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## INHERITANCE OF RESISTANCE TRAITS TO AFRICAN STEM BORER IN GRAIN SORGHUM

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### ABSTRACT

The African stem borer (*Busseola fusca* [Fuller]) is an important insect pest of cereals, mainly maize, sorghum and millets. The pest causes up to 80% reduction in grain yield, depending on the pest population in the field, cultivar and the management practices employed. This reduction in yield translates into food insecurity, especially in semi-arid lands (ASALs) where sorghum is cultivated by small holder farmers. This study investigated the inheritance of resistance traits to the African stem borers in grain sorghum in Kenya. The experimental material consisted of seventeen sorghum lines with varying levels of resistance to the African stem borer. The mating design employed was North Calorina Design 2, where 15 sorghum lines were used as females on two males. The crosses were evaluated in two seasons at University of Embu farm in 2011/2012 short and long seasons replicated twice. Artificial infestation with African stem borer neonates was done 30 days after planting using a camel brush. Data collected included stem borer damage and agro-morphological traits. Genetic analyses were performed using a line x tester method using Genstat statistical software. It was found that both additive and non-additive gene effects were important in conditioning resistance traits to the African stem borer. This implies that expression of high leaf glossiness, plant vigour and bloom waxiness in F1 hybrids is conditioned by additive genes and these traits can be used as morphological markers to select for resistance to the borer in sorghum. ICSB 464 x ICSB 473 was the best combiner for stem borer resistance and grain yield. Parents ICSA 464, ICSB 464 and ICSB 474, were among the good combiners for resistance to the stem borer. These parents can be utilised in developing superior sorghum hybrids resistant to the insect pest.

*Key Words:* Gene action, heritability, *Sorghum bicolor*

### RÉSUMÉ

Le foreur africain de tiges (*Busseola fusca* [Fuller]) est un insecte ravageur important pour les céréales, principalement le maïs, le sorgho et le mil. L' insecte réduit jusqu'à 80% le rendement en grains, en

fonction de la population d' insecte dans le champ, du cultivar et des pratiques de gestion employées. Cette réduction de rendement cause une insécurité alimentaire, en particulier dans les zones semi-arides (ASAL) où le sorgho est cultivé par de petits agriculteurs. Cette étude a examiné la transmission des caractères de résistance aux foreurs africain de tiges chez le sorgho à grains au Kenya. Le matériel expérimental consistait en dix-sept lignées de sorgho présentant différents niveaux de résistance au foreur africain de tiges. Le plan d'accouplement utilisé était le North Calorina Design 2, où 15 lignées de sorgho étaient utilisées en tant que femelles sur deux mâles. Les croisements ont été évalués au cours de deux saisons à la ferme de l'Université d'Embu en 2011/2012 des saisons courtes et longues ont été répliquées deux fois. L'infestation artificielle de nouveau-nés avec des tétranyques a été réalisée 30 jours après la plantation à l'aide d'une brosse à chameaux. Les données collectées comprenaient les dommages causés par les foreurs de tiges et les caractéristiques agro-morphologiques. Les analyses génétiques ont été effectuées à l'aide d'une méthode de test de ligne x utilisant le logiciel statistique Genstat. Il a été constaté que les effets génétiques additifs et non additifs étaient importants pour conditionner les caractères de résistance au foreur de tiges. Cela implique que l'expression de gènes additifs conditionne l'expression d'une brillance élevée des feuilles, de la vigueur des plantes et du fart de la floraison chez les hybrides F1. Ces caractères peuvent être utilisés comme marqueurs morphologiques pour sélectionner la résistance au foreur du sorgho. ICSB 464 x ICSB 473 était le meilleur combineur pour la résistance des foreurs de tiges et le rendement en grains. Les parents ICSCA 464, ICSB 464 et ICSB 474 figuraient parmi les bons combineurs pour la résistance au foreur. Ces parents peuvent être utilisés pour développer des hybrides de sorgho supérieurs résistants à l'insecte ravageur.

*Mots Clés:* Action des gènes, héritabilité, *Sorghum bicolor*

## INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) Moench) is an important indigenous nutritious cereal crop, cultivated by small holder farmers in Sub-Saharan Africa (Sharma *et al.*, 2006). Production of sorghum is constrained by biotic, abiotic and social-cultural challenges. The African stem borer *Busseola fusca* Fuller (Lepidopteran: Noctuidae) is recognised as an economically important insect pest of sorghum, maize and millet (Kfir *et al.*, 2002). *Busseola fusca* is associated with significant grain yield losses ranging between 15 - 80%, depending on the pest population, time of infestation, variety and agroecosystem (Wale *et al.*, 2007). The quantitative losses translate into food insecurity at the household levels, especially during periods where maize fails due to prolonged drought. Qualitative losses include low marketability of the grain, thus the produce does not fetch premium prices in the market. *Busseola fusca* inflicts damage through leaf feeding, dead heart, exit holes and stem

tunneling (Chabi-Olaye *et al.*, 2005). The *B. fusca* larvae remain inside the stems, and thus, are protected from insecticides and natural enemies (Muhammad *et al.*, 2009).

In Kenya, *Busseola fusca* is endemic in high altitudes and co-exists in mid-altitude zones with *Chilo partellus* Swinhoe, (Lepidopteran: Crambidae), which is an introduced pest from Asia (Kfir *et al.*, 2002). In Kenya, much research has been accorded to *C. partellus*, consequently neglecting indigenous economically important stem borers such as the African stem borer. Research on management of *B. fusca* in sorghum has mainly focused on biological control and cultural control, predominantly intercropping, residue management, fertiliser use, and recently, genetic engineering (Chabi *et al.*, 2005; Markus and Gurling, 2006; Amsalu *et al.*, 2008).

