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Influence of environment on soybean [*Glycine max* (L.) Merr.] resistance to groundnut leaf miner, *Aproaerema modicella* (Deventer) in Uganda

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Groundnut leaf miner (GLM) [*Aproaerema modicella* (Deventer)] is a serious problem for soybean cultivation in Uganda causing yield losses of up to 100%. The use of soybean [*Glycine max* (L.) Merr.] cultivars resistant to GLM attack is an important strategy in the integrated pest management program. The aim of this study was to determine the environment × genotype interaction influence on the soybean resistance traits to GLM attack. Eighteen soybean genotypes were evaluated for resistance to GLM attack. The experiment was set up using randomized complete block design replicated three times under natural pest infestation in Budaka (Eastern) and Arua (Northern) districts in Uganda. Data were subjected to analysis of variance, Pearson's phenotypic correlation and cluster analysis. Highly significant ($p < 0.001$) differences among the genotypes were recorded for all the studied traits, except the number of pupae per plant which was significant ($p < 0.05$). GLM incidence and severity had significant negative correlations with rainfall and relative humidity. However, there were significant positive correlations between minimum temperature and GLM incidence as well as severity for most of the genotypes. Soybean genotypes VI046160 and VI046167 could be used as parents in breeding for resistance to GLM pest. Areas with high rainfall and humidity would be recommended for soybean production to minimize infestation by GLM.

Key words: Grain yield, Gelechiidae, incidence, Lepidoptera, natural infestation, severity, weather parameters.

INTRODUCTION

Soybean [*Glycine max* (L.) Merr.] is the most important oil crop in the world (Mattson et al., 2004; Bilyeu et al.,

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2010). Soybean provides the cheapest source of the highest protein content for both human and livestock diets and is an important industrial crop (Ramteke and Husain, 2008; Bhor et al., 2014). Soybean production constitutes 6% of all arable land in the world and has the highest percent increase in the area under production among crops annually (Bilyeu et al., 2010; Tukamuhabwa et al., 2012). In Africa, soybean is used mainly for making infant formula foods and animal feeds (Tukamuhabwa and Oloka, 2016). The crop is attacked by more than 273 species of insect pests (Shirale and Uttamrao, 2010) including groundnut leaf miner (GLM), *Aproaerema modicella* (Deventer) (Lepidoptera: Gelechiidae), which is one of the most devastating oligophagous pests (Shanower et al., 1993a; Praveena et al., 2011). The larvae feed on the leaf mesophyll between the two epidermis layers (Van der Walt et al., 2008b; Buthelezi et al., 2013; Kolhe et al., 2015). Heavy infestations cause leaves to turn brown, with subsequent loss of leaves which in turn reduces the photosynthetically active area leading to yield loss (Du Plessis and Van Denberg, 2011). Groundnut leaf miner causes yield loss of up to 100% on leguminous plants in the tropics (Cugala et al., 2010). In Uganda, the pest has been reported as an economic threat to soybean production in the Eastern and Northern regions causing 54% yield loss (Namara, 2015), yet about 91.2% of the crop is grown in these regions (UBOS, 2010). Chemical control measures are the most widely adopted among the management strategies of the leaf miner in soybean (Okello et al., 2013). However, many 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 and Liu, 2003; Anjani et al., 2007; Mou, 2008). Thus, the development of more reliable alternatives for managing the pest is needed. Host plant resistance offers the potential to reduce dependence on the chemical control which is expensive and environmentally unsound (Hesler and Tharp, 2005). The incidence of some pests and diseases is directly influenced by weather elements, principally rainfall, humidity and temperature (Rao, 2008; Moka et al., 2015). Heavy and persistent rains and high humidity has been shown to reduce GLM population in groundnut and soybean whereas dry weather with bright sunshine hours and occasional rains lead to a rapid buildup of the pest (Gadad et al., 2013; Moka et al., 2015). *A. modicella* is reported to be adapted in a number of agro-ecological areas that differ widely in climates (Buthelezi et al., 2013, 2016). However, information on the interactions between the environment and soybean genotypes on resistance to GLM is lacking. Yet, currently, there is an increasing need to develop resistant varieties that are adapted to a diversity of growing conditions. Recently, Namara (2015) identified 12 moderately resistant genotypes with relatively low severity scores, suggesting a potential to breed soybean for resistance to GLM. Therefore, this study was conducted to determine the influence of the environment on the soybean genotype resistance traits to GLM attack.

MATERIALS AND METHODS

Site characteristics

The study was carried out in Eastern and Northern Uganda. The first experimental location was at the District Agricultural Training and Information Centre, Iki-Iki sub-county in Budaka District (1° 06' N, 34° 00' E) located at an altitude of 1,156 masl. The location has sandy soil (Tukamuhabwa et al., 2012) and receives a mean annual rainfall of 1200 mm, with a mean annual temperature of 24.7°C (Obua, 2013). The second location was at Abi Zonal Agricultural Research and Development Institute in Arua District (3° 04' N, 30° 56' E) with an average altitude of 1215 masl. The area receives a mean annual rainfall of 1250 mm, and has a mean annual temperature of 24°C (Sserumaga et al., 2015); the soil is sandy clay loam (Fungo et al., 2011). These two areas are the hotspots of groundnut leaf miner in Uganda (Page et al., 2000; Epieru, 2004; Okello et al., 2010; Namara, 2015).

