

Full Length Research Paper

Combining ability of maize (*Zea mays*) inbred lines resistant to *Striga hermonthica* (Del.) Benth evaluated under artificial *Striga* infestation

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The parasitic weed *Striga* affects maize on an estimated 20 million ha in Africa, making it a major cause of maize yield reduction from near world average of 4.2 t/ha few decades ago to the present 1.5 t/ha. The objectives of this study were to examine the combining ability of 20 inbred lines and identify single crosses which can be used to develop other hybrids resistant to *Striga hermonthica* (Del.) Benth. Fourteen female lines were mated using North Carolina Design II with all six males. The resulting 84 F₁s along with six commercial checks were evaluated in four separate trials for two rainy seasons during 2010. The trials were conducted on station under both artificial *Striga* infestation and *Striga* free environments using standard procedures at the Kibos and Alupe sites, both in the Kenya's Lake Victoria Basin. Data were recorded on *Striga* counts, *Striga* damage rating (SDR), grain yield and other agronomic traits. General combining ability (GCA) and specific combining ability (SCA) effects were computed using SAS. The new F₁ hybrids outperformed the commercial checks in grain yield and reaction to *Striga*. Single crosses JI-30-3/TESTR 151, JI-30-18/TESTR 151, CML206//56/44-6-3-7-1/TESTR 149 and JI-30-18/TESTR 156 gave the highest yield while single cross JI10-28-#/TESTR 136 gave the lowest yield. The ratio of GCA: SCA mean squares exhibited a predominance of additive gene effects in the inheritance of *Striga* resistance traits as opposed to dominance gene effects. Inbred lines with good GCA for yield and *Striga* resistance traits were identified as TESTR 151, TESTR 156 and OSU231//56/44-6-4-17-3. The high GCA inbred lines and the superior single crosses will provide a basis for future use *per se* and also development of three-way and double cross hybrids to be grown in *Striga* prone areas of the Lake Victoria Basin in eastern Africa.

Key words: Maize, *Striga hermonthica*, general combining ability (GCA), specific combining ability (SCA), host plant resistance, sub-Saharan Africa.

INTRODUCTION

Many African countries often produce less maize than what they consume making them net importers of maize

as maize is an important food crop in sub-Saharan Africa (SSA) and it provides the bulk of the calories in diet

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(Vivek, 2009). The average maize yield is 1.5 t/ha much below the world average of 4.2 t/ha (FAO, 2009). This results to malnourishment due to shortage which affects about 300 million people in Africa (Kim and Adetimirin, 1997). Solutions are needed to various maize production constraints, including low grain yield, susceptibility to pests and diseases, adaptation to the specific growing ecologies and yield loss that result from the devastating effects of *Striga* parasitic weed (Kim, 1994).

Many *Striga* control approaches have been developed, without much success when used singly (Kiruki et al., 2006). The major control strategies are; 1) hand weeding which is probably the oldest and also requires intensive work for several seasons before any benefits can be noticed in the field, 2) use of herbicide resistant maize which has a risk of *Striga* developing resistance to the chemicals, and 3) use of host plant resistance which is the plants ability to prevent attachment of the parasite or to kill or impair development of the attached parasite (Badu-Apraku et al., 2007). Host plant resistance offers the most effective and economical *Striga* control for the resource poor farmers in sub-Saharan Africa.

Host plant resistance (HPR) to *Striga* spp. constitutes two complementary mechanisms: resistance and tolerance (Rodenburg and Bastiaans, 2011). Resistance refers to the ability to reduce or prevent infection and reproduction (Shew and Shew, 1994) while tolerance refers to withstand infection with lower or minimum yield loss (Caldwell et al., 1958). The use of HPR has been limited, though it is the most economically feasible and environmentally friendly means of *Striga* control for the farmer (Rodenburg and Bastiaans, 2011). Series of studies at International Institute for Tropical Agriculture (IITA) found some maize varieties that were tolerant to *Striga* (Kim, 1994). The results from these studies concluded that the genetic control for tolerance and resistance of maize genotypes tested to *S. hermonthica* was polygenic and the inheritance quantitative. Twenty inbred lines and seven synthetics which were found to be tolerant and resistant to *S. hermonthica* were developed from diverse germplasm through artificial infestation with seeds obtained from various host crops (Kim, 1994). Some of these lines were used in the present study to determine their usefulness in variety development.