Host plant resistance is an efficient approach in managing insect pests, especially in Africa where subsistence farmers practice little or no pest management in cereals (Sharma

*et al.*, 2006). Combining host plant resistance with other methods of control, such as cultural strategies, would go along way in integrated stem borer management for improved food security. Understanding the genetic mechanisms underlying *B. fusca* tolerance in sorghum, is imperative for an effective breeding strategy. Estimation of broad and narrow sense heritability in diploids such as sorghum is based on total genetic and additive genetic variance (Falconer and Mackay, 1996). Combining ability is the capability of parents to combine amid each other in hybridisation so that favourable alleles are transmitted to their progenies (Panhwar *et al.*, 2008). The concept of combining ability has been employed in other crops, particularly maize, in determining superior combiners for agronomic, disease and insect pest resistance traits. The objective of this study was to investigate the type of gene action conditioning tolerance to *B. fusca* in sorghum.

## MATERIALS AND METHODS

**Experimental site.** Two experiments were conducted at the University of Embu, field station for two seasons in 2011/2012 (short and long rain seasons). The rainfall pattern at Embu is bi-modal, with two distinct rainy seasons. Long rains occur between March and June; while the short rains fall between October and December (Jaetzold and Schmidt, 1982). Rainfall quantity received varies with altitude, averaging about 1067.5 mm annually and ranging from 640 mm in some areas to as high as 1,495 mm per *annum*. Embu lies between longitude 37°42' E and latitude 0°44' S, at an elevation of 1,510 metres above sea level (Jaetzold and Schmidt, 1982). The site has maximum and minimum daily temperatures of 25 and 14°C. The soils are deep, well weathered Humic Nitisols with moderate to high inherent fertility (Jaetzold and Schmidt, 1982).

**Experimental materials.** The experimental materials consisted of sorghum lines with

varying levels of resistance to *B. fusca* (Table 1). North Calorina mating design 2 was employed, where 15 lines (Gadam, ICSA 464, ICSA 467, ICSA 472, ICSA 474, ICSB 464, ICSB 467, ICSB 474, IESV 91131 DL, IESV 93042 SH, IS 21879, IS 21881, IS 8193, Macia and Seredo) were used as females (lines) and 2 (KARI-Mtama-1 and ICSB 473) as males (testers).

Classification of the sorghum lines into different categories was based on leaf damage, deadheart, exit holes and stem tunneling in 2010 long and short rain seasons (Muturi *et al.*, 2012; Muturi *et al.*, 2014). The test material was sown in an  $\alpha$ -lattice design, consisting of sixteen plots in three blocks, replicated twice. The rows were 2 m long and 0.75 m apart, and the spacing between plants within rows was 0.25 m. Recommended agronomic practices such as weeding and supplemental irrigation were carried out when necessary.

**Stem borer neonates.** First instar neonates of *B. fusca* utilised in this study were obtained from the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya. At 30 days after sowing, five plants in each row were tagged and artificially infested on the whorls with five larvae per plant using a camel hairbrush.

**Data collection.** Data on leaf damage and dead heart were collected per plant basis, at two and four weeks after artificial infestation. Percentages of plants showing leaf and dead heart were computed by expressing the number of plants damaged as a percentage of the total number of plants sampled. At harvest, all the leaves were removed from the tagged plants and the numbers of stem borer exit holes on the stem counted on each sampled plant. The main stem of plants infested with stem borer larvae were split open from the base to the apex using a kitchen knife; and the cumulative tunnel length measured.

Seedling vigor was scored at 30 days after sowing on a scale of 1 - 5, where 1 = low vigour (plants showing minimum growth, less

TABLE 1. Characteristics of sorghum lines used in this study

Genotype	Pedigree	Source of seed	Reaction to <i>Busseolafusca</i>
ICSA 474	(IS 18432 X ICSB 6)11-1-1-2-2	ICRISAT India	MR
Seredo	Seredo	ICRISAT Kenya	MR
ICSB 474	(IS 18432 X ICSB 6)11-1-1-2-2	ICRISAT India	MR
ICSA 464	[(ICSB 11 X ICSV 702)XPS 19349B]5-1-2-2	ICRISAT India	MR
ICSA 472	(ICSB 51 X ICSV 702)7-3-1	ICRISAT India	MR
IS 21879	IS 21879	ICRISAT India	MS
*KARI-Mtama-1	KARI-Mtama-1	ICRISAT Kenya	MS
ICSA 467	[(ICSB 11 X ICSV 700)XPS 19349B]XICSB 13]4-1	ICRISAT India	MS
IESV 93042 SH	IESV 93042 SH	ICRISAT Kenya	MS
*ICSB 473	(ICSB 102 X ICSV 700)5-2-4-1-2	ICRISAT India	MS
Macia	Macia	ICRISAT Kenya	R
IESV91131 DL	IESV91131 DL	ICRISAT Kenya	R
ICSB 464	[(ICSB 11 X ICSV 702)XPS 19349B]5-1-2-2	ICRISAT India	R
ICSB 467	[(ICSB 11 X ICSV 700)XPS 19349B]XICSB 13]4-1	ICRISAT India	R
IS 21881	IS 21881	ICRISAT India	R
Gadam	Gadam	ICRISAT Kenya	R
IS 8193	IS 8193	ICRISAT India	S

R = Resistant, MR = moderately resistant, MS = moderately susceptible, S = susceptible, \*male parents

leaf expansion and poor adaptation, 3 = moderate vigor; 5 = high vigor (tall plants with expanded leaves and robustness) (Aruna and Padmaja, 2009). Leaf glossiness was recorded at 30 days after sowing, on a scale of 1 - 5 where 1 = highly glossy, 3 = moderately glossy, and 5 = non glossy (Dhillon *et al.*, 2005). Waxy bloom was recorded on a scale of 1 - 9; where 1 = no observable bloom, 3 = slightly present, 5 = medium, 7 = mostly bloomy, 9 = completely bloomy at the 50% flowering stage (Dhillon *et al.*, 2005).

Agronomic traits monitored included plant height, days to panicle emergence, 50% flowering and panicle length. Total grain yield and hundred-grain mass were recorded for each of the sampled plants, using a weighing balance (Mettler PM 6000, CH- 8606 GREIFENSEE-ZURICH, made in Switzerland).