Soybean germplasms and experimental procedures

Eighteen soybean genotypes, obtained from the United States of America (USA), International Institute of Tropical Agriculture (IITA), Asian Vegetable Research and Development Center of Taiwan (AVRDC), and Uganda were used in this study (Table 1). These included five susceptible, four moderately susceptible, six moderately resistant, two tolerant and one resistant genotype to GLM.

The experiment was conducted twice during the second rains (September to December) in 2016 and in 2017. This was done because GLM is reported to severely inflict soybean during these periods in Uganda (Namara, 2015). Each plot consisted of a single row of two meters long. The distance between the rows was 60 cm with within row spacing of 5 cm. The plots were laid out in a randomized complete block design with three replicates and a distance of 1 m was kept between the different plots.

Data collection

The data was collected from 30 randomly selected plants per genotype on 40, 60 and 70th days after planting (Ramani and Lingappa, 1988) for GLM incidence and severity damage since GLM peak infestation was reported to occur during reproductive stage (Namara, 2015). Other traits recorded were the number of larvae per plant, number of pupae per plant and seed yield per plot. The GLM incidence (expressed as percent leaf damage) was made by counting the total number of leaves showing folding and mining symptoms from 30 randomly selected plants (Pavviya and Muthukrishnan, 2017). The GLM severity was scored using the standard scale of 1-5 as described by Praveena et al. (2011) in Table 2. The soybean grain yield of each plot was recorded in grams per plot and converted to kg ha^{-1} based on the average of the plots of each cultivar. Data on rainfall, humidity, and temperature for the corresponding months of the study were obtained from the Ugandan National Meteorological Authority.

Data analysis

The analysis of variance (ANOVA) was done for the combined locations using Genstat statistical software 12th Edition (Payne et

Table 1. Description of the soybean genotypes used in the experiment with groundnut leaf miner at District Agricultural Training and Information Centre, Iki-Iki sub-county in Budaka District and at Abi Zonal Agricultural Research and Development Institute in Arua District, Uganda.

Genotype	Pedigree	Maturity group	Origin	GLM reaction[1]
VI046160	CO-2	Early	AVRDC	T
VI046165	NRC-7	Early	AVRDC	T
VI046167	MACS-13	Early	AVRDC	R
BSPS 48C	-	Medium	Uganda	MR
NIIGC4.1-2	-	Medium	Uganda	MR
PI578457A	-	Medium	USA	MR
PI615437	-	Medium	USA	MR
PI605865B	-	Early	USA	MR
Maksoy1N	TGX 1835-10E	Medium	Uganda	MS
Maksoy2N	Maksoy 1N × Duiker	Late	Uganda	S
Maksoy3N	GC 00138-29 × Duiker	Late	Uganda	MR
Maksoy4N	Duiker × GC 00138-29	Late	Uganda	S
Maksoy5N	Nam 2 × GC 00138-299	Medium	Uganda	MS
Namsoy4M	Nam2 × GC00 139-29	Medium	Uganda	MS
Siesta	-	Medium	Uganda	S
Wondersoya	-	Medium	IITA	S
UG5	-	Medium	Uganda	MS
K-local	-	Early	Uganda	S

T: Tolerant; R: resistant, MR: moderately resistant, S: susceptible. The classification of GLM reaction followed Namara[1], (2015).

Table 2. Severity score and resistance category of groundnut leaf miner damage.

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

Source: Praveena et al. (2011).

al., 2009) to estimate the amount of variability for the traits. Prior to analysis, test for homogeneity of variance was applied on all traits. Square root transformation was applied on the number of larvae per plant and grain yield ha^{-1} to improve normality and reduce heterogeneity of the variances (Halverson and Handelsman, 1991). The analysis considered genotype as a fixed factor, and location, season and replication as random factors. Means were separated using the Fisher's protected least significant difference at 0.05% significance level. Pearson's phenotypic correlation estimates were computed for all the studied traits, and the relationship of the genotypes was determined using cluster analysis.

RESULTS

Groundnut leaf miner incidence and severity of soybean genotypes across seasons and locations

The results of ANOVA for GLM incidence and severity of damage on soybean genotypes across seasons and locations are presented in Table 3.

