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ORIGINAL RESEARCH ARTICLE

Gene action conditioning resistance traits to spotted stem borer, Chilo partellus, in grain sorghum

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Abstract
Understanding the mode of gene action conditioning traits of interest in sorghum is important for effective and efficient plant breeding programs. The objective of this study was to establish the nature of gene action for components that contribute to resistance to spotted stem borer, *Chilo partellus*, in grain sorghum. The experimental material consisted of seventeen sorghum lines with varying levels of resistance to *C. partellus*. Genetic analyses were performed using a line x tester method using Genstat statistical software. There was significant variation among the F1 for *C. partellus* resistance and grain yield. The general combining ability (GCA) for deadheart damage was significant ($P \leq 0.01$) implying that this trait was governed by an additive type of gene action. Specific combining ability (SCA) for exit holes and stem tunneling were significant ($P \leq 0.01$) suggesting that these characters were conditioned by both additive and non-additive types of gene action. Lines ICSA 472, ICSA 464, ICSB 474 contributed high levels of resistance to hybrids while IESV 93042 SH, IS 21879 and IESV 91131 DL were good sources of genes for high grain yield. This observation implied that grain yield and stem borer resistance traits should be considered in development of *C. partellus* resistant sorghum since a resistant line doesn't necessarily yield high and vice versa. Generally, results of this study indicated that it would be possible to breed for high *C. partellus* resistance from this set of germplasm for cultivation by farmers in areas where the insect pest causes epidemics.

Keywords Genetic gain · GCA · Heritability · SCA · *Sorghum bicolor* · *Chilo partellus*

Introduction

Sorghum (*Sorghum bicolor* L. Moench) is a food and income security crop to many households in tropical semi-arid lands. The crop's grain output in low resource farming ranges between 0.5–0.8 t/ha compared to potential yields of 10 t/ha (Singh et al. 2012). Lepidopteran spotted stem borer, *Chilo partellus* Swinhoe (Crambidae) is one of the most damaging insect pests of sorghum and maize in Asia and East and South Africa (Nanqing et al. 2004). Stem borers cause an estimated loss of US $266 million annually in sorghum (Sharma et al. 2003). Chemical control is expensive to small holder farmers and unsafe to humans and environment; thus the development of resistant sorghum cultivars is an appriopriate option. The enhancement of resistance to *C. partellus* in sorghum has been difficult, partly due to the lack of information on the inheritance of resistance traits to *C. partellus*.

The larvae of *C. partellus* infest sorghum seedlings and thrive till maturity, resulting in grain yield losses ranging between 15% - 80% (Kfir et al. 2002). The larvae remain protected within stems, thus protected from insecticides and natural enemies (Afzal et al. 2009). *C. partellus* is exotic to Africa and sources of resistance to the pest are limited. However, preliminary studies show that genetic variation in sorghum resistance to *C. partellus* exists (Sharma et al. 2003; Muturi et al. 2012). Utilization of resistance genes identified from genotypes that demonstrate high levels of resistance could be an outstanding contribution in management of this insect pest. The objective of this study was to establish the nature of gene action for components that contribute to resistance or susceptibility to *C. partellus* in grain sorghum.

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Materials and methods

Experiments to investigate inheritance of sorghum resistance traits to *C. partellus* were conducted at the Kenya Agricultural Research Institute (KARI), Kiboko in 2010/2011 during the short and long rainy seasons (March to June and October to December, respectively). Kiboko lies between longitude 37° 75′E and latitude 2° 15’ S at an elevation of 975 m above sea level with an average rainfall of about 280 mm and overall annual mean temperature of 24 °C (Karaya et al. 2009).

Experimental materials

The experimental material consisted of sorghum lines with varying levels of resistance to *C. partellus*. 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 and two (Kari Mtama - 1 and ICSB 473) as males. The use of A/B-pairs (ICSA/B-464, ICSA/B-467 and ICSA/B-474) as independent lines in this experiment was to evaluate how they would combine with the two testers and also study how the resultant F1 would generally respond to *C. partellus*. The test material was sown in an α-lattice design, consisting of 16 plots in three blocks, replicated twice. The rows were 2 m long and 0.75 m apart, with 0.25 m spacing between plants within rows. During planting, the seeds were drilled on furrows of about 5 cm deep. Fertilizer was applied as 20 kg N/ha and 20 kg P/ha at planting time. At 14 days after planting, the crop was sprayed with cypermethrin (synthetic pyrethroid) to manage shoot fly infestation, since the insect pest interferes with screening for resistance to stem borers. Thinning was done at 21 days after planting. Nitrogen was also applied when the sorghum seedlings reached about 50 cm. Supplementary irrigation was applied when needed. The field was kept free of weeds by hand weeding throughout the growth cycle.

Stem borer neonates

The first instar neonates of *C. partellus* used 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 with five *C. partellus* larvae per plant on the whorls using a camel hairbrush. Data was collected from tagged plants.

