INHERITANCE OF RESISTANCE TO SESAME GALL MIDGE IN UGANDA

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ABSTRACT

Sesame gall midge, caused by *Asphondylia sesami* Felt, is an important constraint to sesame (*Sesamum indicum* L.) production in Uganda. Few genotypes have been reported on sesame gall midge, especially hairy genotypes. However, for genetic improvement, there is need to understand the mode of resistance to sesame gall midge in these genotypes. Thirty sesame genotypes were screened for gall midge resistance, under field conditions at Ngetta Zonal Agricultural Research development Institute (ZARDI) in northern Uganda. The spreader row technique was used in order to increase insect pressure on the tested genotypes. The half diallel method 2, model 1 was used to cross 5x5 parents. The result showed that non-additive gene action was important in the inheritance of resistance to sesame gall midge. Cross analysis showed that the GCA x site and SCA x site interactions were significant (P< 0.05), indicating that the additive and non-additive gene actions simultaneously controlled the inheritance for the resistance. The estimate of heritability in narrow sense genetic coefficient of determination (analogue heritable proportion) showed that the resistance was not highly heritable. Estimates of GCA and SCA effects suggest that the parent, Local158, was the best combiner for resistance to gall midge; while the parent AjimoA1-5 was the poorest combiner for the trait. Crosses Local158 x 7029-1-2 and Sesim1 x AjimoA1-5 were the best for the resistance to sesame gall midge. The estimates of genetic effects for resistance to sesame gall midge, showed predominance of additive and additive x additive type of epistasis in the inheritance of the resistance, though dominance also had a role in the cross Sesim1 x 7020-1-2.

Key Words: *Asphondylia sesami,* combining ability, GCA, *Sesamum indicum*

RÉSUMÉ

La cécidomyie du sesame, causée par *Asphondylia sesami* Felt, est une contrainte majeure à la production du sésame (*Sesamum indicum* L.) en Ouganda. Très peu de génotypes résistants à la cécidomyie de sésame ont été enregistrés, en particulier les génotypes à pubescence. Cependant, pour une amélioration génétique, il est nécessaire de comprendre le mode de résistance en jeu. Trente génotypes de sésame ont été évalués en plein champ pour la résistance à la cécidomyie de sésame, à Ngetta, Institut Zonal de Recherche Développement en Agriculture (ZARDI) au nord de l'Ouganda. La technique d'épandage en ligne a été utilisée dans le but d'accroitre la pression d'insecte sur les génotypes testés. La méthode2, modèle 1 de croisements diallèle sans réciproques a été utilisée sur 5x5 parents. Le résultat montre que l'action non additive des gènes est très importante dans l'hérédité de la cécidomyie de sésame. L'analyse des croisements a montré que l'habileté combinatoire générale (GCA) et l'habileté combinatoire spéciale (SCA) montrent varient de façon significative d'un site à un autre (P< 0.05), ceci indique que l'effet additif et non additif des gènes contrôlent l'hérédité de la résistance à la cécidomyie de sésame de façon simultanée. L'évaluation de l'héritabilité au sens strict a montré que le caractère résistant n'est hautement héritable. L'estimation des effets de GCA et SCA suggère que le parent Local158, était le meilleur combineur pour la résistance à la cécidomyie de sésame, tandis que le parent AjimoA1-5 était le pire combineur. Les croisements

Local158 x 7029-1-2 et Sesim1 x AjimoA1-5 étaient les meilleurs pour la résistance à la galle de sésame. Les estimations des effets génétiques pour la résistance à la cécidomyie de sésame a montré la prédominance d'épistasis de type additive et additive x additive dans l'hérédité de la résistance à la galle de sésame, bien que la dominance aussi joue un rôle dans le croisement Sesim1 x 7020-1-2.

Mots Clés: *Asphondylia sesami,* Habileté combinatoire, GCA, *Sesamum indicum*

INTRODUCTION

Sesame (S*esamum indicum* L.) is one of the oldest oilseed crops and it is grown in tropical and sub-tropics in about 70 countries. The seed is rich in oil (50-60 %) (Samara *et al*., 2009). In Uganda it plays a major role as a cash crop, for domestic use and export (Ssekabembe, 2007), especially in eastern and northern Uganda (Munyua and Okwadi, 2013). However, the production in Uganda is below 700 kg ha^{-1} (FAOSTAT, 2013), which is still far below the potential yield of 2000 kg ha^{-1} (Brigham,1985).