The GLM incidence showed highly significant ($p < 0.001$) differences among genotypes for all the three sampling dates across seasons and locations. The season as well as location effects were also highly significant ($p < 0.001$) for all the three sampling dates for GLM incidence. Similarly, the season × genotype interaction showed highly significant ($p < 0.001$) effects at 60 and 70 DAP for incidence whereas the location × genotype interaction had significant ($p < 0.01$) effect at 60 DAP only. The season × location interaction showed highly significant ($p < 0.001$) effects for all the sampling dates for GLM incidence, and the season × location × genotype interaction showed significant ($p < 0.05$ and $p < 0.01$) effects at 60 and 70 DAP, respectively for GLM incidence. Highly significant ($p < 0.001$) differences were

Table 3. Analysis of variance (mean squares) for groundnut leaf miner (GLM) incidence and severity at three recording dates across seasons and locations on 18 soybean genotypes in Uganda.

Source of variation	Df	GLM incidence			GLM severity		
		40 DAP	60 DAP	70 DAP	40 DAP	60 DAP	70DAP
Rep	2	470.88**	20.54	121.82***	2.86***	1.48***	1.32***
Genotype	17	430.64***	311.23***	378.87***	2.03***	1.70***	1.76***
Season	1	45501.60***	121431.14***	98976.35***	270.17***	383.96***	343.71***
Location	1	5060.76***	3669.70***	4608.61***	70.45***	38.16***	29.02***
Season × Genotype	17	132.72	153.85***	200.55***	1.04***	0.85*	0.66***
Location × Genotype	17	89.19	38.33**	23.2	0.78***	0.49***	0.34**
Season × Location	1	3622.98***	1438.77***	2058.36***	42.48***	13.89***	3.32***
Season × Location × Genotype	17	68.57	31.37*	32.07**	0.71***	0.51***	0.37***
Residual	142	89.1	15.78	14.2	0.24	0.14	0.15
Total	215	-	-	-	-	-	-
CV (%)	-	12.2	5.6	5.0	24.4	15.2	12.9

***, **, *Significant at $p < 0.001$, $p < 0.01$, $p < 0.05$, respectively, Df: Degrees of freedom, DAP: days after planting, CV: coefficient of variation.

observed among genotypes for GLM severity on all the three sampling dates. The environmental effects expressed by location and the seasonal effects were also highly significant ($p < 0.001$) for all the sampling dates for severity damage. Similarly, all the interactions showed highly significant ($p < 0.001$) effects for all the sampling dates across locations and seasons, except the genotype × season interaction which was significant ($p < 0.05$) at 60 DAP and location × genotype interaction which was significant ($p < 0.01$) at 70 DAP.

Mean groundnut leaf miner infestation of soybean genotypes across seasons

The results of GLM mean incidence and severity of evaluated soybean genotypes are presented in Table 4. The percentage of incidence for GLM among the genotypes ranged from 85.14 to 98.98% in 2016 and from 43.10 to 65.50% in 2017. The resistant genotype VI046167 recorded the lowest GLM incidence of 85.14% while the moderately resistant genotype K-local recorded the highest incidence value (98.98%) in 2016. In 2017, resistant genotype VI046167 recorded the lowest GLM incidence of 43.10% while the moderately resistant genotype Maksoy4N recorded the highest value (65.5%) across seasons. The mean performance of incidence across seasons and locations revealed that resistant genotype VI046167 recorded the lowest value of 64.12% while moderately resistant genotype Maksoy4N the highest value of 82.09%.

The mean scores for GLM severity ranged from 2.53 to 4.49 in 2016 and from 0.99 to 1.69 in 2017 across seasons. About 88.88% of genotypes exhibited moderate resistance level to GLM with the severity scores of less than 3. Imported genotypes from the Asian Vegetable Research and Development Center (AVRDC), VI046167 and VI046160 which had been reported to be resistant and tolerant to GLM attack respectively, exhibited resistance level with a severity score of < 2 whereas the reported tolerant genotype VI046165 was found to be moderately resistant to GLM attack across seasons and locations. Genotype K-local which was earlier reported as susceptible to GLM (Namara, 2015) had the highest severity score of 2.98 across seasons and locations and exhibited moderately resistance level to GLM attack, plant introductions PI615437, PI605865B and PI578457A which had been reported to be moderately resistant to GLM attack (Namara, 2015) showed moderate resistance level across seasons and locations. Commercial genotypes Maksoy2N and Maksoy4N which had been reported to be susceptible to GLM attack (Namara, 2015), exhibited moderately resistant level across seasons and locations whereas genotypes Maksoy1N, Maksoy5N and Namsoy4M which were known to be moderately susceptible to GLM attack showed moderately resistant level across season and location.

Number of larvae and pupae per plant and grain yield of soybean genotypes across seasons and locations

The ANOVA results for the number of larvae and pupae per plant and grain yield across seasons and locations are presented in Table 5.

Highly significant ($p < 0.001$) differences in the number of larvae and grain yield were observed among the genotypes across seasons and locations. A significant ($p < 0.05$) difference among genotypes for the number of pupae per plant was also observed. The seasons had highly significant ($p < 0.001$) effects on the performance of the genotypes for all the traits. The location had highly significant ($p < 0.001$) effect on the performance of the genotypes for number of larvae and pupae per plant and

Table 4. Mean of soybean genotype performance for groundnut leaf miner (GLM) incidence and severity across seasons and locations in Uganda.