Data collection

Observations on leaf feeding and deadheart damage were recorded on an individual plant basis at two and four weeks after artificial infestation (Kishore Kumar et al. 2006). Percentages of plants showing the leaf feeding and deadheart damage were calculated from the number of plants damaged and the total number of plants sampled. Seedling vigor was scored at 30 days after sowing on a scale of 1–5, where 1 = low vigor (plants showing minimum growth, less 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. At harvest, the tagged main plants were stripped of the leaves and the numbers of stem borer exit holes on the stem counted on each sampled plant. Thereafter, the main stems were split open from the base to the apex and the cumulative tunnel length made by *C. partellus* during feeding was measured in cm. Total grain yield and hundred-grain mass were recorded in grams for each of the sampled plants using a weighing balance (Mettler PM 6000, Switzerland).

Statistical analyses

Data on percentages was arcsin transformed, and counts were log transformed before analysis of variance. General analysis of variance was performed for all the traits observed using Genstat version 14 statistical software (Genstat Release 12 Reference Manual, Part 1 Summary, 2009, VSN International, United Kingdom). Genetic analyses were performed using a line x tester method using Genstat software (Kempthrone 1957; Panhwar et al. 2008). The analysis facilitated an 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 (Panhwar et al. 2008).

Narrow-sense heritability and proportional contribution of females, males, and their interaction were also computed as described by Dhillon et al. (2006). Narrow-sense heritability = (Vgca) / (Vgca+Vsca + VE)} X 100, wher, Vgca = general combining ability variance, Vsca = specific combining ability variance, and VE = error variance (Dhillon et al. 2006). Relative importance of GCA and SCA was estimated according to Baker (1978) as the ratio $\delta^2 GCA_{(f)} + \delta^2 GCA_{(m)} / \delta^2 GCA_{(f)} + \delta^2 GCA_{(m)} + \delta^2 SCA$, where $\delta^2 GCA_{(f)}$, $\delta^2 GCA_{(m)}$ and $\delta^2 SCA$ are the variance components for GCA and SCA, respectively. Genstat statistical software was used to calculate Pearson’s correlation coefficients to determine the association of morphological, agronomic and stem borer resistance/susceptibility traits. The damage parameters were correlated with agronomic traits and morphological trait (bloom waxiness) to detect any relationships, as well as to detect interrelationships between borer damage parameters. Correlated response was expressed as a percentage of predicted response to selection (a measure of direct selection) for each of the traits studied. These correlations support development of a selection criterion. Correlated response implies that it might be possible to achieve genetic gain under selection for a secondary trait than from selection for the desired trait itself (Odiyi 2007).

Results

Leaf feeding, deadheart formation, exit holes and stem tunnel damages

Results of mean squares for deadheart, leaf damage, exit holes and stem tunneling damages are presented in Table 1. The mean squares due to GCAf were significant for all the four *C. partellus* damage traits measured i.e. deadheart (P = <.001), leaf damage (*P* = 0.048), exit holes (P = <.001) and stem tunneling (P = <.001) whereas mean squares due to GCAm were singly significant for deadheart damage (P = <.001). Significant SCA mean squares were recorded for deadheart (*P* = 0.007), exit holes (<.001) and stem tunneling (P = <.001) damages. Proportional contribution to total variance for deadheart and leaf feeding damages was highest among females, followed by female and male interaction and lowest in males. Proportional contribution to total variance for exit holes and stem tunneling damages was highest for female and male interaction and the least from the males. Baker's ratio for deadheart, leaf damage, exit holes and stem tunneling spotted stem borer damages ranged between 30% - 71% while narrow-sense heritability for the same damage traits ranged between 26% - 53%.

Table 1 Mean squares of *Chilo partellus* damage traits on sorghum and narrow sense heritability estimates across seasons at Kiboko, Kenya in 2010/2011 long and short rainy seasons

Source of variation	d.f.	DH	LD	EH	ST
Rep	1	1511.6	985.2	1.1255	3042
Season	1	4789.3**	2960.2**	0.4177 ns	1476.4*
GCA_f	14	778.2**	284.5*	0.6007**	1309.4**
GCA_m	1	2338.1**	72.7 ns	0.2884 ns	173 ns
SCA	14	405**	176.6 ns	0.5059**	1481.5**
Residual	59	162.1	151.5	0.1493	238.9
	Proportional contribution to total variance				
Females		308.05	66.5	0.23	535.25
Males		145.07	−5.25	0.01	−4.39
Females x Males		242.9	25.1	0.36	1242.6
Baker's ratio		0.65	0.71	0.40	0.30
	Narrow-sense heritability (%)				
		53	26	31	26

GCA_f, general combining ability for females; *GCA_m*, general combining ability for males; *SCA*, specific combining ability; *DF*, degrees of freedom; *DH*, deadheart; *LD*, leaf damage; *EH*, exit holes; *ST*, stem tunnels