Combining ability of inbred lines determines the usefulness of the lines in hybrid combinations as the value of the line can best be expressed through the performance of crossing combinations (Hallauer and Miranda, 1981). Sprague and Tatum (1942) introduced the terms general combining ability (GCA) and specific combining ability (SCA). The general combining ability can be determined by using a broad base heterogeneous population as tester, while differences in the SCA can be revealed using a tester with a narrow genetic base (inbred line or single cross (Spitko et al., 2010). Identification of inbred lines with good GCA and SCA effects rely on the availability of genetic diversity among genotypes involved in the breeding program (Legesse et al., 2009).

GCA expresses the mean performance of a parental line in hybrid combinations, while the SCA is a measure of the value of individual combinations as a function of the mean performance of the parental components. GCA and SCA are always relative values and depend greatly on the performance of the specific inbred lines involved in the crosses (Spitko et al., 2010). The value of GCA tends to express additive gene effects, while SCA is more indicative of dominant and epistatic gene effects.

In SSA, maize is grown over a diverse range of environments starting from the lowlands, mid- altitude to the highland ecologies (Derek and Carl, 1997). Some of these regions are infested with *S. hermonthica* which cause a loss of 40 to 60% in grain yield but can go up to 100%. The grain lost is estimated at seven billion tons annually, affecting about 100 million people (Kanampiu and Friesen, 2003). Enhancement of maize production in the *Striga* prone areas can be achieved by identifying elite *Striga* resistant lines which can be used to develop high yielding resistant varieties. The objective of this study were to: 1) estimate the combining ability effects of maize inbred lines from IITA, Kenya Agricultural Research Institute (KARI), and CIMMYT for *Striga* resistance traits, grain yield and foliar diseases, 2) identify promising hybrid crosses which may be used directly or be used in the formation of three way and double cross hybrids which can be grown by the resource poor farmers.

MATERIALS AND METHODS

Genotypes

There were 20 maize inbred lines sourced from three different institutions (Table 1). Materials involved eight *Striga* resistant inbred lines from IITA, the Kenya Agricultural Research Institute (KARI) contributed nine resistant inbred lines, while the International Maize and Wheat improvement Center (CIMMYT) contributed three well adapted inbred lines. Fourteen inbred lines designated as females were factorially mated with six IITA lines using North Carolina Design II to form 84 single cross hybrids in a line x tester mating design.

Field evaluation

Eighty-four single crosses along with six commercial checks were evaluated under both artificial *Striga* infestation and in *Striga* free environments. The F1 hybrids and the parents were tested for two long-rain seasons during 2009 and 2010 each at Kibos (0°40'S, 34°48'E) and Alupe (0°29'N, 34°20'E) in Kenya. Inoculum was prepared by mixing 5 kg of fine sand with 10 grams of *Striga* seeds. Infestation was done by applying the inoculum into an expanded hill of 7 to 10 cm during planting, this way deploying about 3,000 viable *Striga* seeds per hill.

The maize seed was placed on top of the inoculum and covered with soil. The experimental materials were planted in an alpha (0, 1) lattice design with three replications (Patterson and Williams, 1976). The spacing was 75 cm between rows and 25 cm within rows in both sites. The hybrids were over sown with two seeds per hill and later thinned to one to attain a plant density of 53,333 plants per

Table 1. The The list of maize inbred lines tested for the combining ability.

Entry	Pedigree	Source	Remarks
1	CML 444	CIMMYT	Adapted
6	CML204	CIMMYT	Adapted
8	CML312	CIMMYT	Adapted
9	CML206//56/44-6-3-7-1	KARI	Adapted
2	TESTR 153	IITA	<i>Striga</i> resistant
3	JI-30--4	KARI	<i>Striga</i> resistant
4	JI-30--3	KARI	<i>Striga</i> resistant
5	JI-30-18	KARI	<i>Striga</i> resistant
7	TESTR 132	IITA	<i>Striga</i> resistant
10	F1-14-14-24-4-5-4	KARI	<i>Striga</i> tolerant
11	F1-14-79-4-1-3	KARI	<i>Striga</i> tolerant
12	OSU231//56/44-6-4-17-3	KARI	<i>Striga</i> tolerant
13	JI10-76-#	KARI	<i>Striga</i> tolerant
14	JI10-28-#	KARI	<i>Striga</i> tolerant
15	TESTR 136	IITA	<i>Striga</i> resistant
16	TESTR 139	IITA	<i>Striga</i> resistant
17	TESTR 149	IITA	<i>Striga</i> resistant
18	TESTR 150	IITA	<i>Striga</i> resistant
19	TESTR 151	IITA	<i>Striga</i> resistant
20	TESTR 156	IITA	<i>Striga</i> resistant

ha. The six checks included KSTP94 and UA Kayongo as the resistant checks and PHB3253, WH505, H513 and DH04 as susceptible checks.

