

Combining ability and heritability of soybean resistance to groundnut leaf miner

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Abstract Groundnut leaf miner (GLM) (*Aproaerema modicella*) (Deventer) is one of the most destructive pests of soybean and groundnuts. In this study, the mode of inheritance, general combining ability (GCA), specific combining ability (SCA) effects, maternal effects of resistance to GLM and grain yield ha^{-1} were determined. Thirteen soybean parental genotypes and 81 F_2 populations were evaluated for resistance to GLM in a 5×19 alpha lattice diallel design with two replications under natural GLM infestation in northern (Arua) and eastern (Iki-iki) Uganda during September to

December 2016 rainy season. Highly significant differences were observed among parental genotypes and F_2 populations for GLM incidence, severity, and grain yield. The estimates of GCA effects were significant for GLM incidence and severity scores but not for the number of larvae per plant and grain yield ha^{-1} . SCA effects were non-significant for all the studied traits, suggesting that GCA effects were the major component responsible for soybean resistance to GLM with additive gene effects being more important for these traits. Baker's ratio ranged from 0.44–1.0 for most of resistant traits except number of larvae per plant and grain yield ha^{-1} . The results indicated also that cultivars Maksoy1 N, PI615437, PI578457A and NIIGC4.1-2 were good combiners against GLM incidence and severity. Parent PI615437 was a good combiner for grain yield and Maksoy1 N $\times$ PI615437 was a superior cross for grain yield and against GLM incidence. There were no maternal effects for the inheritance of resistance to GLM. The study provides a basis for understanding patterns of inheritance of soybean resistance to groundnut leaf miner for an efficient breeding program.

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Introduction

Soybean, *Glycine max* (L.) Merr. is one of world's leading oil crop, providing the cheapest food and source of proteins for the poor rural communities (Bilyeu et al. 2010). Nutritionally, soybean grains contain about 40% protein, 20% oil, with an optimal supply of essential amino acids and nutrients, and a high-calorie value (Singh et al. 2008). In Uganda, soybean is increasingly becoming an important food and cash crop (Tukamuhabwa et al. 2011) and the land area under soybean production increased from 144,000 to 155,000 hectares between 2004 and 2009, with annual production increasing from 158,000 to 181,000 tonnes, respectively (Tukamuhabwa and Oloka 2016). Northern and Eastern regions account for most of the production in the country with 66.6% and 24.6%, respectively (UBOS 2010). Despite the increasing trend of soybean production in Uganda over the past 10 years, the current yields estimated at about 1200 kg ha⁻¹ are still below the potential of 2000 kg ha⁻¹ reported in other major producing countries in Africa (FAO 2011). According to Tukamuhabwa (2001), the low yields are due to a number of constraints including insect pests, diseases, low soil fertility, drought and lack of inputs among others.

The Groundnut leaf miner (GLM) *Aproaerema modicella* (Deventer) (Lepidoptera: Gelechiidae) is one of the most serious invasive oligophagous pest affecting soybean (*Glycine max* L.) and groundnut (*Arachis hypogaea* L.) production in Indo-Asia and Africa leading to huge yield loss of up to 100% in the tropics (Cugala et al. 2010, Praveena et al. 2011, Buthelezi et al. 2013). In Africa, first report of GLM was on groundnut during 1998 (Page et al. 2000). In Uganda, the pest severely affects soybean (Namara et al. 2015) and groundnut (Page et al. 2000; Epieru 2004; Okello et al. 2010) particularly during the second rainy season (August-December), in Eastern and Northern regions causing up to 54% yield loss in soybean (Namara et al. 2015). GLM damage is characterized by the leaf-mining of larvae between the epidermis and longitudinal folding of individual leaves (Jyothis et al. 2008) leading to decreases in photosynthetic capacity and early defoliation affecting the pod-filling stage (Shanower et al. 1993). Traditionally, GLM pest is controlled by pesticide sprays during the cropping season (Okello et al. 2013), however, previous studies have shown that leaf miners

can develop a high degree of resistance to a broad range of insecticides over a relatively short time (Mou 2008). The resource-poor soybean producers in Sub-Saharan Africa have limited funds for buying pesticides (Munyuli et al. 2003). Given the negative aspects of reliance on pesticides, host-plant resistant cultivars is a more sustainable integrated management approach to leaf miner control (Hill et al. 2009).

Makerere University through the Centre for Soybean Improvement and Development released twelve moderately resistant soybean genotypes (Namara et al. 2015). However, knowledge regarding genetic control and heritability of resistance to GLM and its relationship to other plant traits is needed to be able to develop appropriate procedures in the breeding for resistance. Previous genetic studies on other soybean defoliating insect pests suggested that inheritance of resistance was quantitatively inherited (Rector et al. 2000) and either controlled by a single incompletely dominant (Ojo and Ariyo 1999) or multiple genes (Mebrahtu et al. 1990). The incorporation of the genes for GLM resistance into cultivars with desirable agronomic traits and high yielding is a goal actively pursued in soybean breeding programmes in Uganda. It is important to understand the nature of the gene action to help the breeders to select the suitable parents for the crossing programme (Maphosa et al. 2012). The objective of this study was to determine the mode of inheritance and to identify parents with high combining abilities for soybean GLM resistance.

Materials and methods

Experimental site and germplasm

The study was carried at locations in soybean growing areas of northern and eastern Uganda. The first experimental location was at the District Agricultural Training and Information Centre in Iki-iki sub-county, Budaka district (1°06'N, 34°00'E) located at 1156 m asl with a mean annual rainfall of 1200 mm and temperature of 24.7 °C (Namara et al. 2015). The second location was at Abi Zonal Agricultural Research and Development Institute in Arua (3°04'N, 30°56'E) with an average altitude of 1215 m asl, a mean annual rainfall of 1250 mm and temperature of 24 °C (Sserumaga et al. 2015). These areas are considered hotspot regions of groundnut leaf miner

in Uganda (Okello et al. 2010; Namara et al. 2015). Thirteen soybean genotypes, obtained from the USA, International Institute of Tropical Agriculture (IITA) and Uganda (see Table 1 for their full description). These genotypes were selected based on their GLM reaction as reported by Namara et al. (2015).