The low productivity in Uganda is in part caused by various constraints, including diseases and pests (Ssekabembe *et al*., 2006). Thirty eight insect pest species have been reported to affect sesame, of which sesame gall midge (*Aphondylia sesami* Felt) and webworm (*Antigastra catalaunalis* Dup) are the most devastating (Egonyu *et al.,* 2005).

Midge fly lays eggs on the flower buds; the eggs develop into larvae and start feeding from inside flowers, resulting in the flower abortion or developing abnormal capsules. These manifest in three forms, namely, reinform capsules, double capsules or spherical capsules. These reduce seed yield by up to 100% in susceptible genotypes and under favourable conditions (Mehalingam, 2012). Capsule damage due to gall midge of up to 29-34.3% has been reported in Uganda (Egonyu *et al.,* 2005).

Chemical control has not been effective in controlling gall midge, since larvae hide inside the capsules (Egonyu *et al.*, 2009). Breeding for host plant resistance is believed to be the most effective, efficient and most workable control measure for the resource poor farmers (Bayoumi and El-Bramawy, 2007). Some source of resistance which have been identified among the breeding lines in Uganda (Ogwal *et al.*, 2003), could be utilised in sesame breeding against sesame gall midge, after understanding their inheritance patterns. On the other hand, the source of resistance to insect pests of sesame has been identified among breeding lines in Uganda, and very hairy genotypes have shown low damage by gall midge (Ogwal *et al.*, 2003).

Combining ability studies provide information on additive and non-additive variances (Chandra, 2011), and also identify parents with good general and specific combining abilities. Larger genotypes x environment interaction effects tend to be a problem in breeding, because of lack of predictability response which hinders progress from selection (Haddadi *et al*., 2013). It is, therefore, necessary to identify crosses that present, not only wide adaptation, but also high stability across environments. This study aimed at investigating the nature of gene action governing the inheritance of resistance to sesame gall midge and to identify parents with good GCA and crosses with good SCA effects and help in identification of sources of resistance for breeding.

MATERIALS AND METHODS

Experimental sites. The study was conducted at two stations in Serere district in eastern Uganda, and Ngetta Zonal Agricultural Research Development Institute (ZARDI) in northern Uganda. The Serere site is located at latitudes of 1º30 N and 33º33 E and altitude of 1,085 m above sea level, with average annual rain fall of 1,000-1,200 mm per year (Wambi *et al.*, 2014). Ngetta ZARDI is located at 2º17´N and 32º56´E, at 1,180 m above sea level and receives mean annual rainfall of 1305.3 mm, with a temperature range from 15-32 °C (Otim *et al.*, 2015).

Genetic materials and experimental design. Thirty genotypes, including local varieties, breeding lines and recent introductions at

National Semi-Arid Resources Research Institute (NaSAARI) were used in the study (Table 1). The screening study was conducted under field conditions, in an alpha lattice design (5 plots x 6 blocks), with three replications. Plot size was 5 m x 4 m, containing six rows per plot planted at a spacing of 30 cm x 10 cm. Rows of the most susceptible genotype (Sesim1) were planted between and around the test plots, two weeks earlier, in order to increase pest pressure on the evaluated genotypes.

Five genotypes were crossed in 5x5 half diallel mating design method 2, model-1 (Griffing, 1956). Ten F_1 progenies, along with their parents, were evaluated in a randomised complete block design

TABLE 1. Characteristics of Sesame germplasm lines included in the study conducted at Serere and Ngetta in Uganda

