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## MODE OF INHERITANCE OF RICE RESISTANCE TO AFRICAN RICE GALL MIDGE

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### ABSTRACT

Development of rice (*Oryza sativa*) varieties with improved traits, like resistance to both biotic and abiotic stresses, is crucial, particularly for sub-Saharan Africa (SSA). Among the biotic stresses, the African rice gall midge (*Orseolia oryzivora*) is one of the most devastating pests/insects of rice in the region. The objective of this study was to determine the mode of inheritance of resistance to African rice gall midge (AfRGM) as a basis for developing insect resistant rice varieties in the SSA. Four resistant genotypes and four susceptible locally adapted genotypes of rice were crossed in half diallel crossing design. The F<sub>2</sub> segregants and their corresponding parents, were evaluated in the cage experiment, against AfRGM in a 4 by 9 alpha lattice design, in three replications. Results showed a significant variation (P<0.05) in rice AfRGM resistance among genotypes. Significant general and specific combining abilities were observed, indicating that both additive and non-additive gene effects were important in rice AfRGM resistance. However, the non-additive effects predominated at 42 and 63 days after infection (DAI). High coefficients of genetic determination in the broad sense (0.96, 0.97 and 0.98, respectively), and moderate narrow sense (0.55, 0.45 and 0.39) at 21, 42 and 63 DAI, were obtained, with a moderate Baker's ratio of 0.57, 0.46 and 0.40 in the 21, 42 and 63 DAI, respectively; indicating primarily non-additive inheritance among crosses.

*Key Words:* Additive gene, general and specific combining ability

### RÉSUMÉ

Le développement de variétés de riz (*Oryza sativa*) présentant des caractéristiques améliorées, comme la résistance aux stress biotiques et abiotiques, est crucial, en particulier pour l'Afrique subsaharienne (ASS). Parmi les stress biotiques, la cécidomyie africaine des galles du riz (*Orseolia oryzivora*) est l'un des ravageurs/insectes les plus dévastateurs du riz dans la région. L'objectif de cette étude était de déterminer le mode de transmission de la résistance à la cécidomyie africaine des galles du riz

(CAGR) comme base pour le développement de variétés de riz résistantes aux insectes en ASS. Quatre génotypes de riz résistants et quatre génotypes de riz sensibles adaptés localement ont été croisés selon un modèle de croisement semi-diallel. Les ségrégants  $F_2$  et leurs parents correspondants ont été évalués dans l'expérience en cage, contre la CAGR dans un alpha-plan latinisé 4 x 9, en trois répétitions. Les résultats ont montré une variation significative ( $P < 0,05$ ) de la résistance du riz à la CAGR parmi les génotypes. Des capacités de combinaison générales et spécifiques significatives ont été observées, indiquant que les effets génétiques additifs et non additifs étaient importants dans la résistance du riz à la CAGR. Cependant, les effets non additifs prédominaient 42 et 63 jours après l'infection (JAI). Des coefficients de détermination génétique élevés au sens large (0,96, 0,97 et 0,98 respectivement) et au sens étroit modérés (0,55, 0,45 et 0,39) à 21, 42 et 63 JAI ont été obtenus, avec un rapport de Baker modéré de 0,57, 0,46. et 0,40 dans les 21, 42 et 63 JAI, respectivement ; indiquant principalement un héritage non additif entre les croisements.

*Mots Clés* : Gène additif, capacité de combinaison générale et spécifique

## INTRODUCTION

Development of rice (*Oryza sativa*) varieties with improved traits, particularly resistance to both biotic and abiotic stresses, is crucial in sub-Saharan Africa (SSA). Among the biotic stresses, the African rice gall midge (AfRGM) is by far the main barrier to viable rice production in SSA (Alibu *et al.*, 2016). To effectively develop resistant varieties, it is important to identify resistant genotypes and determine their mode of inheritance to the gall midge. Knowledge of these factors will facilitate incorporation of resistance in susceptible genotypes of superior agronomic characteristics. However, in countries like Uganda, this genetic information is not well established among existing genotypes; thus, hindering the progress of breeding for resistance. Moreover, the estimation of combining ability and gene action is important in identifying parents with superior genes and better performance.

