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Mode of inheritance of resistance to the stalk-eyed fly (*Diopsis longicornis*) in rice

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Abstract

Stalk eyed flies (*D. longicornis* and *D. apicalis*) are pests of economic importance on rice. Of the two species of stalk- eyed fly, *D. longicornis* is the most prevalent and destructive. To determine the mode of inheritance for resistance to the stalk-eyed fly in rice in Uganda, crosses were made among eight parental lines (NERICA4, TXD306, K85, NM7-22-11-B-P-1-1, NERICA1, NERICA6, NAMCHE2 and PAKISTAN) selected on the basis of their response to the stalk-eyed fly, high yield and early maturity. Of the eight, four genotypes [NERICA4, TXD306, and NM7-22-11-B-P-1-1 and K85], exhibited lower levels of deadheart occurrence and were crossed using the North Carolina II mating design with four susceptible genotypes [NERICA1 and NERICA6, PAKISTAN, and NAMCHE2]. Studies on combining abilities were conducted on 16 F_1 hybrids along with the eight parents. Narrow sense coefficients of genetic determination (NSCGD) were low to moderate (0.09 - 0.33) and broad sense coefficients of genetic determination (BSCGD) were moderate to high (0.38 - 0.89) for traits studied. Both GCA and SCA effects were significant for percentage of deadhearts. However, Baker's ratio was less than 0.5 (0.37) for deadhearts, indicating that both additive and non-additive gene effects were involved in resistance to the stalk-eyed fly, although non-additive gene effects were more important. NERICA4 andK85 were found to be good general combiners for increasing resistance. The crosses Pakistan × TXD306 and NERICA1× NM7-22-11-B-P-1-1 were identified as promising lines for advancement.

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Introduction

Rice is the most extensively grown cereal in the tropical and subtropical regions of the world, providing 20% of daily calorie intake (Hasan *et al.*, 2013). Unfornuately, yield losses on the crop are increasing due to insect pest infestations (El-Namaky *et al.,* unpublished). Among the insect pests affecting rice production, the stalk eyed flies (*Diopsis longicornis* and *Diopsis apicalis*) are considered pests of economic importance on rice worldwide (Togola *et al.*, 2011; Fujiie *et al.*, unpublished). Of the two species of stalk eyed fly, *Diopsis longicornis* is the most prevalent and destructive due to its monophagous nature and preference for rice (Heinrichs and Barron, 2004). In contrast, *Diopsis apicalis* is polyphagous and has a wide host range. The species often occurs along with *D. longicornis* but is mostly found in forest ecologies and affects rice mainly during rainy seasons (Pathak *et al.*, 1994). Yield losses of between 10 and 30% have been attributed to these pests. Various cultural practices are used to manage the pests but host resistance is considered the most cost effective (Way and Heong, 1994).

Extensive screening of rice varieties for resistance to the stalk eyed fly has been done in West Africa (Nwilene *et al.*, 2008; Togola *et al.*, 2011; Ogah, 2013). While these studies have not specifically investigated inheritance of stalk eyed fly resistance, resistance to insect pests in rice is reported to be quantitatively inherited and largely governed by both additive and non-additive genes (Sharma *et al.*, 2007, Muturi, 2013). Most of the research so far done in Africa has concentrated primarily on screening for resistance (Togola *et al.*, 2011; Ogah, 2013). In Egypt, F1 populations were used to improve rice for stem borer resistance (El-Namaky *et al.*, unpublished). On-going efforts at the National Crops Resources Research Institute in Uganda are targeting improvement of elite genotypes for resistance to stalk eyed fly, which is currently considered a priority pest (Fujiie *et al.*, unpublished). The current challenge, however, lies in understanding the nature of resistance to stalk eyed fly in order to support further improvement.

The ability of parents to combine well cannot be judged by phenotypic performance and adaptation qualities (Khattak, 2004). Therefore, the choice of parental material and breeding methodology becomes complicated for improvement or development of new cultivars (Thirumeni *et al.,* 2000). Combing ability analysis provides a guideline for the assessment of relative breeding potential and selection of parents (Sarker *et al.*, 2002; Selvaraj *et al.*, 2011) while heritability of traits is a function of a breeding population and the conditions under which a study is conducted. This process provides an indication of the expected response to selection in a segregating population, and is useful in designing an effective breeding strategy (Moose and Mumm, 2008). The general combining ability could identify superior parental genotypes while specific combining ability helps in identification of good hybrids (Saleem *et al.,* 2010). The aim of the current study was to determine the mode of inheritance of resistance to the stalk-eyed fly, *Diopsis longicornis*, in rice. Eight parental lines (Table 1) identified from a cross-section of 50 diverse rice genotypes were used in order to develop F_1 hybrids for evaluation. This process contributed towards a better understanding of the mode of inheritance of resistance.

Materials and methods

Planting materials and experimental design

Eight parental lines were selected on the basis of their resistant to the stalk-eyed fly infestation, high yield and early maturity (Table 2). These lines were selected from three sources: Africa Rice Center, IRRI and NaCRRI. The four recipient (susceptible) genotypes (NERICA 1, NERICA 6, NAMCHE 2 and Pakistan) were grown alongside the four donor (resistant) parents (NERICA 4, TXD306, K85 and NM7-22-11-B-P-1-1) at NaCRRI. The seeds of these lines were soaked and drained, covered and kept moist in order to enhance germination. Soaked seeds were directly planted in buckets filled with well drained top soil. Three seeds were planted per bucket and watered regularly. In order to achieve synchronization in flowering and generate more F_1

population, a two week interval of staggered sowing of seed was practiced.