Genotype	GLM Incidence		GLM severity		Average across seasons and locations			
	2016	2017	2016	2017	IN	FD	SS	GLMR
BSPS48C	96.38	48.68	4.15	1.17	72.53	26.6	2.66	MR
K-local	98.98	63.04	4.49	1.47	81.01	29.8	2.98	MR
Maksoy1N	96.36	55.49	4.21	1.36	75.92	27.9	2.79	MR
Maksoy2N	97.71	61.61	4.15	1.54	79.66	28.4	2.84	MR
Maksoy3N	97.7	51.06	4.06	1.05	74.38	25.6	2.56	MR
Maksoy4N	98.68	65.50	4.25	1.69	82.09	29.7	2.97	MR
Maksoy5N	98.0	53.17	4.05	1.25	75.58	26.5	2.65	MR
Namsoy4M	94.53	49.97	3.65	1.04	72.25	23.5	2.35	MR
NIIGC4.1-2	95.28	57.14	3.54	1.15	76.21	23.4	2.34	MR
PI578457A	94.4	47.32	3.69	1.11	70.86	24.1	2.40	MR
PI605865B	94.65	52.68	3.38	1.26	73.66	23.2	2.32	MR
PI615437	93.61	54.8	3.23	1.08	74.2	21.5	2.15	MR
Siesta	97.8	60.64	4.13	1.45	79.22	27.9	2.79	MR
UG5	95.1	48.99	3.73	0.99	72.05	23.6	2.36	MR
VI046160	88.01	50.74	2.53	1.1	69.38	18.2	1.82	R
VI046165	93.42	53.66	3.86	1.21	73.54	25.4	2.54	MR
VI046167	85.14	43.10	2.53	1.00	64.12	17.7	1.77	R
Wondersoya	96.81	62.89	4.27	1.62	79.85	29.5	2.94	MR
SEDM	2.22	4.31	0.43	0.89	3.3	-	0.29	-
LSD (0.05)	4.48	8.61	0.88	0.2	6.5	-	0.56	-

IN: Incidence (%), FD: foliage damage in % used to score the severity, SS: severity, GLMR: groundnut leaf miner reaction, MR: moderately resistant, R: resistant, SEDM: standard errors of differences of means, LSD: least significant differences of means.

Table 5. Analysis of variance (mean squares) for the number of larvae per plant, number of pupae per plant of groundnut leaf miner (GLM) and grain yield (kg ha^{-1}), across seasons and locations on 18 soybean genotypes in Uganda.

Source of variation	Df	NL	NP	GY
Rep	2	23.76	1.43**	46.04
Genotype	17	70.16***	0.53*	259.44***
Season	1	11462.79***	65.21***	29342.1***
Location	1	8358.47***	15.380***	183.92*
Season × Genotype	17	14.4	0.283	122.1***
Location × Genotype	17	50.1*	0.4911	32.64
Season × Location	1	8435.31***	115.88***	4042.14***
Season × Location × Genotype	17	54.63**	0.2857	87.56*
Residual	142	24.77	0.2938	43.21
Total	215	-	-	-
CV (%)	-	35.8	22.9	34.2

***, **, * Significant at $p < 0.001$, $p < 0.01$, $p < 0.05$, respectively, Df: Degrees of freedom, NL: number of larvae per plant, NP: number of pupae per plant, GY: grain yield in kg ha^{-1}, CV: coefficient of variation.

significant ($p < 0.05$) effect for grain yield. The location × genotype interaction was significant ($p < 0.05$) for the number of larvae per plant and non-significant ($p > 0.05$) for the number of pupae per plant and grain yield. The season × location interaction was highly significant ($p < 0.001$) for all the traits. There was a significant ($p < 0.01$) effect in the number of larvae per plant and significant ($p < 0.05$) effect in grain yield due to season × location × genotype interaction. The season × genotype interaction had highly significant ($p < 0.001$) effect for grain yield and

Table 6. Mean performance of 18 soybean genotypes for the number of larvae and pupae per plant of groundnut leaf miner and grain yield ha^{-1} across seasons and locations in Uganda.

