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RESEARCH PAPER

Genetic resistance of maize inbred lines to *Striga hermonthica*

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Abstract

Maize is one of the most important food security crops in Uganda. It is annually cultivated in an area of 1,063,000 hectares representing 57% of the total area allocated to crop production in the country. However, maize yields are very low due to several biotic and abiotic stresses, institutional and socio-economic constraints. Among the biotic factors, *Striga hermonthica* inflicts significant yield losses reaching up to 100% in highly infested fields. In the present study, the gene action for resistance to *Striga* among selected maize inbred lines was assessed. Ten inbred lines of varying resistance to *Striga hermonthica* were crossed in a 10×10 half diallel to generate 45 single crosses. These were evaluated in three *Striga* endemic locations of Eastern and Western Uganda during 2017A growing season. General combining ability (GCA) effects for AUSNPC were generally low with negative GCA effects of -646.99, -428.21, -338.00 and -76.51 for parents TZISTR1199, TZISTR1192, TZISTR1174 and TZISTR1162. Specific combining ability (SCA) effects were also generally low for area under Striga number progressive curve (AUSNPC) showing good resistance to the parasitic weed.

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Introduction

Maize (*Zea mays* L.*)* is the most widely cultivated cereal crop globally with different germplasm adapted to various environmental conditions including temperate, tropical and sub-tropical zones (Koutsika-Sotiriou, 1999; FAO, 2009). The estimated area under maize production worldwide is 170,398,070 hectares, with an average yield of 5.184 t ha^{-1}(FAO, 2006).

In Uganda, maize is the third most important staple food crop providing up to 11% of the country's caloric requirements, compared to 13% and 18% provided by cassava and bananas, respectively (FAO, 2009). Maize is widely consumed throughout Uganda and is a major ingredient in livestock and poultry feeds. The maize Stover is on the other hand used as fuel in form of firewood and as mulch in banana and coffee plantations (Bigirwa *et al.*, 2001). In spite of its great importance in Uganda, maize productivity is still low with yields as low as 2.399 t ha^{-1} that are far below its yield potential of 9.59 t ha^{-1} in USA (FAOSTAT, 2010) and up to 7.00 t ha^{-1} in Uganda (FAO, 2009). Various production constraints are being blamed for the wide gap between on-station and on-farm yields and these include low grain yield, poor resistance to pests and diseases, poor adaptation to various agro ecologies and yield loss resulting from the devastating effects of weeds, particularly *Striga*, a parasitic weed (Kim, 1994).

Striga hermonthica (Del) Benth infestation constitutes a serious threat to maize productionin Africa and is one of the major contributors to hunger, malnutrition and food insecurity across sub-Saharan Africa (Ejeta and Butler, 1993). Amudavi *et al.*, (2007) and Hearne *et al.*, (2009) reported a loss of 30-50% to Africa's agricultural economy on 40% of its arable land due to *Striga* infestation. Several control methods have been adopted including the application of nitrogenous fertilizers to increase soil fertility (Watson and Ciotola, 1999), intercropping maize with catch and trap crops to induce suicidal *Striga* germination (Kureh *et al.*, 2000), use of herbicide resistant maize caltivars (Kanampiu *et al*, 1998), crop rotation and timely weeding (Ejeta and Gressel, 2007) although none of these measures is completely effective (Ejeta and Gressel, 2007). Host resistance has particularly been reported to be an effective and affordable component of integrated *Striga* control strategy since resistant cultivars reduces both the production of new *Striga* seed and the *Striga* seed bank in the soil (Yoder and Scholes, 2010). Identifying source germplasm with different resistance mechanisms can facilitate combining several resistance genes to obtain more durable and stable polygenic resistance to *Striga*in maize (Ejeta *et al.*, 2000; Menkir, 2006). There is also need to study gene action responsible for resistance to *Striga* in maize single cross hybrids in order to design the most appropriate selection techniques for improvement of resistance to *Striga*. Therefore, the objective of the study reported in this paper was to determine the gene action responsible for resistance to *Striga* in Uganda.

Materials and methods

Plant materials

Fifty six inbred lines were evaluated in farmers' abandoned naturally *Striga* infested fields in Nakyere, Namutumba district of Eastern Uganda during 2016B growing season using a 7×8 alpha lattice design with two replications. Ten inbred lines (Table 1) of varying resistance to *Striga hermonthica* were selected from the preceding study of 2016B and all possible crosses were made among the inbred lines using 10 × 10 half diallel to generate 45 single-crosses during 2017A growing season.

Evaluation of single crosses

Seed of the successful crosses were harvested and single crosses were evaluated in a 9×5 alpha lattice replicated two times in three farmers' abandoned naturally *Striga* infested fields at Nakyeere in Namutumba district; Ngerekyomu in Tororo district (Eastern Uganda) and Kinyamaseka in Kasese district (western Uganda) during 2017B growing season.