The North Carolina II (NC II) mating design was used for crossing on the basis of its superiority for evaluation of inbred lines for combining ability as well as its ability to facilitate measurement of both GCA and SCA (Nduwumuremyi *et al.*, 2013). Prior to pollination, female recipient parents were emasculated by removing pollen early in the morning using a vacuum emasculator. Pollen of the respective male donor parents were collected on the same day before pollen shedding. Pollen was then introduced on the stigma of the female parents; all the crosses were done manually. After the pollination, all panicles were covered again with a brown paper bag. The pollinated panicles were identified with tags indicating the names of female and male parents; and the date of pollination. The fertilized panicles were harvested after maturation for evaluation.

The F_1 generation was treated with 70% ethanol by soaking in petri-dishes for three to four minutes. Naked seeds were then washed gently with double distilled water two times and rinsed for five to ten minutes, which helped to minimize contamination. These seeds were initiated on a white tissue and placed in petri-dishes and watered regularly. Germination of F_1 started three to four days after initiation.

The P_1 and P_2 seeds were sowed in the nursery for germination. Seven days after germination, young F_1 seedlings were transplanted to plastic cups filled with sterilized top soil and watered. At 16 days, the eight parents and sixteen F_1 progeny were transplanted into buckets of one foot height filled with top soil. An alpha lattice design with three replications was used for evaluation. Three seedlings were transplanted per bucket. The buckets were placed in a cage and covered with a nylon mesh of 0.5mm gauge for infestation as described in chapter three. At 7 days after transplanting (DAT), 446 adult stalk-eyed flies were introduced to each screening cage to achieve a density of 50adults per square meter.

Data collection and analyses

Data collection followed guidelines in the international standard for evaluation of rice resistance to biotic and abiotic factors (Visalakshmi *et al.,* 2014). The data collected on pest infestation or damage, plant agronomic and yield traits are described below. Pest damage in rice was evaluated on the basis of proportion of deadhearts (Elanchezhyan and Arumugachamy, 2015). In this study, deadheart data were collected at seedling and tillering stages (vegetative phase), which are considered critical periods for damage by the stalk-eyed fly in rice (Togola *et al.,* 2011). Stalk-eyed fly damage data were collected at 7, 14, 21 and 28 days after transplanting, in cage. Affected numbers of tiller per three hills were counted and expressed over the total number of tillers observed to compute for percentage of deadhearts

$$\text{\% deadhearts} = \frac{\text{Number of deadhearts observed}}{\text{Total number of tillers observed per ten hills}} \text{ x } 100$$

Days to flowering was recorded as maximum flowering stage (70 to 75 days after sowing, at 50% heading), where the three hills were sampled. Panicle length was recorded as the distance (cm) from the last node of the rachis to tip of the main panicle for each hill sampled and the average was recorded. Number of effective panicles was counted for three hills per pot and sampled. Plant height was recorded at the ripening stage for three hills per pot.

This was done by taken the length of main culm (cm) from the soil level in the pot to the tip of its panicle. Grain weight for each hill harvested was recorded. In order to determine the 1000-grain weight, a thousand clean sun-dried grains were counted from total grain weight of three hills per pot after which the grains were weighed (g) and the average was taken at 14% seed moisture content. A thousand grains were then floated for about 3 to 4 minutes and the filled grain was separated from the empty grain and weights were then taken. The rice genotypes were placed into different resistance categories based on the pest damage rating scale (Elanchezhyan and Arumugachamy, 2015) (Table 2).

The analyses of combining ability for agronomic traits and gene action were performed for the experimental design, including parents and progeny in order to estimate error variances using the method prescribed by Dabholkar (1992).

The error variances were computed to test for significance of the general combining ability (GCA) and specific combining ability (SCA) of both male and female parents and to evaluate the effects of GCA and SCA in the F_1' response to stalk-eyed fly damage or deadhearts. Analyses of combining ability in the NC II were performed according to Ozimati *et al.* (2014). The linear model used was as follows: $Y_{ij} = \mu + f_i + m_j + (fxm)_{ij} + e_{ij}$ where: Y_{ij}= effects observed due to r_{th} replications, i_{th} female and j_{th} male; μ = Overall mean of the experiment; f_i= GCA effects due the i_{th} female parent; m_j= GCA effects due the j_{th} male parent; $(fxm)_{ij}$ = effect of the interaction between i_{th} female and j_{th} male; and e_{ij} is the experimental error.