The general combining ability allows for the identification superior parental genotypes; while specific combining ability enables identification of specific parental combination that produce good hybrids (Saleem *et al.*, 2009). Heritability is estimated by calculating the fraction of genotypic variation to phenotypic variation, and permits determination of the degree to which a trait is transmissible from a parent to its offspring,

and the influence of environmental difference (Allard, 1960). This information is useful as the basis for determining breeding methods and the population to use to achieve meaningful resistance. This is done by analysing the genetic parameters of the parents and their segregating  $F_2$  populations. The objective of this study was to determine the mode of inheritance of resistance to the AfRGM in SSA.

## MATERIALS AND METHODS

**Study sites.** This experiment was conducted at two sites, the National Crop Resources Research Institute (NaCRRI) Namulonge in central Uganda; and at Lira in northern Uganda. NaCRRI is located at latitude  $0^\circ 31' N$ , and longitude  $32^\circ 35' E$ ; while Lira is located at latitude  $2^\circ 14' 59'' N$ , and longitude  $32^\circ 53' 59'' E$ . NaCRRI is located at an altitude of 1,150 meters above sea level (masl); while Lira is located at 1,074 masl. Atmospheric temperatures range from 13.0 to 28.5 °C at NaCRRI; and 22.5 to 25.5 °C at Lira site. Mean annual rainfall is 1300 mm for NaCRRI and 1400 mm for Lira site.

**Rice materials.** As for the parental genotypes, eight rice varieties from two sources were selected as parents for population development (Table 1). Four genotypes which consistently showed resistance reaction to AfRGM under both

TABLE 1. Rice genotypes and their sources screened to obtain parents for inheritance of resistance to the African rice gall midge (AfRGM)

Genotypes	Source	Pedigree name	Reaction to AfRGM
NERICA-6	NaCRRRI	WAB450-1-B-P-160-HB	Resistant
NERICA-4	NaCRRRI	WAB450-1-B-P-91-HB	Resistant
NERICA-1	NaCRRRI	WAB 450-1-B-P-38-HB	Resistant
METP-7	NaCRRRI	ART34-76-2-8D-2	Resistant
K85	NaCRRRI	Unknown	Susceptible
KOMBOKA	NaCRRRI	IR 79253-55-1-4-6	Susceptible
NAMCHE-1	NaCRRRI	WAB95 BB 40 HB	Susceptible
E22	NaCRRRI	NM7-22-11- B-P-1-1	Susceptible

NaCRRRI = National Crops Resources Research Institute

screening conditions, were selected based on screening results of the study (Desta, 2021). The four genotypes were classified as resistant to AfRGM based on IRRI 2014 AfRGM damage scale (0 - 9); and the other four were susceptible to AfRGM.

**Population development.** The parental genotypes were planted in plastic buckets (pots) of 25 cm depth and 30 cm width; filled with forest soil. In each pot, three seeds were staggered-planted at four weekly intervals, to synchronise flowering dates of the genotypes. A half-diallel mating design was used to generate populations.

To avoid injury to floral parts and to obtain viable seeds with artificial emasculation, hybridisation was done with the aid of a vacuum emasculator late in the mornings (9:00 am-12:00 noon) and late afternoons (3:00-5:00 pm) on panicles that had already started flowering (Herrera and Coffman, 1974).

Immature and deformed or mature spikelet's, were cut off at the bottom of the panicle, leaving only the emasculated spikelet's on the panicle. In addition, for leafy genotypes, bottom leaves were removed to minimise competition for nutrient. After emasculation, panicles were covered with pollinating bags, secured with paper clips to exclude exterior pollen.

A flowering panicle of the male parent was cut carefully and dusted onto the emasculated panicle, gently tapped onto the receptive stigma, and covered with the pollinating bag. For each cross, the date and parent's name, starting with that of the female parents, were written on the back of the pollen bag to avoid confusion during harvest. Mature seeds from successful crosses, were harvested and bagged separately according to the cross number.