The hybrids were planted in two row plots measuring 5m in length. Planting was done at a spacing of 75cm by 25cm at the rate of two seeds per hole. 8 g of

Diammonium Phosphate (DAP) were banded below the maize seed. The maize seedlings were thinned to one per stand at 14days after crop establishment. Low fertilizer dosage (50kg/ha NPK 20-10-10) was applied by broadcast to minimize the likelihood of nitrogen (N) suppressing *Striga* emergence (Olakoja and Olaoya, 2005). Hand weeding was done to remove all other weeds other than *Striga*. Cypermethrine was applied to control fall army worm and stem borer infestation.

Data collection

Striga related traits assessed included *Striga* count/m^2 at 8,10, and 12 weeks after crop emergence, *Striga* vigour (using a scale of 0-9), where 0= no emerged *Striga*plants and 9= very vigorous *Striga* plants (average height >40cm with >10 branches) (Kroschel, 2001), plant damage scores (using a scale of 0-9), where 1=Normal plant growth, no visible symptoms and 9 = Complete leaf scorching of all leaves, causing premature death or collapse of host plant and no ear formation (Kim, 1994), area under *Striga* number progress curve (AUSNPC) and area under *Striga* severity progress curve (AUSVPC) (Rodenburg *et al.,* 2005). The AUSNPC was calculated as follows;

$$AUSNPC = \sum_{i=0}^{n-1} \left(\frac{Y_i + Y_{(i+1)}}{2} \right) \left(t_{(i+1)} - t_i \right)$$

wheren is the number of *Striga* assessment dates, Yi the *Striga* number at the ith assessment date, tithe days after planting at the ith assessment date, t is 0, and Yis 0.The AUSVPC was estimated similarly, with Yi representing the *Striga* severity score. *Striga* severity score is a product of the *Striga* vigour and the number of *Striga* plants at each assessment date.

Data analysis

The analysis of variance (ANOVA) for all traits under study was carried out using Genstat release 14.1 statistical package (Payne *et al.,* 2011). The 10×10 half-diallel analysis was executed to estimate general combining ability (GCA) and specific combining ability (SCA) effects using Griffing's diallel analyses, Model 1 (fixed genotype effects), Method IV (Crosses only) (Griffing, 1956), according to model; $Y_{ijk}=\mu + g_i + g_j + s_{ij} + e_{ijk}$.,where; Y_{ijk}: Observed measurement for the ij$_{th}$ cross in the k$_{th}$ replication/environment combination, μ: Overall mean, g_i and g_j: GCA effects for the i$_{th}$ and j$_{th}$ parents respectively, s_{ij}: SCA effects for the i$_{th}$ and j$_{th}$ parents, e_{ijk}: Error term associated with the ijth cross evaluated in the kth replication/environment combination. The interaction terms were used to test for the significance of the corresponding main effect (Zhang and Kang, 1997).

The environments and replications within environments were considered random and therefore tested against the residual error term. Mean squares of parents were estimated from the GCA effects while that of single-crosses were obtained from the SCA effects of the diallel analysis. These were further used to estimate GCA: SCA ratios (Beil and Atkins, 1967; Haussmann *et al.*, 1999).

Results and discussion

Analysis of variance

Table 2 presents the combined analysis of variance for the general and specific combining abilities for the parental inbred lines and the single hybrids respectively.

The observed significant mean squares of location and genotypes for *Striga* traits indicated that the three environments were distinct and that there were genetic variations among the single-cross hybrids, suggesting that selection of such traits for further improvement was feasible. Similar findings were reported by Badu-Apraku *et al.,* (2011).

The significant G×E interaction for *Striga* traits suggested differences in expression of traits of the set of hybrid genotypes across the locations. The expression of almost all traits was influenced by the environmental differences further suggesting the need to develop specific varieties for specific environments to take into account the high influence of the environment on the expression of traits. Similar results were reported by Olakojo *et al.,* (2005) when they assessed the performance of newly developed *Striga lutea* (Lour) tolerant maize genotypes including seven *Striga* tolerant open pollinated maize varieties. The significant mean square estimates of GCA observed indicated the important role of additive genes in the inheritance of such traits. The traits with significant mean squares for SCA indicated that the non-additive gene effect contributed significantly to the inheritance of such traits and thus, selection of such traits for further improvement could be achieved through recurrent selection, and backcrossing methods.

Table 1. List of parental inbred lines used.

Name	Source	Response to Striga	Estimated yield (t ha^{-1})
CML442	CIMMYT	Susceptible	0.5
CML312	CIMMYT	Susceptible	0.2
1368STR	IITA	Resistant	0.9
TZISTR1181	IITA	Resistant	1
TZISTR1162	IITA	Resistant	0.8
TZISTR1192	IITA	Resistant	1.1
TZISTR1174	IITA	Resistant	1.2
TZISTR1198	IITA	Resistant	0.9
TZISTR1199	IITA	Resistant	1.2
TZISTR1132	IITA	Resistant	0.9

Source: Experiment in 2016B growing season.