*, ** Data significant at ≤0.05 and ≤ 0.01 probability level respectively

Agronomic and morphological traits

The results on analysis of variance for agronomic and morphological traits are presented in Table 2. Mean squares due to GCAf were significant for plant height (P = <.001), days to 50% flowering (P = <.001), days to panicle emergence (P = <.001), panicle length (P = <.001), total grain weight (P = <.001), hundred grain mass (P = <.001) and bloom waxiness (P = <.001). Mean square GCAm were significant for panicle length (*P* = 0.038), total grain weight (P = <.001) and hundred grain mass (P = <.001). SCA mean squares were significant for total grain weight (P = <.001), hundred grain mass P = <.001, panicle emergence (P = <.001), days to 50% flowering (P = <.001), panicle length (P = <.001), plant height (P = <.001) and bloom waxiness (*P* = 0.013). Proportional contribution to total variance was greatest among females for plant height and panicle length. Proportional contribution to total variance was greatest in the interaction between females and males for days to 50% flowering, days to panicle emergence, panicle length, total grain weight, hundred grain mass and bloom waxiness. Baker's ratio ranged between 34% - 89% while narrow sense heritability for the same traits ranged between 31% - 87%.

Chilo partellus sorghum damage, agronomic performance and morphological traits

The results of the performance of sorghum crosses are presented in Table 3. Agronomic, morphological and major stem borer damage parameters traits were significant except for leaf feeding damage. This could be attributed to the high seasonal/environmental influence on the trait. Cross that showed the least leaf feeding damage was ICSB 474 X Kari mtama 1. Crosses ICSA 464 X Kari mtama 1, ICSA 472 X ICSB 473, ICSB 464 X ICSB 473 and ICSB 474 X ICSB 473 showed the least dead heart damage. The least stem exit holes damage was recorded on ICSA 467 X ICSB 473 while Macia X ICSB 473, ICSA 464 X Kari mtama 1, ICSA 467 X ICSB 473, ICSA 472 X ICSB 473 showed the least stem tunneling damage. Panicle length ranged from 17 to 30 cm with a mean of 24 cm. Longest panicles were recorded on ICSB 464 X Kari-mtama 1 and IS 8193 X ICSB 473, while Seredo X Kari-mtama 1 produced the smallest panicles. The tallest cross was ICSA

Table 2 Mean squares from line x tester analysis of agronomic and morphological traits in sorghum in 2010/2011 long and short rainy seasons, Kiboko Kenya

Source	Df	PH	FL	PE	PL	TGW	HSM	BW
Rep	1	33.5	0.13	70.53	1.07	272.4	7.55	0.03
GCA_f	14	12,470.4**	208.2**	54.56**	169.52**	5185**	3.12**	8.23**
GCA_m	1	2324.2	4.8	16.13 ns	66.2*	16,102.5**	12.13**	2.7*
SCA	14	4687.9**	149.59**	53.99**	170.25**	4853.4**	3.60**	3.2**
Residual	539	518.3	15.57	7.4	12.46	531.3	0.26	0.4
	Proportional contribution to total variance							
Females		5976.1	96.3	3276.3	437	2326.9	1.4	47.9
Males		120.4	−0.7	62.5	10.5	1038.1	0.8	−0.1
Females x Males		4169.6	134	8060.4	53.7	4322.1	3.3	133.6
Baker's ratio		0.59	0.42	0.34	0.89	0.43	0.4	0.59
	Narrow-sense heritability (%)							
		0.56	0.39	0.31	0.87	0.41	0.38	0.56

GCAf, general combining ability for females; *GCAm*, general combining ability for males; *SCA*, specific combining ability; *Df*, degrees of freedom; *PH*, plant height; *FL*, days to 50% flowering; *PE*, days to panicle emergence; *PL*, panicle length; *TGW*, total grain yield; *HSM*, hundred seed mass; *BW*, bloom waxiness

*, ** Data significant at ≤0.05 and ≤ 0.01 probability level respectively, ns = non-significant

474 X Kari-mtama 1 while Gadam X ICSB 473 was the shortest. Days to 50% flowering ranged from 62 to 82 days on Seredo X ICSB 473 and ICSA 464 X Kari-mtama 1 respectively. ICSA 464 X Kari-mtama 1 and Seredo X ICSB 473 took the longest and shortest days to panicle emergence respectively.

Cross IESV 91131 DL X Kari-mtama 1 produced the highest total grain weight while ICSB 464 X Kari-mtama 1 weighed the least. Highest hundred grain mass was observed on IESV 91131 DL X Kari-mtama 1, ICSB 474 X Kari-mtama 1, IESV 93042 SH X ICSB 473 and ICSA 474 X Kari-mtama 1 while Seredo X Kari-mtama 1 recorded the least. Bloom waxiness ranged from 3.5 (slightly present) on ICSA 472 X ICSB 473 to 8.0 (mostly bloomy) on Gadam X Kari-mtama 1, IESV 91131 DL X Kari-mtama 1 and IESV 91131 DL X ICSB 473 at 50% flowering stage.