The harvested F<sub>1</sub> seeds were placed in an air-dry oven, for 7 days at 50 °C, in order to break the dormancy (Herrera and Coffman, 1974). The F<sub>1</sub> seeds were later surface sterilised with 0.1 % Tween 20 for 20 minutes; followed by 70 % ethanol and washed twice with distilled water. Sterilised seeds were placed in sterile petri-dishes, on moistened tissue paper, and incubated for 48 hours at 30 °C.

Pre-germinated F<sub>1</sub> seeds were transferred into small cups until they became strong enough for transplanting (Sama *et al.*, 2016). Thereafter, seedlings were transplanted into the pots, filled with forest soil, and kept in the screen house for two to three weeks. Morphological markers, including plant height, colour, shape and size of the leaves, tillering, days-to-flowering and maturity; were used to differentiate successful crosses from selfed plants, and by planting the parent's side-by-side with the crosses.

**Experimental design.** The experiment was conducted under cage conditions at NaCRRI, Namulonge. The  $F_2$  segregating population with parents, were evaluated in a 4 x 9 alpha lattice design, replicated three times. A spacing of 20 cm between pot rows and between blocks, and 15 cm between pots was used in order to ease management of the experiment. Each  $F_2$  segregant was planted in a pot, which in turn was kept inside the cage. The infestation process with *AfRGM* was done in the early mornings.

Sixty small glass bottles were prepared and tissues put inside the glass for keeping moisture and creating conducive environment for the gall midge (Ogah *et al.*, 2010). A few water drops were added on the tissue to maintain a moist conditions. The male and female gall midge pupae were separated based on the physical structure; and arranged in a ratio of 2 males to 3 females pupae per small glass bottler. Then, each glass was introduced into each genotype cage by tightening the glass on the tag stick and add small dropps of water applied, until the pupa became an adult and started to fly (Moses Ekobu, NaCRRI, personal communication). Other agronomic practices, such as weeding and watering, were done regularly as needed.

The experimental area had a size of 3.6 m x 15.8 m, and for each genotype, 60 cm x 60 cm cage was used. A spacing of 20 cm between each cage and 60 cm between the replications was used. Infestation was done in accordance with the method of Ogah *et al.* (2010), where 3 females and 2 males of *AfRGM* were released in each cage (Yao, 2012). A total of 180 females and 120 males of gall midge was used. The infestation was done 21 days after planting (Ogah *et al.*, 2010).

**Data collection and analysis.** Data collection included total number of tillers, number and scales of infested tillers, number of tillers infestation (percentage), number of gall

midges per plant after 21, 41 and 63 days of artificial infestation (IRRI, 2014).

The data collected were analysed using ANOVA of GenStat (18<sup>th</sup> edition, Payne *et al.*, 2015), using alpha lattice Restricted Maximum Likelihood (ReML) algorithm. The genotypes were considered a fixed effect; while blocks and replications were random effects. Means of significant treatments were separated using Least Significant Difference (LSD) at  $P < 0.05$  level of significance.

To select a good combination of parents, heritability, general combining ability and specific combining ability were calculated using Griffing (1956), method II model I. The Linear Model used was as follows:

$$Y_{ijk} = \bar{Y} \dots + G_i + G_j + S_{ij} + R_k + e_{ijk}$$

Where:

$Y_{ijk}$  = the observed change value for the  $ijk^{th}$  experimental unit,  $\bar{Y} \dots$  = the grand mean,  $G_i + G_j$  = the GCA effect for the  $i^{th}$  and  $j^{th}$  parents, respectively;  $R_k$  = the effect of the  $k^{th}$  replications, and  $e_{ijk}$  = experimental error.

Broad and narrow sense coefficients of genetic determination (BS-CGD; NS-CGD) were computed on cross means, using the formula described by Dabholkar (1999). The formula helps to estimate the proportion of phenotypic variation that is due to genetic causes; while the latter focuses on the proportion of additive gene effects.