**Statistical analyses.** Data on percentages were arcsin transformed; while those of counts were log transformed before analysis of variance to normalise the data. General analysis of variance was performed for all the traits observed using GenStat version 14 statistical software (GenStat 12 VSN 2009). Genetic analyses were performed using the Line X tester method using the same software (Panhware *et al.*, 2008).

The analysis facilitated estimate of the variances from expected mean squares and general combining ability (GCA) effects, representing additive gene effects and specific combining ability (SCA), denoting non-additive gene effects. The sums of squares of the crosses were partitioned into GCA and SCA effects, and their interaction with the environment was estimated. Narrow-sense heritability and proportional contribution of females, males, and their interactions were also computed.

Narrow-sense heritability =  
 $(V_{gca}) / (V_{gca} + V_{sca} + V_{E}) \times 100$ ;

Where:

$V_{gca}$  = general combining ability variance,

$V_{sca}$  = specific combining ability variance, and

$V_E$  = error variance (Dhillon *et al.*, 2006).

Relative importance of GCA and SCA was estimated according to Baker's (1978) as:

$$[\delta^2 GCA_{(f)} + \delta^2 GCA_{(m)}] / [\delta^2 GCA_{(f)} + \delta^2 GCA_{(m)} + \delta^2 SCA]$$

Where:

$\delta^2 GCA_{(f)}$ ,  $\delta^2 GCA_{(m)}$  and  $\delta^2 SCA$  are the variance components for GCA and SCA, respectively.

Correlation analysis was also performed to understand the association between the morphological and traits linked with sorghum resistance to *B. fusca*.

## RESULTS

### Plant damage and morphological traits.

The results of plant damage and morphological traits are presented in Table 2. The mean squares due to GCAf were significant ( $P = < 0.05$  or  $P = < 0.01$ ) for leaf damage, exit holes, stem tunneling and vigor. Significant GCAm were observed on exit holes, leaf glossiness and bloom waxiness. Significant SCA mean squares were observed on exit holes and stem tunneling damages. Baker's ratio estimates for leaf feeding, deadheart, exit holes and stem tunneling damages ranged between 15 - 46%; while that of leaf glossiness, seedling vigor and bloom waxiness ranged between 38 - 43%. Narrow sense heritability for leaf damage, deadheart, exit holes and stem tunnels ranged from 4 to 26%; while that of glossiness, vigor and bloom waxiness ranged between 38 - 56%.

**Agronomic traits.** Data of plant height, panicle emergence, days to 50% flowering, panicle length, total grain weight and hundred grain mass are presented in Table 3.

TABLE 2. Mean squares for general and specific combining ability for various damage by the African stemborer and morphological traits and heritability in sorghum

Source of variation	d.f	DH	LD	EH	ST	GL	VG	BW
Rep	1	913.7	2382.6	0.59ns	640.9	0.8	0.3	0.469
Season	1	2397.3*	2207.3*	0.01ns	396.1ns	0.6ns	4.9**	7.3*
GCAf	14	323.4ns	726.8*	0.13*	770.5**	0.9ns	0.9**	2.2ns
GCAm	1	136.9ns	949.2ns	0.73**	9.4ns	2.1*	0.7ns	21.3**
SCA	14	480.8ns	621.9ns	0.30**	842.4**	0.4ns	0.2ns	2.2ns
Residual	59	335.6	368.9	0.07	151.2	0.5	0.234	1.494
<b>Proportional contribution to total variance</b>								
Females		6.1	178.95	0.03	309.65	0.17	0.27	0.37
Males		13.25	38.69	0.04	9.45	0.1	0.03	1.32
Females x males		145.2	253	0.23	691.2	0.07	0.01	0.75
Baker's Ratio		0.15	0.46	0.25	0.3	0.79	0.97	0.69
<b>Narrow sense heritability (%)</b>								
		4	26	21	26	38	56	43

\*, \*\* Data significant at < 0.05 and < 0.01 probability level respectively; ns = non-significant; DH = Deadheart %, LD = Leaf damage (%), EH = Exit holes, ST = stem tunneling, GL = Glosiness, VG = vigour, BL = Bloom waxiness, DF = Degrees of freedom, GCAf = general combining ability for females, GCAm = general combining ability for males, SCA = specific combining ability

TABLE 3. Mean squares for general and specific combining ability for various agronomic traits and heritability estimates in sorghum

Source of variation	d.f.	PH	PE	FL	PL	TGW	HGM
Rep stratum	1	608	44.4	61.6	58.3	341.1	1
Season	1	15790.1**	745.0**	1540.8**	2760.6**	6.6ns	1.1ns
GCA <sub>f</sub>	14	8449.9**	33.8*	34.8*	55.7**	447.0**	4.9**
GCA <sub>m</sub>	1	3322.9*	99.0*	116.0*	19.8ns	316.3*	2.1*
SCA	14	6020.1**	15.1ns	20.5ns	130.0**	372.8**	2.4**
Residual	539	668.2	17.6	18.1	11.1	76.8	0.5

  

Proportional contribution to total variance							
Females		3890.85	22.32	8.37	22.32	185.11	2.2
Males		176.98	0.58	6.53	0.58	15.96	0.11
Females X Males		5351.9	118.97	2.39	118.97	295.99	1.95
<b>Baker's Ratio</b>		0.43	0.16	0.86	0.16	0.4	0.54

  

Narrow sense heritability (%)							
		40	15	42	15	35	49

\*, \*\* Data significant at < 0.05 and < 0.01 probability level respectively; ns = non-significant; PH = Plant height, PL = Panicle length, FL = 50% flowering, PL = Panicle length, TGW = Total grain weight, HGM = Hundred grain mass, DF = Degrees of freedom, GCA<sub>f</sub> = general combining ability for females, GCA<sub>m</sub> = general combining ability for males, SCA = specific combining ability

Mean squares due to GCA<sub>f</sub> and GCA<sub>m</sub> were significant (P<0.05) for plant height, panicle emergence, days to 50 % flowering, total grain weight, hundred grains mass except for GCA<sub>m</sub> for panicle length. SCA mean squares were significant for plant height, panicle length, total grain weight and hundred grains mass. Baker's ratio for agronomic traits ranged between 16 - 86% while narrow sense heritability estimates ranged between 15 - 49%.