Entries	Origin	Level of resistance*
Local158-1	Egypt	Resistance
Local158-2	Egypt	Resistance
Local158-3	Egypt	Resistance
Local158-4	Egypt	Resistance
Local158-5	Egypt	Resistance
Renner1-3-1-1	USA	Unknown
Renner1-3-1-16	USA	Unknown
7029-1-2	Thailand	Susceptible
Sesim2	Uganda	Moderate resistance
Sesim1	Uganda	susceptible
Adong4-4	Uganda	Susceptible
AjimoA1-5	Uganda	Susceptible
AjimoA1-6	Uganda	Susceptible
Oyamhairy	Uganda	Susceptible
(Sesim2//5181)-2-2-1	Uganda	Unknown
Em15-1-5	Uganda	Unknown
ICEASE00020	Uganda	Unknown
1438-1-10-2-1	Uganda	Unknown
(Local158//7029)-7	Uganda	Unknown
1438-1-6-3	Uganda	Unknown
1438-1-6-1-1	Uganda	Unknown
(Local158//6022)-2-1	Uganda	Unknown
49-7	Uganda	Unknown
ICEASE0005	Uganda	Unknown
(AjimoA1-6//7029)-1-9	Uganda	Unknown
Em15-3-2	Uganda	Unknown
1438-1-6-18-1	Uganda	Unknown
(Y-1//Local158)-1-2-1	Uganda	Unknown
(AjimoA1-6//7029)-1-1	Uganda	Unknown
(A1)-1-1-1	Uganda	Unknown

*Information from NaSARRI

(RCBD), with three replications in two sites. In each location, the single row plot of 2 m long was used. The experiment was allowed natural infestation as no protection measures were undertaken, but all the agronomic practices were applied to ensure good crop growth.

Generation mean analysis was carried out in five crosses of susceptible x susceptible (Sesim1 x 7029-1-2, AjimoA1-5 x 7029-1-2), resistant x susceptible (Sesim2 x AjimoA1-5, Local158 x Sesim1), and resistance x resistance (Sesim2 x Local158). The F_1 of each cross was backcrossed to both parents to produce BC_1 and BCP_2 generations; while some of the F_1 plants were selfed to produce F_2 seeds. The five populations were planted in a RCBD, with three replications. The number of rows varied as follows: one row for non-segregating generations P_1, P_2 and F_1; eight rows for the F_2 and six rows for the BCP_1 and BCP_2. All recommended agronomic practices were applied, except chemical spray against pests.

Data collection

Screening. Galled capsules were recorded at 8, 10 and 12 weeks after crop emergence, by counting the number of formed and galled capsules on 10 randomly selected plants per tested genotype in each plot. The level of incidence was obtained by dividing the number of infested capsules by the total number of capsules per plant and multiply by 100.

Genetic study. Five randomly selected plants were used for recording damaged capsules and total number of capsules per plant in the diallel. For generation mean analysis, the number of selected plants was varied as follows: 15 plants in P_1, P_2 and F_1, 45 plants in BCP_1 and BCP_2 and 60 plants in F_2 in each replication.

Data analysis

Screening. The percentage of galled capsules per cultivar was used for analysis of variance. Means were separated using Fisher's protected Least Significant Difference test, at 5% probability level. The 12 weeks score was used because it had a high F value, which separated means clearly. The resistance was categorised by the scale of

0–10 (resistance), 11–20 (moderate resistance), 21–30 (moderate susceptible), 31–50 (susceptible) and above 50 (highly susceptible) used by Solanki *et al.* (2006) for categorising resistance for leaf webber, and capsule borer in sesame was used.

Genetic analysis. Analysis of variance for single sites and across sites was computed using GenStat statistical (14th Edition) Software. The Griffing (1956) method 4, Model 1, which includes only direct F_1 crosses without parents and reciprocals, was used to estimate general and specific combining ability effects. The GCA and SCA values and the respective variance components were calculated and used to determine Baker's ratio in order to estimate the relative importance of additive and non-additive gene effects (Baker, 1978).

$$BR = \frac{(2\sigma^2 GCA)}{(2\sigma^2 GCA + \sigma^2 SCA)}$$

Where: BR= Baker's ratio, $2\sigma^2 GCA$ = variance due to GCA, and $2\sigma^2 SCA$ = variance due to SCA. Since the parents were considered to be fixed effects factor, heritability was estimated on entry mean basis, in forms of broad-sense coefficient of genetic determination (BS.CGD), which is the total genetic variations and narrow sense coefficient of genetic determination (NS.CGD) the heritable proportion (Dabholkar, 1992).

$$BS.CGD = \frac{(2\sigma^2 GCA + \sigma^2 SCA)}{(2\sigma^2 GCA + \sigma^2 SCA + \sigma^2 e)}$$

Where: BS.CGD = Estimated broad sense heritability; $\sigma^2 GCA$ = Variance due to additive effects; $\sigma^2 SCA$ = Variance due to dominance effects; and $\sigma^2 e$= Environmental error variance

$$NS.CGD = \frac{(2\sigma^2 GCA)}{(2\sigma^2 GCA + \sigma^2 SCA + \sigma^2 e)}$$

Where: NS.CGD= Estimated narrow sense heritability; $\sigma^2 GCA$= Variance due to additive effects; $\sigma^2 SCA$= Variance due to dominance effects; and $\sigma^2 e$ = Environmental error variance.

