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Combining Ability for Grain Yield, Agronomic Traits and *Striga hermonthica* Resistance of Yellow Endosperm Maize

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Abstract

Maize production is constrained by *Striga hermonthica* in Mali leading to high yield losses. Breeding resistant hybrid maize is a promising alternative for increasing farmers' income. The objective of this study was to evaluate the response of test crosses to *Striga hermonthica* and identify high yielding and adopted hybrid. Forty-five F1 hybrids and three checks were evaluated under *Striga*-infested and *Striga*-free conditions in Sanankoroba and Sotuba rainy season. Data collection was carried on grain yield, anthesis silking interval, plant aspect, plant height, days to 50% tasselling and silking, *Striga* damage ratings and *Striga* count at 8 and 10 weeks after planting. General combining ability (GCA) of line and Specific combining ability (SCA) of hybrids effects were significant for most traits under both conditions. GCA effects had greater proportion of variance than SCA effects suggesting additive gene effects controlling the inheritance of yield and *Striga* resistance. Parental lines *TZISTR112*, *TZISTR1214*, *TZISTR1222*, *TZISTR1223*, tester *TZISTR1207* and *TZISTR106* were the best combiner for grain yield under both conditions and they could be used in hybrid development.

Keywords: Maize; *Striga hermonthica*; Combining ability; Resistance; Yield

Introduction

Maize is one of the most important food crops in the world and together with rice and wheat, provides at least 30% of the food calories to more than 4.5 billion people in 94 developing countries [1]. This crop is gaining momentum compared to other cereals, both in terms of productivity and use in human and animal food. In Mali, the area covered by maize is 803,136 ha with an average yield of 2.17 t/ha [2]. With this performance, Mali comes first in terms of productivity among the West African countries that produce maize [3]. However, this yield is low compared to Mexico 3.71 t/ha and the United States 10.96 t/ha [4]. This low yield is generally caused using open pollinated and local varieties, biotic and abiotic factors. One of the major biotic factors is *Striga hermonthica*. Since 1990, maize varieties production has been hampered by *Striga*. In 2005, a total of 25 African countries were infested by *Striga* as reported by De Groote et al. [5]. In Mali and other maize growing countries, the cultivated area infested by *Striga* ranged from 30% to 40% [6]. Farmers have reported losses between 20% and 80% and were eventually forced to abandon highly infested fields [7]. About 300 million people in Africa are affected by *Striga* damage [8,9] causing yield loss estimated at 10 million tons grain this loss can be economically estimated to $ US 7 billion [10,11].

There is need for high yielding hybrids with resistance to *Striga hermonthica* present on the farmer's field.

The use of *Striga* resistant hybrids will increase maize production, productivity and lead to improved incomes and livelihoods of farmers as well as enhance the sustainability of the seed companies. Reports of genetic resistance to *Striga* have been reported for maize [12,13]. Inbreeds with stable resistance to *Striga hermonthica* could be useful as parents of hybrids for marketing in *Striga hermonthica* infested areas [14]. *Striga* resistant lines were introduced to Mali from IITA to develop high yielding hybrids with resistance to *Striga hermonthica*. These inbreeds must be evaluated for combining ability to develop hybrids which exhibit high heterosis. The combining ability is prerequisite for developing economically viable hybrid maize varieties. Genotypes that support reduced *Striga hermonthica* emergence can form an important basis for developing resistant hybrids. The broad objective of this study was to enhance the productivity of maize in *Striga* endemic areas. The specific objectives were (i) to identify parental lines for resistance to *Striga* and yield under *Striga*-infested and *Striga*-free conditions, (ii) to identify maize hybrids for resistance to *Striga* and yield under *Striga*-infested and *Striga*-free conditions and (iii) assess the general and specific combining ability of inbreed lines and their hybrids under *Striga*-infested and *Striga*-free conditions.

Material and Methods

Site description

The experiments under *Striga*-infested and *Striga*-free conditions were conducted at CRRA Sotuba (North-West) in central Mali at an altitude of 320 m and in Sanankoroba. Sotuba is situated in southern Mali at an altitude of 320 m, latitude 12°39'47" N, longitude 7°54'50" E and isohyet 600-1000 mm. The soil at this site is sandy with low water holding capacity, low inherent soil fertility and low organic matter content. Sanankoroba is situated in southern Mali at an altitude of 379 m (masl), latitude 12° 23'51.67" N, longitude 7°56'22.10" E. Sanankoroba is a *Striga* endemic zone in Mali and a preferred location for testing maize for responses to *Striga hermonthica* infestation. The experimental

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station of Sotuba has an infested field for evaluating genotypes response to *Striga hermonthica* infestation.

Planting materials

Fifteen Striga resistant maize inbreed lines and three testers with different reaction pattern to Striga hermonthica were crossed in line by tester fashion to generate 45 F1 hybrids in the Regional Agronomic Research Centre of Sotuba/ Mali. The inbreed lines and testers were obtained from the International Institute of Tropical Agriculture (IITA). The three testers were TZSTRI106, TZSTRI1207 and TZSTRI1033. They have different reaction to Striga hermonthica. Inbreed tester TZSTRI106 is a Striga resistant line derived from a backcross containing Zea diploperennis in its genome, TZSTRI1207 is a Striga tolerant line derived from a backcross containing a temperate inbreed line (B73) and TZSTRI1033 is a Striga susceptible line derived from a bi-parental cross between a temperate line (B73) and a line from Thailand (KI21).

Experimental design and field management

The hybrid trial was composed of 48 entries made up of 45 testcrosses obtained from a line by tester cross plus three hybrids checks. The checks included one tolerant hybrid, Mata (TZE-Y Pop DT STRC4 × TZEI 13) and two susceptible hybrids. Farako and Tieba. The 48 hybrids along with the 18 parents were evaluated in Sotuba and Sanankoroba during the growing season of 2014 and 2015 under Striga-infested and Striga-free conditions.