The relative importance of additive *versus* non-additive gene effects was determined according to the ratio established by Baker (1978). All negative values of estimated variance components were considered as zero in the formulae of coefficient of genetic determination. Narrow sense coefficient of genetic determination (NS-CGD) and Barker's ratio (BR) were calculated on genotype mean basis as follows:

$$BS - CGD = (2 * \sigma_{GCA}^2 + \sigma_{SCA}^2) / (2 * \sigma_{GCA}^2 + \sigma_{SCA}^2 + \frac{\sigma_e^2}{r})$$

$$NS - CGD = 2 * \sigma_{GCA}^2 / (2 * \sigma_{GCA}^2 + \sigma_{SCA}^2 + \frac{\sigma_e^2}{r})$$

$$BR = 2 * \sigma_{GCA}^2 / (2 * \sigma_{GCA}^2 + \sigma_{SCA}^2)$$

Where:

r = number of replications,  $\sigma_{GCA}^2$  and  $\sigma_{SCA}^2$  = variance component estimates of GCA and SCA, respectively; and  $\sigma_e^2$  = the variance due to experimental error.

## RESULTS

**Combining ability.** Analysis of variance of  $F_2$  segregating populations evaluated under controlled conditions EW are presented in Table 2. There were highly significant ( $P < 0.001$ ) differences among genotypes for AfRGM on tillers damage scores at 21, 42 and 63 days after infestation (DAI).

The narrow sense coefficient of genetic determination were 0.55, 0.45 and 0.39 at 21,

42, and 63 DAI, respectively (Table 2). The broad sense coefficient of genetic determination was 0.96, 0.97 and 0.98 at 21, 42 and 63 DAI, respectively. The relative importance of additive to non-additive gene action were 0.57, 0.46 and 0.40 at 21, 42 and 63 DAI, respectively,

The parents had significantly different general combining ability (GCA) effects ( $P < 0.001$ ) for all damage assessment periods. The specific combining ability (SCA) effects of the crosses were also significantly different ( $P < 0.001$ ) for all damage level assessment dates.

Estimates of the effects of GCA for individual parental rice lines for AfRGM are presented in Table 3. Accordingly, the desirable GCA effect for parents and SCA for crosses were negative values. Significant effects ( $P < 0.001$ ) of GCA and SCA variation among genotypes were observed. The four parents used in this study, NERICA-6, NERICA-4, NERICA-1 and METP-7, had highly significant but negative GCA effects of the parents (Table 3).

According to IRRI (2014) scoring scale, four parents contributed to tiller damage

TABLE 2. Analysis of variance of general and specific combining abilities for African Rice Gall Midge resistance

Sources of variation	DF	21_DAI	42_DAI	63_DAI
Replications	2	2.07 <sup>ns</sup>	2.84 <sup>ns</sup>	0.54 <sup>ns</sup>
Crosses	31	5.99 <sup>***</sup>	11.65 <sup>***</sup>	10.89 <sup>***</sup>
GCA	7	16.21 <sup>***</sup>	26.17 <sup>***</sup>	21.45 <sup>***</sup>
SCA	24	3.01 <sup>***</sup>	7.42 <sup>***</sup>	7.8 <sup>***</sup>
Error	62	0.25	0.39	0.27
Additive component ( $\sigma^2$ GCA)		1.86	3.01	2.47
Dominance component ( $\sigma^2$ SCA)		2.76	7.03	7.54
Bakers' ratio (BR)		0.57	0.46	0.40
BS-CGD		0.96	0.97	0.98
NS-CGD		0.55	0.45	0.39

\*\*\* = Significant at 0.001 probability, ns = non-significant, DF = degree of freedom, DAI = days after infestation, GCA = general combining ability, SCA = specific combining ability, BS-CGD = broad sense coefficient of genetic determination, and NS-CGD = narrow sense coefficient of genetic determination

TABLE 3. Tiller damage mean scores and general combining ability (GCA) effects of the rice parents