The results on the interaction of *C. partellus* resistance traits from the three A/B pairs used in this study are presented in Table 4. Among the four resistance traits evaluated, interaction effects of the male and female parents were significant for exit holes and stem tunneling.

Nature of gene action

Results of the general combining ability (GCA) effects for the tested sorghum materials are presented in Table 5. The GCA effects suggested that lines ICSA 472 and ICSA 464 and ICSB 474 exhibited the maximum negative GCA effect of −6.10, −4.97 and − 3.94 respectively for *C. partellus* damages pooled together. Tester ICSB 473 displayed higher negative significant GCA effect of −1.17. This implied that the afore mentioned materials showed good general combining ability to the sorghum spotted stem damage traits evaluated. IESV 91131 DL showed the highest significant positive GCA effects of 7.57 followed by Seredo (4.14) and IS 21881 (3.71) for the four damages parameters pooled.

Maximum GCA significant positive effects for plant height among females were observed on ICSA 474 (33.89), ICSB 467, and ICSB 474 (23.19) while among males ICSB 473 displayed higher GCA effect of 1.98. On the other hand, low negative GCA effect of −38.08 and − 15.91 were observed for plant height on Gadam and IESV 91131 DL respectively suggesting that these parents contributed alleles for dwarfness in the crosses. High significant positive GCA effects for days to 50 % flowering among females were recorded on ICSA 464 (12.72), ICSA 472 (6.72) and Macia (2.47) while a negative GCA effect for the same trait was observed on Gadam (−6.03). High positive significant GCA effects for panicle length were observed on females ICSB 464 (3.74) and ICSB 467 (3.52). Significant positive GCA effects for grain yield were recorded on IESV 93042 SH (20.37), IS 21879 (17.21), IESV 91131 DL (11.65) and Gadam (10.91). High positive significant GCA effects for bloom waxiness was observed on IESV 91131 DL (2.45) and Gadam (1.45) while the lowest and negative GCA effects for the same trait were observed on IS 21881 (−0.3).

Specific combining ability results for damage, agronomic and morphological traits measured are presented in Table 6. The best specific combiners that showed significant negative effects for deadheart, leaf feeding, exit holes and stem tunneling damages were Macia X ICSB 473, IS 21881 X ICSB 473, ICSB 474 X ICSB 473 and ICSA 472 X Kari mtama 1 respectively. Cross IS 21879 X ICSB 473 showed the highest positive significant SCA for plant height. Hybrid ICSA 464 X Kari mtama 1 depicted significant good SCA effects for total grain yield while IESV 93042 SH X Kari mtama 1 showed significant undesirable for SCA for the same trait.

Table 3 Means for *Chilo partellus* damage, agronomic and morphological traits for sorghum F_1 crosses

F1 hybrids	DH	LD	EH	ST	PH	PE	FL	PL	TGW	HGM	BW
Gadam X ICSB 473	13	37	7	25	125	62	68	21	40	2.2	6.0
Gadam X Kari mtama 1	32	28	3	20	129	64	71	22	53	2.7	8.0
ICSA 464 X ICSB 473	7	40	7	18	154	63	70	23	42	2.5	5.0
ICSA 464 X Kari mtama 1	1	35	3	9	175	62	67	24	17	1.6	5.0
ICSA 467 X ICSB 473	7	36	2	9	142	62	70	24	19	1.8	5.0
ICSA 467 X Kari mtama 1	7	40	11	25	176	67	73	27	39	2.5	4.0
ICSA 472 X ICSB 473	1	28	4	9	183	68	75	19	16	2.4	3.5
ICSA 472 X Kari mtama 1	26	27	5	11	156	61	69	22	20	1.9	5.0
ICSA 474 X ICSB 473	13	40	5	12	194	64	70	23	14	2.1	5.0
ICSA 474 X Kari mtama 1	26	33	11	18	204	64	71	24	30	2.9	5.5
ICSB 464 X ICSB 473	1	30	6	17	159	60	70	26	49	2.6	7.0
ICSB 464 X Kari mtama 1	20	31	10	37	174	55	62	30	13	2.5	5.5
ICSB 467 X ICSB 473	7	40	10	18	192	62	69	27	17	1.9	5.0
ICSB 467 X Kari mtama 1	7	35	8	27	174	63	70	28	45	2.3	5.0
ICSB 474 X ICSB 473	1	32	6	35	186	60	67	27	26	2.4	5.0
ICSB 474 X Kari mtama 1	26	15	3	10	191	60	66	24	45	3.0	6.0
IESV 91131 DL X ICSB 473	45	33	10	34	159	64	72	24	33	2.4	8.0
IESV 91131 DL X Kari mtama 1	23	33	10	33	140	64	71	23	61	3.0	8.0
IESV 93042 SH X ICSB 473	23	28	6	22	154	60	68	24	56	2.9	4.5
IESV 93042 SH X Kari mtama 1	26	32	3	10	157	61	68	25	55	2.7	5.0
IS 21879 X ICSB 473	20	30	6	24	161	63	69	24	52	2.0	5.0
IS 21879 X Kari mtama 1	19	36	5	18	139	65	72	24	53	2.5	7.0
IS 21881 X ICSB 473	20	45	5	17	155	62	69	25	34	2.4	5.0
IS 21881 X Kari mtama 1	32	46	7	16	167	67	74	23	43	2.4	5.5
IS 8193 X ICSB 473	32	52	6	23	159	59	65	30	43	1.9	5.5
IS 8193 X Kari mtama 1	23	30	5	17	145	65	72	21	39	2.0	6.0
Macia X ICSB 473	16	37	4	8	173	69	75	22	17	1.6	5.0
Macia X Kari mtama 1	45	32	9	22	180	71	76	25	49	2.7	5.0
Seredo X ICSB 473	25	35	5	26	153	65	73	27	48	2.6	7.5
Seredo X Kari mtama 1	36	46	4	14	161	66	72	17	19	1.4	5.0
F value	0.007	0.325	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001
LSD	18.01	17.42	0.24	9.60	14.14	3.82	5.54	2.19	14.32	0.32	0.89
CV	26	36	10	16	14	4	5	15	35	22	18