In each location, the 45 single cross hybrids and 3 checks were arranged in a 6 × 8 alpha lattice design with three replications and the parents were arranged in a RCBD with three replications. Hybrids and parents were randomized within each replicate. An experimental plot consisted of a 5m long single row with plants within a row spaced 0.25m apart and 0.75m distance between rows. The fields were planted with two seeds and later thinned to one plant per hill at two weeks after emergence to give a population density of 53,333 plants per hectare. A compound fertilizer at both Sotuba and Sanankoroba consisted of two applications. The first application was carried out 30 days after planting at the rate of 30 kg ha-1 each of N, P and K. Urea was used as top-dressing at the rate of 30 kg/ha^{-1} N two weeks later. Under Striga-infested environments weeds were manually controlled.

Artificial *Striga* infestation procedure

The artificial *Striga* infestation was carried as described by Kim [15] and Kim & Winslow [16]. Matured *Striga* plants were collected in infested maize field from previous season in Sanankoroba. Then the mature *Striga* plant were air dried for 7-9 days. After drying, the *Striga* plants were threshed and seed collected were stored for a minimum of six months to allow the conditioning of the seeds and breakage of dormancy. Germination test was conducted as described by Menkir [13] and germinable *Striga* seed were thoroughly mixed with finely sieved sand at the ratio 1:99 by weight. The sand served as the carrier and provided adequate volume for rapid and uniform infestation. For the field infestation, artificial inoculation with *Striga* seeds was carried out by digging small holes at the crop planting hill along the ridge and infesting with about 3000 germinable *Striga* seeds (8.5g sand/*Striga* mixture). Field infestation was done using by Menkir et al. [17] method. Apart from the *Striga* seed infestation, management practices were the same for both *Striga*-infested and non-infested plots**.**

Data Collection

Under both *Striga*-free and *Striga*-infested conditions, ten traits including grain yield (Yield), days to 50% silking (DYSK), days to 50% anthesis (DYTS), anthesis silking interval (ASI), ear aspect (EASP), ear height (EHT), ears per plant (EPP), plant aspect (PASP), plant height (PLHT) and husk tip cover (HUSK) were measured from each experiment at each location. Under *Striga* infestation, additional data were collected on *Striga* related traits such as *Striga* damage ratings (STRA) and *Striga* emergence count (STRC) at 8 and 10 weeks after planting (WAP). *Striga* damage rating was on a scale of 1-9 as described by Kim [18] where 1=Normal plant no visible symptoms growth, 2=Small and vague purplish- brown blotches visible leaf, 3=Mild leaf blotching with some purplish-brown necrotic spots, 4=Extensive blotching and mild wilting, slight but noticeable stunting and reduction in ear and tassel size, 5=Extensive leaf blotching wilting and some scorching moderate stunting; ear and tassel size reduction., 6=Extensive leaf scorching with mostly grey necrotic spots some stunting and reduction in stem diameter ear size and tassel size, 7=Definite leaf scorching with grey necrotic spots and leaf wilting and rolling severe stunting and reduction in stem diameter ear size and tassel size often causing stalk lodging brittleness and husk opening at a late growing stage, 8=Definite leaf scorching with extensive grey necrotic spots conspicuous stunting leaf wilting rolling severe stalk lodging and brittleness reduction in stem diameter ear size and tassel size and, 9=Complete scorching of all leaves causing premature death or collapse of host plant and no ear formation.

Ear aspect which is the assessment of the general appeal of the ears without the husks was rated on a scale of 1-9, where 1=excellent with no disease/insect damage, large cobs, uniform ears and fully filled grains, 2=very good with no disease/insect damage and fully filled grains, one or two irregularity in cob size, 3=good with no disease/insect damage and fully filled grains, one or two irregularity in cob size, 4=mild insect damage, no disease, fully filled grains, one or two irregularity in cob size poor, 5=mild disease/insect damage and fully filled grains, one or two irregularity in cob size, 6=severe disease/insect damage and fully filled grains, smaller cobs, non-uniform cob size, 7=severe disease/insect damage, scanty grain filling, few ears, non-uniformity of cobs, 8=severe disease/insect damage, scanty grain filling, very few ears and, 9=only one or no ears.

The factors considered included ear size; uniformity of size, color and texture; extent of grain filling and insect and disease damage.

Husk tip cover was rated on a scale of 1-5 where 1 indicates very tight husks extending beyond the tip and 5 indicates exposed ear tip.

Data Analysis

SAS was used to perform analysis of variance for alpha lattice design.

The analysis of combining ability was based on the model described by Kempthorne, Comstock & Robinson [19,20]. The general combining ability (GCA) and specific combining ability (SCA) effects were estimated for each environment and across environments.

The statistical model used for the combined analysis is as follows:

a. Model of combining ability for each environment

$$Y_{ijk}=\mu+r_k+f_i+m_j+(f \times m)_{ij}+e_{ijk}$$

Yijk: The observed measurement for the kth replication of the ixjth progeny; μ: experimental mean; fi: is the effect of the ith line (GCAlinei); I=1, 2, 3….21; tj: is the effect of the jth tester (GCAtesterj); j=1, 2, 3; (f x m) ij: is the interaction effect of the ith line with the jth male (SCAij);

rk: effect replication within environment; k=1, 2; eijk: is the error effect associated with the ijkth observation;

b. Model of combining ability for across environments

Yijkm=μ+rk+li+tj+ (l x m) ij + (f x s) im + (t x s) jm + (l x t x s) ijm+eijkm

Yijkm: The observed measurement for the kth replication at the mth environment of the ixjth progeny; (l x s) im: is the interaction effect of the ith line and mth environment; im=1….n; (t x s) jm: is the interaction effect of the jth tester and mth environment; jm=1……n; (l x t x s) ijm: is the interaction effect of the ith line and jth tester at the mth environment; ijm=1, n; rk: effect replication within environment; k=1,..n; eijkm: is the error effect associated with the ijkmth observation [21];

c. Estimation of GCA and SCA effects

GCA was computed as:

GCAl=Xl – μ and

GCAt=Xt – μ

Xl and Xt=Mean of female and male respectively

GCAl and GCAt=General combining ability of female and male respectively; μ = Overall mean of crosses in the trial

SCA will be computed as:

SCAij=Xi – Ej=SCAij=Cross (ij) mean – [GCAlinei+GCAtesterj+μ]

Xi=Observed mean value of the cross; Ej=Expected mean value of the cross based on the 2 GCAs of its parents;