The variance components estimated from the SCA and GCA effects were calculated for each trait using expected mean squares (Nduwumuremyi *et al.*, 2013). Furthermore, the variance components which are associated with GCA and SCA were used to estimate the relative importance of GCA, as suggested by Baker (1978) with the following formula: $2\sigma^2GCA/ (2\sigma^2GCA + \sigma^2SCA)$ the closer the ratio was to unity, the greater the predictability of progeny performance based on GCA effects alone. Estimates were also obtained for the broad sense coefficient of genetic determination (BSCGD) and narrow sense coefficient of genetic determination (NSCGD) for resistance to stalk-eyed fly and other agronomic traits in rice. The BSCGD was calculated using the formula: H^2 = δ2GCAf + δ2GCAm+ SCAf / δ2GCAf + δ2GCAm+ SCAfm+ δ2e, where: the fixed effect equivalent of broad sense heritability). The NSCGD was established from the formula: h^2 = δ2GCAf + δ2GCAm / δ2GCAf + δ2GCAm+ SCAfm+ δ2e where: the fixed effect equivalent of narrow sense heritability).

Results

Performance of 16 progeny and 8 parental lines for stalk-eyed fly damage and tiller number in rice

The analysis of variance and the mean for 16 progeny and 8 parental lines for pest damage and other agronomic trait are presented in Tables 3 and 4, respectively. Significant differences occurred between mean square for tillers counts among the eight parents and their crosses.

Table 1. Characteristics of parents used to determine the mode of inheritance of rice resistance to stalk-eyed fly.

Variety name	Parent	Maturity period (days)	Reaction to stalk-eyed fly
TXD306	Male	125 -135	Resistant
K85	Male	120 -130	Resistant
NM7-22-11-B-P-1-1	Male	100-120	Resistant
NERICA4	Male	95-100	Resistant
Pakistan	Female	120 -135	Susceptible
NAMCHE2	Female	120 -130	Susceptible
NERICA1	Female	95-100	Susceptible
NERICA6	Female	95-100	Susceptible

Table 2. Standard Evaluation System for screening for resistance to rice stem borers.

Scale code	% Dead hearts	Level of resistance
0	No visible damage	Highly Resistant
1	1-10%	Resistant
3	11-20%	Moderate resistant
5	21-30%	Moderate susceptible
7	31-60%	Susceptible
9	>60%	Highly susceptible

Source: (Elanchezhyan and Arumugachamy, 2015)

The differences in tiller number of the genotypes were significant at all intervals of scoring of the infestation. Stalk-eyed fly damage was significant ($P<0.001$) at all intervals of data collection (Table 3). The greatest damage to stalk-eye fly was generally observed at 14 and 21 days starting at 7 days after infestation (Table 4). Three of the four male parental lines reacted as resistant with deadheart damage between 6.1 to 7.7%. The fourth parental line reacted as moderately resistant with a damage of 14.4% (Table 4). Two female parental lines reacted as moderately susceptible and the other two as susceptible.

Table 3. Mean squares of analysis of variance of 8 parental lines and 16 crosses evaluated under screen cage conditions for resistance to stalk eyed fly.

Mean squares for Tiller number			Mean squares for percentage of deadheart						
Source of variation	Df	7DAITNO	14DITTNO	21DAITNO	28DAITNO	7DAIDH	14DAIDH	21DAIDH	28DAIDH
Replications	2	0.74	0.59	0.84	0.99	0.37	5.7	2.13	1.58
Rep.Block	15	-	0.27	0.52	-	-	-	-	-
Genotype	23	1.22***	0.47*	1.13*	8.49*	120.61***	316.65***	356.56***	209.96***
Residual	32	0.27	0.18	0.46	0.65	1.29	3.5	3.54	1.52
LEE	36	-	0.2	0.48	-	-	-	-	-

*= significant, *** = highly significant, DAITNO= days after infestation tiller number, DAIDH= days after infestation percent deadhearts, LEE= lattice effective error.

Ten of the sixteen progeny reacted as resistant with mean deadheart damage from 4.55 to 9.48%. The remaining six progeny reacted as moderately resistant with the mean deadheart damage ranging from 11.16 to 16.03 (Table 4). The analysis further revealed significant differences in tiller numbers between the genotypes used. Generally, the progeny were found better in both tillers and deadhearts performance than the parents (Table 4).

Table 4. The mean number of tillers and damage of deadhearts in the eight parental lines and 16 crosses evaluated under screen cage condition for resistance to stalk eyed fly (*Diopsis longicornis*).

