.67***	8.22***	6.3***	6.9***	191.76	205.19***	-9.46***	-12.13***	-10.79*
SB-93	-6.33***	-5.58***	-1.68*	-2.84***	72.4	38.21	14.5***	18.79***	16.64**
SB-98	-2.63**	-4.18***	-2.39*	-1.61*	-242.89*	-125.89*	-2.23*	-4.52**	-3.38

***Significant at $P \leq 0.001$, **Significant at $P \leq 0.01$, and *Significant at $P \leq 0.05$

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 significant positive SCA effects at Mwea ($P < 0.05$) while at Embu it was significant but negative. Crosses Nyala x SB-93 and SB-25 x SB-98 had significant positive SCA effects ($P < 0.05$) at Embu but insignificant 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 9). GCA/SCA ratio was close to zero (Table 7).

Pod shattering

Pod shattering varied significantly among the study genotypes ($P < 0.001$). There was significant interactions between genotypes and locations ($P < 0.001$) (Table 4). Pod shattering varied from 2.8 to 60.4% with a mean of 24.4%. Embu and Mwea had 23.2% and 25.5% of pod shattering. Among the parental lines, resistance to pod shattering ranged from 2.8 % with SB-8 to 56.7% with SB-93. Two genotypes, SB-8 and Nyala, were classified as resistant, four, 835/5/30, 915/5/12, SB-19 and SB-98 were intermediate, while two, SB-25 and SB-93, were highly susceptible to pod shattering. Pod shattering score among

the F_1 progenies ranged from 9 to 60.4% across the environments. The F_1 progenies of cross Nyala x SB-8 had the lowest pod shattering while SB-25 x 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 6).

Pod shattering had GCA effects highly significant at $P < 0.01$. Significant interactions were observed between GCA and environments at $P < 0.05$ (Table 7). Based on the AVRDC scale used, negative significant GCA values were desirable for reduced 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 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 7). 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 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. 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 9). GCA/SCA ratio was less than 1 and close to zero (Table 7).

DISCUSSION

Agronomic traits

Days to 75% maturity varied significantly among genotypes suggesting that parents and F_1 progenies were genetically diverse. Parental lines, matured from the 96th day from the sowing to the 127th day while most of progenies were the medium maturing (between 100 and 115 days) and some were late maturing (beyond 115 days). These findings 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.

Significant environmental interactions with GCA or SCA at $P < 0.01$ 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. (2002).

The highly significant GCA and SCA for duration to maturity ($P < 0.01$) 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), Tukamuhabwa et al. (2002), Agrawal et al. (2005), Gavioli et al. (2006) and Sher et al. (2012). GCA/SCA ratio close to zero suggested that non-additive gene effects played a bigger role than additive gene effects. These results are in line with those found by Gadag et al. (1999), Sharma (2004) and 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

Gavioli 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. 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 not significant at Mwea. However, early maturity did not result in significant high yield increase among the F_1 progenies. These results 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.

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 GCA and SCA effects ($P < 0.01$) suggested that both additive and non-additive gene action controlled the inheritance of the trait. Sharma (2004), Agrawal et al. (2005), Gavioli 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 et al. (2005), Gavioli et al. (2006), Shiv et al. (2011) and Wanderi (2012) whose findings showed the preponderance of additive gene action over non-additive.

Significant environmental interactions with GCA and SCA effects at $P < 0.01$ suggested that additive and non-additive gene effects were not stable across environments. This makes selection for superior parents or crosses across environments more difficulty as reported by Tukamuhabwa et al. (2002). These findings are in line with Cruz et al. (1987) who found significant interactions between environments and GCA and SCA effects.

Parental lines SB-19, 915/5/12, Nyala, SB-93 and SB-98 had significant negative GCA effects suggesting they

Table 9. SCA effects of studied characters of 28 F₁ progenies grown at Embu and Mwea Research stations during the 2016-2017 short rain season