Crosses and mating design

A full diallel mating design developed by Griffing (1956) was used for this study. Five seeds from each of the 13 parents were planted in perforated plastic pots of diameter 25 cm and height 30 cm containing sterilized loam and sandy soils in the screen house at the Makerere University Agricultural Research Institute Kabanyolo (MUARIK), from October 2015 to April 2016. Staggered planting of parents was done to synchronize flowering and to ensure continuous availability of flowers for crossing. Plants were watered after every two days until they reached physiological maturity. The F_1 seeds were planted alongside their respective parents in the screen house and allowed to self-pollinate to produce the F_2 populations. The pods of the crosses (F_2) were harvested at physiological maturity on a plant basis.

Field evaluation of parents and F_2 populations for GLM resistance

The 13 parental genotypes together with their 81 F_2 plants were grown in an alpha-lattice design with five blocks $\times$ 19 genotypes per block. A two-meter long

row was planted at a spacing of 60×5 cm per genotype in each of the five blocks, replicated twice. The last row in each replication consisted of a particular genotype added in order to fit the design. Planting was done in the second growing season of 2016 (September to December) the period when the pest is reported to occur under natural insect infestation in two GLM hotspot locations of Iki-iki sub-county in Budaka and Abi Zonal Agricultural Research and Development Institute in Arua district, Uganda (Namara et al. 2015). Data were recorded for incidence, severity and number of leaf miner larvae (average from 10 randomly selected F_2 plants per each genotype) per plot at 40, 60, 70 and 80 days after planting in order to monitor the infestation levels at the different crop stages (Ramani and Lingappa 1988). The data on GLM incidence was obtained by counting the total number of leaflets and damaged leaflets from 10 randomly selected plants per plot and expressed as percentage leaflet damage (Praveena et al. 2011). The GLM severity was given by using a standard scale of 1–5 (Praveena et al. 2011) (Table 2). The yield per hectare was estimated from dry seed weight per plot.

Data analysis

Differences in resistance traits among the parental genotypes and their crosses across the four sampling times and their interactions were examined using Restricted Maximum Likelihood (REML) analysis in

Table 1 Genotypes used as parents in the study

Genotypes	Origins	Maturity	Incidence (%)	Severity score	Resistance level to GLM	G.Y kg ha ⁻¹
PI615437	USA	Medium	97	2.7	MR	442.0
BSPS 48C	Uganda	Medium	98	2.5	MR	312.4
PI578457A	USA	Medium	95	2.9	MR	377.2
NIIGC4.1-2	Uganda	Medium	98	2.8	MR	366.1
Maksoy1 N	Uganda	Early	99	3.8	MS	393.2
Siesta	Zimbabwe	Medium	94	4.4	S	389.1
Maksoy4 N	Uganda	Late	100	3.7	S	281.9
Maksoy2 N	Uganda	Late	99	3.9	MS	272.7
Maksoy3 N	Uganda	Late	93	3.0	MR	346.9
Maksoy5 N	Uganda	Medium	97	3.1	MS	430.4
K-local	Uganda	Early	97	4.4	S	290.2
Namsoy4 M	Uganda	Late	97	4.5	S	281.0
Wondersoya	IITA	Medium	97	3.8	MS	307.2

Source: (Namara et al. 2015). *MR* moderately resistant, *MS* moderately susceptible, *S* susceptible, *G.Y* Grain yield ha⁻¹

Table 2 Severity score and resistance category of GLM damage (Preveena et al. 2011)

Foliage damage (%)	Severity score	Category
0	1	Immune
1–20	2	Resistant
21–40	3	Moderately resistant
41–60	4	Moderately susceptible
61–100	5	Highly susceptible

Genstat statistical software 12th Edition (Payne et al. 2009) to estimate the amount of variability for the traits. Means were separated using Fisher's LSD test at 5% probability level.

The statistical model used for this analysis was described by Smith et al. (2005) as follows:

$$y_{ijklm} = \mu + \rho_i + l_j + b_{m(l)} + \rho_{lji} + \varepsilon_{ijklm}$$

where y_{ijklm} = the observed value for the i th genotype from j th location, m th block nested within the l th replication; μ = the general mean effect; ρ_i = is the i th genotype effect (considered as fixed effect); l_j = is the j th location effect (considered as fixed effect); $b_{m(l)}$ = is the effect of m th block nested within the l th replication (considered as random); ρ_{lji} = is the interaction effect of j th location and i th genotype (considered as fixed effect) and ε_{ijklm} = is the experimental error considered as random.

$$Y_{ijklc} = \mu + C_l + G_{ij} + S_{ij} + R_{ij} + (CG)_{il} + (CG)_{jl} + (CS)_{ijl} + (CR)_{ijl} + e_{ijklc},$$

where Y_{ijklc} is the observed value of each experimental unit; μ is the overall mean; C_l is the environmental effect; G_{ij} is the GCA effect for i th or j th parent; S_{ij} is the SCA effect for ij th F_2 plants; R_{ij} is the reciprocal effect for ij th or ji th F_2 plants; $(CG)_{il}$ is the interaction between GCA effect for i th parent and environments; $(CG)_{jl}$ is the interaction between GCA effect for j th parent and environments; $(CS)_{ijl}$ is the interaction between SCA effect for ij th F_2 plants and environments; $(CR)_{ijl}$ is the interaction between reciprocal effect for ij th or ji th F_2 plants and environments and e_{ijklc} is the random residual term.