Trial management practices including fertilization and weeding were done differently for each of the *Striga* infested and *Striga* free environment. For the *Striga* infested trials, the first weeding was done mechanically using a hoe but subsequent weedings were done by hand to uproot only other weeds but not *Striga*. Data for all agronomic traits were recorded on a per plot basis for each experiment. Data recorded included *Striga* counts at 6, 8, 10, and 12 weeks after planting (WAP) by counting *Striga* plants which emerged in each plot.

Striga damage rating was recorded at the 10th WAP using a 1-9 scale (1 = clean with no damage and 9 = heavily damaged). Days to 50% pollen shed and days to 50% silking were recorded when half of the total maize plants in a plot produced pollen or silked, respectively. Disease data was recorded on maize streak virus (MSV), gray leaf spot (GLS), rust and *Exserohilum turcicum* using a 1-5 scale (1 = no disease and 5 = severely diseased). Grain yield (tha⁻¹) was computed from unshelled cobs by assuming 0.8 shelling percent and adjusting it to 12.5% moisture content.

Statistical analysis

Combined analyses of variance were conducted for all the traits measured for each environment separately. Log₁₀ transformation was done on the *Striga* counts. Using:

$$Y = \text{Log}_{10}(x+1)$$

Where, Y = Transformed data and x = actual *Striga* counts. Line x tester analyses of variance were performed to estimate (GCA) and (SCA) effects and variance according to the factorial model by Comstock and Robinson (1948).

$$Y_{hijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + R_h + \epsilon_{hijk}$$

Where Y_{hijk} = the observation of the k-th full-sib progeny in a plot in h-replication of the i-th paternal parent and the j-th maternal parent; μ = the general mean; α_i = the effect of the i-th male parent; β_j = the effect of the j-th female parent; $(\alpha\beta)_{ij}$ = the interaction of paternal and maternal genotypes; R_h = the effect of h-th replication and ϵ_{hijk} = the environment effect and remainder of the genetic effect between full sibs on the same plot.

The SAS software (SAS, 2003) was used with the effects of environment and replicates considered as random while those of the genotype were considered as fixed. The mean squares of variance for the lines (females) and the testers (males) and their interaction effects were determined. The GCA effects of all 20 lines and SCA effects of the 84 single cross hybrids were determined. Test for significance of GCA and SCA effects were performed by computing the standard error for lines, testers and crosses and then tested against the t-test by taking the degree of freedom of the pooled error mean square.

RESULTS

Agronomic performance under artificial *Striga* infestation

Highly significant differences ($P \leq 0.001$) were observed in grain yield, days to 50% silking, SDR, *Striga* emergence counts (6th, 8th, 10th and 12th WAP), and disease severity caused by MSV, *Turcicum*, GLS and leaf rust. The grain yield of the crosses ranged 2.3 to 6.8 tha⁻¹ and the trial mean was 5 tha⁻¹ while the yield of the six commercial checks ranged 3.8 to 4.1 tha⁻¹ with a mean of 4 tha⁻¹

Table 2. Performance of selected F1 hybrids under artificial *Striga* infestation.