	Tiller number					*Percentage of deadheart*					
Genotypes	7DAITNO	14DAITO	21DAITNO	28DAITNO	Mean	7DAI%DH	14DAI%DH	21DAI%DH	28DAI%DH	Mean	Status
NERICA 4	2.97	4.39	7.23	8.63	5.81	4.80	6.00	9.23	4.23	6.07	R
TXD306	1.80	4.65	5.56	10.44	5.61	6.27	9.48	4.84	4.93	6.38	R
K85	2.69	4.54	6.42	9.22	5.72	3.60	7.76	14.33	5.40	7.77	R
NM7-22-11-B-P-1-1	2.26	4.29	6.52	7.42	5.12	7.87	13.97	20.66	15.43	14.48	MR
NAMCHE2	3.17	4.91	6.99	8.02	5.77	18.53	33.23	40.33	23.57	28.92	MS
NERICA1	2.32	4.27	6.38	7.30	5.07	21.79	36.50	34.13	25.80	29.56	MS
NERICA6	1.87	3.87	6.05	2.62	3.60	19.97	41.70	35.00	27.67	31.08	S
Pakistan	3.32	4.88	6.96	7.40	5.64	27.53	34.26	36.80	27.97	31.64	S
NERICA6 x K8	3.44	4.81	7.57	8.31	6.03	5.27	6.53	4.10	2.30	4.55	R
NAMCHE2 x K85	2.15	5.13	7.33	8.11	5.68	4.50	7.50	6.77	4.25	5.75	R
NAMCHE2 x NERICA 4	3.22	4.64	7.13	8.44	5.86	5.10	6.40	8.97	6.00	6.62	R
NERICA1 x TXD306	3.22	4.40	6.89	7.44	5.49	5.93	13.67	6.73	4.66	7.75	R
Pakistan x K85	3.56	4.44	7.01	7.78	5.70	6.70	17.00	5.10	4.79	8.40	R
NERICA6 x NM7-22-11-B-P-1-1	3.11	4.92	7.21	7.96	5.80	6.63	13.10	9.25	5.60	8.65	R
NERICA1 x NERICA 4	2.71	4.91	6.01	7.44	5.27	6.53	17.47	6.93	4.76	8.92	R
NERICA6 x NERICA 4	3.44	4.80	6.88	8.44	5.89	8.23	14.27	7.80	5.66	8.99	R
Pakistan x NERICA 4	2.29	5.04	7.02	7.50	5.46	7.07	13.67	11.84	5.23	9.45	R
Pakistan x TXD306	2.38	3.81	7.48	8.19	5.47	7.79	13.17	14.07	2.90	9.48	R
NAMCHE2 x NM7-22-11-B-P-1-1	3.22	4.78	6.98	9.40	6.10	5.67	8.80	13.05	17.13	11.16	MR
NERICA1 x K85	1.50	3.78	5.21	8.11	4.65	6.70	19.53	14.50	5.00	11.43	MR
NERICA6 x TXD306	2.13	4.07	7.08	8.56	5.46	5.63	14.17	22.66	7.33	12.45	MR
NERICA1 x NM7-22-11-B-P-1-1	2.43	4.92	7.33	8.19	5.72	11.46	25.33	8.58	4.83	12.55	MR
NAMCHE2 x TXD306	3.44	4.71	7.52	12.89	7.14	11.87	21.30	12.33	7.08	13.15	MR
Pakistan x NM7-22-11-B-P-1-1	3.78	4.65	7.31	8.44	6.05	15.00	25.27	10.50	13.37	16.03	MR
Grand Mean	2.77	4.57	6.84	8.18	5.59	9.60	17.50	14.94	9.83	12.97	
Parental Mean	2.55	4.48	6.51	7.63	5.24	13.80	22.86	24.42	16.88	19.49	
Offspring Mean	2.88	4.61	7.00	8.45	5.73	7.51	14.82	10.20	6.31	9.71	
LSD 0.05	0.86	0.74	1.14	1.32		1.87	3.08	3.09	2.02		
%CV	18.82	7.98	8.24	9.83		11.84	10.69	12.60	12.53		

DAITNO= Total number of tillers with days after infestation, DAI%DH= Days after infestation percent deadheart, R= resistant, MR= moderate resistant, and S= susceptible,

Performance of 16 progeny and 8 parental lines for other agronomic traits in rice evaluated for resistance to the stalk- eyed fly

The analysis of variance and the Means performance of 8 parents and their 16 progeny for agronomic traits are presented in Table 5 and 6. Significant differences were observed among the genotypes for days to flowering, plant height, panicle length', average grain weight per pot ($P<0.001$), leaf ratio and panicle number ($P<0.05$). The differences among genotypes were not significant for 1000 grain weight, filled grain weight and empty grain weight (Table 5).

Table 5. Mean squares of the analysis of variance for 8 parental lines and their 16 F1 progeny for agronomic trait characters under screen cage conditions for resistance to stalk eyed fly.

Mean		Agronomic traits								Yield traits
SOV	df	DF	PH	LR	PL	PNO	AGW/POT	1000GW	FGW	EGW
Replication	2	0.6728	49.37	19.26	6.65	0.92	5.3	2.04	2.25	0.51
Rep.Block	15	-	39.79	4.887	-		22.2	-	1.62	-
Genotype	23	81.41***	137.67***	7.82*	13.98***	3.55*	131.91***	1.83^{ns}	1.52^{ns}	0.68^{ns}
Residual	32	0.9176	17.75	3.371	2.805	1.95	7.14	1.352	1.378	0.45
LEE	36	-	21.48	3.726	-	2.44	9.08	-	1.44	-

df = degree of freedom, ns = not significant, * = significant, *** = highly significant, DF=Day to flowering, PH (cm) =Plant height, LR (cm) = Leaf ratio, PNO = Panicle number, PL (cm) = Panicle length, AGW/pot (g)= Average grain weight per pot, 1000GW (g) = A thousand grain weight, FGW (g) = Filled grain weight, and EGW (g) = Empty grain weight.

The mean of parents for day to flowering was between 79.67 and 89.78 days while F_1 progeny had a mean of 73.89-77.67 days. The parent's height ranged from 80.97-111.10 while the progeny had a plant height mean range of 88.46-104.64. Parents had a panicle length between 17.43-22.70 cm; progeny had panicle mean between 20.78-26.22 cm; and parents had a panicle number mean of 4.90-8.67 while progeny had the panicle number mean of 6-9 (Table 6).