**Stem borer damage, agronomic and morphological traits.** Results for exit holes, stem tunneling, plant height, panicle length, total grain yield and hundred grain mass were significant (Table 4). Cross IESV 93042 SH X ICSB 473 suffered the least deadheart damage; while ICSB 467 X KARI-Mtama-1 suffered the most to the most damage.

Cross ICSB 464 X ICSB 473 suffered the least leaf feeding damage; while IS 21881 X KARI-Mtama-1 suffered the most damage. ICSA 467 X ICSB 473 and ICSB 464 X ICSB 473 scored the least exit holes damage; while IS 8193 X KARI-Mtama-1 suffered the most damage. ICSB 464 X ICSB 473 had the least stem tunneling damage; while ICSB 464 X KARI-Mtama-1 suffered the most damage. Cross ICSB 464 X ICSB 473 scored the least deadheart, leaf feeding, stem tunnels and exit holes damages combined, and also scored the highest hundred grain mass. Panicle length ranged from 17 to 26 cm on crosses ICSA 474 X ICSB 473 and ICSA 467 X KARI-Mtama-1. Cross ICSB 474 X KARI-Mtama-1 was the tallest (154 cm); while ICSB 464 X ICSB 473 was the shortest (104 cm). Days to 50 % flowering ranged from 65 - 76 days for Gadam X KARI-Mtama-1 and IS 21881 X

TABLE 4. Damage, agronomic and morphological traits for sorghum F1 hybrids

F1 hybrids	DH	LD	EH	ST	PH	FL	PL	TGW	HGM	BW	GL	VG
ICSA 467 X KARI-Mtama-1	35.8	38.9	0.7	14.0	128	72	26	38.3	3.1	6.5	2.8	3.3
ICSB 474 X KARI-Mtama-1	13.3	16.4	0.8	19.3	153	71	23	31.0	2.9	6.8	2.9	3.5
IESV 91131 DL X KARI-Mtama-1	19.6	54.5	0.7	17.8	112	71	24	30.2	3.1	4.5	3.4	3.4
ICSA 472 X ICSB 473	26.0	26.3	0.7	15.6	137	75	17	29.1	3.1	5.5	3.5	3.4
ICSB 467 X KARI-Mtama-1	51.1	45.0	0.7	20.5	125	71	23	26.9	3.1	6.0	2.9	3.1
ICSB 464 X ICSB 473	16.4	15.9	0.4	9.1	104	72	18	25.6	4.0	7.0	2.8	3.3
ICSA 472 X KARI-Mtama-1	32.3	48.8	0.5	12.6	145	73	21	24.4	2.7	6.0	2.7	2.9
ICSA 464 X KARI-Mtama-1	23.1	48.5	0.6	13.3	120	71	24	24.3	2.8	5.8	3.0	2.9
ICSA 474 X ICSB 473	26.3	44.4	0.6	16.7	119	72	17	23.9	2.9	7.0	2.3	3.8
IESV 91131 DL X ICSB 473	26.3	48.2	0.7	27.7	106	72	19	23.6	2.9	7.0	3.0	3.4
ICSB 474 X ICSB 473	38.9	26.3	0.7	19.2	145	71	18	23.1	2.7	6.8	2.9	4.0
ICSA 467 X ICSB 473	35.2	38.7	0.4	10.9	120	72	20	22.9	2.7	7.0	2.3	3.0
IS 21879 X ICSB 473	25.7	32.6	0.6	28.6	121	75	19	22.9	2.3	7.0	2.3	3.4
IS 21881 X KARI-Mtama-1	32.0	64.6	0.8	20.0	115	71	24	22.8	2.6	6.0	3.4	2.4
Gadam X KARI-Mtama-1	22.5	28.1	0.7	13.3	118	65	22	22.2	2.9	5.5	3.3	3.0
ICSA 464 X ICSB 473	24.8	17.9	0.6	9.3	112	72	20	21.9	3.1	6.3	2.3	3.4
IS 21879 X KARI-Mtama-1	32.6	44.4	0.7	19.7	129	76	22	21.5	2.2	6.5	2.9	3.0
IESV 93042 SH X KARI-Mtama-1	32.0	42.4	0.6	14.0	138	72	23	21.5	2.5	6.1	3.6	3.1
Gadam X ICSB 473	16.4	35.5	0.7	15.6	110	68	18	21.3	2.9	7.0	3.5	2.3
IESV 93042 SH X ICSB 473	9.8	54.8	0.7	23.6	130	72	18	21.3	2.8	5.5	3.1	3.3
Seredo X ICSB 473	35.2	26.3	0.7	27.7	120	69	20	20.8	2.4	6.5	3.0	3.1
IS 8193 X ICSB 473	35.8	38.4	0.8	22.3	129	69	20	20.5	2.2	7.0	2.9	3.4
Macia X ICSB 473	42.1	36.1	0.7	24.0	111	70	19	20.4	2.9	6.5	3.1	3.2
IS 21881 X ICSB 473	19.3	19.3	0.6	19.5	107	76	20	19.9	2.4	6.3	3.4	2.7
Seredo X KARI-Mtama-1	47.9	26.0	0.8	22.2	128	67	25	19.7	2.8	4.0	3.1	3.0
ICSB 464 X KARI-Mtama-1	35.2	16.4	0.8	36.9	112	71	22	19.5	2.5	6.5	3.1	3.4
ICSA 474 X KARI-Mtama-1	19.6	41.8	0.8	22.4	127	71	22	19.4	2.9	7.0	2.8	3.5
Macia X KARI-Mtama-1	19.9	32.3	0.7	19.1	119	71	24	19.4	2.7	4.8	3.3	3.1

TABLE 4. Contd.