Ij=crosses, ij=1…n

Grain yield under *Striga*-infested environments was calculated as follows [22]: GY=fwt × ((100-m))/85 × 10000/ ((8 ×Φ)) ×0.8

Where, GY=grain yield (kg ha^{-1}); Fwt=field weight of harvested ears per plot (kg); m=moisture content grain at harvest 10,000=land area per hectare (m2); 8=area harvested per plot (0.75 m × 0.25 m × 18), 0.75 m is the larger of a row and 0.25 m is the distance between 2 holes and 18 is the number of inner plants from the 20 plants per plot which will be harvested. Φ=number of hills/plot (20) and 0.80=shelling percentage. 85=is the adjustment of grain yield at 15% moisture content

Results

Combining ability of lines × testers under *Striga*-infested and *Striga*-free conditions

The genotypes effects were significant (P ≤ 0.05) for most traits under *Striga*-infested and *Striga*-free conditions except ASI under *Striga*-free conditions.

Lines and tester mean square were significant for all traits under *Striga*-infested and *Striga*-free conditions except ASI of line under *Striga*-free conditions, STRA at 8 and 10 WAP and STRC at 8 and 10 WAP under *Striga*-infested, ASI of tester under *Striga*-free conditions, and Yield and ASI of tester under *Striga*-infested (Table 1).

Line and tester by site interactions were significant for most traits under *Striga*-infested and *Striga*-free conditions except PLHT of line by site under *Striga*-free conditions, and yield and STRA and STRC at 8 and 10 WAP of line by site under *Striga*-infested conditions; yield and STRA and STRC at 8 and 10 WAP of tester by site under *Striga*-infested conditions.

Line and tester by year interactions were significant for most traits under *Striga*-infested and *Striga*-free conditions except yield and ASI of line by year under *Striga*-free conditions, and STRA and STRC at 8 and 10 WAP of line by year under *Striga*-infested conditions; yield and STRA and STRC at 8 and 10 WAP of tester by year under *Striga*-infested conditions, and ASI of tester by year under *Striga*-free conditions, and yield and STRA and STRC at 8 and 10 WAP under *Striga*-infested conditions. Line, tester, line by year and tester by year mean square were not significant for ASI under *Striga*-free conditions. Line × tester mean square was significant for all trait under *Striga*-free condition but was not significant for STRA and STRC at 8 and 10 WAP under *Striga*-infested conditions. Line x tester by site interactions were significant for all trait under *Striga*-free condition but was not significant for STRA at 10 WAP and STRC at 8 and 10 WAP under *Striga*-infested conditions. Line × tester by year interactions were significant for all trait under *Striga*-free condition but was not significant for PLHT, STRA at 8 and 10 WAP and STRC at 8 and 10 WAP under *Striga*-infested conditions.

		***Striga*-free conditions**			***Striga*-infested conditions**						
Sources of variation	**d.f**	**Grain Yield**	**ASI**	**PLHT**	**Grain Yield**	**ASI**	**PLHT**	**STRA 8 WAP**	**STRA 10 WAP**	**STRC 8 WAP**	**STRC 10 WAP**
Site	3	1049282.4ns	6.13^{*}	99540.36^{**}	110066912.3^{**}	28.17^{**}	75382.52^{**}	30.83^{**}	13.90^{*}	4.31^{**}	0.95^{*}
Year	1	140153317.9^{**}	28.47^{**}	23522.62^{**}	7382736^{**}	8.07^{*}	298249.47^{**}	14.34^{**}	6.67ns	2.46^{**}	0.41^{*}
GCALine	14	134252052.4^{**}	0.55ns	1236.64^{**}	1349627.2^{**}	2.47^{*}	1152.40^{**}	1.30ns	1.42ns	0.05ns	0.05ns
GCATester	2	1566743.8^{*}	0.10ns	5219.81^{**}	494986.6ns	0.64ns	3954.08^{**}	10.96^{*}	7.12^{*}	1.07^{**}	1.33^{**}
Site x GCALine	42	13644832.3^{**}	2.61^{*}	374.04ns	584004.9ns	2.25^{*}	783.23^{**}	1.25ns	1.29ns	0.12ns	0.15ns
Year x GCALine	14	716423.5ns	0.77ns	1102.84^{**}	2040459.2^{**}	1.83^{*}	693.28^{*}	1.28ns	0.96ns	0.04ns	0.07ns
Site x GCATester	6	1745432.1^{*}	4.23^{*}	2362.69^{**}	676138.2ns	11.76^{**}	7967.86^{**}	0.74ns	4.80ns	0.06ns	0.03ns
Year x GCATester	2	3782049.3^{*}	1.64ns	5036.05^{**}	597430.2ns	1.05ns	2611.05^{**}	4.10ns	1.81ns	0.48^{*}	0.90ns
SCA	28	19451800.3^{**}	2.07^{*}	1194.59^{**}	1102226.8^{**}	2.00^{*}	529.23^{**}	1.69ns	1.43ns	0.12ns	0.11ns
Year x SCA	28	3841517.5^{**}	1.85^{*}	1054.69^{**}	1729755.2^{**}	1.67^{*}	351.06ns	1.14ns	1.15ns	0.10ns	0.11ns
Site x SCA	84	4172841.8^{**}	3.05^{**}	741.97^{**}	828702.7^{**}	2.33^{**}	544.54^{*}	2.40^{*}	2.30ns	0.10ns	0.09ns
Year x Site x SCA	135	1625563.5^{**}	2.93^{**}	2616.78^{**}	3842522^{**}	4.09^{**}	3204.97^{**}	2.81^{**}	2.68^{*}	0.36^{**}	0.23^{**}
Pooled error	718	6278365.6^{**}	1.20	283.66	389173.5	1.1	334.56	1.4	1.91	0.09	0.11

Table 1: Mean squares of grain yield and other traits of single cross hybrids under Striga-free and Striga-infested conditions. *Significant at P=0.05; **Significant at P=0.01; GY= grain yield; EPP=number of ears per plant; PLHT=plant height; ASI=anthesis-silking interval; EASP=ear aspect; EHT=ear height and PASP=plant aspect, STRA 8=Striga damage rating at 8 WAP; STRA 10=Striga damage rating at 10 WAP; STRC 8=Striga emergence count at 8 WAP; and STRC 10=Striga emergence count at 10 WAP; WAP=week after planting.