Rank	Genotype	Grain yield (t/ha)	50% days to anthesis	<i>Striga</i> damage rating (Score 1-9)	<i>Striga</i> count 6 WAP/M ²	<i>Striga</i> count 8 WAP/M ²	<i>Striga</i> count 10 WAP/M ²	<i>Striga</i> count 12WAP/M ²	<i>E. turcicum</i> (score 1-5)	Gray leaf spot (Scored 1-5)
1	CML 444/ TESTR 136	6.8	66.0	1.3	0.03	0.33	0.67	0.93	2.3	1.3
2	TESTR 153/TESTR 136	6.8	66.0	1.7	0.03	0.27	0.75	0.96	2.3	1.2
3	JI-30--4/TESTR 136	6.4	65.4	1.8	0.04	0.52	1.01	1.18	1.8	1.3
4	JI-30--3/ TESTR 136	6.4	65.8	2.3	0.13	0.79	1.23	1.38	1.9	1.6
5	JI-30-18/ TESTR 136	6.4	65.7	1.7	0.08	0.49	1.04	1.25	1.9	1.2
6	CML204/TESTR 136	6.4	66.3	1.7	0.08	0.57	1.13	1.31	2.1	1.5
7	TESTR 132/TESTR 136	6.3	64.3	1.4	0.06	0.67	1.19	1.34	2.3	2.0
8	CML312/TESTR 136	6.2	64.5	2.7	0.04	0.47	1.02	1.17	1.8	1.4
9	CML206//56/44-6-3-7-1/TESTR 136	6.2	64.5	1.8	0.01	0.53	0.94	1.09	2.1	1.2
10	F1-14-14-24-4-5-4/ TESTR 136	6.2	65.4	1.6	0.08	0.48	0.97	1.26	2.6	1.4
11	F1-14-79-4-1-3/ TESTR 136	6.1	63.8	1.7	0.02	0.37	0.78	0.98	2.4	1.4
12	OSU231//56/44-6-4-17-3/ TESTR 136	6.1	64.8	1.5	0.04	0.41	0.73	1.02	2.3	1.4
13	JI10-76-#/ TESTR 136	6.0	64.4	3.2	0.04	0.55	1.03	1.20	2.3	1.3
14	JI10-28-#/TESTR 136	6.0	64.9	1.4	0.11	0.48	0.88	1.08	2.2	1.2
15	CML 444/TESTR 139	6.0	64.5	1.5	0.03	0.42	0.75	0.91	2.4	1.2
16	TESTR 153/TESTR 139	5.9	62.6	2.5	0.06	0.47	0.90	1.06	2.1	1.2
17	JI-30--4/TESTR 139	5.9	67.3	2.2	0.08	0.65	1.15	1.33	2.7	1.5
18	JI-30--3/ TESTR 139	5.9	67.2	1.6	0.06	0.45	0.96	1.07	2.8	1.2
19	JI-30-18/TESTR 139	5.8	64.9	2.1	0.07	0.57	1.04	1.18	2.3	1.7
20	CML204/TESTR 139	5.8	66.5	1.7	0.02	0.32	0.79	0.93	2.5	1.6
90	COMMERCIAL CHECK-1	2.1	68.5	4.6	0.04	0.54	1.00	1.23	2.4	1.4
87	COMMERCIAL CHECK-2	2.5	62.3	3.3	0.08	0.65	1.09	1.26	2.8	1.8
81	COMMERCIAL CHECK-3	3.0	68.9	2.7	0.01	0.09	0.36	0.65	2.3	1.4
89	COMMERCIAL CHECK-4	2.3	67.0	4.7	0.13	0.76	1.22	1.35	2.5	1.4
82	COMMERCIAL CHECK-5	3.0	64.7	5.3	0.07	0.65	1.07	1.20	2.7	2.0
85	COMMERCIAL CHECK-6	2.9	65.3	5.0	0.10	0.53	1.00	1.15	2.8	1.9
	Mean (Trial)	2.48	64.63	4.10	0.07	0.53	0.97	1.12	3.14	1.57
	CV (%)	39.26	3.95	36.07	195.42	65.24	33.01	28.1	14.59	31.1
	LSD(0.05)	1.29	2.13	1.25	0.11	0.29	0.26	0.26	0.31	0.42
	Significance	**	***	***	NS	***	***	***	**	**

*, **and *** indicates significance differences at P<0.05, P<0.01 and P<0.001, respectively.

(Table 2). F1 hybrids were in the same maturity bracket as the commercial checks under. It also

exhibited a lower mean score for the SDR (2.4) as opposed to the commercial checks (4.3) (Table 2).

The F1 single cross hybrids (registered low disease incidences) than commercial checks

Table 3. Coefficient of phenotypic correlation between agronomic and the *Striga* resistance traits of 84 maize hybrids under artificial *Striga* infestation.

Parameter	AD	ASI	PH	EH	EPP	YLD	SDR	STR6	STR8	STR10	STR12	MSV	TURC
AD													
ASI	0.25**												
PH	0.33***	-0.20*											
EH	0.38***	-0.23*	0.87***										
EPP	0.22*	-0.22*	0.24*	0.36***									
YLD	0.30***	-0.17	0.51***	0.55***	0.51***								
SDR	-0.24*	0.37***	-0.76***	-0.76***	-0.42***	-0.67***							
STR6M2TR	0.03	0.02	0.14	0.12	0.14	0.22*	-0.01						
STR8M2TR	0.01	0.18	-0.03	-0.01	0.18	0.29**	0.06	0.47***					
STR10M2TR	0.1	0.12	0.01	0.0002	0.21*	0.35***	0.01	0.44***	0.87***				
STR12M2TR	0.21*	0.1	0.07	0.06	0.27**	0.44***	-0.06	0.37***	0.81***	0.94***			
MSV	0.25**	0.31***	0.19	0.09	-0.001	0.30***	-0.01	0.31***	0.36***	0.38***	0.43***		
TURC	-0.48***	-0.16	-0.28**	-0.35***	-0.44***	-0.82***	0.44***	-0.21*	-0.29**	-0.34***	-0.44***	-0.36***	
GLS	-0.13	0.20*	-0.25	-0.24**	-0.02	-0.18	0.32**	-0.01	0.17	0.28**	0.26**	0.18	0.01