Crosses	Days to 75% maturity		Plant height		Grain yield		Pod shattering		
	Embu	Mwea	Embu	Mwea	Embu	Mwea	Embu	Mwea	Across env.
835/5/30 x 915/5/12	0.96	-0.46	7.46**	3.23*	550.12**	388.12**	-1.26	1.29	0.02
835/5/30 x Nyala	2.56	1.64	-3.79	-3.75*	-367.89	-327.13*	-1.14	-1.98	-1.56
835/5/30 x SB-19	-4.04*	0.14	0.42	-0.27	-277.34	-151.96	-0.44	-0.86	-0.65
835/5/30 x SB-25	1.76	-0.96	-6.25*	-2.04	-602.3**	-549.7***	1.48	-0.19	0.65
835/5/30 x SB-8	0.26	-1.06	-3.19	-2.08	-80.5	-154.17	2.5**	-0.22	1.14
835/5/30 x SB-93	0.26	-2.26	0.95	-0.66	-524.28*	-301.41*	-1.06	0.517	-0.27
835/5/30 x SB-98	-0.44**	-0.66	1.49	-0.23	-42.17	20.73	1.21	0.53	0.87
915/5/12 x Nyala	2.96*	-1.56	-3.13	-0.26	-220.76	-174.1	-3.51***	-1.77	-2.64
915/5/12 x SB-19	-0.64	0.94	-4.24	-2.44	646.00**	439.82**	1.43	-0.66	0.39
915/5/12 x SB-25	-3.84*	-0.16	1.58	0.29	-42.29	-85.63	1.63	-0.27	0.68
915/5/12 x SB-8	0.66	-0.26	-3.68	-2.33	489.56*	721.49***	4.42***	-2.28	1.07
915/5/12 x SB-93	2.66	-1.46	-1.88	1.16	-495.29*	-458.14**	0.58	5.67	3.13
915/5/12 x SB-98	0.96	0.14	0.99	1.76	-112.13	-178.46	-0.53	-2.7	-1.62
Nyala x SB-19	-0.04	1.04	1.5	0.25	-134.16	-82.46	1.97*	-3.96	-0.99
Nyala x SB-25	-1.24	-0.06	6.0*	3.65*	-147.48	59.9	1.81*	2.18	1.99
Nyala x SB-8	-1.74	-0.16	1.06	0.77	-55.27*	366.25**	2.82**	3.13	2.98
Nyala x SB-93	-0.74	0.64	0.54	0.35	581.16**	122.75	0.76	-2.3	-0.77
Nyala x SB-98	-0.74	-0.76	-5.08*	-2.88*	-1.08	-90.94	-0.41	1.98	0.79
SB-19 x SB-25	4.16*	0.44	-3.28	-2.53	-118.52	-207.65	1.88*	3.53	2.71
SB-19 x SB-8	1.66	-0.66	1.61	-1.57	-457.72*	-342.62*	-3.94***	7.6*	1.83
SB-19 x SB-93	-0.34*	-0.86	4.75*	2.67	140.16	-32.7	-1.6	-1.29	-1.45
SB-19 x SB-98	-1.04	-0.26	-1.87	-1.9	-483.99*	-250.56*	0.23	1.34	0.79
SB-25 x SB-8	3.46*	0.24	0.12	1.49	708.18**	913.8***	-10.51***	-4.56	-7.54**
SB-25 x SB-93	-4.54**	1.04	-0.25	-0.6	276.27	-136.42	1.31	5.83*	3.6
SB-25 x SB-98	-1.24	0.64	1.63	-0.66	461.95*	133.89	-1.04	-0.75	-0.9
SB-8 x SB-93	0.96	0.94	-3.52	-1.97	-292.74	-476.6***	1.43	-2.95	-0.76
SB-8 x SB-98	-0.74	0.54	-5.06*	-4.21**	-356.05	-577.6***	2.91**	-0.15	1.38
SB-93 x SB-98	0.26	0.34	1.49	2.87*	-202.4	-154.3	-2.81	-0.11	-1.46

***Significant at $P \leq 0.001$, **Significant at $P \leq 0.01$, and *Significant at $P \leq 0.05$

contributed towards reduced plant height. F₁ progenies 835/5/30 x Nyala and Nyala x SB-98 had significant negative SCA effects indicating that they were the best for reduced plant height.

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 F₁ 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 F₂ population generated from 28 F₁ 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).

Significant environmental interactions with GCA and SCA ($P < 0.01$) 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. (2002) 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); 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 suggesting that selection for grain yield in soybeans may be more effective in the F₂ and later generations.

Genotypes 835/5/30 and SB-8 had significant GCA effects among parents while 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 had significant SCA effects among progenies. They were therefore the best combiners towards high grain yield 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 weight. Cho and Scott (2000) suggested that selection should be effective at later generations if SCA is predominant.

Pod shattering

Highly significant environmental interactions with GCA and SCA suggested instability of additive or non-additive effects across environments. Therefore selection for low pod shattering resistance of widely adapted parents or crosses across a full range of environments may be difficult. The findings agreed with Tukamuhabwa et al. (2002) 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 (2002) 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. This indicated 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 F₁ 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 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. 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 recorded 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 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). Hence, it appeared that favorable genes for resistance to pod shattering and high yield might have accumulated in parents SB-8 followed by 835/5/30; these two genotypes could be gainfully utilized in soybean breeding programs as suggested by Jenson (1970) and Gadag et al. (1999). Only the F₁ 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. At Embu, F₁ progenies of crosses SB-25 x SB-8, SB-19 x SB-8 and 915/5/12 x Nyala had significant negative SCA effects.

Conclusion and recommendation

Parents 835/5/30 and SB-93 were the best combiners for

early maturity while none of progeny was significantly the best for early maturity throughout the two sites. Parents SB-19, 915/5/12, Nyala, SB-93 and SB-98 significantly contributed towards reduced plant height while 835/5/30 x Nyala and Nyala x SB-98 were significantly the best throughout the two sites. Parents SB-8 and Nyala were the best combiners for improving resistance to pod shattering. None of the F₁ progenies recorded a significant negative SCA effect for pod shattering at Mwea. However at Embu, SB-25 x SB-8 recorded the highest significant negative SCA effects, followed by SB-19 x SB-8 and 915/5/12 x Nyala suggesting that they would produce the most promising shattering resistant progenies. Finally, parent 835/5/30 significantly was the best combiner for high grain yield, slightly followed by SB-8 while 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 were significantly the best crosses among progenies in both sites.

Significant differences were observed for both GCA and SCA effects. 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 that non-additive gene action was predominant over additive gene action. This implied that heterosis breeding and selection at later generations should be the best approach to improve pod shattering resistance ability and other selected agronomic traits in soybeans. Significant interactions among GCA or SCA with the environment could be a major problem in the development of stable soybean pod shattering resistance varieties with other preferred agronomic 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 breeding programs.

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Conflict of interests

The authors declare that they have no conflicting interests

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