Genotypes	*Striga*-free conditions			*Striga*-infested conditions						
	GY	ASI	PLHT	GY	ASI	PLHT	STRA8 WAP	STRA10 WAP	STRC8 WAP	STRC10 WAP
TZISTR110	-327.82	0.57	1.08	265.00	0.04	1.38	0.10	-0.07	-0.27**	0.04
TZISTR112	158.03	-0.43	-2.49	59.25	0.40	-1.68	0.02	0.24	0.01	-0.02
TZISTR113	-237.15	-0.16	-3.00	-152.26	-0.16	-6.98	-0.26	-0.10	-0.1	0.07
TZISTR1028	532.33**	-0.02	0.04	-200.90	-0.16	-7.31	-0.04	0.26	0.37**	-0.02
TZISTR1211	-506.22**	0.34	0.71	-307.74*	0.04	-6.07	-0.01	0.04	-0.21**	0.05
TZISTR1214	272.48	-0.02	-1.52	52.01	-0.1	-4.09	-0.23	-0.04	0.15*	0.03
TZISTR1218	-87.76	-0.24	-3.80	-28.69	-0.16	9.42	0.13	-0.04	-0.18**	-0.05
TZISTR1222	240.47	0.12	11.53**	288.31	-0.08	13.02**	0.07	0.07	0.04	0.08
TZISTR1223	647.59**	-0.16	-0.4	302.45*	-0.21	1.09	0.07	0.04	-0.35**	0.06
TZISTR1226	36.38	-0.16	3.35	-220.19	-0.02	-1.45	-0.29	-0.15	0.09	0.02
TZISTR1227	156.24	-0.02	1.96	-97.21	-0.1	6.96	0.10	-0.04	-0.32**	-0.08
TZISTR1230	-83.08	0.01	-5.55	-21.84	0.12	-2.63	0.07	0.01	0.01	-0.04
TZISTR1235	-121.56	0.07	1.63	6.11	0.34	-2.5	0.24	-0.04	0.43**	0.00
TZISTR1237	-248.27	-0.13	-1.88	-28.90	-0.13	1.57	-0.04	-0.1	0.15*	-0.05
TZISTR1238	-431.65**	0.21	-1.65	84.60	0.20	-0.74	0.07	-0.07	0.18*	-0.09
SE ± line	*192.74*	*0.37*	*4.40*	*174.02*	0.34	6.37	0.25	0.26	0.08	0.09
TZISTR1033	-240.35	-0.06	2.81	-58.76	-0.06	-4.07	-0.03	0.1	0.36**	0.13**
TZISTR106	44.24	0.01	-4.07	9.74	0.01	2.81	-0.09	-0.37*	-0.31**	-0.06**
TZISTR1207	196.11	0.06	1.26	49.02	0.06	1.26	0.12*	0.27	-0.05**	-0.07**
SE ± testers	*167.38*	*0.18*	*4.18*	*70.77*	*0.30*	*7.68*	*0.07*	*0.19*	*0.02*	*0.01*

Table 2: General combining ability effects of lines and testers under Striga-free and Striga-infested conditions. *Significant at P=0.05; **Significant at P=0.01; GY=grain yield; ASI=anthesis-silking interval; PLHT=plant height; STRA 8=Striga damage rating at 8 WAP; STRA 10=Striga damage rating at 10 WAP; STRC 8=Striga emergence count at 8 WAP; and STRC 10=Striga emergence count at 10 WAP; WAP=week after planting.

SCA mean squares were larger than GCA mean squares for grain yield, days to silking, anthesis-silking interval, plant height, ear aspect, plant aspect and husk cover (Table 2).

Mode of gene action controlling measured traits

The proportion of the GCA over the total genetic effect of the sum of squares was used to determine the relative importance of GCA and SCA effects. The predictability based on GCA [23] is higher when the ratio is almost equal to one. Across environments the SCA percent contribution was greater than GCA line plus GCA tester percent contribution for most traits except DYSK, DYTS, and Husk. The SCA percent contribution varied from 67% (grain EPP) to 53% (PLHT and EASP). GCA line percent contribution varied from 41% (Husk) to 15% (EASP). The line percent contribution was the highest from Husk (41%) followed by EHT (35%), PASP (34%), ASI (33%), EPP (28%), PLHT (25%), and grain yield (20%), respectively. While the contribution of tester varied from 37% (DYSK) to 1% (ASI) (Figure 1a). Under *Striga*-free conditions, the relative contribution of SCA was greater than GCA (GCA line +GCA tester) for all traits measured. The highest SCA percent contribution was 87.93% (ASI) and the lowest percent contribution was 50.54% (DYSK). Lines percent contribution varied from 44% (Husk) to 12% (ASI), the lines contribution was greater than the testers contribution for all traits measured (Figure 1b) under *Striga*-free conditions. Under *Striga*-infested conditions the percent contribution of SCA was greater for grain yield and *Striga* related traits (Figure 1c). The lines and testers contributed similarly for husk tip cover. However, the relative contribution for lines was greater for GY, ASI, PLHT, EHT and STRA 10WAP.

GCA effects of line and testers for various traits under *Striga*-infested and *Striga*-free conditions. Among the lines, *TZISTR112*, *TZISTR1214*, *TZISTR1222* and *TZISTR1223* exhibited positive GCA effects for GY under *Striga*-infested and *Striga*-free conditions. Among

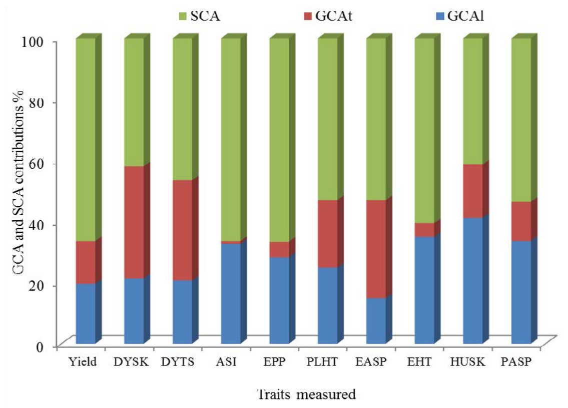

Figure 1a: GCA and SCA across environment.