*, **and *** indicates significance differences at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively. Yld = Yield, AD = 50% days to anthesis, SD = 50% days to silking, ASI = anthesis silking interval, PH = Plant height, EH = ear height, GLS = Gray leaf spot, *Turc* = *E.turcicum*, SDR = *Striga* damage rating, STR8 = *Striga* counts 8WAP, STR10 = *Striga* counts 10WAP and STR12 = *Striga* counts 12 WAP

(Table 2). The genotypes differed significantly for reaction to leaf blight caused by *E. turcicum* and gray leaf spot (GLS) caused by *Cercospora zeae-maydis*. The mean score for *E. turcicum* was 3.14 and the range was 1.8 to 4.2 on a scale of 1-5. For gray leaf spot the mean was 1.57 while the range was 1.2 to 2.2 (Table 2).

The relationship between yield performance and the *Striga* resistance traits of the hybrids was investigated by a simple linear phenotypic correlation in a combined analysis for the two sites (Table 3). A highly significant ($P < 0.001$) and negative correlation was observed between grain yield and SDR ($r = -0.67^{***}$). A positive and significant correlation was observed between *Striga* counts per m^2 and yield 6 WAP, $r = 0.22$, and 8 WAP. *Striga* counts 10 WAP and 12 WAP was highly significantly correlated to yield across

sites ($r = 0.44$) and ($r = 0.30$), respectively.

Combining ability analysis

Significant GCA mean squares ($P < 0.001$) were observed in most of the traits except ears per plant (EPP), indicating that there were some differences in the agronomic performance of the inbred lines used as the parents of the hybrid combinations in a line x tester experiment (Table 4). The site x GCA interaction was highly significant ($P < 0.001$) for grain yield, EPP, ear aspect, days to 50% anthesis, days to 50% silking, GLS and *E. turcicum*, indicating that the GCA effects were specific to the sites. This underlines that selection based on performance across the sites.

The ratio of the GCA: SCA mean squares were higher than unit in all the traits observed, suggesting that the additive gene action effects could be more important than the dominance gene action for the agronomic traits. The GCA mean squares under the *Striga* infested environment were highly significant ($P \leq 0.001$) for most of the traits except for SDR suggesting that dominance effects were more important (Table 5). The GCA mean squares for the *Striga* resistant traits were 1.78, 1.96, 5.31, 13.04 and 14.98 times larger than the SCA mean squares. This also suggested that the additive gene action was more important than dominance gene action for *Striga* resistance for these genotypes.

Significant GCA effects were observed on yield, days to 50% anthesis, SDR and *Striga* counts 6, 8, 10 and 12 WAP. Inbred lines TESTR

Table 4. Analysis of variance (mean squares) of a 14x6 factorial cross of maize inbred lines in a *Striga* free environment.

Source	Degrees of freedom	Grain yield (t/ha)	Ears per plant (no.)	Ear aspect (Score 1-5)	50% days to anthesis (days)	Plant height (Cm)	Ear height (Cm)	Gray leaf spot (score 1-5)	<i>Exserohilum turcicum</i> (score 1-5)
REP	2	1.566	0.028*	0.404	38.727***	15043.742***	9102.257***	0.311**	0.226
SITE	3	370.593***	0.321***	19.784***	1411.408***	224643.525***	78776.281***	39.257***	13.268***
LINE (GCA)	13	71.975***	0.111***	17.628***	204.825***	3383.093***	1898.636***	1.253***	20.100***
TESTER (GCA)	5	31.089***	0.018	6.973***	136.556***	11817.577***	5689.251***	3.068***	1.243***
SITE*LINE	39	4.402***	0.032***	0.755***	4.558***	150.906	161.930	0.114***	0.981***
SITE*TESTER	15	10.825***	0.030***	0.656***	4.854***	278.214	308.920**	0.202***	0.898***
LINE*TESTER (SCA)	65	2.258***	0.018***	0.587***	3.069***	309.510**	151.837	0.140***	0.335***
SITE*LINE*TESTER	195	1.168***	0.012	0.308***	2.134	204.635	172.945*	0.078**	0.165
GCA/SCA		31.88	6.17	30.03	66.74	10.93	12.50	8.95	60.00
ERROR	670	0.781	0.011	0.176	2.078	199.566	138.3	0.061	0.147
CV		19	11.01	14.9	2.2	6.79	10.61	17.01	13.66

*, **and *** indicates significance differences at P<0.05, P<0.01 and P<0.001, respectively.