The relative importance of GCA and SCA was estimated using the general predicted ratio (GPR) for all the traits and computed as illustrated by Baker (1978);

$$GCA = (2 \times MSQGCA) / \{(2 \times MSQGCA) + MSQSCA\}$$

where; $MSQGCA$ and $MSQSCA$ are the sum of mean squares for GCA and SCA, respectively.

Heritability of resistance to GLM was estimated on trait basis using the fixed effects model (Baker 1978). Broad sense heritability (H) and narrow sense heritability (h^2) on different traits (Kayaga et al. 2017) were determined as follows:

$$H = \frac{2\sigma^2 GCA + \sigma^2 SCA}{2\sigma^2 GCA + \sigma^2 SCA + (2 * \sigma^2 GCA * Location + \sigma^2 SCA * Location) / 2 + (Error / 2)}$$

$$h^2 = \frac{2\sigma^2 GCA}{2\sigma^2 GCA + \sigma^2 SCA + (2 * \sigma^2 GCA * Location + \sigma^2 SCA * Location) / 2 + (Error / 2)}$$

Estimation of heritability, general and specific combining ability

The general and specific combining abilities for each trait were analyzed according to Griffing's Model 1 (Griffing 1956) and method 3 over environments outlined as follows:

where, $\sigma^2 GCA$ = general combining ability variance; $\sigma^2 SCA$ = specific combining ability variance.

Results

A combined (over locations) analysis of variance showed that there were highly significant ($P < 0.001$)

Table 3 Analysis of variance for resistance traits to GLM in a diallel cross of 94 genotypes (parents and crosses) across locations, 2016

Source of variation	DF	GLM Incidence				GLM Severity				NL	GY
		40DAP	60DAP	70DAP	80DAP	40DAP	60DAP	70DAP	80DAP		
Location	1	3197.26**	1565.25**	412.36**	112.29*	415.90***	141.11***	75.22***	20.78***	24,179.55**	1,518,357*
Location × Replication	2	12.07	5.02	2.27	3.44	0.55	0.01	0.08	0.0012	61.77	21,366*
Location × Rep × Block	18	13.34**	9.08**	4.99***	3.39*	0.39	0.20***	0.30***	0.15***	22.14	4321
Genotype	93	67.03***	78.19***	36.6***	19.09***	1.36***	1.15***	0.67***	0.42***	129.12*	24,135***
Genotype × Location	93	51.89***	71.56***	30.74***	19.39***	0.91***	0.85***	0.54***	0.35***	177.6***	16,720***
Residual	171	6.41	4.29	1.96	1.69	0.30	0.07	0.06	0.04	31.47	3625
LEE	91	25.97	35.95	15.51	9.73	0.46	0.44	0.29	0.18	88.15	8217.423
CV		2.8	2.3	1.5	1.4	17	6.9	6.1	4.4	27.4	84.3

***, **, * Significant at 0.001; 0.01, and 0.05 probability levels, respectively; DAP days after planting, NL number of larvae per plant, G.Y grain yield in kg ha^{-1} , LEE Lattice effective error and CV coefficient of variation

genotypic differences among the 94 genotypes for GLM incidence across all of the four sampling dates (Table 3). The location effects were significant ($P < 0.01$) for GLM incidence at 40, 60 and 70 DAP and ($P < 0.05$) at 80 DAP. The genotype × location interaction was also highly significant ($P < 0.001$) for all the sampling dates. There were highly significant ($P < 0.001$) genotypic differences among the genotypes, location as well as the interaction between genotype and location for soybean severity to GLM attack in all the four sampling dates. Groundnut leaf miner reached peak severity at 40 DAP during the vegetative growth stage as indicated by the highest mean sum of squares value. A combined analysis of variance also revealed significant ($P < 0.05$) genotypic differences in the number of larvae per plant among the genotypes, location ($P < 0.01$) as well as the interaction between genotype and location ($P < 0.001$). There were also significant ($P < 0.001$) differences in grain yield among the 94 genotypes and location ($P < 0.05$). In addition, there was a significant ($P < 0.001$) genotype × location interaction effects.

The mean scores of parental genotypes and 15 selected F_2 populations (10 least and 5 most damaged) for GLM incidence, severity, number of larvae per plant and grain yield ha^{-1} are presented in Table 4. The incidence of GLM among the parental genotypes ranged from 88.6% to 98.9% in Arua and 95.2 to 100% in Iki-iki. Moderately susceptible genotype PI57857A recorded the lowest GLM incidence while the susceptible genotype K-local recorded the highest value (99.5%) across locations.

The mean of parental genotypes for GLM severity damage ranged from 3.1 to 4.4 across locations. Plant introductions PI615437 showed moderate susceptibility level with the lowest severity score of 3.1 whereas the genotype K-local had the highest severity score across locations. Most of the commercial genotypes (Maksoy1 N, Maksoy2 N, Maksoy3 N, Maksoy4 N and Maksoy5 N) showed a high level of susceptibility to GLM attack with the exception of Namsoy4 M which showed moderate susceptibility level with a severity score of 3.3.

The mean numbers of larvae per plant ranged from 19 to 27.5 among parental genotypes. Moderately susceptible genotype PI578457A recorded the lowest mean number of larvae per plant (19) whereas susceptible genotype Maksoy4 N the highest (27.5).