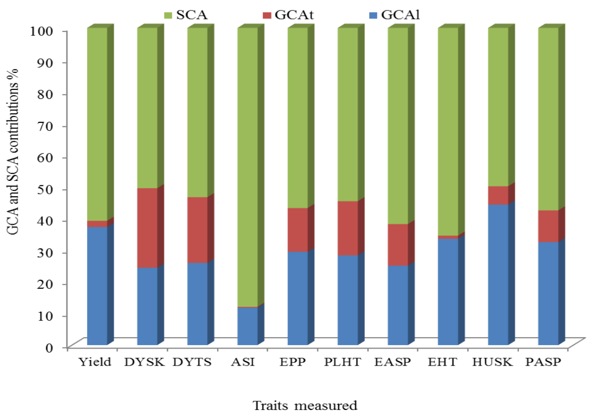

Figure 1b: GCA and SCA under Striga-free.

the testers, *TZISTR106* and *TZISTR1207* exhibited positive GCA effects for GY under *Striga*-infested and *Striga*-free conditions. Parental line, *TZISTR1223* and tester *TZISTR1207* manifested desirable GCA effect for GY and STRC. Also, parental line, *TZISTR1214* exhibited desirable GCA for STRA. Lines, *TZISTR110*, *TZISTR113*, *TZISTR1218*, *TZISTR1227* and tester, *TZISTR106* exhibited desirable GCA for STRA and STRC (Table 2).

Six crosses exhibited significant positive SCA effects for grain yield while seven had negative SCA effects under *Striga*-free conditions (Table 3). Cross *TZISTR106/TZISTR1230* recorded the highest positive SCA effect for grains yield while the lowest was recorded by the cross *TZISTR1207/TZISTR1222*. Seven crosses displayed significant negative SCA effects for both DYSK and DYTS, four had negative and three positive SCA effects. Eight crosses showed significant SCA for ASI; four