Table 5. Analysis of variance (mean squares) of a 14x6 factorial cross of maize inbred lines under artificial *Striga* infestation.

Source	Degrees of freedom	Grain yield (t/ha)	50% days to anthesis (days)	Plant height (Cm)	Ear height (Cm)	Ears per plant (no.)	<i>Striga</i> damage rating (Score 1-9)	<i>Striga</i> count per M2 (6 WAP)	<i>Striga</i> count per M2 (8 WAP)	<i>Striga</i> count per M2 (10 WAP)	<i>Striga</i> count per M2 (12 WAP)	Gray leaf spot (score 1-5)	<i>Exserohilum turcicum</i> (score 1-5)
REP	2	1.493**	149.738	1850.131**	127.797	0.005	0.371	0.005	1.004***	1.772***	1.230***	0.210	0.354
SITE	3	3.568***	806.996***	220507.063***	53380.479***	0.362***	6.567***	1.374***	12.397***	8.004***	8.240***	12.953***	2.186***
LINE GCA	13	5.749***	192.822***	2412.596***	1941.884***	0.089***	0.060	0.015*	0.381***	0.787***	0.999***	1.854***	19.491***
TESTER GCA	5	1.965***	58.461	11400.264***	7264.425***	0.033*	0.248	0.017*	0.538***	1.593***	1.553***	5.891***	1.295***
SITE*LINE(GCA)	32	0.429	81.043	327.452	230.885	0.022*	0.148	0.015**	0.071	0.099	0.097	0.199***	0.564***
SITE*TESTER(GCA)	15	0.495	80.595	403.742	186.636	0.025*	0.223	0.014*	0.106**	0.168**	0.116	0.554***	0.509*
LINE*TESTER(SCA)	65	0.466*	77.840	254.836	190.080	0.017	0.034	0.008	0.072	0.060	0.067	0.206***	0.409**
SITE*LINE*TESTER(SCA)	123	0.368	76.810	312.302	187.551	0.014	0.073	0.008	0.055	0.056	0.062	0.112	0.285
GCA/SCA		12.337	2.477	9.467	10.216	5.144	1.780	1.955	5.308	13.041	14.979	9.000	47.655
ERROR	245	0.33	77.7	344.305	199.62	0.015	0.226	0.009	0.059	0.078	0.078	0.109	0.284
CV		21.09	13.62	9.1	12.36	12.2	289.62	95.66	54.53	30.74	25.78	21.54	20.15

*, **and *** indicates significance differences at P<0.05, P<0.01 and P<0.001, respectively.

151, TESTR 156 and OSU231//56/44-6-4-17-3 exhibited significant positive GCA effects for yield (Table 6). However, inbred line TESTR 156

exhibited significant positive GCA effects for the *Striga* resistance traits. Inbred lines J110-76-# and J110-28-# were the best general combiners for the

Striga resistance traits as they had significant (P ≤ 0.001) negative GCA effects for SDR and *Striga* counts although they had significant negative

Table 6. The GCA effects of the parental materials under artificial *Striga* infestation.