Table 4 Mean performance of parents and 15 selected F_2 populations for GLM incidence, severity and number of larvae per plant and grain yield across locations

Parents	GLMR	I Arua	I Iki-iki	I Locations	S Arua	S Iki-iki	S Locations	NL	GY
Maksoy1 N	HS	93.8	100.0	96.9	4.3	4.6	4.0	19.7	98.2
Maksoy2 N	HS	95.9	100.0	97.9	4.0	4.7	3.9	23.7	44.2
Maksoy3 N	HS	97.4	100.0	98.7	4.0	4.6	3.9	22.7	40.5
Namsoy4 M	MS	95.2	95.2	95.2	4.0	3.7	3.3	25.9	74.6
Maksoy4 N	HS	97.0	100.0	98.5	4.3	4.7	4.2	27.5	4.8
Maksoy5 N	HS	96.4	100.0	98.2	4.2	4.4	3.8	19.6	63.5
BSPS48C	HS	94.5	98.1	96.3	4.1	4.7	4.0	20.2	19.1
K_Local	HS	98.9	100	99.5	4.7	4.9	4.4	20.9	58.3
NIIGC4-12	MS	91.6	98.7	95.1	3.1	4.3	3.4	24.6	195.8
PI578457A	MS	86.2	100	93.3	2.9	4.7	3.5	19	103.1
PI615437	MS	88.6	100	94.3	2.2	4.4	3.1	16.8	242.1
Siesta	HS	96.4	100	98.2	4.2	4.5	3.9	23.3	61.8
Wondersoya	HS	91.4	100	95.7	2.5	4.8	4.1	21	7
F_2 Crosses									
Maksoy1 N $\times$ PI615437	MR	94.7	57.5	76.1	3.07	2.5	2.8	7.5	511.6
PI615437 $\times$ PI578457A	MR	90.7	93.8	92.2	2.13	3.9	3	13.9	170.1
NIIGC4.1-2 $\times$ PI615437	MR	90.1	98.9	94.5	2.01	4.0	3.0	19.1	196.8
Maksoy1 N $\times$ PI578457A	MS	99.1	96.6	97.8	3.46	4.1	3.8	17.3	68.4
NIIGC4.1-2 $\times$ PI578457A	MS	86.6	95.4	91.01	2.89	4.0	3.5	15.5	131.5
PI615437 $\times$ NIIGC4.1-2	MS	84.3	97.1	90.7	2.4	4.3	3.4	11.1	137.6
PI578457A $\times$ PI615437	MS	89.9	95.9	92.9	2.82	3.7	3.25	11.2	107.3
PI578457A $\times$ Siesta	MS	95.6	100	97.8	2.66	4.7	3.7	16.2	341.8
NIIGC4.1-2 $\times$ Maksoy1 N	MS	93.5	100	96.7	2.29	4.6	3.4	15.7	61.3
Maksoy5 N $\times$ PI578457A	MS	93.1	91.9	92.5	2.44	3.9	3.2	23.5	73.2
Maksoy2 N $\times$ Siesta	HS	99.2	100	99.6	4.63	4.7	4.9	14.8	0
BSPS48C $\times$ NIIGC4.1-2	HS	99.8	100	99.9	4.36	4.9	4.6	20.1	0
PI578457A $\times$ Maksoy4 N	HS	96.1	96.6	96.3	3.47	4.6	4.0	26.9	0
Wondersoya $\times$ PI615437	HS	97.5	95.4	96.5	4.01	4.5	4.2	42.3	114.7
Maksoy1 N $\times$ Maksoy2 N	HS	98.2	100	99.2	4.23	4.6	4.4	6.3	22.65

GLMR Groundnut leaf miner reaction, I GLM incidence, S GLM severity, I Locations Incidence across locations, S Locations Severity across locations, MR = moderately resistant, MS moderately susceptible, HS highly susceptible, Dap days after planting, NL = Number of larvae per plant, G.Y grain yield in kg ha^{-1}

Grain yield ranged from 4.8 to 195.8 kg ha⁻¹ among parental genotypes across locations. Moderately susceptible genotype NIIGC4.1-2 recorded the highest grain yield (195.8 kg ha⁻¹) and susceptible genotype Maksoy4 N the lowest yields (4.8 kg ha⁻¹) across location.

The mean score of incidences of GLM attack for the F₂ populations ranged from 76.1% to 99.6% across locations. The F₂ population of cross Maksoy1 N × PI615437 recorded the lowest GLM incidence (76.1%) while Maksoy2 N × Siesta recorded the highest GLM incidence (99.6%). The incidence for crosses ranged from 57.5–100% in Iki-iki and 84.3–100% in Arua, respectively. The mean scores for GLM severity ranged from 2.8 to 4.9 among crosses across locations. There were no categories of immune or resistant genotypes observed in this evaluation, however, about 3.7% of F₂ crosses were moderately resistant with GLM severity scores of 2.8–3.0 across locations while 34.5% of F₂ populations were moderately susceptible with severity scores ranging from 3.1 to 3.9, and 60.4% were highly susceptible to GLM attack with mean score of 4.1–4.9. The F₂ populations of cross Maksoy1 N × PI615437 recorded the lowest GLM severity score (2.8) across location. Other crosses with moderately resistant levels of GLM severity score (3.0) across locations were PI615737 × PI578457A and NIIGC4.1-2 × PI615473.

The mean numbers of larvae per plant ranged from 42.3 among crosses at 40 DAP across locations. The F₂ population of cross Wondersoya × PI615437 recorded the highest number of larvae per plant (42.3) whereas the crosses Maksoy1 N × Maksoy2 N and Maksoy1 N × PI615437 recorded the lowest numbers of larvae per plant of 6.3 and 7.5, respectively across locations. Grain yield ranged from 0 to 511.6 kg ha⁻¹ across locations. The highest yield (511.6 kg ha⁻¹) across locations was from the cross Maksoy1 N × PI615437 while the lowest yields (0 kg ha⁻¹) was from crosses BSPS48C × NIIGC4.1-2, Maksoy2 N × Siesta and PI578457A × Maksoy4 N.