Genotypes	*Striga*-free conditions			*Striga*-infested conditions						
	GY	ASI	PLHT	GY	ASI	PLHT	STRA8 WAP	STRA10 WAP	STRC8 WAP	STRC10 WAP
TZISTR1033/TZISTR1227	737.81**	0.12ns	2.48ns	609.03**	0.18ns	-5.75ns	-0.24ns	0.03ns	-0.01ns	0.02ns
TZISTR106/TZISTR1218	695.98**	0.08ns	-5.15ns	548.50**	0.08ns	0.63ns	0.06ns	0.06ns	-0.03ns	-0.10ns
TZISTR1207/TZISTR1214	557.29**	0.10ns	6.62*	508.43**	0.22ns	4.68ns	0.17ns	0.13ns	-0.01ns	0.01ns
TZISTR1033/TZISTR1235	458.76**	0.79**	4.04ns	454.00**	0.15ns	-7.08*	-0.15ns	-0.39ns	-0.02ns	-0.08ns
TZISTR1033/TZISTR1223	331.95*	0.26ns	-7.65**	302.44**	-0.05ns	-4.78ns	-0.24ns	-0.11ns	0.04ns	0.07ns
TZISTR1033/TZISTR1028	324.88**	0.12ns	-2.66ns	300.76**	-0.19ns	5.37ns	0.29ns	0.33ns	-0.03ns	0.03ns
TZISTR106/TZISTR1237	269.82ns	0.06ns	-0.20ns	299.03**	0.30ns	4.28ns	0.04ns	-0.19ns	0.00ns	0.07ns
TZISTR1207/TZISTR113	269.49ns	-0.34ns	-2.82ns	287.79*	0.11ns	-3.04ns	0.48*	0.63*	0.06ns	-0.04ns
TZISTR1207/TZISTR1226	264.72ns	-0.01ns	3.56ns	241.47*	0.30ns	4.61ns	-0.30ns	-0.14ns	-0.09ns	-0.08ns
TZISTR1033/TZISTR113	234.74ns	0.26ns	4.73ns	195.27ns	-0.10ns	11.37**	-0.26ns	-0.44*	0.03ns	0.07ns
TZISTR106/TZISTR1222	233.17ns	-0.11ns	0.77ns	194.00ns	-0.34ns	-1.90ns	0.04ns	-0.33ns	-0.03ns	0.00ns
TZISTR106/TZISTR1230	222.60ns	-0.17ns	5.02ns	191.09ns	0.30ns	2.73ns	0.43*	0.37ns	0.01ns	0.02ns
TZISTR106/TZISTR1226	200.56ns	0.17ns	6.59*	183.54ns	-0.06ns	5.47ns	0.34ns	0.45ns	0.01ns	0.07ns
TZISTR1207/TZISTR1218	171.60ns	-0.09ns	3.18ns	170.66ns	-0.14ns	-6.35*	-0.08ns	-0.12ns	0.04ns	0.10ns
TZISTR1033/TZISTR110	136.57ns	0.37*	1.54ns	154.76ns	0.12ns	-1.41ns	0.96**	-0.03ns	-0.13*	-0.10ns
TZISTR1207/TZISTR112	108.78ns	0.35ns	5.46ns	138.80ns	0.22ns	-3.13ns	0.23ns	-0.14ns	-0.09ns	-0.05ns
TZISTR1033/TZISTR1222	100.22ns	0.15ns	10.12**	114.47ns	0.15ns	11.93**	-0.26ns	0.58*	0.05ns	0.03ns
TZISTR1033/TZISTR112	65.69ns	-0.54**	-4.06ns	99.53ns	0.18ns	1.69ns	-0.18ns	0.11ns	0.05ns	0.07ns
TZISTR1207/TZISTR1237	56.32ns	0.21ns	-3.91ns	76.57ns	-0.17ns	0.37ns	-0.44*	-0.37ns	-0.09ns	-0.07ns
TZISTR106/TZISTR1214	52.84ns	0.11ns	-7.34*	44.93ns	-0.40*	-7.43*	-0.19ns	0.06ns	0.04ns	0.03ns
TZISTR1207/TZISTR1238	47.67ns	-0.29ns	3.32ns	41.45ns	0.08ns	3.46ns	0.11ns	0.02ns	-0.01ns	-0.04ns
TZISTR106/TZISTR1211	33.08ns	-0.08ns	0.21ns	41.09ns	0.13ns	1.71ns	-0.27ns	-0.16ns	-0.01ns	-0.07ns
TZISTR1033/TZISTR1211	24.75ns	-0.57**	5.07ns	21.71ns	-0.38*	-1.37ns	0.10ns	0.00ns	-0.07ns	-0.02ns
TZISTR106/TZISTR1238	-12.73ns	0.31ns	-1.56ns	20.97ns	-0.45*	-7.73*	0.34ns	-0.05ns	0.01ns	0.03ns
TZISTR1207/TZISTR1235	-48.99ns	-0.48*	-5.40ns	-37.25ns	-0.31ns	1.52ns	0.00ns	0.36ns	0.06ns	0.07ns
TZISTR106/TZISTR1223	-80.76ns	-0.08ns	3.78ns	-50.30ns	0.13ns	10.51**	-0.02ns	0.39ns	-0.05ns	-0.07ns
TZISTR1033/TZISTR1238	-87.58ns	-0.02ns	-1.76ns	-62.42ns	0.37*	4.27ns	-0.46*	0.03ns	0.00ns	0.01ns
TZISTR1207/TZISTR1211	-128.16ns	0.49*	3.48ns	-62.79ns	0.25ns	-0.34ns	0.17ns	0.16ns	0.08ns	0.09ns
TZISTR1207/TZISTR110	-153.85ns	0.11ns	-5.19ns	-65.30ns	-0.09ns	2.10ns	-0.55*	0.47*	0.18**	0.13*
TZISTR1207/TZISTR1230	-172.96ns	0.03ns	2.94ns	-74.67ns	0.00ns	5.24ns	-0.47*	-0.14ns	0.02ns	0.05ns
TZISTR106/TZISTR110	-178.10ns	-0.32ns	-8.50**	-89.46ns	-0.04ns	-0.70ns	-0.41*	-0.44*	-0.05ns	-0.03ns
TZISTR106/TZISTR1028	-196.72ns	-0.39*	2.06ns	-109.02ns	0.41*	-6.38*	-0.07ns	-0.41ns	0.09ns	0.03ns
TZISTR1033/TZISTR1230	-225.31ns	-0.15ns	-0.28ns	-116.42ns	-0.30ns	-7.98*	0.04ns	-0.22ns	-0.04ns	-0.08ns
TZISTR106/TZISTR1227	-251.99ns	0.19ns	-1.40ns	-136.23ns	0.19ns	0.14ns	-0.19ns	0.37ns	0.09ns	0.06ns
TZISTR1207/TZISTR1028	-280.38ns	-0.18ns	3.86ns	-191.74ns	-0.22ns	1.01ns	-0.22ns	0.08ns	-0.06ns	-0.07ns
TZISTR106/TZISTR112	-306.11ns	-0.04ns	-10.89**	-238.33*	-0.40*	1.44ns	-0.05ns	0.03ns	0.05ns	-0.02ns
TZISTR1207/TZISTR1223	-334.95*	-0.27ns	4.11ns	-252.14*	-0.09ns	-5.73ns	0.25ns	-0.28ns	0.00ns	-0.01ns
TZISTR1207/TZISTR1222	-349.75*	-0.31ns	1.36ns	-308.47**	0.19ns	-10.03**	0.23ns	-0.26ns	-0.02ns	-0.03ns
TZISTR1033/TZISTR1237	-388.07*	-0.16ns	-10.16**	-375.60**	-0.13ns	-4.64ns	0.40*	0.56*	0.09ns	0.00ns
TZISTR106/TZISTR1235	-389.88*	0.27ns	-4.55ns	-416.75**	0.16ns	5.56ns	0.15ns	0.03ns	-0.04ns	0.01ns
TZISTR1033/TZISTR1226	-455.76*	0.08ns	-1.91ns	-425.01**	-0.24ns	-10.08**	-0.04ns	-0.31ns	0.08ns	0.01ns
TZISTR1207/TZISTR1227	-622.97*	-0.21ns	0.72ns	-472.80**	-0.36*	5.61ns	0.42*	-0.39ns	-0.08ns	-0.07ns
TZISTR106/TZISTR113	-728.59**	0.01ns	1.97ns	-483.07**	-0.01ns	-8.34*	-0.21ns	-0.19ns	-0.09ns	-0.03ns
TZISTR1033/TZISTR1214	-128.16ns	0.49*	3.48ns	-553.36**	0.18ns	2.75ns	0.01ns	-0.19ns	-0.04ns	-0.04ns
TZISTR1033/TZISTR1218	-153.85ns	0.11ns	-5.19ns	-719.16**	0.06ns	5.72ns	0.01ns	0.06ns	-0.01ns	0.00ns
SE±	127.3403	0.22316	3.43793	293.15	0.49	7.51	0.50	0.49	0.10	0.10

Table 3: Specific combining ability of crosses for yield and other traits under *Striga*-free and *Striga*-infested conditions. *Significant at P=0.05; **Significant at P=0.01; GY, grain yield; DYSK=days to 50% silking; DYTS=days to 50% anthesis; EPP=number of ears per plant; PLHT=plant height; ASI=anthesis-silking interval; EASP=ear aspect; EHT=ear height; HUSK=husk tip cover; PASP=plant aspect; STRA 8=*Striga* damage rating at 8 WAP; STRA 10=*Striga* damage rating at 10 WAP; STRC 8=*Striga* emergence count at 8 WAP; and STRC 10=*Striga* emergence count at 10 WAP; WAP=week after planting.