Regression analysis (generalised linear model) was used to estimate the genetic effects (additive, dominance, additive x additive and additive x dominance) from six generations using Bernardo method (2010), by fitting the model one by one until the lack of fit became non-significant.

RESULTS AND DISCUSSION

Characterisation of genotypes. None of the genotypes was free from gall midge attack (Table 2). Out of the 30 genotypes screened, 8 were moderately resistant with galled capsules ranging from 16.5 to 19.7%. The introduced genotypes, Local 158-5, Local 158-4, Local 158, Local 158-1 and Local 158-2, with hairy stems, capsules and leaves showed better resistance to sesame gall midge than the non-hairy cultivars.

Similar results were reported by Ogwal *et al.* (2003) among breeding lines in Uganda. Singh *et al.* (1990) also reported that sesame genotypes with dense trichomes on the leaf surface, flowers and pods experienced less damage by web worm than the other genotypes. Genotype Sesim2, a commercial variety in Uganda, with purple colour on leaves, flowers and pods showed moderate resistance to sesame gall midge compared with other local variety with green colour on leaves, flowers and pods.

Orientation of insects towards the plant is influenced by plant architecture and colour, but the colour stimulus plays the most important role (Dent, 1993). Genotype Renner1-3-1-16, which is greenish and hairless also showed moderate resistance to gall midge, suggesting that they may possess biochemical repellants (antixenosis) or antibiotic.

Combining ability and heritability. The estimates of GCA and SCA effects from single and across two sites are presented in Table 3. Only Local158 had a significant (P< 0.01), but negative GCA effect for percent galled capsules under Ngetta conditions, and non-significant negative GCA effects at Serere and across sites.

The parent, Sesim2, also showed a consistent non-significant negative GCA effect in single site and across sites (Table 3), which is the trend for resistance that would be passed onto crosses in

TABLE 2. Capsules infestation score (%) during season 2013b (October- January 2014) at Ngetta in Uganda

Genotypes	Origin and description	Gall midge infestations		Genotypes	Origin and description	Gall midge infestation	
		Mean	Reaction			Mean	Reaction
Local158-5	Egypt/ hairy	16.5	MR	Em15-1-5	Uganda /Breeding line	27.9	MS
Local158-4	Egypt/ hairy green	17.7	MR	(A1)-1-1-1	Uganda /Breeding line	29.7	MS
Local158-1	Egypt/ hairy green	17.7	MR	49-7	Uganda /Breeding line	30.4	MS
Local158-2	Egypt/ hairy green	18.0	MR	ICCASE00020	Unknown	30.8	MS
Sesim2	Released/purple/ few hair	18.6	MR	(AjimoA1-6//7029)-1-1	Uganda /Breeding line	31.0	S
(Local158//7029)-7	Uganda/Breeding line	19.1	MR	(AjimoA1-6//7029)-1-9	Uganda /Breeding line	31.2	S
Renner1-3-1-16	USA/ green	19.6	MR	1438-1-6-18-1	Uganda /Breeding line	31.8	S
(Local158//6022)-2-1	Uganda /Breeding line	19.7	MR	1438-1-6-3	Uganda /Breeding line	32.0	S
Renner1-3-1-1	USA/green	20.1	MS	7029-1-2	Thailand/ green	32.8	S
(Y-1//Local158)-1-2-1	Uganda /Breeding line	20.4	MS	1438-1-10-2-1	Breeding line	32.8	S
Local158-3	Egypt/ hairy green	20.4	MS	1438-1-6-1-1	Uganda /Breeding line	33.3	S
Oyamhairy	Uganda /Local/ hairy	22.4	MS	AjimoA1-6	Uganda /Local/ green	34.6	S
Em15-3-2	Uganda /Breeding line	25.1	MS	Sesim1	Uganda /Released/ green	37.0	S
(Sesim2//5181)-2-2-1	Uganda /Breeding line	25.6	MS	AjimoA1-5	Uganda /Local/ green	37.4	S
ICCASE0005	Unknown	26.8	MS	Adong4-4	Uganda /Local/ green	40.5	S