Fl hybrids	DH	LD	EH	ST	PH	FL	PL	TGW	HGM	BW	GL	VG
ICSB 467 X ICSB 473	26.0	23.1	0.6	23.1	117	70	21	17.6	2.7	6.8	2.8	3.1
IS 8193 X KARI-Mtama-1	19.3	19.6	0.8	24.0	137	68	24	15.4	1.4	4.5	3.9	2.8
F value	0.167	0.083	<.001	<.001	<.001	0.064	<.001	<.001	<.001	0.139	0.736	0.423
LSD (0.05)	25.92	27.18	0.16	7.64	16.06	4.15	2.07	5.44	0.42	1.73	1.02	0.68
CV (%)	65.4	54.8	6.6	63.5	17.8	4.1	15.9	38	24.6	19.8	24	15.3

DH = Deadheart %, LD = Leaf damage (%), EH = Exit holes, ST = stem tunneling, PH = Plant height, FL = 50 % flowering, PL = Panicle length, TGW = Total grain weight, HGM = Hundred grain mass, BL = Bloom waxiness, GL = Glossiness, VG = vigour

ICSB 473, respectively. Cross ICSA 467 X KARI-Mtama-1 produced about three times more grain weight than IS 8193 X KARI-Mtama-1, which produced the least. Hundred grain mass ranged from 1.4 to 4.0 g on IS 8193 X KARI-Mtama-1 and ICSB 464 X ICSB 473, respectively.

**Gene action.** Results for leaf damage, deadheart, exit holes and stem tunnels GCA effects are shown in Table 5. Maximum GCA effects for leaf damage, deadheart and stem damages were displayed by genotypes Gadam, ICSB 464 and ICSA 464, respectively. Generally, ICSB 473 (male) contributed favourable alleles for resistance to *B. fusca*. Seredo scored the highest positive GCA effects on dead heart, stem exit holes and stem tunneling damages. IESV 91131DL showed the highest undesirable GCA effect towards leaf feeding damage. Maximum GCA effect for plant height was observed on ICSB 474; while Gadam scored the maximum negative GCA effects for plant height (Table 5). Highest positive GCA effects for days to 50% flowering among females were recorded on IS 21879 and IS 21881; while a negative maximum GCA effect was recorded on Gadam. High positive significant GCA effect for total grain yield was observed on ICSA 467 among lines and KARI-Mtama-1 among the males. A high GCA effects for bloom waxiness were observed on ICSA 474, ICSA 467 and ICSB 474. Seedlings of ICSA 474 and ICSA 467 were highly vigorous and glossy; while for IS 8193 and IS 21881, they were non-glossy and the least vigorous.

Results on specific combining ability for the different damages, agronomic and morphological characteristics are presented in Table 6. There were significant differences in SCA effects among crosses with regard to leaf damage, exit holes, stem tunnels, plant height, panicle length, grain yield and leaf glossiness. Most of the other SCA estimates were negative, low or not significant. Crosses that showed the least negative SCA effects for deadheart, leaf and stem damages were ICSB

TABLE 5. General combining ability (GCA) effects of females and males for damage, agronomic and morphological traits in sorghum

Females	DH	LD	EH	ST	PH	FL	PL	TGW	HGM	BW	GL	VG
Gadam	-8.50	-3.30	0.03	-4.95	-21.90	-3.53	-1.45	-1.28	0.15	0.07	0.38	-0.56
ICSA 464	-4.10	-1.90	-0.08	-8.13	-5.80	0.47	-0.37	0.02	0.20	-0.18	-0.36	-0.03
ICSA 467	7.50	3.80	-0.08	-6.98	-5.30	2.47	-0.02	7.56**	0.14	0.57	-0.45	-0.04
ICSA 472	1.10	2.50	-0.06	-5.28	-16.10	-1.65	0.33	3.72*	0.17	-0.43	0.10	-0.03
ICSA 474	-5.10	8.10	0.02	0.15	26.50*	2.22	-1.00	-1.37	0.15	0.82*	-0.50	0.47*
ICSB 464	-2.20	-18.90	-0.06	3.58	14.50*	-1.90	2.10*	-0.46	0.53**	0.57	-0.06	0.16
ICSB 467	10.50	-1.00	-0.04	2.45	6.40	0.47	1.82*	-0.80	0.13	0.20	-0.18	-0.03
ICSB 474	-1.90	-13.70	0.05	-0.15	28.80*	-2.53	0.88	4.03*	0.12	0.57	-0.12	0.60*
IESV 91131 DL	-5.10	16.30*	0.02	3.35	5.80	-3.15	0.88	3.83*	0.26*	-0.43	0.19	0.22
IESV 93042 SH	-7.10	13.60	-0.01	-0.60	-13.40	1.85	-0.15	-1.65	-0.09	-0.37	0.38	0.03
IS 21879	1.10	3.50	-0.02	4.75*	-16.50	3.10	-0.72	-0.82	-0.49	0.57	-0.43	0.03
IS 21881	-2.30	6.90	0.03	0.36	1.60	0.47	0.20	-1.70	-0.26	-0.05	0.38	-0.62
IS 8193	-0.50	-6.10	0.13*	3.75	7.20	0.22	0.70	-5.12	-0.92	-0.43	0.38	-0.09
Macia	3.00	-0.90	0.03	2.15	-13.30	0.60	-2.20	-3.12	0.07	-0.55	0.23	0.01
Seredo	13.50*	-8.90	0.05	5.55*	11.60*	0.85	-0.97	-2.83	-0.16	-0.93	0.07	-0.12
Males												
ICSB 473	-1.05	-2.75	-0.03	0.12	2.37	-0.98	0.18	-0.72	0.06	0.42*	-0.13	0.08
KARI-Mtama-1	1.08	2.85	0.04	-0.13	-2.34	0.98	-0.19	0.73	-0.06	-0.42	0.13	-0.08