Entry	Genotype	Grain yield (t/ha)		50% days to anthesis (d)	<i>Striga</i> damage rating (Score 1-9)	<i>Striga</i> counts 8 WAP	<i>Striga</i> counts 10 WAP	<i>Striga</i> counts 12 WAP	<i>E. turcicum</i> (Score 1-5)	Gray leaf spot (Score 1-5)
		INF	No-INF							
1	CML 444	1.7	0.3	1.7	-1.06***	-1.06***	0.1**	0.08*	0.01	-0.1*
2	TESTR 153	-0.14	-0.66**	-0.14	0.13	0.13	0	0	0.38***	0.25***
3	JI-30--4	0.04	0.37	0.04	-0.09	-0.09	-0.05	-0.04	-0.31***	0.07
4	JI-30--3	1.04	0.85***	1.04	0.23	0.23	-0.06	-0.06	-0.3***	0
5	JI-30-18	0.7	0.66**	0.7	0.2	0.2	0.05	0.05	-0.48***	-0.01
6	CML204	1.63	0.33	1.63	0.19	0.19	0.03	0.07	-0.23**	0.19***
7	TESTR 132	1.48	-1.55***	1.48	0.88***	0.88***	-0.11**	-0.15***	0.53***	-0.29***
8	CML312	0.08	0.91***	0.08	0.01	0.01	0.23***	0.26***	-0.08	0.07
9	CML206//56/44-6-3-7-1	-0.12	1.12***	-0.12	-0.04	-0.04	0.07*	0.07*	-0.62***	-0.25***
10	F1-14-14-24-4-5-4	-1.12	0.63**	-1.12	0.23	0.23	0.1**	0.06	-0.25**	0.14**
11	F1-14-79-4-1-3	-2.78**	0.11	-2.78**	0.03	0.03	-0.04	-0.03	-0.22*	-0.12*
12	OSU231//56/44-6-4-17-3	2.2*	0.36	2.2*	-0.24*	-0.24*	-0.23*	-0.54**	-0.37***	-0.05
13	JI10-76-#	-3.03**	-1.41***	-3.03**	-0.97***	-0.97***	-0.14***	-0.17***	0.77***	0.16**
14	JI10-28-#	-1.65	-2.01***	-1.65	0.03	0.03	-0.15***	-0.18***	1.18***	-0.06
15	TESTR 136	-0.17	-0.37	-0.99	-0.29*	-0.29*	-0.03	-0.05*	0.11*	-0.19***
16	TESTR 139	-0.44**	-0.52*	0.36	0.61***	0.61***	-0.01	-0.02	-0.1*	0.24***
17	TESTR 149	-0.11	0.16	0.36	-0.53***	-0.53***	0	0.01	0.1*	0.03
18	TESTR 150	-0.05***	0.06	0.14	0.18	0.18	0.03	0.02	-0.06	0.08
19	TESTR 151	0.41**	-0.02	0.57	-0.23*	-0.23*	-0.14***	-0.13***	0.01	-0.26***
20	TESTR 156	0.36**	0.7**	-0.43	0.26*	0.26*	0.16***	0.16***	-0.06	0.08

WAP = Weeks after planting, INF- Artificially infested with *Striga*, NO-INF- *Striga* free environment. *, **and *** indicates significance differences at P<0.05, P<0.01 and P<0.001, respectively.

GCA effects for yield. These two inbred lines were also found to be very susceptible to *E. turcicum*.

Significant ($P \leq 0.01$) positive SCA effects for yield were observed among the F1 hybrids. These were found out in crosses involving parents 7x2, 13x4, and 14x2. Hybrids 13x4 and 14x2 also had favorable SCA effects for *Striga* resistance traits (Table 7), making them the best F1 hybrids which could be grown in *Striga* infested fields. Hybrid 7x6 had favorable SCA effects for *Striga* resistance and diseases but a significant negative SCA effects for yield.

DISCUSSION

Host plant resistance with reduced *Striga* emergence is considered as the best strategy for long term control of *Striga* in sub-Saharan Africa. *Striga* resistant F1 hybrids with low *Striga* emergence were identified. However, susceptible F1 hybrids which supported few and many *Striga* plants were also present. Resistant maize cultivars should be able to support few emerged parasites, and sustain low *Striga* damage symptoms and produce high grain yields

(Rodenburg and Bastiaans, 2011). In this case an inbred line which supports few *Striga* plants and finally succumbs to the effect of the parasite is considered not useful in the development of host plant resistance materials (Kim and Adetimirin, 1997).

The usefulness of the inbred lines in hybrid combinations is determined through studying their combining ability (Hallauer and Miranda, 1981). For the present study therefore, the desirable and *Striga* resistant lines would show negative GCA effects for SDR and *Striga* counts and a positive

Table 7. The SCA effects of the best performing F1 hybrids under artificial *Striga* infestation.

Cross	Grain yield (t/ha)	50% days to anthesis (d)	<i>Striga</i> counts 6 WAP	<i>Striga</i> counts 8 WAP	<i>Striga</i> counts 10 WAP	<i>Striga</i> counts 12 WAP	<i>E. turcicum</i> (Score 1-5)	Gray leaf spot (Score 1-5)
1X2	-0.09	-0.09	-0.16	0.7**	0	0.01	-0.31*	-0.05
2X5	-0.33	-0.22	0.48	0.42	0.1	0.06	0.05	-0.31***
6X5	-0.13	-0.32	0.17	0.09	0.07	0.03	0.07	-0.26**
6X6	0.34	2.27	-0.14	0.08	-0.02	-0.03	0.02	-0.22**
7X2	0.74**	-1.21	-0.36	0.06	0.06	0.16*	-0.2	-0.15
7X3	0.34	0.29	-0.14	0.02	-0.04	-0.07	-0.31*	0.02
7X4	0.39	-0.74	0.66*	0.05	0.08	0.08	-0.29*	-0.11
7X6	-0.99	2.75	0.08	0.01	-0.2***	-0.19**	-0.43**	-0.07
8X1	0.41	0.04	0.17	-0.04	-0.12*	-0.04	-0.13	-0.17*
9X3	0.36	0.47	0.11	-0.11	0.03	0.01	-0.33*	-0.02
11X3	0.06	3.54	-0.46	-0.22	-0.12*	0.02	-0.03	-0.03
13X4	0.83**	0.68	0.09	-0.4	-0.06	-0.66*	-0.44**	-0.06
14X2	0.89**	-0.25	-0.09	-0.43	0.01	-0.72*	-0.19	-0.09
14X5	-0.07	0.13	0.16	-0.62*	-0.09	-0.14*	-0.29*	0.2*