Parental lines	Reactions	21_DAI		42_DAI		63_DAI	
		Mean	GCA effects	Mean	GCA effects	Mean	GCA effects
NERICA-6	Resistant	0.00	-0.56*	0.00	-0.70***	0.00	-0.91***
NERICA-4	Resistant	0.00	-1.46***	1.00	-1.53***	0.00	-1.28***
NERICA-1	Resistant	0.00	-1.01**	0.00	-1.61***	0.00	-1.13***
METP-7	Resistant	0.00	-1.75***	0.00	-2.43***	0.00	-2.28***
KOMBOKA	Susceptible	4.33	0.87**	7.00	1.84***	6.33	1.53***
NAMCHE-1	Susceptible	4.33	1.57***	7.00	1.77***	6.33	1.12***
K85	Susceptible	5.67	1.31***	7.00	1.51***	7.00	1.97***
E22	Susceptible	5.00	1.24***	7.00	1.42***	5.67	1.33***
Minimum		0.00		0.00		0.00	
Maximum		5.67		7.00		7.00	
LSD(5%)		1.21		1.07		1.30	
S.E. <sub>GCA</sub>			0.05		0.01		0.05

\*, \*\*, \*\*\*\* = Significant at 0.05, 0.01 and 0.001 probability, respectively, S. E = standard error for GCA, and DAI = Days after infestation

resistance at 21, 42, and 63 DAI (Table 3). Based on the mean value of tiller damage scores, METP-7 was the best parent for the transfer of resistance to AfRGM. This was followed by NERICA-4. On the other hand, a highly positive significant ( $P < 0.001$ ) GCA effect was obtained on the locally adapted genotypes, KOMBOKA, NAMCHE-1, K85 and E22. These genotypes contributed average scores of 1.25, 1.6 and 1.5 tillers damage units towards susceptibility at 21, 42, and 63 DAI, respectively. Generally, GCA effects were less than SCA effects, as illustrated by Baker's ratio (Table 3).

The specific combining ability of crosses are shown in Table 4. For rice AfRGM tiller damage, two crosses (NERICA-6 X METP-7 and NERICA-4 X NERICA-1) had no significant SCA effects ( $P > 0.05$ ); while the other eight crosses had highly significant ( $p < 0.001$ ) SCA effects for all periods assessed (21, 42, and 63 DAI). The most desirable SCA effects were obtained in crosses NERICA-6 X E22; followed by NERICA-1 X K85, NERICA-1 X KOMBOKA and NERICA-4 X

KOMBOKA (Table 4). Four crosses had positive and undesirable SCA effects, i.e., NERICA-6 X NERICA-1, NERICA-4 X E22, METP-7 X KOMBOKA and NERICA-1 X NAMCHE-1 at 21, 42, and 63 DAI (Table 4).

**Parents and crosses tillers damage.** Based on tiller damage mean scores (Table 3), the four parents, NERICA-6, NERICA-4, NERICA-1 and METP-7 confirmed their resistance status at all tiller damage assessment periods (21, 42 and 63 DAI). All resistant parents showed the most resistant status in all tiller damage assessment periods, except NERICA-4, which recorded 1.0 at 42 DAI. Generally, all resistant parents were classified under highly resistant (zero score) and resistant (1) mean scores at 21, 42 and 63 DAI. The most susceptible parents were K85 and E22 with mean tiller damage scores at 21, 42 and 63 DAI.

The F<sub>2</sub> family tillers damage mean scores for resistance to AfRGM are presented in Table 4. The average tiller damage scores ranged from 0 to 6.33 at 21 DAI and 0 to 7.67 at both

TABLE 4. Tiller damage means scores and specific combining ability effects of the F2 families to African rice gall midge