Genotype	NL		NP		GY		YSL
	2016	2017	2016	2017	2016	2017	
BSPS48C	20.2	6.6	8.8	2.4	10.0	308.4	108.2
K-local	20.9	6.4	9.5	3.9	34.2	649.8	246.1
Maksoy1N	19.7	6.4	10.1	1.7	50.8	804.4	315.5
Maksoy2N	23.7	9.5	6.7	1.7	23.9	602.7	217.5
Maksoy3N	22.7	11.8	6.9	2.7	25.9	1428.6	461.3
Maksoy4N	27.4	11.9	9.5	2.8	3.4	444.2	133.6
Maksoy5N	19.8	4.8	7.5	1.6	30.1	995.7	343.8
Namsoy4M	25.9	5.4	7.4	2.9	48.1	1406.8	494.5
NIIGC4.1-2	24.6	7.6	5.3	3.1	106.3	1264.2	526.6
PI578457A	18.1	5.0	9.2	2.2	52.7	1100.6	409.5
PI605865B	20.5	6.3	9.8	2.4	45.2	951.3	353.6
PI615437	17.1	5.7	5.3	2.2	147.6	1629.5	690.2
Siesta	22.3	6.7	7.2	1.9	32.1	793.7	286.9
UG5	22.4	5.5	7.7	2.7	67.2	1551.4	566.9
VI046160	18.4	6.0	5.8	1.9	359.2	806.7	560.7
VI046165	17.1	2.4	4.1	1.1	109.1	1726.2	676.6
VI046167	19.5	4.5	8.1	1.2	146.4	753.1	391.1
Wondersoya	20.9	6.7	7.8	3.7	3.5	686.5	199.8
SEDM	5.6	1.9	0.6	0.3	2.8	6.8	5.4
LSD (0.05)	10.9	3.8	1.1	0.5	5.5	13.5	10.6

NL: Number of larvae per plant, NP: number of pupae per plant, GY: grain yield in kg ha^{-1}, YSL: yield across seasons and locations, SEDM: standard errors of differences of means, LSD: least significant differences of means. The number of pupae, grain yield and yield across seasons and locations are back-transformed values.

non significant ($p > 0.05$) effect for the number of larvae and pupae per plant.

Mean performance of various genotypes for different traits

The results of number of larvae and pupae per plant and grain yield in kg ha^{-1} of evaluated soybean genotypes are presented in Table 6.

The number of GLM larvae per plant among the genotypes ranged from 17.1 to 27.4 in 2016 and 2.4 to 11.9 in 2017 across seasons and locations with the moderately resistant genotype Maksoy4N having the highest number of larvae per plant (27.4) while the moderately resistant genotype VI046165 recorded the lowest value (2.4).

The number of pupae per plant ranged from 4.1 to 10.1 in 2016 and from 1.1 to 3.9 in 2017. The highest number of pupae per plant was recorded on the moderately resistant genotype Maksoy1N with a value of 10.1, while moderately resistant genotype VI046165 had the lowest value of 4.1 in 2016. In 2017, the moderately resistant genotype K-Local had the highest number of pupae of 3.9 per plant and the moderately resistant genotype VI046165 the lowest value of 1.1.

The mean performance for grain yield per hectare across seasons showed that the resistant genotype VI046160 recorded the highest soybean grain yield with 359.2 kg ha^{-1}, whereas the lowest grain yield ha^{-1} was recorded by the moderately resistant Maksoy4N (3.4 kg ha^{-1}) in 2016. In 2017, the moderately resistant genotype VI046165 recorded the highest soybean grain yield with 1726.2 kg ha^{-1} while the moderately resistant genotype BSPS48C had the lowest grain yield of 308.4 kg ha^{-1}. The results showed that the grain yield ranged from 108.20 to 690.2 kg ha^{-1} across seasons and locations with the moderately resistant plant introduction PI615437 recording the highest value of 690.2 kg ha^{-1}.

Relationships of different traits

The correlation coefficients among the studied soybean resistance traits to GLM are presented in Table 7. GLM incidence at 40 DAP was highly significantly ($p < 0.001$) positively correlated to the GLM mean severity ($r = 0.82$ and $r = 0.73$) at 40 and 60th DAP, respectively, significantly ($p < 0.01$) correlated to the GLM mean incidence ($r = 0.59$) at 60th DAP and GLM severity (0.62)

Table 7. Correlation matrix for different traits in soybean genotypes affected by the groundnut leaf miner (GLM) in Uganda.

Trait	IN40DAP	IN60DAP	IN70DAP	S40DAP	S60DAP	S70DAP	NL	NP
IN40	-							
IN60	0.59**	-						
IN70	0.58*	0.67**	-					
S40DAP	0.82***	0.73***	0.74***	-				
S60DAP	0.73***	0.66**	0.79***	0.96***	-			
S70DAP	0.62**	0.71***	0.91***	0.87***	0.89***	-		
NL	0.53*	0.52*	0.33	0.44	0.43	0.32	-	
NP	0.51*	0.15	0.25	0.40	0.45	0.29	0.43	-
GY	-0.38	-0.20	-0.36	-0.36	-0.42	-0.46	-0.42	-0.61**

***, **, * Significant at $p < 0.001$, $p < 0.01$, $p < 0.05$, respectively, NL: number of larvae per plant, NP: number of pupae per plant, IN: GLM incidence, S: severity score, DAP: days after planting, GY: grain yield in kg ha^{-1}.

at 70th DAP, and significantly ($p < 0.05$) correlated to GLM incidence (0.58) at 70th DAP, number of larvae per plant (0.53) and number of pupae per plant (0.51).