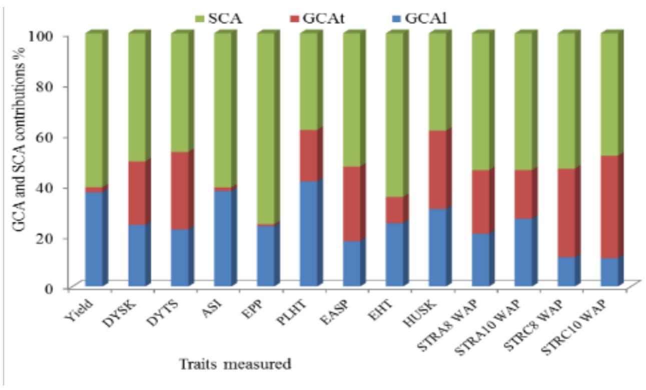

Figure 1c: GCA and SCA under Striga infestation.

had negative and four positive SCA effects. For EPP, seven crosses displayed significant SCA effects, five had negative and two positive SCA effects. Six crosses showed significant SCA for PLHT; four had negative and two positive SCA effects.

Twenty-four hybrids showed significant SCA for EASP; eleven had negative and thirteen showed positive SCA effects. The entire crosses showed significant SCA for EHT; twenty had negative and twenty-four showed positive SCA effects. Twelve hybrids showed significant SCA for PASP; half had negative and the other half had positive SCA effects (Table 3).

Under *Striga*-infested condition; nineteen crosses exhibited significant SCA effects for grain yield; ten had negative and nine displayed positive SCA effects. Cross *TZISTR1033/TZISTR1227* recorded the highest positive SCA effect for grains yield while the lowest was recorded by the cross *TZISTR1207/TZISTR1226*. Twelve crosses displayed significant negative SCA effects for both DYSK and DYTS, eight had negative and four positive SCA effects. Seven crosses showed significant SCA for ASI; five had negative and two positive SCA effects. For EPP, twelve crosses displayed significant SCA effects, seven had negative and five positive SCA effects. Twelve crosses showed significant SCA for PLHT; nine had negative and three positive SCA effects. Thirteen hybrids showed significant SCA for EASP; six had negative and seven showed positive SCA effects. Except *TZISTR1207/TZISTR1214* and *TZISTR106/TZISTR110*, all the other crosses showed significant SCA for EHT; eighteen had negative and twenty-five showed positive SCA effects. Twenty-five hybrids showed significant SCA for PASP; thirteen had negative and the twelve had positive SCA effects. Crosses *TZISTR1207/TZISTR113* and *TZISTR1033/TZISTR1237* showed significant positive SCA effects negative for *Striga* damage ratings at 8 and 10 WAP, while *TZISTR106/TZISTR110* showed significant negative SCA effects. Sixteen crosses showed negative SCA effect for *Striga* emergence counts at 8 and 10 WAP (Table 3).

Discussion

In the present study a desirable line and tester for resistance to *Striga* would show negative GCA effects for *Striga* damage ratings and *Striga* emergence counts and positive GCA effects for grain yield under *Striga*-infested conditions.

There were significant environmental effects for all the parameters measured. The significant environmental variation for all traits under both *Striga*-infested and *Striga*-free conditions indicates that each environment was unique and highly variable, emphasizing the need for testing in more than one environment over several years. Similarly, the significant genotype x environment interactions detected for grain yield and most other traits is an indication that the inbred lines should be tested in several environments to identify stable, *Striga* resistant inbred lines for hybrid production. Similar results were reported by Menkir et al., Badu-Apraku et al. and Ifie et al. [14,24-27].

GCA lines and GCA testers mean squares were significant for all traits except ears per plant. Both GCA for inbreed and SCA effects for hybrids were significant ($P<0.05$) for yield under *Striga*-infested and *Striga*-free conditions, indicating the importance of additive and non-additive effects for controlling grain yield. This finding corroborates with Menkir [13] who reported that *Striga* resistance is controlled by non- additive gene action. GCA tester was greater than GCA line for some traits except for grain yield and ASI, under both conditions. This indicates that the major contribution of additive variance for grain yield and ASI was due to the line. This finding disagrees with Duarte et al. [28] who suggested that the improvement of grain yield is under the higher frequency of favorable alleles for testers than lines.

Parental lines *TZISTR112*, *TZISTR1028*, *TZISTR1214*, *TZISTR1222*, *TZISTR1223*, *TZISTR1226* and *TZISTR1227* were the best general combiners for grain yield under *Striga*-free condition. These lines have favorable alleles for yield and can be used in maize breeding programs to develop high yielding hybrid maize for farmers. Lines *TZISTR113*, *TZISTR1028*, *TZISTR1214*, *TZISTR1218*, *TZISTR1223*, *TZISTR1226*, *TZISTR1227*, *TZISTR1237* and tester *TZISTR1033* had negative value of ASI under both *Striga*-infested and *Striga*-free conditions. The highly significant line x tester means squares for grain yield indicate that non-additive gene effects must be considered if maximum improvement of yield is to be achieved. These results are similar to those of Gethi and Smith, Yallou et al. and Badu-Apraku et al. [29-31] who showed that SCA effects is more important than GCA effects for host plant damage inheritance. The significant GCA line and GCA tester and SCA for grain yield and other traits under *Striga* infestation indicates that there were differences in the performance of the inbred lines as parents in hybrid combinations. The non-significant GCA tester x site and GCA line × site interactions for most traits under *Striga* infestation indicate that the performance of crosses between parental lines were stable across the *Striga* environments. This suggests that the selection of superior *Striga* resistant hybrid is better across different *Striga* environments. This finding disagrees with the finding of Makumbi et al. [32]. *Striga* emergence had low SCA effects for all the hybrids which indicate good resistance to *Striga* emergence under the infestation conditions. This agrees with Adeosun et al. [33] who reported that tolerant plants have little *Striga* emergence. While Kim [18] recommended *Striga* damage ratings for assessing crop genotypes for tolerance to *Striga* infestation. Furthermore, Rodenburg and Bastiaans, Badu-Apraku and Lum [34,35] concluded that resistant maize cultivars should be able to support few emerged parasites and sustain low STRA reduced emergence, resulting from effective host-plant resistance, which is a good strategy for long-term control of *Striga* in Africa.