Table 6. Mean performance of parents and their crosses for agronomic traits and resistance to the stalk-eyed fly.

	Agronomic traits						*Yield traits*		
Genotypes	DF	PH	LR	PL	PNO	AGW/Pot	1000GW	FGW	EGW
TXD306	83.67	102.65	22.36	22.63	8.67	48.31	19.33	16.27	3.10
NERICA 4	83.67	100.68	21.60	22.70	5.67	44.65	20.33	18.04	2.33
K85	79.67	80.94	17.72	22.16	7.33	42.92	18.33	16.17	2.17
NM7-22-11-B-P-1-1	87.00	107.16	18.92	21.96	6.00	33.83	20.00	17.44	2.47
NAMCHE2	87.33	98.92	19.97	17.43	5.33	41.02	20.00	17.26	2.73
NERICA 6	88.00	111.10	17.50	17.49	4.90	47.36	19.33	17.67	1.60
NERICA 1	89.78	99.83	21.57	18.62	5.56	44.39	19.00	17.28	1.67
PAKISTAN	88.33	103.87	23.64	18.16	8.00	46.13	20.00	17.15	2.90
NAMCHE2 x NERICA 4	76.11	94.82	20.96	21.89	6.00	29.61	19.83	17.26	2.60
NAMCHE2 x NM7-22-11-B-P-1-1	77.56	90.84	17.69	22.89	6.00	35.69	20.00	17.68	2.37
NAMCHE2 x K85	75.00	95.52	18.94	26.22	9.00	28.16	20.67	17.83	3.20
NAMCHE x TXD306	76.89	88.46	19.94	24.11	6.00	31.32	19.63	17.96	1.70
NERICA1 x TDX306	77.44	102.81	20.68	21.44	6.33	31.78	19.67	16.82	2.80
NERICA 6 x NERICA 4	75.44	102.98	20.96	21.44	6.00	35.89	20.67	17.65	3.03
NERICA 6 x TXD306	76.89	98.22	22.26	22.89	7.00	30.50	19.67	17.22	2.40
NERICA 1 x K85	75.22	91.95	20.05	21.02	8.00	44.01	21.33	18.44	2.93
NERICA 1 x NERICA 4	75.00	100.90	21.51	22.89	7.33	42.88	21.33	18.94	2.43
NERICA1 x NM7-22-11-B-P-1-1	73.89	94.53	20.94	22.44	7.33	44.42	20.67	18.11	2.47
NERICA6 x K85	75.56	101.60	18.07	21.78	8.33	31.78	20.33	17.52	2.77
NERICA x NM7-22-11-B-P-1-1	75.56	104.62	19.64	21.56	7.00	44.59	20.00	17.78	2.27
Pakistan x K85	75.33	95.93	21.05	20.78	7.33	36.58	21.33	18.80	2.53
Pakistan x NERICA4	75.89	95.43	21.59	25.11	6.33	45.80	19.00	16.29	2.77
Pakistan x NM7-22-11-B-P-1-1-	77.67	103.03	21.23	23.44	7.00	31.88	19.00	17.47	1.47
Pakistan x TXD306	76.00	104.24	19.35	22.00	6.33	38.30	20.33	18.07	2.30
Grand Mean	79.10	98.63	20.25	21.76	6.78	38.41	20.02	17.60	2.43
Parental Mean	85.93	100.64	20.41	20.14	6.43	43.58	19.54	17.16	2.37
Offspring Mean	75.97	97.87	20.30	22.62	6.96	36.45	20.22	17.74	2.50
LSD 0.05	1.57	7.67	3.20	2.75	2.30	4.99	1.91	1.99	1.10
%CV	1.21	3.83	7.75	7.68	20.59	6.34	5.82	5.59	27.33

DF=Day to flowering, PH (cm) =Plant height, LR (cm) = Leaf ratio, PNO= Panicle number, PL (cm)= Panicle length, AGW/pot= Average grain per pot, 1000 GW (g) = A thousand grain weight, FGW (g)= Filled grain weight, EGW= Empty grain weight (g).

In general, parents' performance was better for plant height, average grain weight, leaf ratio and while better performance for panicle number, panicle length and early flowering was displayed by the progeny (Table 6).

Estimates of combining ability and variance components for resistance to stalk eyed fly, agronomic and yield traits of parents and progeny

Analyses of variance for combining ability showed that mean squares of genotypes, GCA female and GCA male were significant for days to flowering and plant height; panicle length, panicle number, average grain weight and tiller number GCA female were significant while GCA male were not significant; 1000 grain weight, percentage deadhearts and empty grain weight were significant for GCA male while GCA female were not significant. On the other hand, the variances for all traits were not significant for SCA except panicle length, average grain weight, tiller number and percentage deadhearts which were significant (Table7).

Table 7. Analyses and variance components of stalk-eyed fly damage, agronomic traits for parents and progeny of rice evaluated for general and specific combining abilities.