SE = 3.8
LSD 0.05 = 6.1
C.V% = 14.1

Scale: 0-10= Resistance, 11-20= Moderate resistance, 21-31= Moderate susceptible, 31-50= susceptible and above 50 highly susceptible, MR = moderate resistance, MS = moderate susceptible, S = susceptible (Solanki *et al.,* 2006)

TABLE 3. General combining ability effects (GCA) of Sesame genotypes at Serere and Ngetta in Uganda

Parents	Serere	Ngetta	Across locations
GCA			
Sesim1	2.83	3.54	3.19
Sesim2	-3.2	-3.09	-3.14
AjimoA1-5	-0.41	12.01***	5.80
Local 158	-2.55	-9.56**	-6.05
7029-1-2	3.33	-2.89	0.22
SCA			
AjimoA1-5 x 7029-1-2	-2.27	7.77*	2.75
AjimoA1-5 x Local 158	2.47	8.73*	5.59
Local 158 x 7029-1-2	-3.47	-22.27***	-12.88**
Sesim1 x 7029-1-2	5.38*	8.23*	6.80
Sesim1 x AjimoA1-5	-1.89	-13.27**	-7.58
Sesim1 x Local 158	-0.21	10.80**	5.30
Sesim1 x Sesim2	-3.28	-5.77	-4.52
Sesim2 x 7029-1-2	0.37	6.27	3.32
Sesim2 x AJimoA1-5	1.70	-3.23	-0.76
Sesim2 x Local 158	1.21	2.73	1.97
Standard error	2.24	3.82	4.53

Significance level, * = P<0.05, ** = P<0.01 and *** = P<0.001

which it would be involved. On the other hand, parent AjimoA1-5 showed a significant (P<0.001) positive GCA effect at Ngetta, which was an undesired direction for the trait of interest for hybridisation (Dabholkar, 1992). In the case of SCA effects, the results showed that the cross Sesim1 x 7029-1-2 had a significant (P<0.05) positive effect at Serere and Ngetta, and was rated a poor combiner.

Crosses, Sesim1 x AjimoA1-5 and Local158 x 7029-1-2, were the best combiners for resistance to gall midge in single and across environment (Table 3). On the other hand, the crosses AjimoA1-5 x 7029-1-2 and AjimoA1-5 x Local158, with positive significant (P<0.05) SCA effect and Sesim1 x Local158 with significant (P<0.01) positive effects were recorded as the poor combiners for resistance to gall midge under Ngetta conditions. Crosses of good combiners would be desirable in hybridisation for resistance to gall midge according to Dabholkar (1992).

In this study, it was observed that combining good x good parents not always results in desirable SCA effects as in cross of Sesim2 x Local 158 (moderate x moderate resistant parents) resulted in undesirable SCA effects and Sesim1 x

AjimoA1-5 (poor x poor parents) result in desirable SCA effects. Similar observations were reported by Nsabiyera *et al.* (2013) in hot pepper and Hannan *et al.* (2007) in tomato.

Mean squares due to GCA and SCA are presented in Table 4. The results from Serere showed no variations among the genotypes GCA and SCA for resistance to gall midge, but there were significant (P<0.001) variations among genotypes under Ngetta conditions. This suggests evidence of influence of environment in the expression of mode of inheritance.

The combined analysis of variance across the two locations showed differences, again suggesting that multi-locations may be necessary for resistance selection. This was further confirmed by σ^2GCA x location and σ^2SCA x location, indicating that the crosses had dissimilar performance for resistance to sesame gall midge for the two sites. This clearly shows that when developing a breeding programme for resistance to gall midge, environmental factors ought be considered. This was also proposed by Nzuve *et al.* (2013) while working on grey leaf spot and yield traits in maize inbred lines. The variance due to SCA x location was greater than

that due GCA x location, suggesting that non-additive gene action was more important than additive. The important role of non-additive gene action was further demonstrated by low Baker's ratio (0.31), thus suggesting that best progeny cannot be obtained by crossing two parents with low capsules infestation (Baker, 1978). The improtant role of non-additive gene action was earlier reported in sesame, for resistance to leaf webber and capsule borer, by Gnanasekaran *et al*. (2010). Similar results were reported earlier by Solanki *et al*. (2006).