Crosses combinations	Parental status	21_DAI		42_DAI		63_DAI	
		Mean	SCA effects	Mean	SCA effects	Mean	SCA effects
NERICA-6 X NERICA-4	R X R	0.00	-0.17 <sup>ns</sup>	0.00	-1.15 <sup>s</sup>	0.00	-0.82 <sup>ns</sup>
NERICA-6 X NERICA-1	R X R	4.33	3.71 <sup>***</sup>	5.00	3.93 <sup>***</sup>	6.33	5.36 <sup>***</sup>
NERICA-6 X METP-7	R X R	0.00	0.12 <sup>ns</sup>	0.00	-0.25 <sup>ns</sup>	0.00	0.19 <sup>ns</sup>
NERICA-6 X KOMBOKA	R X S	2.67	0.16 <sup>ns</sup>	7.67	3.15 <sup>***</sup>	7.00	3.37 <sup>***</sup>
NERICA-6 X NAMCHE-1	R X S	5.00	1.8 <sup>***</sup>	6.33	1.89 <sup>**</sup>	0.00	-3.22 <sup>***</sup>
NERICA-6 X K85	R X S	2.33	-0.61 <sup>ns</sup>	4.67	0.48 <sup>ns</sup>	5.00	0.93 <sup>s</sup>
NERICA-6 X E22	R X S	0.00	-2.88 <sup>***</sup>	0.00	-4.1 <sup>***</sup>	0.00	-3.43 <sup>***</sup>
NERICA-4 X NERICA-1	R X R	0.00	0.28 <sup>ns</sup>	0.00	-0.23 <sup>ns</sup>	0.00	-0.6 <sup>ns</sup>
NERICA-4 X METP-7	R X R	0.00	1.02 <sup>*</sup>	0.00	0.59 <sup>ns</sup>	0.00	0.55 <sup>ns</sup>
NERICA-4 X KOMBOKA	R X S	0.00	-1.6 <sup>**</sup>	0.00	-3.68 <sup>***</sup>	0.00	-3.26 <sup>**</sup>
NERICA-4 X NAMCHE-1	R X S	0.00	-2.3 <sup>***</sup>	0.00	-3.61 <sup>***</sup>	0.00	-2.86 <sup>**</sup>
NERICA-4 X K85	R X S	2.33	0.29 <sup>ns</sup>	6.33	2.98 <sup>***</sup>	7.67	3.96 <sup>***</sup>
NERICA-4 X E22	R X S	3.00	1.02 <sup>*</sup>	7.00	3.74 <sup>***</sup>	7.00	3.94 <sup>***</sup>
NERICA-1 X KOMBOKA	R X S	0.00	-2.06 <sup>***</sup>	0.00	-3.6 <sup>**</sup>	0.00	-3.41 <sup>***</sup>
NERICA-1 X NAMCHE-1	R X S	3.67	0.91 <sup>*</sup>	7.00	3.47 <sup>***</sup>	7.00	4.0 <sup>**</sup>
NERICA-1 X K85	R X S	0.00	-2.49 <sup>***</sup>	0.00	-3.27 <sup>***</sup>	0.00	-3.85 <sup>***</sup>
METP7 X KOMBOKA	R X S	3.00	1.69 <sup>***</sup>	7.00	4.22 <sup>***</sup>	5.00	2.75 <sup>***</sup>
METP7 X NAMCHE-1	R X S	0.00	-2.01 <sup>***</sup>	0.00	-2.71 <sup>***</sup>	0.00	-1.85 <sup>***</sup>
METP-7 X K85	R X S	0.00	-1.75 <sup>***</sup>	0.00	-2.45 <sup>***</sup>	0.00	-2.7 <sup>**</sup>
METP-7 X E22	R X S	0.00	-1.69 <sup>***</sup>	0.00	-2.36 <sup>***</sup>	0.00	-2.06 <sup>***</sup>
KOMBOKA X NAMCHE-1	S X S	5.67	1.03 <sup>*</sup>	7.00	0.02 <sup>ns</sup>	5.67	0.01 <sup>ns</sup>
NAMCHE-1 X K85	S X S	6.33	1.26 <sup>**</sup>	7.00	0.35 <sup>ns</sup>	7.00	0.89 <sup>ns</sup>

Rice resistance to African rice gall midge



TABLE 4. Contd.

Crosses combinations	Parental status	21_DAI		42_DAI		63_DAI	
		Mean	SCA effects	Mean	SCA effects	Mean	SCA effects
NAMCHE-1 X E22	S X S	6.33	1.32**	7.00	0.44 <sup>ns</sup>	6.33	0.87 <sup>ns</sup>
K85 X E22	S X S	6.33	1.59***	7.00	0.7 <sup>ns</sup>	7.00	0.69 <sup>ns</sup>
S.E. <sub>SCA</sub>			0.45		0.57		0.47
Minimum		0.00		0.00		0.00	
Maximum		6.33		7.67		7.67	
LSD (5%)		1.49		1.97		1.56	

\*, \*\*, \*\*\* = significant at 0.05, 0.01 and 0.001 probability, respectively, ns= non-significant, S. E.= standard error for SCA, R = resistant, S = susceptible, DA I= days after infestation

42 and 63 DAI. In all the three periods, twelve crosses had the highest degree of resistance, with a mean score of zero and these crosses had in common parents NERICA-6, NERICA-4, NERICA-1, and METP-7. The rest of the crosses had lower degree of resistance with the mean scores ranging from 2.33 to 7.0 in the three assessments periods.