\*, \*\* Data significant at <0.05 and <0.01 probability level respectively; DH = Dead heart %, LD = Leaf damage (%), EH = Exit holes, ST = stem tunneling, PH = Plant height, FL = 50 % flowering, PL = Panicle length, TGW = Total grain weight, HGM = Hundred grain mass, BL = Bloom waxiness, GL = Glosiness, VG = vigour

TABLE 6. Specific combining ability estimates of F1 hybrids from line x tester analysis of various characters in sorghum

F1 hybrids	DH	LD	EH	ST	PH	FL	PL	TGW	HGM	BW	GL	VG
Gadam X ICSB 473	6.29	7.71	0.01	6.86*	0.15	5.40**	-1.23*	1.97	-0.31	0.27	0.26	-0.01
Gadam X KARI-Mtama-1	10.84	-1.21	-0.07	3.78*	19.72	7.33	3.60	0.61	2.36	-0.39	-0.49*	0.88
ICSA 464 X ICSB 473	3.99	17.91	-0.09	6.86*	11.15	-0.60	-0.03	-0.13	-0.21*	-0.03	0.56	0.19
ICSA 464 X KARI-Mtama-1	5.69	-14.21*	0.03	10.08	-6.68	2.33	0.30	0.01	2.16	0.31	0.71	-0.27*
ICSA 467 X ICSB 473	-13.21*	-3.09	0.01	6.16	-11.35	-1.60	-0.93	-29.61	-0.51	-0.73	0.76*	-0.31*
ICSA 467 X KARI-Mtama-1	-7.96*	-4.41	0.23**	8.48	14.92	-4.67*	0.40	-0.99	2.56	-0.39	0.71	-0.22*
ICSA 472 X ICSB 473	-3.51	-12.99*	0.21	7.56*	19.05	-2.60*	1.57	-0.23	-0.11	-0.23	0.06	0.09
ICSA 472 X KARI-Mtama-1	1.24	7.99	-0.07	3.78	6.02	2.33	-2.80	-7.19*	2.16	1.11	0.31*	-0.23*
ICSA 474 X ICSB 473	9.19	-5.99	-0.14	-2.24	-8.25	0.40	-0.53	4.77*	-0.31*	-1.23	0.76*	-0.51*
ICSA 474 X KARI-Mtama-1	7.64	-10.11	0.08*	2.68*	-27.78	-2.67	2.00*	-1.99	2.36	-0.39	0.71*	-0.62*
ICSB 464 X ICSB 473	-6.41	19.41	-0.19*	-16.74	-29.85	0.40	-5.83	-1.43	0.09	-0.73	0.46*	-0.41*
ICSB 464 X KARI-Mtama-1	10.84	18.39	0.23	10.28	-30.08	0.33	1.10	2.41	1.26	-0.39	0.21	-0.12
ICSB 467 X ICSB 473	-22.31*	-9.19*	0.01	-0.34	-0.15	-1.60	-3.33	-2.73*	-0.51*	-0.23	0.66*	-0.11
ICSB 467 X KARI-Mtama-1	1.24	11.19	0.03	-3.72*	-19.78	1.33	-0.90	4.31	2.56	-0.19	0.21	0.08
ICSB 474 X ICSB 473	15.49*	19.41	-0.09	0.86	-39.55	1.40	-2.13	-6.83	-0.31*	-1.03*	0.66*	-0.51*
ICSB 474 X KARI-Mtama-1	-11.66	7.99	-0.07	0.18	-5.18*	1.33*	-0.10	-1.19	2.56	-0.19	0.11	-0.82
IESV 91131 DL X ICSB 473	9.19	-18.69	0.01	2.36*	-11.15	3.40	-0.73	-6.03	-0.51	-5.36	0.16	-0.41
IESV 91131 DL X KARI-Mtama-1	0.94	-13.91*	-0.07	-8.32	-7.38	2.33	-1.50	-1.69*	2.36	-0.39	0.01	-0.27*
IESV 93042 SH X ICSB 473	-3.21	-6.59	0.11	6.16	-3.05	3.40	-0.53	2.67*	0.09	-0.33	-0.04	-0.11
IESV 93042 SH X KARI-Mtama-1	-4.76	-20.51	0.01	-3.62*	22.82	0.33	0.30	0.61	2.46	1.11	-0.09	-0.12
IS 21879 X ICSB 473	-3.81	-8.59*	0.01	0.46	11.15	-13.60	1.17	2.67*	0.39*	-0.73	0.66*	-0.01
IS 21879 X KARI-Mtama-1	-5.36	1.69	0.07	-9.22	14.72*	-16.67	-0.20	-0.99	2.96	-12.63	0.71	-0.22*
IS 21881 X ICSB 473	-3.21	-28.79*	-0.06	0.16	-23.65	3.40	-1.03	1.37	0.19	-0.23	0.16	0.59
IS 21881 X KARI-Mtama-1	-4.76	14.99	0.03	-0.12	13.32	2.33	0.10	2.01	2.66	0.31	-0.39	0.48
IS 8193 X ICSB 473	9.49	16.21	-0.09	-3.84*	10.45	2.40	2.07	8.77	1.19	1.27*	-0.34*	0.19
IS 8193 X KARI-Mtama-1	7.94*	-4.11	-0.17*	-4.62	-31.88**	2.33	-4.00	1.41	3.06	-0.39	0.11	-0.22*
Macia X ICSB 473	11.87*	3.51	0.01	1.06	15.75	-1.60	2.67	4.77*	-0.11	0.97	0.26	-0.11

Resistance traits to African stem borer in grain sorghum

TABLE 6. Contd.