Expression of genetic variability for traits associated with resistance to *Striga hermonthica* in maize, including grain yield under *Striga* infestation, host plant damage symptom rating and number of emerged *Striga* plants, is largely dependent on the presence of severe infection with the parasite. In this study, there were significant GCA lines and SCA mean squares for all traits except ears per plant, *Striga* damage rating and *Striga* emergence count. This indicates the presence of genotypic variability among inbred lines used as female parents. This finding is in disaccord with finding of Gethi and Smith [29] who reported significant GCA mean squares for *Striga* emergence counts and non-significant GCA mean squares for *Striga* damage rating. The proportion of the SCA mean squares over GCA for grain yield and most other traits under *Striga* infestation indicates that non-additive as well as additive effects are important and that non-additive genetic effects were more important than additive effects. This is consistent with the findings of Badu-Apraku et al. and Choukan [36,37] that GCA and SCA are mostly used to identify inbred line with good characters. Lines, *TZISTR1214*, *TZISTR1226* and *TZISTR1237* exhibited desirable negative GCA effects for *Striga* damage rating. However, lines *TZISTR110*, *TZISTR113*, *TZISTR1218*, *TZISTR1227* and tester, *TZISTR106* exhibited desirable negative GCA effects for *Striga* damage rating and *Striga* emergence count making them good combiners for maize *Striga* resistance traits and can be used to improve maize for *Striga* resistance. Lines *TZISTR1214*, *TZISTR1223*, tester *TZISTR106* and *TZISTR1207* had significant positive GCA effect for grain yield and negative effect for *Striga* damage rating and *Striga* emergence count. These lines and testers are good combiners for grain yield and maize *Striga* resistance traits. Testers TZISTR106 and *TZISTR1207* resistant and tolerant to *Striga* respectively, had significant negative GCA effect for *Striga* emergence count while the susceptible Tester *TZISTR1033* had significant positive GCA effect for STRC. This is in disagreement with Rodenburg and Bastiaans [34] who suggested that *Striga* emergence count would not be a sufficient criterion to point out genetic control of *Striga* tolerance of maize.

Lines *TZISTR113*, *TZISTR1218* and *TZISTR1227* had significant negative effect for grain yield and negative effect for *Striga* counts, they can be utilized as source of *Striga* resistance in maize breeding. Significant negative GCA for ASI indicates that the silk and pollen shed are done together ensuring good synchronization. Line *TZISTR112*, testers *TZISTR106* and *TZISTR1207* had significant positive effect for grain yield and negative effect for ASI, these line and testers had pollen grain and silking appearing at the same time which ensures good synchronization under *Striga* infestation despite the fact that the parasitic weed can delay flowering period. They are therefore suitable for hybrid seed production. Testers *TZISTR106* and *TZISTR1207* had positive GCA effect for grain yield this finding is in agreement with finding of Karaya et al. [38]. Lines *TZISTR1222*, *TZISTR1223*, testers *TZISTR106* and *TZISTR1207* had positive GCA for grain yield and negative effects for plant height indicating that they can resist to plant height reduction due to *Striga* effect on plant.

Reduced emergence, resulting from effective host-plant resistance, is a good strategy for long-term control of *Striga* in Africa. Host plant damage rating refers to the general appearance of a host plant caused by *Striga* [18]. The specific combining ability results indicated that hybrids *TZISTR1033/TZISTR1235*, *TZISTR1207/TZISTR1226*, *TZISTR1033/TZISTR110*, *TZISTR1207/TZISTR112*, *TZISTR1207/TZISTR1237* and *TZISTR106/TZISTR1211* are good specific combiners for grain yield and maize *Striga* related traits. TZISTR106/TZISTR110 showed significant negative SCA effects for *Striga* damage rating. In this study, hybrids resistant to *Striga hermonthica* were developed from resistant tester (*TZISTR106*) × resistant lines, tolerant tester (*TZISTR1207*) × resistant line and susceptible tester (*TZISTR1033*) × resistant line. *TZISTR1033/TZISTR1227*, *TZISTR106/TZISTR1218*, *TZISTR1207/TZISTR1214*, *TZISTR1033/TZISTR1235*, *TZISTR1033/TZISTR1223* and *TZISTR1033/TZISTR1028* had significant positive SCA effect for grain yield under *Striga*-free and *Striga*-infested conditions.

Both GCA for inbred and SCA effects for hybrids were significant ($P<0.05$) for grain yield under *Striga*-free conditions, indicating the importance of additive and non-additive effects for controlling grain yield. This finding agrees with Derera et al. [39] on maize hybrids yield under drought conditions.

In this study, testers were used to evaluate the combining abilities of lines; therefore, negative GCA estimates for these testers would be more interesting because the better expression of the favorable alleles from different lines depends on the frequency of unfavorable alleles from the testers as reported by Barata and Carena [40]. While crosses including *TZISTR1033/TZISTR1214*, *TZISTR1207/TZISTR1222*, *TZISTR1207/TZISTR1235*, *TZISTR106/TZISTR1208*, *TZISTR106/TZISTR1223* and *TZISTR106/TZISTR1230* were the best specific combiners for grain yield. Among them, *TZISTR1207/TZISTR1222*, *TZISTR1207/TZISTR1235* and *TZISTR106/TZISTR1230* were the best specific combiners for resistance to stalk lodging. *TZISTR106/TZISTR1230* was the best specific combiners for earliness.

Conclusion

For the 18 inbred lines studied, SCA was greater than GCA line and GCA tester. Non-additive gene action plays a predominant role in the inheritance of grain yield and most traits under *Striga* infestation. GCA line effects were more important for grain yield, anthesis-silking interval and plant and ear height than GCA tester effects under *Striga* infestation. Inbred parents *TZISTR112*, *TZISTR1214*, *TZISTR1222*, *TZISTR1223*, tester *TZISTR106* and *TZISTR1207* were the best general combiners for grain yield under both *Striga*-infested and *Striga*-free conditions. These lines could be used for heterosis breeding in maize. Lines *TZISTR113*, *TZISTR1214*, *TZISTR1226* and *TZISTR1237* were identified as best combiners for *Striga* damage ratings at 8 and 10 WAP. Inbred line *TZISTR1218* and *TZISTR1227* were the best general combiner for *Striga* emergence count at 8 and 10 WAP. These lines could be exploited in maize breeding programs as they have beneficial alleles for resistance to *Striga*. Hybrids with yield higher than the check were identified.

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