Combining ability

The analysis of variance of combining ability among the 81 F₂ progeny indicated that the GCA effects were significant ($P < 0.05$) for the GLM incidence only at

40 DAP (Table 5). The analysis revealed highly significant ($P < 0.001$) location effects among the F₂ progenies for GLM incidence at 40, 60 and 70 DAP. The SCA analysis and reciprocal crosses showed non-significant effects for incidence at all the four sampling dates. The interaction of the GCA effects and location (GCA × L) was highly significant ($P < 0.001$) at 70 DAP, significant ($P < 0.01$) at 80 and ($P < 0.05$) at 60 DAP. The interaction of the SCA effects and location (SCA × L) was significant ($P < 0.01$) for incidence at 40 and 60 DAP, and ($P < 0.05$) at 80 DAP. The interaction of reciprocal effects and location (R × L) were significant ($P < 0.001$) for all the four planting dates for GLM incidence. Baker's ratio was 1.0 for GLM incidence for all the sampling dates, except at 70DAP. The broad sense heritability (BSH) estimates for GLM incidence were low and ranged from 0.06 to 0.38 across locations. Narrow sense heritabilities (NSH) estimates at different DAP were also low and had the same values as BSH for all the sampling dates, except at 70DAP.

The mean sums of squares of the GCA were significant ($P < 0.001$) for GLM severity at 40 DAP and ($P < 0.05$) at 60 DAP but non-significant at 70 DAP and 80 DAP. Highly significant ($P \leq 0.001$) location effects were recorded for GLM severity at all the four planting dates. The interaction of GCA effects with the location was highly significant ($P < 0.001$) for GLM severity at 70 DAP and 80 DAP, and significant ($P < 0.01$) at 60 DAP. The interaction of SCA effects with location was highly significant ($P < 0.001$) at 40 DAP and significant ($P < 0.01$) at 60 DAP for GLM severity damage. Also, the interaction of reciprocal crosses with the location was significant ($P < 0.01$) at 40 and 60 DAP, and not-significant at 70 and 80 DAP for GLM severity damage. Baker's ratio for GLM severity damage was 1.0 at all the four sampling dates. The estimates of broad sense heritability for GLM severity damage across locations was moderate (estimated value 0.54) at 40 DAP but low at 60, 70 and 80 DAP. Narrow sense heritabilities at different DAP had the same values as BSH except at 70 DAP.

The sum of mean squares for number of larvae per plant was highly significant ($P < 0.001$) for location, significant ($P < 0.005$) for reciprocal crosses and non-significant for GCA and SCA. Baker's ratio for the number of larvae per plant was zero across locations.

Table 5 Combined ANOVA for GCA and SCA, heritability of 81 Soybean crosses over two locations

Source of variation	D.F	GCA Mean squares GLM Incidence			GCA Mean squares GLM severity			NL	GY
		40_dap	60_dap	70_dap	80_dap	40_dap	60_dap	70_dap	80_dap
Location	1	1149.33***	560.46***	107.44***	14	171.84***	52.82***	28.85***	7.31***
Crosses	80	36.87	44.08	19.42	10.63	0.74*	0.61	0.33	0.20
GCA	12	89.74*	78.45	28.97	17.13	2.77***	1.95*	1.05	0.61
SCA	44	24.65	23.93	12.79	7.24	0.32	0.26	0.18	0.11
Reciprocal crosses	24	32.83	63.84	26.78	13.61	0.49	0.59	0.25	0.16
Crosses × Location	80	26.48***	39.69***	15.88***	9.39***	0.478***	0.45***	0.30***	0.17***
GCA × Location	12	22.18	35.01*	24.19***	11.48**	0.17	0.58**	0.83***	0.44***
SCA × Location	44	25.23**	30.92**	11.03	7.26*	0.56***	0.39**	0.21	0.13
Recip × Location	24	30.93***	58.12***	20.62***	12.24***	0.47**	0.50**	0.20	0.10
Error	171	12.98	17.98	7.75	4.87	0.23	0.22	0.15	0.09
$\sigma^2_{GC A}$	3.57	2.30	2.30	0.25	0.30	0.14	0.07	0.01	0.01
$\sigma^2_{SC A}$	– 0.21	– 2.50	0.63	– 0.01	– 0.09	– 0.05	– 0.01	– 0.01	– 0.01
$\sigma^2 R$	0.47	1.43	1.54	0.34	0.34	0.01	0.02	0.01	0.01
$\sigma^2_{GCA} \times ENV$	0.97	1.80	1.74	0.70	0.70	– 0.01	0.04	0.07	0.04
$\sigma^2_{SCA} \times ENV$	8.77	9.27	2.34	1.71	1.71	0.24	0.12	0.04	0.03
$\sigma^2 R \times ENV$	8.97	20.07	6.43	3.69	3.69	0.12	0.14	0.03	0.01
NSH (h^2)	0.38	0.23	0.06	0.13	0.13	0.54	0.41	0.12	0.16
BSH (H)	0.38	0.23	0.14	0.13	0.13	0.54	0.41	0.12	0.16
BR	1	1	1	0.44	1	1	1	1	1

GCA the general combining ability, SCA the specific combining ability, Recip. Reciprocal crosses, BR the general predicted ratio, NL number of larvae per plant, G.Y grain yield in kg ha⁻¹, BSH (H) Broad sense heritability, NSH (h^2) Narrow sense heritability, σ^2 GCA variance due to GCA; σ^2 SCA variance due to SCA; $\sim \sigma^2$ R variance due to reciprocal crosses. σ^2 GCA × ENV Variance due to interaction between GCA and Environment, σ^2 SCA × ENV Variance due to interaction between SCA and environment, σ^2 R × ENV Variance due to interaction between reciprocal crosses and environment

Table 6 GCA estimates of individual parents, SCA and reciprocal effects of 15 selected F₂ populations for GLM severity score and incidence, number of larvae per plant and grain yield across locations