Fl hybrids	DH	LD	EH	ST	PH	FL	PL	TGW	HGM	BW	GL	VG
Macia X KARI-Mtama-1	14.86	-1.81	-0.07	-4.62	3.82	2.33	1.20	1.51	2.36	0.11	-0.09	-0.02
Seredo X ICSB 473	19.11*	9.81	-0.09	-7.54	-11.35	1.40	3.60*	4.47	-0.21*	1.77*	0.46*	-0.01
Seredo X KARI-Mtama-1	20.66	7.99	-0.07	-2.82	-18.88	-0.67	-2.10	1.11	2.86	0.11	0.01	0.08

\*, \*\* Data significant at <0.05 and <0.01 probability level respectively; DH = Deadheart %, LD = Leaf damage (%), EH = Exit holes, ST = Stem tunneling, PH = Plant height, FL = 50% flowering, PL = Panicle length, TGW = Total grain weight, HGM = Hundred grain mass, BL = Bloom waxiness, GL = Glossiness, VG = vigour

467 X ICSB 473, IS 21881 X ICSB 473 and ICSB 464 X ICSB 473, respectively. Cross ICSA 467 X KARI-Mtama-1 was the best specific combiner for panicle length and total grain yield. Crosses ICSA 474 X ICSB 473 and ICSB 474 X ICSB 473 recorded the highest seedling vigour. Cross ICSB 464 X ICSB 473 showed the highest hundred grain mass and was resistant to stem tunneling and exit holes damage.

**Association between *B. fusca* damage parameters, agronomic and morphological traits.** Results for correlation between damage parameters, agronomic and morphological traits are presented in Table 7.

Bloom waxiness was significantly and positively correlated with days to 50% flowering, and days to panicle emergence ( $r = 0.38^*$  and  $r = 0.35^*$ , respectively). Days to 50% flowering correlated positively and highly significantly with days to panicle emergence ( $r = 0.96^{**}$ ). Plant height significantly and positively correlated with vigour ( $r = 0.49^{**}$ ) and panicle length ( $r = 0.51^{**}$ ). A positive and significant association was observed between panicle length and vigour ( $r = 0.36^*$ ). Exit holes positively and significantly correlated with stem tunnels ( $r = 0.61^{**}$ ), and with non-glossy leaves ( $r = 0.49^{**}$ ). A positive and highly significant relationship was observed between dry panicle weight and total grains ( $r = 0.94^{**}$ ) and with hundred grain mass ( $r = 0.52^{**}$ ). Hundred grain mass positively and significantly correlated with total grain yield ( $r = 0.54^{**}$ ).

Bloom waxiness negatively and significantly correlated with leaf glossiness ( $r = -0.57^{**}$ ). Days to 50% flowering negatively and significantly correlated with leaf glossiness ( $r = -0.70^{**}$ ). Leaf glossiness was negatively and highly significantly associated with days to panicle emergence ( $r = -0.63^{**}$ ) and vigour ( $r = -0.46^{**}$ ). A negative relationship was observed between exit holes and hundred grain mass ( $r = -0.40^*$ ) and exit holes and days to 50% flowering ( $r = -0.36^*$ ). A negative and highly significant association was observed between dry panicle weight and stem tunnels

TABLE 7. Correlation matrix between damage parameters, agronomic and morphological characters in sorghum

	BW	DH	DPW	EH	FL	GL	HGM	LD	PE	PH	PL	ST	TGW	VG
BW	-													
DH	0.01	-												
DPW	0.03	0.09	-											
EH	-0.31	0.08	-0.06	-										
FL	0.38*	0.1	-0.02	-0.36*	-									
GL	-0.57**	-0.16	-0.22	0.49**	-0.70**	-								
HGM	0.17	-0.09	0.52**	-0.40*	-0.09	-0.29	-							
LD	-0.06	0.09	0.16	0.05	-0.06	0.02	0.01	-						
PE	0.35*	0.08	0.0	-0.3	0.96**	-0.63**	-0.15	0.08	-					
PH	0.32	0.14	0.17	0.06	-0.08	-0.28	0.25	-0.26	-0.15	-				
PL	0.33	0.18	0.15	0.19	0.0	-0.07	0.03	-0.09	-0.07	0.51**	-			
ST	0.03	0.17	-0.36*	0.61**	0.11	0.14	-0.46**	-0.08	0.07	0.18	0.39*	-		
TGW	0.08	0.02	0.94**	-0.08	0.01	-0.18	0.54**	0.18	0.02	0.17	0.22	-0.38*	-	
VG	0.25	0.07	0.25	-0.03	0.32	-0.46**	0.26	-0.18	0.26	0.49**	0.36*	0.15	0.25	-

\*, \*\* Data significant at <0.05 and <0.01 probability level, respectively; BW = bloom waxiness, DH = Deadheart damage, DPW = dry panicle weight, EH = exit holes, FL = days to flowering, GL = leaf glossiness, HGM = hundred grain mass, LD = leaf damage, PE = panicle emergence, PH = plant height, PL = panicle length, ST = stem tunneling, TGW = total grain weight, VG = seedling vigour

( $r = -0.36^*$ ). A negative relationship was also observed between hundred grain mass and stem tunnels ( $r = -0.46^{**}$ ). Stem tunneling negatively and significantly correlated with total grain yield ( $r = -0.38^*$ ).

## DISCUSSION

General combining ability (GCA), as well as specific combining ability (SCA) were significant (Tables 2 and 3), suggesting that additive and non-additive gene effects were important in conditioning resistance traits to *B. fusca*. The negative GCA effects for damage (leaf damage, deadheart, stem tunnels and exit holes) signified contribution of the genotype towards resistance; while positive GCA effects on the parents suggested that the those parents contributed towards *B. fusca* damage susceptibility in the crosses. The significance of GCAf mean squares for leaf damage, exit holes, stem tunneling, seedling vigour; and significant GCAm for exit holes, seedling vigoUr and bloom waxiness implied presence of additive genes in controlling these traits. The significance of GCAf and GCAm in controlling exit holes implies that both female and males influenced the trait. GCA (female) contribution was predominant over GCA (male) for leaf damage and stem tunneling, suggesting that that there might be maternal effects. Baker's ratio estimates indicated that leaf damage was conditioned by both additive and non-additive genes since GCA SCA ratio was almost 1:1. Thus, the response of hybrids to leaf damage could be predicted based on the GCA of the parents. This observation is supported by Aruna and Padmaja (2009) who reported that the potentiality of parents to produce better offspring with a pool of superior genes in regard to sorghum shoot damage by shoot insect pests is based on their GCA effects.