Traits	SOV	Female GCA	Male GCA	Female.Male SCA	Residual	LEE	Baker's ratio	NSCGD	BSCGD
	Df	3	3	9	35	47			
Days to flowering	MS	49.82*	96.38**	96.38^{ns}	18.55	5.45	0.25	0.18	0.73
	VC	3.7	7.58	33.94					
PH	MS	198.10***	37.42***	86.22^{ns}	19.23	6.43	0.38	0.27	0.72
	VC	15.97	2.58	30.88					
LR	MS	6.42^{ns}	4.32^{ns}	4.98^{ns}	4.15	1.30	0.24	0.10	0.42
	VC	0.43	0.25	2.09					
PL	MS	26.68**	5.20^{ns}	9.85*	4.19	1.40	0.39	0.23	0.60
	VC	2.11	0.32	3.75					
P.NO	MS	6.62*	1.52^{ns}	2.27^{ns}	2.41	0.80	0.35	0.14	0.39
	VC	0.48	0.06	1.03					
AGW/pot	MS	207.89**	51.32^{ns}	67.39*	29.89	8.64	0.44	0.28	0.64
	VC	16.6	3.56	25.34					
1000GW	MS	1.31^{ns}	4.86**	1.39^{ns}	1.25	0.42	0.42	0.19	0.46
	VC	0.07	0.37	0.6					
FGW	MS	1.20^{ns}	1.36^{ns}	1.14^{ns}	1.24	0.34	0.24	0.09	0.38
	VC	0.07	0.08	0.48					
EGW	MS	0.02^{ns}	1.44*	0.69^{ns}	0.48	0.16	0.25	0.11	0.44
	VC	-0.01	0.11	0.28					
TNO	MS	2.12***	0.43^{ns}	0.96***	0.21	0.06	0.37	0.33	0.89
	CV	0.17	0.03	0.34					
%DH	MS	74.97^{ns}	174.93**	86.23*	38.58	11.73	0.37	0.30	0.82
	VC	5.27	13.60	31.65					

SOV= source of variation, df = degrees of freedom, ns = not significant,* = significant($P<0.05$); ** = highly significant ($P<0.01$); and *** = highly significant $P<0.001$); DF = days to flowering, PH(cm) =Plant height, LR(cm) = Leaf ratio, PL(cm) =panicle length, P.NO= panicle number, AGW/pot (g) = Average grain weight per pot, 1000 GW(g) = A thousand grain weight, FGW(g) = filled grain, EGW(g) = Empty grain weight, TNO = tiller number, %DH = percent deadhearts; LEE= lattice effective error, BSCGD= broad sense coefficient of genetic determination, NSCGD = narrow sense coefficient of genetic determination.

Heritability and bakers' ratio was estimated for each trait and the results are presented below (Table 7). Baker's ratio was below 0.5 for all traits, ranging from 0.24 to 0.42 (Table 7). Damage of deadhearts displayed low narrow sense heritability, with a range of 0.09 to 0.33. Broad sense heritability (BSCGD) values were high (0.60 – 89) for all traits except for panicle number, leaf ratio, filled grain weight and empty grain weight where the values were moderate between 0.38 and 0.46 (Table 7).

Estimates of the general combining ability

Results of the GCA for stalk-eyed fly damage and other agronomic traits for 8 parents are presented (Table 8). Results showed K85 and NERICA4 showed a significant negative GCA for percentage deadhearts. On the other hand, positive significant GCA effects were displayed by NM7-22-11-B-P-1-1 and TXD306 for percentage deadhearts while other genotypes were not significant. NAMCHE2 had positive significant GCA and NERICA1 had negative significant GCA effect for tiller number. Significant negative GCA effects and significant positive GCA effects were obtained for plant height for the genotypes NAMCHE2 and NERICA6, respectively. The genotypes NAMCHE2 had significant negative GCA effect for panicle number. On the other hand, NERICA6 and Pakistan had positive significant GCA effects for panicle number. NAMCHE2 and NERICA6 had significant positive and negative GCA effects for panicle length. The genotypes K85 and NAMCHE2 displayed negative significant GCA effects for average grain weight while NERICA1 had positive significant GCA effects for average grain weight. TXD306 had positive significant GAC effects for 1000 grain weight and empty grain weight while TXD306 had negative significant GCA effects for empty grain weight (Table 8).

Table 8. General combining ability (GCA) effects of 8 parents for tiller number and stalk stalk-eyed fly damage.

	Parental lines							
Traits	K85	NERICA4	NM7-22-11-B-P-1-1	TXD306	NAMCHE2	NERICA6	NERICA1	Pakistan
TNO	-0.14	-0.04	0.20	-0.02	0.53***	0.05	-0.60***	0.02
%DH	-3.35*	-3.40*	2.84*	3.91**	-1.24	1.16	0.79	-0.71
DF	-2.44**	-1.96**	1.54**	2.86**	-1.29*	1.79*	0.07	-0.56
PH	-2.11	0.26	0.66	1.18	-5.97**	3.79***	1.14	1.04
LR	-0.81	0.83	-0.06	0.04	-1.01	0.09	0.08	0.85
PNO	-0.02	0.14	0.02	-0.14	-0.71*	0.69*	-0.2	0.23*
PL	0.12	0.51	0.04	-0.67	1.45**	-1.19*	-0.84	0.58
AGW/POT	-2.45*	1.15	1.07	0.23	-5.48***	-1.02	4.61***	1.89
1000GRW	0.69*	-0.02	-0.18	-0.49	-0.19	-0.05	0.52	-0.27
FGW	0.45	-0.18	0.00	-0.27	-0.04	-0.2	0.49	-0.26
EGW	0.38*	0.23	-0.29	-0.32*	-0.01	0.11	0.01	-0.11

Values without stars are not significant, *significant (P<0.05); ** = highly significant (P<0.01); and *** = highly significant (P<0.001); TNO = tiller number;% DH= percentage deadhearts; DF= days to flowering, PH (cm)= plant height, LR(cm)= Leaf ratio, PNO= panicle number; PL (cm)= panicle length; AGW/pot = average grain weight per pot ,1000 GW (g)= A thousand grain weight, FGW (g)= filled grain weight, EGW (g)= empty grain weight.