DH, Deadheart damage; *LD*, leaf feeding damage; *EH*, exit holes; *ST*, stem tunnels; *PH*, plant height (cm); *PE*, days to panicle emergence; *FL*, 50% flowering; *PL*, Panicle length (cm); *TGM*, total grain mass (gm); *HGM*, hundred grain mass (gm); *BW*, bloom waxiness

Table 4 Interaction effect of stem borer resistance traits from the three A/B-pairs (ICSA/B-464, ICSA/B-467 and ICSA/B-474) involved in this experiment

Source of variation	d.f.	DH	LD	EH	ST
Female parent ignoring male parent	6	393.8	189.2	0.44 *	781*
Female parent eliminating male parent	6	358.7	190.9	0.44*	766.9*
Male parent ignoring female parent	1	1562.3*	4.4	1.44**	2957.6**
Male parent eliminating female parent	1	1211.2*	21.3	1.41**	2873.2**
Female parent. Male parent	5	224.2	190.3	0.64**	2516.3**
Residual	232	199.2	344.6	0.18	285.2
Total	244	259.7	292.7	0.2	353.7

d.f., degrees of freedom; *DH*, deadheart; *LD*, leaf feeding damage; *EH*, exit holes; *ST*, stem tunnels

*, ** Data significant at ≤0.05 and ≤ 0.01 probability level respectively

Table 5 General combining ability effects of females and males for *Chilo partellus* damage on leaf feeding, deadheart and stem damages, agronomic and other traits in sorghum

Females	DH	LD	EH	ST	PH	FL	PE	PL	TGM	HGM	BW
Gadam	3.52	−1.96	−1.14	2.87	−38.08	−6.03	−2.62	−2.71	10.91**	0.08	1.45**
ICSA 464	−15.85	3.34	−1.24	−6.12	−1.08	12.72**	5.63*	−0.63	−10.61	−0.27	−0.55
ICSA 467	−12.55	3.64	0.34**	−2.68	−6.51	0.72	0.38	1.38*	−11.45	−0.15	−1.05
ICSA 472	−6.15	−6.79	−1.89	−9.56	4.92	6.72**	4.13**	−3.53	−17.26	−0.21	−1.3
ICSA 474	0.65	1.44	1.71**	−1.26	33.89**	2.72*	0.88	−0.88	−13.02	0.18*	−0.8
ICSB 464	−9.35	−7.79	1.94**	7.38**	1.39	−1.03	−0.37	3.74**	−4.49	0.21*	0.7**
ICSB 467	−12.55	2.58	2.76**	2.81	17.79**	−2.03	0.38	3.52**	−4.05	−0.2	−0.55
ICSB 474	−6.15	−10.96	−1.41	2.78	23.19**	−6.53	−4.37	1.12*	0.31	0.35**	−0.05
IESV 91131 DL	14.59**	−1.56	3.44**	13.82**	−15.91	−3.53	−0.62	−0.46	11.65**	0.4**	2.45**
IESV 93042 SH	5.39	−4.49	−1.76	−3.73	−9.54	−0.78	1.38	0.17	20.37**	0.5**	−0.8
IS 21879	0.32	−1.49	−0.96	1.14	−15.31	2.47*	−0.12	−0.16	17.21**	−0.09	0.45*
IS 21881	6.82	11.41*	0.14*	−3.55	−4.61	−5.78	−3.37	−0.11	3.37	0.1	−0.3
IS 8193	8.12*	6.24	−0.51	0.39	6.79*	−2.53	−0.37	1.54*	5.95*	−0.37	0.2
Macia	11.72*	0.04	0.39**	−4.82	11.39**	2.47*	1.13	−0.6	−7.21	−0.21	−0.55
Seredo	11.45*	6.34	−1.76	0.52	−8.31	0.47	−2.12	−2.41	−1.71	−0.31	0.7**
Males											
ICSB 473	−4.42	0.78	−0.5	−0.54	1.98	0.2	0.37	0.33	−5.18	−0.14	−0.15
Kari- mtama 1	4.41**	−0.78	0.51**	0.54	−1.97	−0.2	−0.37	−0.33	5.18	0.14*	0.15
LSD Female	17.9**	15.19 ns	0.17**	6.7*	11.7*	7.0**	4.8**	1.7**	10.5**	0.2**	1.1**
Male	6.6**	5.55 ns	.06*	0.06*	2.5	4.2*	2.6*	1.8 ns	4.8**	3.8**	0.4 ns