GCA effects														
Parents	GLM incidence				GLM Severity				IA	SS	NL	GY		
	40DAP	60DAP	70DAP	80DAP	40DAP	60DAP	70DAP	80DAP						
Maksoy1 N	- 1.25	- 0.72	- 1.15	- 0.96	- 0.02	- 0.06	- 0.03	- 0.08	- 2.80**	- 0.06	- 3.90*	22.38		
Maksoy2 N	1.85	2.20	1.22	1.01	0.45**	0.47***	0.34**	0.24**	2.20*	0.38***	1.16	- 47.62**		
Maksoy3 N	2.10*	- 0.20	- 0.07	0.22	0.52***	0.17	0.10	0.06	1.45	0.25**	2.81	- 19.72		
Namsoy4 M	0.52	- 0.29	- 0.25	- 0.30	0.22	- 0.21	0.03	0.02	0.24	0.02	1.74	4.28		
Maksoy4 N	0.34	1.54	0.43	0.51	- 0.12	0.31*	0.21*	0.17*	0.79	0.14	1.41	- 45.02**		
Maksoy5 N	1.37	1.18	0.71	0.67	- 0.32**	0.05	0.00	0.03	- 0.39	- 0.10	2.06	3.68		
BSPS48C	3.24***	2.40*	1.54*	1.03	0.49***	0.27*	0.18	0.15*	2.86**	0.33***	1.80	- 45.02**		
K Local	- 0.20	3.05*	1.41	0.92	- 0.14	0.45**	0.31*	0.22*	0.57	0.21*	0.51	- 45.22*		
NIIGC4 - - 12	- 1.79**	- 1.36	- 0.65	- 0.43	- 0.03	- 0.24**	- 0.12	- 0.12*	- 0.81	- 0.13*	0.45	18.48		
PI578457A	- 1.99*	- 1.78*	- 1.26*	- 0.78	- 0.28**	- 0.34***	- 0.18*	- 0.15*	- 1.33	- 0.26***	- 0.31	30.58*		
PI615437	- 3.42***	- 3.80***	- 1.98***	- 1.71***	- 0.67***	- 0.46***	- 0.47***	- 0.34***	- 2.50**	- 0.54***	- 3.16*	65.88***		
Siesta	1.53	1.61	1.06	0.68	0.05	- 0.01	0.04	0.10	1.38	0.05	- 2.98	3.68		
Wondersoya	2.09**	1.20	1.38*	0.90	0.46***	0.351***	0.20*	0.16*	1.91*	0.34***	0.27	- 34.22*		
Crosses														
1 N × 2 N	0.84	2.17	1.26	- 0.64	0.18	- 0.05	0.07	0.07	3.00	0.02	- 10.93*	- 20.52		
1 N × 5 N	2.48	2.06	1.29	- 0.71	0.03	0.14	- 0.07	- 0.10	- 6.60*	- 0.03	- 1.50	- 2.25		
1 N × PI615437	- 4.82	- 8.88*	- 8.15***	5.94***	0.06	- 0.34	- 0.15	- 0.17	- 5.74*	- 0.12	2.31	132.22*		
5 N × 1 N	2.48	2.06	1.29	- 0.71	0.03	0.14	- 0.07	- 0.10	- 6.60*	- 0.03	- 1.50	- 2.25		
5 N × PI578457A	- 5.14	- 1.81	- 2.86	- 0.11	- 0.69	- 0.38	- 0.621*	- 0.13	- 2.42	- 0.52*	2.07	- 31.29		
BSPS × Wonder	- 2.89	- 1.82	- 1.90	1.23	- 0.46	- 0.54	- 0.44	- 0.33	- 2.67	- 0.52	- 4.80	99.65*		
K - local × 3 N	1.67	0.81	0.00	0.45	0.07	0.05	0.04	- 0.04	0.91	0.08	- 10.07*	7.28		
NIIGC × PI57	- 6.40*	- 5.52	- 1.65	2.20	0.26	- 0.65	- 0.19	- 0.22	- 3.77	- 0.18	- 7.64	24.58		
PI57 × NIIGC	- 6.40*	- 5.52	- 1.65	2.20	0.26	- 0.65	- 0.19	- 0.22	- 3.77	- 0.18	- 7.64	24.58		
PI57 × Siesta	0.15	- 0.20	1.54	- 0.80	0.27	- 0.17	- 0.49	- 0.24	0.91	- 0.16	- 0.04	235.16***		
PI615437 × 1 N	- 4.82	- 8.88*	- 8.15***	5.94***	0.06	- 0.34	- 0.15	- 0.17	- 5.74*	- 0.12	2.31	132.22*		
PI615 × K - local	- 5.49*	0.08	- 0.19	- 1.48	0.33	- 0.33	- 0.26	0.01	- 2.28	- 0.03	8.28	- 71.63		
Siesta × Wonder	- 0.67	- 1.75	- 1.11	0.88	0.08	- 0.10	- 0.03	- 0.03	- 1.15	- 0.04	- 2.21	14.00		
Wonder × 4 M	1.11	0.18	0.20	- 0.10	- 0.20	0.26	0.10	0.05	0.18	0.01	3.33	- 29.26		
Wonder × PI57	4.56	3.42	1.16	- 0.57	0.21	0.66	0.41	0.22	2.10	0.37	3.81	- 43.19		
Reciprocal effects														
1 N × 5 N	0.55	0.88	0.48	0.275	- 0.47	0.419	0.37	0.25	- 11.45***	0.11	1.42	9.91		
1 N × NIIGC	- 4.14	1.62	1.05	0.37	0.00	0.61	0.53	0.48*	- 1.125	0.44	9.01	- 9.8		
1 N × PI615437	- 8.32***	- 15.32***	- 11.61***	- 8.55***	- 0.59	- 0.91*	- 0.60*	- 0.61*	- 9.95***	- 0.61*	- 8.18	221.2***		

Both the broad sense heritability and narrow sense heritability estimates of the number of larvae per plant also had zero values. The mean sums of squares of interaction for grain yield and locations were highly significant ($P < 0.001$) but non-significant for GCA, SCA and reciprocal crosses. The broad sense heritability was low (0.07), and both the narrow sense heritability and Baker's ratio for grain yield had zero values.