Estimates of the specific combining ability

The estimates of the specific combining ability (SCA) effects for crosses in relation to agronomics traits and stalk-eyed fly damage are presented in Table 9. With respect to inheritance of resistance to the stalk-eyed fly damage or deadhearts inheritance, the progeny NERICA1 x NM7-22-11-B-P-1-1 and. Pakistan x TXD306 showed significant and negative SCA effects for resistance to stalk-eyed fly. On the other hand positive significant SCA effects was displayed by NERICA1 x NM7-22-11-B-P-1-1 for tiller number and displayed negative significant SCA effect for plant height while other agronomic traits had not significant SCA effects. Pakistan x TXD306 showed positive significant SCA effects for plant height and average grain weight while other traits had not significant SCA effect. The progeny NERICA6 x NM7-22-11-B-P-1-1 exhibited highly significant and positive SCA effects for resistance to the borer; the hybrid, however, exhibited negative significant SCA effects for plant height and positive significant SCA effects for average grain weight respectively .The analyses further revealed that, Pakistan x TXD306 had the highest negative significant SCA value for resistance to stalk-eyed fly.

Discussion

The present study was conducted to determine the mode of inheritance of resistance to stalk-eyed fly in rice. The results showed significant differences among rice genotypes for both agronomic traits and resistance to the stalk-eyed fly for the eight parents and 16 crosses evaluated. The exceptions, however, occurred for 1000 grain weight, filled grain weight and empty grain weight, which did not differ significantly (<0.05) among these materials. In general, parental genotypes and progeny exhibited variation in response to stalk-eyed fly attack at 14 and 21 days after infestation.

Table 9. Estimate of the specific combining ability (SCA) effects of 16 crosses evaluated for agronomic traits and stalk-eyed fly damage.

Crosses	*TNO*	*%DH*	*DF*	*PH*	*LR*	*PNO*	*PL*	*AGW/pot*	*1000GW*	*FGW*	*EGW*
NAMCHE2 x K85	-0.34	-0.12	0.95	4.95**	0.44	-0.54	2.32*	-0.43	-0.05	-0.32	0.35
NAMCHE2 x NERICA4	-0.32	0.75	1.77	2.62*	0.58	1.30	-2.39*	-2.96*	-0.18	-0.23	-0.10
NAMCHE2 x NM7-22-11-B-P-1.1	-0.30	-0.58	-0.36	-2.46*	-1.55	0.09	-0.93	3.78*	0.15	0.00	0.19
NAMCHE2 x TXD306	0.96***	-0.04	-4.95	-17.04***	-1.50	-2.27	3.90*	-0.39	0.09	0.49	-0.47
NERICA6 x K85	0.50*	-4.39	-1.51	1.65	-1.65	0.73	0.52	-2.30	-0.53	-0.38	-0.21
NERICA6 x NERICA4	0.25	-3.13	-1.73	0.22	-0.13	-1.44	-0.20	-2.55	0.51	0.33	0.21
NERICA6 x NM7-22-11-B-P-1.1	-0.36	3.26***	-0.36	-2.46*	-1.55	0.09	-0.93	4.16**	0.37	0.00	0.19
NERICA6 x TXD306	-0.38	4.25	0.69	-4.30**	1.30	0.35	0.28	0.69	-0.35	0.08	-0.24
NERICA1 x K85	-0.35	3.38	0.04	-4.70**	0.36	-0.38	-0.59	3.28	-0.10	-0.22	0.06
NERICA1 x NERICA4	0.26	-0.25	-0.91	1.41	-0.10	-0.21	0.90	0.22	0.60	0.91	-0.29
NERICA1 x NM7-22-11-B-P-1.1	0.57*	-6.25*	-0.97	-3.15*	1.13	0.08	1.04	0.72	0.25	-0.07	0.19
NERICA1 x TXD306	-0.48*	3.11	1.84	6.45***	-1.39	0.52	-1.35	-4.22**	-0.75	-0.62	0.03
Pakistan x K85	0.19	1.13	0.51	-1.90	0.84	0.19	-2.25*	-0.56*	0.69	0.92	-0.21
Pakistan x NERICA4	-0.18	2.63	0.87	-4.25**	-0.35	0.35	1.69	5.29**	-0.93	-1.00	0.17
Pakistan x NM7-22-11-B-P-1.1	0.086	3.57	-1.22	3.19*	-0.06	-0.52	0.49	-8.66***	-0.77	0.11	-0.61
Pakistan x TXD306	-0.10	-7.32*	-0.17	2.95*	-0.43	-0.02	0.07	3.92*	1.02	-0.02	0.65

Those values without stars are not significant, *= significant, ** = significant, *** = highly significant TNO = tiller number, % DH= percent deadhearts, DF = days to flowering, PH = plant height (cm), LR(cm)= leaf ratio (cm), PNO= panicle number, PL(cm)= panicle length, AGE/pot (g)= average grain weigh/ pot, 1000 GW(g)= A thousand grain weight, FGW (g)= filled grain weight, EGW (g)= empty grain weight.