WAP = Weeks after planting. *, ** and *** indicates significance differences at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

GCA effects for grain yield under *Striga* infested conditions. In our study TESTR 151 and OSU231//56/44-6-4-17-3 would be considered superior and desirable. Inbred line TESTR 156 exhibited a significant positive GCA effects for grain yield and a positive GCA effects for *Striga* resistance traits making it not suitable for *S. hermonthica* resistance. Inbred lines JI10-76-# and JI10-28-# exhibited high GCA effects for *Striga* resistance traits but negative GCA effects for grain yield. These lines can therefore be utilized only as source of resistance to *Striga* in maize breeding. The importance of additive gene action was observed for grain yield and the *Striga* resistance traits as opposed to non-additive gene action. Similar findings were reported by Yallou et al. (2009) who reported the importance of additive gene effects while studying combining ability of maize inbred lines containing genes from *Zea diploperennis*. The relative importance of GCA and SCA variance was examined by expressing it as the ratio of additive to total genetic variance. The closer this ratio is to unity, the greater the predictability based on GCA alone (Baker, 1978). In our study, the additive gene effects were found to be more important than the dominance effects. The importance of the GCA effects was 12% under *Striga* infested environment and 31% under *Striga* free environment. Makumbi et al. (2010) reported GCA effects of 51 to 79% in well watered environment and 40 to 64% under water stressed environment. The significant GCA effects as opposed to SCA effects for the SDR and *Striga* counts indicate that the genetic variation for resistance to *S. hermonthica* among the lines was mainly controlled by additive type of gene action. This is in agreement with findings of Gethi and Smith (2004) findings who reported

significant GCA mean squares for *Striga* counts but contrary on SDR. However, these results are in contrast to that of Kim (1994), who found higher SCA mean squares than GCA mean squares for *Striga* counts and higher GCA mean squares than SCA mean squares for SDR. *Striga* infestation coupled with other stresses such as foliar diseases including *E. turcicum* and gray leaf spot are major causes that has hampered maize production in the sub-Saharan Africa over the last two decades, making it to remain at 1.5 t/ha well below the world average of 4.2 t/ha (FAO, 2003, Kanampiu et al., 2007). It is therefore important to develop genetic materials with good levels of resistance to these diseases. Quite a good number of F1 hybrids with good and acceptable scores were identified. In the development of maize hybrids, resistance to *Striga* should be tested under both *Striga* free and *Striga* infested environments following procedures developed by Kim (1991) and Hausmann et al. (2000). This helps in identifying superior inbred lines in both environments which would be ideal for the farmers as *Striga* infestation in the field is not uniform and the parasite infestation in the field is erratic. In *Striga* free environments TESTR 156 and OSU231//56/44-6-4-17-3 had positive and significant GCA effects for yield making them superior under both environments. Inbred lines JI-30-3, JI-30-18, CML 312, CML 206, and F1-14-14-24-4-5-4 showed positive and highly significant GCA effects for grain yield under *Striga* free environments.

Conclusion

The outcome of the present studies confirms the

availability of inbred lines for developing maize hybrids with good levels of resistance to *S. hermonthica*. The importance of additive gene action was demonstrated in breeding for *Striga* resistance as opposed to non-additive gene action. Inbred lines with good GCA for yield and *Striga* resistance traits were identified as TESTR 151, TESTR 156 and OSU231//56/44-6-4-17-3. These inbred lines would be of great importance in the breeding for *Striga* resistance in maize. Single crosses 7x2, 13x4, and 14x2 were identified as the best performing hybrids under *Striga* infested environment. They would therefore be recommended to be grown by farmers in the *Striga* prone areas. Inbred lines JI10-76-# and JI10-28-# which are mutants from KARI Muguga might be a very good source of resistance as they gave very good GCA effects for the *Striga* resistance traits.

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