Analysis of combining ability (GCA) effects of individual parents, specific combining ability (SCA) and reciprocal effects for F_2 populations.

The results of GCA effects of individual parents, SCA and reciprocal effects of 15 selected crosses (best performing) for GLM incidence and severity at the four sampling dates, the number of larvae per plant and grain yield ha^{-1} across locations are presented in Table 6. GCA effects for GLM incidence ranged from -2.80 to 2.86 across locations. Parents Maksoy1 N and PI615437 exhibited significant ($P < 0.01$) negative GCA effects for GLM incidence across locations. In contrast, significant ($P < 0.01$) positive GCA effects for incidence trait were observed for the parent BSPS48C and ($P < 0.05$) for parents Wondersoya and Maksoy2 N.

The general combining ability effects for GLM severity score ranged from -0.54 to 0.38 across the locations. GCA effects combined across locations indicated that parents PI615437 and PI578457A were good combiners for GLM severity score with highly significant ($P < 0.001$) negative GCA effects whereas parent NIIGC4.1-2 had significant ($P < 0.05$) negative effects. Parents BSPS48C, Maksoy2 N and Wondersoya showed highly significant ($P < 0.001$) positive GCA effects for GLM severity score and significant ($P < 0.01$) effect was observed for parent Maksoy3 N and ($P < 0.05$) for K-local.

The GCA effects for the number of larvae per plant ranged from -3.90 to 2.81 across locations. Significant ($P < 0.05$) and negative GCA effects for the number of larvae per plant were observed for Parents Maksoy1 N and PI615437. GCA effects for grain yield ha^{-1} ranged from -47.62 to 65.88 across locations. Significant ($P < 0.01$) negative GCA effects for grain yield ha^{-1} were observed for parents BSPS48C, Maksoy2 N, Maksoy4 N and ($P < 0.05$) for parents K-local and Wondersoya. In contrast, highly significant ($P < 0.001$) positive GCA effect

Table 7 Correlation matrix for different traits

Traits	NL	G.Y	I.A
NL	–		
G.Y	-0.363^{***}	–	
I.A	0.227^*	-0.585^{***}	–
S.A	0.382^{***}	-0.676^{***}	0.571^{***}

NL number of larvae per plant, G.Y Grain yield kg ha^{-1} , I.A Incidence across locations, S.A Severity across locations

was observed for parent PI615437 and ($P < 0.05$) for PI578457A across locations.

SCA effects combined across locations indicated that the F_2 populations of crosses Maksoy1 N $\times$ PI615437, Maksoy1 N $\times$ Maksoy5 N, Maksoy5 N $\times$ Maksoy1 N and PI615437 $\times$ Maksoy1 N were significant ($P < 0.05$) and negative for GLM incidence across locations. A significant ($P < 0.05$) negative SCA effect was also observed for GLM severity for the F_2 populations of cross involving Maksoy5 N and PI578457A. The SCA effects for number of larvae per plant were also significant ($P < 0.05$) and negative for the F_2 populations of crosses Maksoy1 N $\times$ Maksoy2 N and K-local $\times$ Maksoy3 N across location. Highly significant ($P < 0.001$) positive SCA effects across locations were observed for grain yield for the F_2 cross involving PI57457A and Siesta and significant ($P < 0.05$) effects for the F_2 populations of crosses Maksoy1 N $\times$ PI615437, BSPS48C $\times$ Wondersoya and PI615437 $\times$ Maksoy1 N.

Highly significant ($P < 0.001$) and negative reciprocal effects for GLM incidence were observed in the F_2 progenies of crosses Maksoy1 N $\times$ PI615437 and Maksoy1 N $\times$ Maksoy5 N across locations. In contrast, the F_2 populations of the crosses Maksoy5 N $\times$ Maksoy1 N and PI615437 $\times$ Maksoy1 N recorded highly significant ($P < 0.001$) and positive reciprocal effects. Significant ($P < 0.05$) and negative reciprocal effects for GLM severity were observed in the F_2 populations of crosses Maksoy1 N $\times$ PI615437 and Namsoy4 M $\times$ NIIGC4.1-2. On the other hand, significant ($P < 0.05$) and positive reciprocal effects were recorded for the F_2 crosses NIICG $\times$ Namsoy4 N and PI615437 $\times$ Maksoy1 N. Highly significant ($P < 0.001$) positive reciprocal effects for grain yield ha^{-1} were observed in the F_2 population of the cross involving Maksoy1 N and PI615437, however,

highly significant ($P < 0.001$) and negative effects were observed in the F_2 population of cross PI615437 $\times$ Maksoy1N.

Table 6 GCA estimates of individual parents, SCA and reciprocal effects of 15 selected F_2 populations for GLM severity score and incidence, number of larvae per plant and grain yield across locations.

Relationships of different resistance traits

The correlation coefficients among the studied soybean resistance traits to GLM are given in Table 7.

There was a highly significant ($P < 0.001$) negative correlation between grain yield ha^{-1} and the number of larvae per plant ($r = -0.363$), but a highly significant ($P < 0.001$) positive correlation between the GLM severity and number of larvae per plant ($r = 0.382$) and a significant ($P < 0.05$) positive correlation between GLM number of larvae per plant and the incidence ($r = 0.227$). GLM incidence and severity were highly significantly ($P < 0.001$) positively correlated ($r = 0.571$), but the grain yield ha^{-1} was negatively correlated to the incidence ($r = -0.585$) and severity ($r = -0.676$).