DH, Deadheart; *LD*, leaf damage; *EH*, exit holes; *ST*, stem tunnels; *PH*, plant height; *FL*, 50% flowering; *PE*, days to panicle emergence; *PL*, Panicle length; *TGM*, total grain mass; *HGM*, hundred grain mass; *BW*, bloom waxiness

*, ** Data significant at ≤0.05 and ≤ 0.01 probability level respectively, ns = non-significant

Discussion

This study found out that from Baker's ratio, general combining ability (GCA) and specific combining ability (SCA) for deadheart damage, leaf damage, exit holes and stem tunnel damages were important. This observation implied that these damage traits are conditioned by both additive and non-additive types of gene actions. The reason for considering leaf damage, deadheart formation, exit holes and stem tunnel damages is due to the fact that selecting for resistance based on a single parameter is not effective and reliable (Singh et al. 2012). Additive type of gene action was predominant for leaf feeding and deadheart damages while both additive and non-additive types of gene action were important for number of stem borer exit holes and stem tunnels. This observation is in agreement with Sharma et al. (2007) who reported that GCA and SCA controlled leaf feeding in sorghum. However, a study on combining ability in *C. partellus* resistance maize reported additive gene action to be predominant for leaf damage, number of exit holes and stem tunnel length (Karaya et al. 2009).

The negative combining ability effects for leaf feeding, deadheart formation, stem tunnels and exit holes damages suggested contribution of the genotype towards resistance, while positive combining ability effects implied contribution to susceptibility in the crosses. Selection of resistant parents with high negative GCA effects to these traits could be effective for development of new sorghum cultivars resistant to insect pests (Aruna and Padmaja 2009). The moderate values for narrow sense heritability in the present study suggested that conventional pedigree and early generation selection methods can be effective for initial improvement in sorghum resistance against *C. partellus.*

Several authors have reported similar observations with the current study in different backgrounds. Pathak (1990) reported that both additive and non-additive genes are important for inheritance of stem borer resistance but, additive gene effect is more important. A study conducted on genetics of resistance to the pink stem borer (*Sesamia nonagrioides*) in maize showed that genetic effects of traits related to stem and ear damage by the pink stem borer fitted an additive-dominant model (Butrón et al. 2009).

In the current study, the relative significance of GCA to SCA variances as depicted from Baker's ratio implied that the additive type of gene action conditioned deadheart and leaf damage. Selection of resistant parents to these traits could thus be effective for development of *C. partellus* resistant sorghum cultivars. GCA for leaf damage was non-significant and other results are dependent/interlinked to this major stem

Table 6 Specific combining ability estimates of F1 hybrids from line x tester analyses of various traits in sorghum