GLM incidence at 60 DAP was found to be highly significantly ($p < 0.001$) positively correlated to the GLM mean severity (0.73 and 0.71) at 40 and 70th DAP, respectively; significantly ($p < 0.01$) correlated to GLM severity (0.66) at 60th DAP, and incidence (0.67) at 70th DAP and ($p < 0.05$) to the number of larvae per plant (0.52). The GLM incidence at 70 DAP was highly significantly ($p < 0.001$) positively correlated to the severity ($r = 0.74$; $r = 0.79$ and $r = 0.91$) at 40, 60 and 70th DAP, respectively. The GLM severity at 40 DAP had highly significant ($p < 0.001$) positive correlation with the severity score (0.96 and 0.87) at 60 and 70th DAP, respectively. Similarly, GLM severity at 60 DAP had a highly significant ($p < 0.001$) positive correlation with the GLM severity at 70 DAP (0.89). A significant ($p < 0.01$) negative correlation was observed between the number of pupae and the grain yield (-0.61).

The correlation coefficients of soybean resistance traits to GLM with the weather factors are given in Table 8. There was a negative significant ($p < 0.01$) correlation between relative humidity in the morning (9 am) with GLM incidence ($r = - 0.99$) for the genotype Maksoy1N and ($P<0.05$) negative correlations (-0.99, -0.99, -0.99 and -0.99) for the genotypes BSPS48C, K-local, Maksoy3N and VI046167, respectively. The relative humidity in the evening was also negatively significantly ($p < 0.05$) correlated to the GLM incidence for the genotype Maksoy2N. A significant ($p < 0.01$) positive correlation between the minimum temperature and GLM severity for the genotype UG5 and significant ($p < 0.05$) positive correlations for all the studied genotypes were also observed except for Maksoy1N, Maksoy3N, VI046160, VI046167, VI046165 and Wondersoya. A significant ($p < 0.01$) negative correlation between rainfall and GLM incidence ($r = -0.997$) for Maksoy2N and significant ($p < 0.05$) for PI605865B was observed. Genotypes were grouped into two clusters. The first cluster comprised two sub-clusters A and B. Sub-cluster A consisted of eight genotypes from different origins, six Ugandan genotypes, one from IITA and one from the AVRDC Taiwan. Genotypes VI046165 from the AVRDC and the Ugandan genotype Maksoy4N had the same genetic distance and were genetically distinct from the rest in the same group. The second sub-cluster B had seven genotypes from different origins, four Ugandan genotypes and three plant introduction lines (PIL) from the USA. However, plant introduction PI615437 was found to be genetically distinct from others genotypes in the same sub cluster. The second-cluster C comprised two resistant genotypes from the AVRDC with the same genetic distance. These genotypes were independently distinct from the rest of genotypes.

Cluster analyses

The results of the cluster analysis performed using nine traits are as shown in Figure 1.

DISCUSSION

The results demonstrated highly significant differences among the genotypes for GLM incidence and severity, indicating genetic variability among the soybean genotypes for these traits, and suggesting that it is possible to genetically improve soybean for resistance to GLM (Table 3). Namara (2015) and Ptaware et al. (2001) identified soybean lines with varying degrees of resistance to GLM in Uganda and India, respectively. The highly significant season × genotype and location × genotype interaction effects observed across seasons and locations in sampling dates for GLM incidence and severity showed that the effect of GLM on genotypes was highly dependent on the seasons and environments. Liu et al. (2015) reported that the impacts of mining on plant leaves differ from season to season. Similarly, Buthelezi

Table 8. Relationships of groundnut leaf miner incidence and severity on 18 soybean genotypes in 2016 with weather factors in Uganda.

WP	BSPS48C		K_local		Maksoy1N		Maksoy2N		Maksoy3N		Maksoy4N		Maksoy5N		Namsoy4M		NIIGC4.1-2	
	IN	S	IN	S	IN	S	IN	S	IN	S	IN	S	IN	S	IN	S	IN	S
MaxT	0.76	0.64	0.82	0.62	0.78	0.6	0.93	0.66	0.75	0.61	0.99	0.64	0.72	0.64	0.75	0.65	0.63	0.66
MinT	0.99	0.99*	0.98	0.99*	0.98	0.99	0.89	0.99*	0.99	0.99	0.79	0.99*	0.99*	0.99*	0.99	0.99*	0.99*	0.99*
RHM	-0.99*	-0.98	-0.99*	-0.97	-0.99**	-0.96	-0.96	-0.98	-0.99*	-0.97	-0.88	-0.97	-0.99	-0.97	-1.00	-0.98	-0.97	-0.98
RHE	-0.96	-0.9	-0.98	-0.89	-0.97	-0.88	-0.99*	-0.91	-0.95	-0.88	-0.97	-0.9	-0.94	-0.89	-0.95	-0.9	-0.89	-0.91
R	-0.94	-0.87	-0.97	-0.86	-0.95	-0.85	-1**	-0.88	-0.93	-0.85	-0.98	-0.87	-0.92	-0.87	-0.93	-0.88	-0.86	-0.88