## DISCUSSION

**Combining ability.** The significant differences among the progenies tested, along with their parents in the three cases of tiller damage assessments periods (Table 2), indicate that both additive and non-additive gene actions were involved in the inheritance of resistance to AfRGM. However, the non-additive portion being greater than the additive, suggests that the former gene effects contributed more to rice AfRGM resistance than its latter counterpart. Similar results were reported on rice on tillers damage scores by Yao (2012) in a study in Côte d'Ivoire.

The significant contribution of both additive and non-additive genes contributed to inheritance of resistance to AfRGM (Table 2), concurs with the findings of Ubor *et al.* (2015), who found out that both genes contribute to inheritance in sesame resistance to AfRGM. The negative GCA values obtained in genotypes NERICA-6, NERICA-1, NERICA-4 and METP-7 (Table 2), underscores their importance of contributing resistance against rice AfRGM in their crosses. Parents with high negative GCA effects are potentially superior, and may be included in rice breeding programmes to select new inbred lines in advanced generations (Yao, 2012; Yao *et al.*, 2016).

The proportion of additive to non-additive gene effects for rice AfRGM resistance was moderate, as estimated by Baker's ratio of 0.57, 0.46 and 0.40 for 21, 42, and 63 DAI, respectively (Table 2). This implies that both additive and non-additive genes effects are involved in the inheritance of AfRGM resistance (Baker, 1978; Yao *et al.*, 2016). The



additive gene effects were more important than their non-additive counterparts (0.57) at 21 DAI. In this early stage of 21DAI, progenies have a high predictability of performance of the parents from the GCA effects. This suggests that breeding methods that involve selection of rice progenies in the early generation improve rice against tiller damage. These methods include pedigree breeding, pure line selection, mass selection, single seed decent and progeny selection. However, the non-additive gene effects were larger than their additive gene counterpart effects (0.46) at 42 DAI *versus* (0.40) at 63 DAI. Weelar *et al.* (2017) reported similar results on stalk eye fly on different rice genotypes. In addition, Weelar (2017) reported that progenies have low predictability for performance of the parents from the GCA effects. Therefore, methods that involve a delay in selection of genotypes would be appropriate for improving tillers damage. The modified bulk methods of selection are proposed for Uganda to be employed in this rice breeding effort.

The moderate narrow sense coefficient of genetic determination obtained for rice tiller damage, suggests that 45 % (at 42 DAI) of the inheritance to rice AfRGM resistance was governed by additive genes, transmissible to the progeny (Viana *et al.*, 2001, Yao *et al.*, 2016). This implies that phenotypic selection would be moderately effective heritability (Fehr, 1987).

The high broad sense coefficient of genetic determination (97 % at 42 DAI) for inheritance to rice AfRGM resistance observed in the present study, indicated that the proportion of genotypic to environmental factors is very high. This conforms to the reports by Yao (2012) on heritability of 96.6% for rice resistance to AfRGM in  $F_2$  populations.

### CONCLUSION

This study has revealed that resistance to rice AfRGM is controlled by both additive and non-additive gene effects. The estimated narrow-

sense coefficient of genetic determination is fairly low, implying that later-generation selection would be effective. The estimated Baker's ratios are also low, suggesting that low predictability of progenies performance from parents' general combining ability effect. The progeny performance in this set of crosses is only better in specific crossing combinations and; therefore, could not be predicted for a wide range of crosses. Overall, genotypes METP-7 and NERICA-4 are promising sources of resistance to rice AfRGM, since they had very good aptitude of transmission of AfRGM resistance.

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