F1 hybrids	DH	LD	EH	ST	PH	PL	TGW	HGM	BW	FL	PE
Gadam X Kari mtama 1	1.43	5.97*	3.22	0.17	37.88	3.81**	−9.71*	0.03	−0.60	6.23*	0.33
Gadam X ICSB 473	−8.44*	−2.07	−9.44	−5.91*	33.94	1.60	−12.10*	−0.19*	−2.30	5.83	1.57
ICSA 464 X ICSB 473	12.54	−6.73	−0.03	2.30	9.10*	0.95	−1.38	−0.05	0.70*	−15.67	−8.93
ICSA 464 X Kari mtama 1	14.73*	0.03	2.51**	9.94*	−11.62	0.31	22.60**	0.595	0.40	−9.77	−2.17
ICSA 467 X ICSB 473	16.96	−6.73	−4.03	−4.55*	−12.92*	−3.15	1.72	−0.08	1.70	1.83*	0.57
ICSA 467 X Kari mtama 1	8.13	−0.57	3.36	29.55	21.28	0.384	21.18	0.37	0.40	−3.27	−1.17*
ICSA 472 X Kari mtama 1	14.723*	7.03	1.21	29.48	−19.72	5.61**	13.90	−0.165	1.9**	−0.27	−2.67
ICSA 472 X ICSB 473	−2.44	6.57	2.22	9.27*	5.18	1.45	20.62**	0.58	0.70*	−13.17	−5.43
ICSA 474 X Kari mtama 1	−2.74	−3.67	−14.63	7.24*	−31.32	24.66	15.63	0.115	1.90	−5.27	−0.17
ICSA 474 X ICSB 473	−1.42	0.77	−4.33	−4.73*	−41.12	0.35	10.41	−0.47	0.20	−0.17	−1.43
ICSB 464 X Kari mtama 1	3.96	13.33*	−3.73	2.07	3.58	−1.59*	−18.70	−0.41	1.40	0.23	−1.17*
ICSB 464 X ICSB 473	14.73	2.27	−0.14*	2.79	11.02*	−5.90	27.67	0.00	0.20	1.83	2.07
ICSB 467 X Kari mtama 1	16.96*	−4.27	−3.73	0.87	28.92	−2.64*	13.20*	−0.41**	0.4	2.23	0.83
ICSB 467 X ICSB 473	8.13	−0.93	−8.93	−6.50*	−11.32*	−4.40	−5.10	0.14	0.70*	1.83*	−1.43
ICSB 474 X ICSB 473	−2.44	0.77	−1.71	9.87	−28.22*	25.60*	−4.76*	−0.49**	−0.3	9.83**	7.57
ICSB 474 X Kari mtama 1	14.723*	3.13	3.12	−15.43*	−22.82	−2.59*	4.14	−0.215*	0.4	3.23*	1.33*
IESV 91131 DL X ICSB 473	−30.27	0.77	−3.03	−13.23*	22.78	0.50	−20.56	−0.55	−2.3	4.83*	0.57
IESV 91131 DL X Kari mtama 1	1.06	2.33	−3.84	−14.41*	4.38*	0.414	−2.73	−0.26*	−2.6	2.23	0.83
IESV 93042 SH X ICSB 473	−2.44	1.47	3.77	10.07	6.14	−0.80	−15.10*	−0.14	0.70*	1.33	−1.43
IESV 93042 SH X Kari mtama 1	−17.57*	7.53	−0.24*	−2.61	8.68*	0.464	−25.64*	−0.76	0.9	0.23	−1.17*
IS 21879 X ICSB 473	−4.87	−2.53	1.92	−4.61*	24.08*	−0.20	−12.56*	−0.02	−1.3	3.33	0.57
IS 21879 X Kari mtama 1	4.26	5.53*	0.81	2.32	1.88	0.514	−21.85*	0.20*	0.4	−8.27	−0.17
IS 21881 X ICSB 473	−8.74*	−12.73*	−0.53	2.52	−3.62	0.50	−2.89	0.04	0.2	4.333*	1.57
IS 21881 X Kari mtama 1	−4.87	−10.07	0.26*	4.57*	8.18	−0.29	−3.85	−0.25*	0.15	7.23	5.33**
IS 8193 X ICSB 473	−17.27	3.97	−0.54	2.82	17.48*	2.55	0.85	0.46**	−0.3	3.33*	0.57
IS 8193 X Kari mtama 1	1.06	16.47*	1.57*	−3.61	34.28	−5.64	−12.75*	0.28*	−0.1	1.73	0.33
Macia X ICSB 473	−21.74**	1.57	−2.18	−1.40	−17.22*	−0.99	−8.17	−0.18	0.70*	2.33	2.57*
Macia X Kari mtama 1	−1.67	−1.67	1.41	11.04*	−10.22	2.18*	22.60*	0.61	0.4	−7.27**	−4.67**
Seredo X ICSB 473	−12.24	−12.53*	2.82*	−6.39	2.08	7.20	21.40*	−0.41**	0.70*	−11.67**	61.32
Seredo X Kari mtama 1	10.67*	−0.17	0.71	5.87*	9.88*	−2.39	−18.00*	1.034	−2.1	10.73**	4.33**

DH, Deadheart damage; *LD*, leaf feeding damage; *EH*, exit holes; *ST*, stem tunnels; *PH*, plant height; *PL*, Plant length; *TGW*, total grain yield; *HGM*, hundred grain mass; *BW*, bloom waxiness; *FL*, days to 50% flowering; *PE* , days to panicle emergence

*, ** Data significant at ≤0.05 and ≤ 0.01 probability level respectively

borer criteria. This finding implied that leaf damage alone may not be adequate and effective to measure resistance to *C. partellus*.

The comparative significance of SCA to GCA for exit holes and stem tunneling implied that non additive mode of gene action was predominant over additive gene action for these stem damage traits. The significance of GCA as well as SCA for agronomic and morphological traits studied suggested the presence of both additive and non-additive gene actions. A study involving a different sorghum population reported leaf feeding damage, overall plant resistance, panicle initiation and plant height to be conditioned by dominance type of gene action (Sharma et al. 2007). Specific combining ability was greater than GCA males for maturity dates and grain components implying that female parents might have been influential in determining days to maturity and grain yield.