Discussion

Significant variations were found among the 94 genotypes (parents and crosses) for all the resistance traits to GLM, which indicated that there was adequate genetic variability among the studied soybean genotypes (Table 3). This finding suggested the possibility of selecting genotypes that possess resistant genes to GLM that could be introgressed into susceptible cultivars with acceptable attributes. Similar observations were made by El-Bramawy and Osman (2012) who reported significant genotypic variations in the number of miners per 100 leaflets, number of larvae per 100 leaflets and seed yield per plant in *Vici faba*. (Namara et al. 2015) reported significant genotypic differences for GLM incidence at 40 DAP, severity at 40, 54, 68 and 82 DAP and yield in soybean. Significant environmental effects were observed for all the traits studied indicating that certain genotypes reacted differently in different locations but in all cases GLM reached peak severity early (40 DAP) during the vegetative stage as indicated by the highest mean square values and suggested that any select for

GLM resistance and any GLM pesticide application should begin at 40 DAP. The high GLM damage level recorded in genotypes suggested that these species were able to successfully adapt to the environmental field conditions (Table 4) and confirmed the findings of Du Plessis (2011) and Buthelezi et al. (2013). Taware et al. (2001) also reported GLM peak infestation at 20 days after germination during the vegetative stage. Gianessi et al. (2002) reported that foliage loss greater than 35% during soybean vegetative stage caused economic yield loss due to the reduction in the light interception by the soybean canopy. In contrast, Namara et al. (2015) recorded the peak infestation during the soybean crop reproductive stage at Serere and Iki-iki.

The significant GCA effects for GLM incidence and severity suggested significant role of additive gene effects in the inheritance of soybean resistance to GLM (Table 5). Baker's ratio which reveals the relative importance of GCA effect with respect to SCA effect, was high for these traits at all the sampling dates except at 70 DAP. The predominance of GCA effects over SCA effects implied that additive gene action was more important than non-additive gene action for resistance to GLM, and that GCA was the major component responsible for the differences among the genotypes. This implied that early generation selection would be effective and resistant hybrids could be predicted from GCA effects of parents (Nyadanu et al. 2017). EL-Garhy et al. (2015) reported the predominance of additive gene effects in determining resistance to cotton leaf worm defoliator and yield components in soybean in Egypt. Anderson et al. (1990) reported significant parental GCA and SCA effects for leaf miner *A. modicella* (Deventer) damage in a diallel cross in peanut with a preponderance of additive gene action. The broad sense and narrow sense heritabilities had the same values for GLM incidence and severity and was attributed to the fact that the SCA variance component was zero for most of the traits studied. The broad sense and narrow sense heritability values for GLM incidence, severity score across locations were generally low (range 0.06–0.41) except at 40 DAP (0.54) (Table 5), and suggested the low genetic contribution towards the phenotypic variance (Holland et al. 2003). The low heritabilities observed for these traits at the different DAP were attributed to the high significant environmental and genotype $\times$ environment interaction

effects across locations (Acquaah 2012). The implication is that the resistance to defoliator pests in soybean is a quantitatively inherited trait (Rector et al. 2000; Warrington et al. 2008).

The GCA mean sums of squares for the number of larvae per plant and grain yield were non-significant across locations which indicated the high involvement of non-additive gene action in the expression of these traits (Acquaah 2012). The Backer ratio was low for the number of larvae per plant and grain yield ha^{-1} , indicating the predominance of non-additive gene effects in the inheritance of the traits. The involvement of non-additive gene effects in the inheritance of soybean grain yields was previously reported by Kiryowa et al. (2008) and Wanderi (2012). The broad sense and narrow sense heritabilities for GLM number of larvae per plant and grain yield ha^{-1} were low, again indicating that these traits were influenced by non-additive action and therefore, response to selection for resistance to GLM would be low if directed on GLM number of larvae per plant and grain yield (Holland et al. 2003).

Parents Maksoy1 N, PI615437, PI578457A and NIIGC4.1-2 exhibited highly significant negative GCA effects for GLM incidence and severity across locations, indicating a high contribution of the parents to soybean resistance to GLM within the progenies (Table 6). These genotypes were good sources of resistance genes and could transmit the trait to their progenies. Crosses Maksoy1 N $\times$ PI615437, Maksoy1 N $\times$ Maksoy5 N, Maksoy5 N $\times$ Maksoy1 N, PI615437 $\times$ Maksoy1 N and Maksoy5 N $\times$ PI578457A exhibited significant and negative SCA effect for GLM damage whereas cross Maksoy1 N $\times$ PI615437 was the best performing for grain yield, suggesting that these crosses could be selected and used in breeding programme for improving GLM resistance in soybean varieties for farmers. Maksoy1 N $\times$ PI615437 could also be used for grain yield improvement. Results also showed that mean sum of squares for reciprocals crosses were non-significant for the GLM incidence, severity, the number of larvae per plant and grain yield, indicating the absence of maternal inheritance in F_2 crosses for these the traits, however, some crosses exhibited significant and negative reciprocal effects for resistance to GLM, which suggested that they were associated to maternal inheritance from female parents. Finally, the significant negative correlation of

GLM severity ($r = -0.676$) and incidence (-0.585), respectively, with yield imply that increase in GLM severity and incidence would cause a significant decrease in the grain yield (Table 7).

Conclusion

The results showed that the resistance to GLM in soybean is controlled mostly by additive gene effects indicating that resistance to GLM could be improved through early selection. Soybean genotypes Maksoy1 N, PI615437, PI578457A and NIIGC4.1-2 were good general combiners for resistance to GLM and important parents to introgress resistance to farmer acceptable but moderately susceptible genotypes.

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