The significance of SCA over GCA as estimated from Baker's ratio for deadheart, exit holes and stem tunnels damage suggested that these characters were controlled largely by non-additive type of gene action (Table 2).

Both additive and non-additive genes conditioned plant height, panicle weight and grain yield in the current study. A study conducted by Sharma *et al.* (2007) on inheritance of resistance to spotted stem borer in sorghum reported that these traits were mainly controlled by additive type of gene action. The significance of SCA variance implies that cross combinations would be efficient in breeding for deadheart, exit holes and deadheart. Also, the observation suggests that inheritance depended on the resistance and susceptibility levels of the parents used in the cross. This also indicates that the GCA alone could not give a complete prediction of hybrids' deadheart and stem tolerance to *B. fusca*.

This observation is supported by findings on inheritance of resistance in maize to *B. fusca* in South Africa, that estimates of combining ability show greater SCA than GCA in most crosses (Taylor *et al.*, 2003). Moreover, a study conducted by Andre *et al.* (2003) on inheritance of resistance in maize to *B. fusca* revealed that SCA was greater than GCA in most crosses. Gene effects for *B. fusca* resistance in sorghum are not fixable, owing to the presence of significant non-heritable interaction present in  $F_1$ . In order to fix the genes of interest, unconventional methods such as DNA marker technology can be considered to fix the genes.

Narrow sense heritability estimates for leaf damage, exit holes and stem tunneling were moderate (ranged between 21-26%), implying that genetic gain is likely to be realised in selection. The moderate heritability estimates for leaf glossiness, seedling vigour and bloom waxiness imply that genetic gain is likely to be realised when selection is done. Genetic gain may not be realised for deadheart as estimated from the narrow sense heritability, since the values are too low. There is need to consider other options such as DNA marker technology to fix the desired genes. Further analysis using Baker's ratio equation to estimate the preponderance mode of gene action, suggested days to 50% flowering was largely conditioned

by additive genes. Additive genes conditioned plant height, panicle weight and grain yield. A study conducted by Mohammed (2015) on quantitative genetic analysis of agronomic and morphological traits in sorghum reported that plant height and grain yield is controlled by both additive and non-additive type of gene action. Muturi *et al.* (2019) reported that plant height and yield related traits are controlled by both additive and non-additive types of gene action.

Parents such as IESV 91131 DL and KARI-Mtama-1, which scored high positive GCA effect with regard to leaf damage, deadheart, exit holes and several parameters, might have contributed alleles for susceptibility to borer damage in the crosses (Table 5). The maximum negative GCA effects observed on some parents, such as ICSB 464 and ICSB 473, implied that these parents contributed positive alleles in the crosses in which they were involved with genes that could augment resistance to *B. fusca* damage. The low negative SCA effects observed on some crosses, such as ICSB 464 X ICSB 473, implied this cross was among the best specific combinations for stem borer damage. Sharma *et al.* (2007) who studied inheritance to spotted stem borer in sorghum reported that parents possessing significant SCA effects for two or more resistance traits for either or more parents have good potential for use as breeding stock in the development of sorghum hybrids resistant to stem borer.

The negative relationship observed between stem tunnels, exit holes, total grain yield and hundred grain mass (Table 7) implies that stem damage contributed to significant reduction in grain yield. This observation may imply that selection for reduction in stem tunneling would lead to increased sorghum grain yield. The probable explanation could be due to the fact that stem tunneling causes obliteration of vascular tissues that are important in translocation of nutrients and water from the soil to the photosynthetic sites and from the source to the sink organs. This explanation is

supported by Kfir *et al.* (2002) who reported that stem tunneling and feeding by stem borer destroys the growing point of sorghum, causes early leaf aging thus interfering with translocation of metabolites and nutrients that result in malformation of the grain and results to direct damage to ears in maize plant. The reverse relationship observed between hundred grain mass with exit holes and stem tunnels, implies that stem damage contributed to significant reduction in grain yield. It is worth noting that among the stem borer damage traits, stem tunneling and exit holes damage contributed to lowering of grain yield. This suggests that the two traits were key in demonstrating host resistance to *B. fusca* damage. A study conducted by Odiyi *et al.* (2007) against the effect of *Sesamia calamistis* (Hampson) and *Eldana saccharina* (Walker) in maize observed that stem tunneling was the major trait contributing to yield loss. Sorghum genotypes with highly glossy, non-vigorous seedlings suffered lower damage compared to the non-glossy but highly vigorous ones. This may be attributed to the fact that the highly glossy, shiny leaf surfaces were not ideal for the attachment of the stem borer neonates and their habitation due to high levels of cuticular wax accumulation. Similar observations have been reported for sorghum shootfly, using some other populations, where highly glossy lines were resistant to shoot fly attack (Dhillon *et al.*, 2005).

Tall plants were observed to have high vigour and produced long panicles (Table 7). This implies that tall plants had photosynthetic advantage and were efficient in channeling assimilates to the sink organs hence higher grain yields from such genotypes. Songa *et al.* (2001) reported that maize plants with many leaves (>10), taller (>150 cm) with big stem diameter (>2.1 cm) had significantly increased yield. The positive and significant relationship between exit holes and stem tunnels, suggests a close and direct relationship between these two damage traits and, therefore, one of them could be used to predict the other. Moreover,

either of the two stem damage traits can be used as *B. fusca* resistance trait thus reduction in phenotyping costs in terms of funds, labour and time involved in data collection.

This study also showed that the two stem damage traits i.e stem tunneling and exit hole damages are controlled by non-additive type of gene action. An inverse association was observed between bloom waxiness and leaf glossiness in the population under study. This suggests that the two resistance traits are conditioned by different alleles. Generally, there was no significant correlation between bloom waxiness and stem tunneling; bloom waxiness and deadheart and this may suggest that there are other factors of resistance at work in the population under study and those factors were not assessed in this study.

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