Broad sense heritability was medium (0.43) (Table 4), indicating the significant role of environmental effects in the variations observed for resistance to gall midge (Akinwale *et al.*, 2011).

TABLE 4.   Variance component for resistance to gall midge

Source of variation	Serere	Ngetta	Across sites
σ^2 GCA	5.7	56.8	7.4
σ^2 SCA	4.2	187.5	33.5
σ^2 GCA x site	-	-	23.8
σ^2 SCA x site	-	-	62.3
BS.CGD	0.61	0.91	0.43
NS.CGD	0.44	0.34	0.13
Baker's ratio	0.73	0.38	0.31

*= P<0.05, ** = P<0.01 and *** = P<0.001= significance levels. , σ^2 GCA = variance due to GCA, σ^2 SCA = variance due to SCA, σ^2 GCA x sit e= variance due to interaction between genotype by site and σ^2 SCA x site= variance due to interaction between crosses by site, BS.CGD and NS.CGD = broad sense and narrow sense coefficients of genetic determination respectively

The narrow sense heritability was very low (0.13), indicating that resistance to sesame gall midge had a high environmental effect and non-additive gene effects, making the value of NS.CGD to be low. During improvement of resistance through selection, early selection would not be effective due to the masking effects of the environment.

The estimates of genetic effects for resistance to sesame gall midge are presented in Table 5. Gene effects varied among crosses; thus, simple additive/dominance model was adequate to explain the inheritance of resistance in crosses Local x Sesim1 and Sesim2 x AjimoA1. This suggests that improvement can be achieved through pedigree breeding procedure. The inheritance was more complex in the crosses, Sesim1 x 7029-1-2, AjimoA1-5 x 7029-1-2 and Sesim2 x Local 158 as shown by the significant lack of fit.

In general the inheritance of resistance in these crosses was controlled by additive x additive epistasis, though dominance and additive were also having effect in crosses Sesim1 x 7029-1-2 and AjimoA1-5 x 7029-1-2, respectively, for the improvement selfing within those crosses would be the best approach to capture the epistasis and dominance effects.

CONCLUSION

Genotypes used in this study possess reaction to sesame gall midge, indicating that materials are diverse. Genotypes, Local158, Sesim2 and Renner1-3-1-1 with moderate resistance can be

TABLE 5.   Estimates of genetic effects of five crosses of Sesame in a study conducted in Serere in Uganda

Source of variation	Sesim1 x 7029-1-2	ajimoA1-5 x 7029-1-2	Local158 x Sesim1	Sesim2 x AjimoA1-5	Sesim2 x Local158
a	2.8	12.3*	91.7***	64.0*	0.3
d	33.0***	6.0	0.7	15.5	1.8
aa	15.6**	16.4*	-	-	20.5*
ad	4.0	3.6	-	-	1.6
Lack of fit	2.0*	1.8*	-	-	11.7*
Total	11.5	7.6	-	-	7.2
Residual	1.3	2.2			2.8

Significant differences at * = P<0.05, ** = P<0.01 and *** = P<0.001. a = additive, d = dominance, aa = additive x additive and ad = additive x dominance

good sources for future breeding. The estimated low (0.31) Baker's ratio indicated that non-additive gene effect is more important than additive gene effects in determining sesame gall midge resistance in sesame genotypes evaluated in this study. The results from generation mean analysis show predominance of additive and additive x additive type of epistasis in the inheritance of resistance to sesame gall midge, though dominance also has a role in the cross Sesim1 x 7020-1-2. With respect to GCA effects, parents Local158 and sesim2 are the best combiners for resistance to gall midge. On the other hand, for SCA effect, the cross Local 158 x 7029-1-2 would be the best choice. The low narrow sense heritability (0.13) obtained in this study implies that improvement through selection at early generation may not be effective. Moderate (0.43) broad sense heritability obtained in this study indicates the role of environmental effects on the expression of the resistance.

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