Generally, the F1 resultants from *C. partellus* resistant ‘A’ lines and restorer lines had significantly lower leaf damage, deadhearts, exit holes and stem tunneling damages. This finding implies that resistance is requisite in both male and female parents to obtain progenies with resistance to *C. partellus.* This observation is supported by several authors who noted that parental performance in evaluation of sorghum to shoot fly damage could be a good predictor of the resultant F1 performance (Rao et al. 1974; Dhillon et al. 2006). Females ICSA 472 and ICSA 464 and male ICSB 473 demonstrated the highest negative significant GCA effects in regard to leaf feeding, deadheart formation, exit hole and stem tunnels damages combined. This observation suggested that these sorghum lines have good general combining ability to the *C. partellus* sorghum damage traits. These novel parents could be utilized in development of *C. partellus* resistant sorghum cultivars for cultivation by famers in regions where *C. partellus* is endemic. An interesting observation in the current study was observed on IESV 91131 DL. The sorghum line recorded high significant positive GCA in regard to deadheart, exit holes and stem tunnels damages and depicted high significant positive GCA to total grain yield and hundred grain mass. A possible reason could be that the genotype contributed genes for tolerance to spotted stem borer damage since crosses involving this particular line also had relatively high total grain yield. Tolerance is the inherent ability of a plant not to compromising yield or quality while supporting pest population that would otherwise damage a susceptible variety (Reese et al. 1994).

Generally, leaf feeding damage was non-significant. This could be attributed to several factors such as the high influence of seasons, the sorghum plants might have healed faster and may be leaf damage scoring rather than incidence would be a better way of measuring leaf damage. This observation may imply that stem tunneling, exit holes and deadheart formation may be more dependable and effective traits for consideration in evaluating materials for *C. partellus* resistance. A similar observation was made by Prasad Shyam et al. (2011) on the assessment of resistance to *C. partellus* on sweet sorghum. It is also striking that among all damage parameters, deadheart formation showed reasonable narrow sense heritability. The low narrow sense heritability on leaf feeding, exit holes and stem tunneling could be due to the environmental influence on the characters. Resistance to *C. partellus* is a multi-mechanism, low-heritability quantitative trait that is highly influenced by the environment (Sharma et al. 2006; Singh et al. 2012).

There was a disconnect that was observed among the F1 hybrids between total grain yield SCA and traits used to measure resistance. For instance hybrid ICSA 464 X Kari mtama 1 had unfavorable SCA effects for resistance to *C. partellus* but showed good SCA effects for total grain yield. This observation implied that in the development of *C. partellus* resistant hybrids, both grain yield and the characters used to measure resistance should always be considered to complement the alleles for different traits of interest.

Genotypes that were completely bloomy suffered low leaf feeding, deadheart and stem damages as a result of *C. partellus* attack. This suggested that bloom waxiness possibly contributed to the resistance mechanism. Bloom wax may have interfered with stem borer larvae movement and leaf feeding. The positive and highly significant association between exit holes and stem tunnel imply a positive and direct relationship between the two damage parameters and so either of the two traits can be used to predict the other. In addition, selecting for exit holes would also ensure selecting for stem tunneling thus possibility of selecting for more than one trait. The negative significant correlation between panicle length and days to flowering implied that late maturing sorghum genotypes were high grain yielders. The highly significant and positive correlation between panicle length and stem tunnel implied that plants with a long panicle would suffer intense damage since a large surface area was available for *C. partellus* feeding hence grain yield would be negatively affected. In addition the positive correlation between panicle length and stem tunnel may imply tolerance mechanism of resistance where by the panicle size would not be affected by stem borer damage.

Conclusion and recommendation

This study suggested that *C. partellus* leaf feeding and deadheart damages were governed by additive type of gene action while exit holes and stem tunneling were conditioned by both additive and non-additive types of gene action. Genetic gain is likely to be realized through conventional breeding for these traits since the narrow sense heritability estimates were moderate. The significance of GCA and SCA mean squares suggests the importance of both additive and non-additive types of gene action respectively for all the traits studied. Generally, results of this study indicated that it would be possible to breed for high *C. partellus* resistance from this set of germplasm. Parents ICSA 464, ICSA 472, ICSB 474 and ICSB 474 were among the best parents that showed reduced damage to leaf feeding, deadheart and stem damages due to *C. partellus.* IESV 91131 was good for *C. partellus* tolerance, earliness and high total grain yield. The SCA effects revealed that cross IESV 93042 SH X Kari mtama 1 was significantly the best for deadheart and exit holes damages, Seredo X ICSB 473 was the best for leaf feeding damage and ICSB 467 X ICSB 473, the best for stem tunneling damage. Cross ICSA 464 X Kari mtama 1 was the best option for grain yield. These could be used in development of sorghum hybrids for high grain yield and resistance to *C. partellus* for cultivation by farmers in areas where the insect pest causes epidemics.

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