WP	PI578457A		PI605865B		PI615437		Siesta		UG5		VI046160		VI046165		VI046167		Wondersoya	
	IN	S	IN	S	IN	S	IN	S	IN	S	IN	S	IN	S	IN	S	IN	S
MaxT	0.92	0.69	0.96	0.7	0.49	0.74	-0.77	-0.67	-0.62	-0.63	-0.37	-0.55	-0.63	-0.69	-0.5	-0.49	-0.57	-0.7
MinT	0.91	0.99*	0.86	0.99*	0.97	0.99*	0.97	0.99*	1**	0.99**	0.96	0.99	0.99*	0.99	0.99	0.98	0.99*	0.99
RHM	-0.97	-0.99	-0.93	-0.99	-0.92	-0.99	-0.93	-0.97	-0.98	-0.98	-0.99	-0.99	-0.98	-0.97	-0.99*	-0.99*	-0.99	-0.96
RHE	-1*	-0.93	-0.99	-0.93	-0.8	-0.95	-0.82	-0.89	-0.92	-0.92	0.96	-0.95	-0.91	-0.88	-0.97	-0.97	-0.94	-0.87
R	-0.99	-0.9	-0.99*	-0.91	-0.68	-0.88	-0.7	-0.79	-0.83	-0.83	-0.96	-0.88	-0.82	-0.78	-0.91	-0.91	-0.86	-0.77

**, *Significant at $p < 0.01$, $p < 0.05$, respectively, IN: GLM incidence, S: GLM severity, WP: weather parameters, MaxT: maximum temperature, MinT: minimum temperature, RHM: relative humidity in the morning (0900 h), RHE: relative humidity in the evening (1500 h), R: rainfall.

et al. (2012) also reported that the epidemic of GLM is sporadic and its severity varies from location to location and from year to year. The variation among seasons and locations had predominant effects on the traits suggesting that soybean genotypes performed differently in different seasons and locations with high damage level observed in 2016 compared to 2017 which was a result of below normal rainfall of 28.6 to 78.2 mm during experimentation and high temperatures (29.3 to 33°C) recorded in 2016 compared to 2017, especially in Iki-iki (UNMA, 2016, 2017), that might explain the GLM population buildup and infestation. GLM incidence and severity are reported to vary depending on temperature, rainfall and humidity (Du Plessis, 2011; Arunachalam and Kavitha, 2012; Gadad et al., 2013) with an average of high GLM damage levels in Africa than in Asia where the pest originated due to environmental conditions (Du Plessis, 2011).

The study clearly showed a high significant season and location effects on GLM number of larvae and pupae per plant and significant season × location × genotype and location × genotype interactions for the number of larvae per plant. This indicated that the number of larvae and pupae per plant differed from season to season and from location to location with a high number of larvae and pupae per plant observed in 2016 compared to 2017. Fluctuations in *A. modicella* populations were reported to occur between locations, seasons and years by Logiswaran and Mohanasundaram (1986) and Shanower et al. (1992) in India, and in South Africa by Van der Walt (2007) and Buthelezi et al. (2016). The highly significant difference in the number of larvae among genotypes across seasons and locations (Table 5) could be attributed to the fact that the incidence of soybeans GLM is influenced not only by the performance of the genotype but also weather conditions (Du Plessis, 2011; Moka et al., 2015). Maksoy4N, a moderately resistant genotype to GLM recorded the highest number of larvae across seasons (27.4) while VI046167 resistant genotypes had the lowest number of larvae per plant 2.4 (Table 6). The number of larvae per plant was very high compared to the economic threshold level of 5-10 larvae per plant in Uganda and India (Kenis and Cugala, 2006; Van der Walt et al., 2008a). The high population levels in the areas of invasion suggested that this species was able to successfully adapt to the environmental field conditions, establish in the areas of soybean production in Eastern and Northern Uganda and confirmed the findings of Cugala et al. (2010) and Du Plessis (2011).