The finding was in close conformity with Togola *et al.* (2011) who reported high infestation at 10 and 20 days infestation using a different set of populations. The high damage at 14 to 21 days in the present experiment could be probably due to the high sugar content, low phenolic content and occurrence of silica compounds in the stem tissue at maximum tillering stage (Padhi, 2004). Secondly, rice plants at maximum tillering stage (40 to 42 days after sowing, approximately 21 days after transplanting) do not have vigor to withstand insects attack; therefore the level of resistance to stalk-eyed fly was probably poor (Padhi and Sen, 2002). This period also falls within the most critical period for infestation by the fly as described by Togola *et al.* (2011). The 16 progeny, however, showed enhanced resistance to the stalk-eyed fly, when compared with the male parents from which the resistance gene was transferred. The eight parental genotypes, for the most part, exhibited a slightly different response for damage (resistance), compared to the previous assessment at screening. Since the parental lines were already released varieties, these differences in performance could possibly be attributed to differences in environmental factors such as: water supply, which are reported to influence infestation and performance (Togola *et al.,* 2011). Even more, soil nutrient status with respect to nitrogen, potassium and others have been found to influence infestation (Mochiah *et al.*, 2011). The effect of soil nutrient status on genotypic response was not evaluated on this study and could be an area for further study.

In this study, analyses showed significant GCA and SCA effects for percentage of deadhearts, indicating additive and non-additive gene effects contributed to the variation observed. This is consistent with the findings of Kenga *et al.* (2004). The present study further revealed that, for resistance to stalk-eyed fly, the parental lines displayed significant and non-significant negative and positive GCA effects, indicating that both undesirable and desirable traits were inherited by the progeny from the parents. Negative GCA effects are desirable traits in selecting superior parents for resistance to the borers because they indicate a larger contribution of genetic effects to resistance; while positive values contribute towards high susceptibility (Kenga *et al.*, 2004; Saleem *et al.*, 2010). The highest negative significant GCA effects for resistance to the stalk-eyed was displayed by the male parents NERICA4 and K85 while the highest positive significant GCA effect for resistance to the stalk-eyed fly were displayed by TXD306, followed by NM7-22-11-B-P-1-1. Parents with negative GCA effects are known to be good combiners and therefore desirable genotypes for use in breeding programs (Kenga *et al.*, 2004). The male parents, NERICA4 and K85, would thus be prime candidates for further use in breeding for stalks- eyed fly resistance in rice in Uganda.

Crosses Pakistan x TXD306 and NERICA1 x NM7-22-11-B-P-1-1 exhibited a combination of negative significant and non-significant GCA effects for deadheart while positive significant SCA effects were realized for plant height, tiller number and average grain weight. These traits would, therefore, form a basis for selection. These crosses, thus, appear to be the most promising lines for advancement and further evaluation needs to be conducted at F_2. Parents with negative GCA effects do not show good hybrid combinations and there is often difficulty in predicting the resistance levels that can be attained in the progeny on the basis of GCA alone. Therefore, testing of specific male-female combinations is appropriate (Kenga *et al.,* 2004). The contribution of additive and non-additive genes to inheritance of resistance to stalk eyed fly is similar to Sharma *et al.* (2007) who reported additive and non-additive genes action in the inheritance of resistance to deadhearts in sorghum using the spotted borer and the stem borer *Chilo partellus*. Muturi(2013) also reported additive and non-additive effects govering resistance to the stem borer *Busseola fusca* (Noctuiade) and *Chilo partellus* (Crambidae) in sorghum.

In the present study, the narrow sense coefficient of genetic determination was moderate (0.30) and broad sense coefficient of genetic determination was high (0.82) for percentage of deadhearts. Both GCA and SCA effects were significant for this trait. However, the value of Baker's ratio was less than 0.5 (0.37) for deadhearts indicating that non-additive gene effects are more important than additive gene effects in determining resistance to the stalk-eyed fly as also reported by Yao (2012) on inheritance of resistance to the African gall midge in rice; which pest falls within the same order as the stalk-eyed fly (*Diptera*). Control of a trait by both additive and non-additive genes is known to result in low heritability of the said trait due to masking effects of the environment. Singh *et al.* (1994) reported the same in their research on inheritance of resistance to the African gall midge in sugarcane.

Conclusion

In conclusion, since resistance to the stalk eyed fly in rice seems to be controlled by both additive and non-additive genes, selection in early generations (F_1 and F_2) is not effective. Therefore, selection can be appropriate in later generations, between F_4 and F_6. Advancement of selected breeding lines (Pakistan × TXD306 and NERICA1× NM7-22-11-B-P-1-1) is, therefore, recommended for further evaluation for resistance to the stalk borer in later generations. The parental lines NERICA4 and K85 are recommended as good general combiners.

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