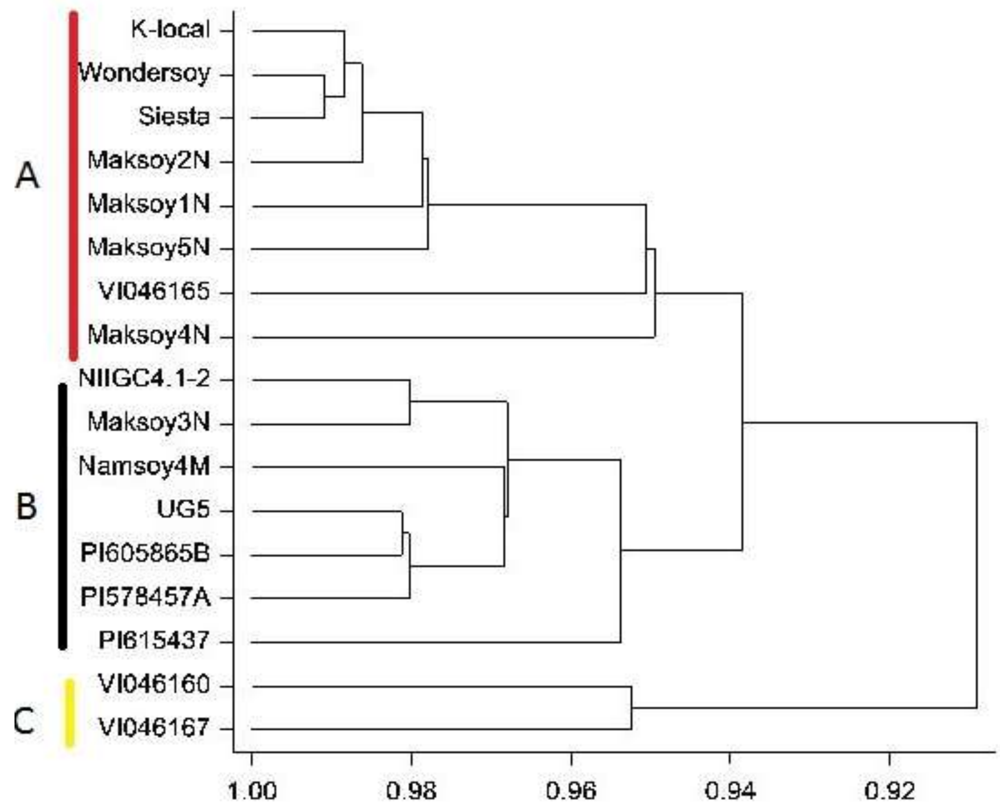

Figure 1. Ward's cluster dendrogram of the 18 soybean genotypes based on eight traits. A: Sub-cluster 1, B: sub-cluster 2, C: second cluster.

The study clearly showed that *A. modicella* is a priority pest and thus strategies for its effective management are pertinent. Cugala et al. (2010) reported an average of 29 to 38 larvae per groundnut plant in Mozambique. Van der Walt et al. (2008a) reported that in the absence of natural mortality factors, GLM numbers can increase by a factor of up to 20 per generation. With this increase, by the pod filling stage, the GLM has the potential to build up to a high population.

This study identified VI046160 and VI046167 as resistant genotypes across seasons and locations in terms of lower severity score (<2) and higher grain yield. Genotype PI615437 was the best performer in terms of grain yield recorded and recorded a relatively low severity score. The highly significant positive correlations observed between the GLM mean incidence and severity at different DAP suggested a linear relationship between these traits, implying that an increase in GLM incidence would lead to increased severity damage. However, a highly significant negative correlation ($r = -0.61$) observed between the number of pupae per plant and grain yield suggested that increase in pupae density would lead to lower grain yield. This arises because GLM pupation occurs in the webbed leaflets, and has the potential of decreasing the photosynthetic active leaf area affecting the growth and yield of the plant (Kenis and Cugala, 2006; Van der Walt et al., 2008b).

The results of this study clearly indicated that GLM incidence and severity depended on the environmental conditions. In this study, negative significant correlations were observed between morning and evening relative humidity with GLM incidence and severity, and significant negative correlations were observed between rainfall and GLM incidence along with severity for most of genotypes studied. Positive correlations were, however, recorded between the minimum temperature and the GLM incidence and severity (Table 8). Increased GLM incidence and severity with a rise in temperature and a decrease in relative humidity and rainfall was previously reported by Lewin et al. (1979), Joshi and Patel (2010), Arunachalam and Kavitha (2012) and Gadad et al. (2013). Shanower et al. (1993b) suggested that under mid-range temperature conditions (25 and 30°C), adults of GLM lived relatively longer and egg production was maximized. This could be the reason why *A. modicella* severely inflicts soybean during the second season (August to December) in Uganda (Namara, 2015), since the first rainy season (March to May) is less influenced by El Niño-Southern Oscillation (ENSO) phases, and records heavy and persistent rains and high humidity;

thus having lower inter-annual variability which tend to reduce GLM population compared to the second rainy season where dry weather with bright sunshine hours and occasional rains lead to a rapid buildup of the pest (Conway et al., 2005; Asadullah et al., 2008). The result from the cluster analysis showed that the geographical origins were not associated with the genetic diversity among genotypes. The sub-cluster A included the moderately resistant genotypes to GLM with high severity score close to 3 with low grain yield except for the genotype VI046165. These are mixtures of late and early maturity cultivars, suggesting genetic diversity among them. The sub-cluster B included genotypes with severity score less than 2.5 and therefore recorded as moderately resistant with medium maturing cultivars. The similarity of genotypes VI046167 and VI046160 suggested that these genotypes can equally be used as a source of resistant genes in the breeding program against leaf miner. Genetic patterns obtained from the cluster analysis would help soybean breeders make better choices when selecting among the available genotypes for parents.

Conclusion

Groundnut leaf miner incidence and severity depended on the temperature, relative humidity and rainfall. The study also indicated a possibility for improving soybean genotypes for resistance to GLM as a result of the genetic variability. The genotype VI046160 and VI046167 were recommended as resistant. It is recommended that a study be undertaken in order to understand the physical impact of rainfall on groundnut leaf miner eggs, larvae and on adult's emergency.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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