The observed significant mean square of GCA×E interaction indicated variations in the combining abilities of the inbred lines and emphasized the need for testing the inbred lines under different environments with the view to assess performance and stability. Similar observations were made by Menkir *et al.*, (2003) and Badu-Apraku *et al.*, (2007a) in a similar study. The lack of significant mean square estimates of SCA×E interaction for some traits suggested that expressions of such traits among the single cross hybrids were consistent across environments and therefore, good selection progress for improvement of such traits was feasible under any environment.

General combining ability effects for Striga traits

General combining ability (GCA) effects of the parental inbred lines for *Striga* traits are presented in Table 3.

Table 2. Analysis of Variance for Striga traits across locations.

Source of variation	D.f	Striga count				Striga severity		Striga vigor		
		SC/m^2 (8wap)	SC/m^2 (10wap)	SC/m^2 (12wap)	AUSNPC (m^2)	SS (10wap)	SS (12wap)	SV (10wap)	SV (12wap)	AUSVPC (m^2)
Location(E)	2	1632.5**	13583.6***	42447.7*	38387312***	1936594***	1487328***	51.9***	5.1***	5.82E+09***
REP	3	2686.9***	21980.3***	30989.0**	61056577**	2623417***	1382949***	59.3**	39.5***	6.93E+09***
Cross(G)	44	477.0	1751.8	1398.1***	4097567*	132474.5	63512.5	14.4***	7.6	3.32E+08
GCA	9	895.5	3476.6*	2628.4*	8367264*	215567.5*	105393.3	26.1*	12.3	5.55E+08*
SCA	35	401.4	1419.5	1081.7***	3179240	111107.8	52743.1	11.8***	6.8	2.74E+08
GXE	88	354.0	1781.2*	1126.6*	3641193	108866.5	51789.8	2.6	2.0*	2.68E+08
E×GCA	18	504.4	2340.2	1774.2*	5120955	127590.7	73484.8*	2.8	1.8*	3.43E+08
E×SCA	70	348.1	1774.8	960.1	3487003	104051.7	46211.1	2.6	2.1	2.48E+08
Residual	108	309.0	1631.1	814.4	3168332	96655.1	42824.6	3.6	2.5	2.29E+08
GCA: SCA (%)		79.2	61.4	58.4	79.6	92.4	78.9	35.6	85.1	90.4

SC: *Striga* count, SV: *Striga* vigor, SS: *Striga* severity, AUSNPC: Area under *Striga* progressive curve, AUSVPC: Area under *Striga* severity progressive curve, E: Environment, wap: weeks after planting.

In breeding for resistance to *Striga*, the lower the value of *Striga* related trait, the better was the resistance of the genotypes with respect to the trait. GCA effects for *Striga* shoot count, *Striga* severity, *Striga* vigor, area under *Striga* number progressive curve and area under *Striga* severity progressive curve, were low in this study, which indicated high resistance of the parents to *Striga hermonthica* emergence.

Table 3. GCA effects for Striga traits across locations.

Parents	Striga count				Striga severity		Striga vigor		
	SC/m^2 (8wap)	SC/m^2 (10wap)	SC/m^2 (12wap)	AUSNPC (m^2)	SS (10wap)	SS (12wap)	SV (10wap)	SV (12wap)	AUSVPC (m^2)
TZISTR1199	-7.02***	-11.36**	-13.04***	-646.99**	-90.03**	-80.42**	-0.84***	-0.56***	-5113.73**
TZISTR1192	-3.41*	-8.77*	-7.87*	-428.21*	-79.45*	-49.53*	-0.59**	-0.32*	-3869.44*
TZISTR1132	0.15	3.34	3.20	155.87	21.82	22.75	-0.09	-0.04	1336.933
TZISTR1174	-4.10*	-7.17*	-4.79*	-338.00*	-68.89*	-39.95*	-1.03***	-0.71***	-3265.15*
1368STR	2.16	13.74**	9.31**	580.57**	95.94**	55.81*	0.34*	0.24	4552.6**
TZISTR1162	-1.70	-0.34	-2.51	-76.51	-25.07	-22.19	-0.54**	-0.47**	-1417.9
TZISTR1181	5.48**	7.16*	7.60*	408.66*	64.88*	44.76*	0.87***	0.61***	3289.392*
TZISTR1198	6.56**	6.57	8.03**	420.57*	73.85*	52.56*	1.12***	0.43*	3792.558*
CML312	2.92	5.30	2.51	225.34	28.52	18.64	0.23	0.08	1415.058
CML442	-1.03	-8.48	-2.44	301.30*	-21.58	-2.43	0.52*	0.73***	-720.317

SC: *Striga* count, SV: *Striga*vigor, SS: *Striga* severity, AUSNPC: Area under *Striga* progressive curve, AUSVPC: Area under *Striga* severity progressive curve, E: Environment, wap: weeks after planting.

This reduced the rate of *Striga* multiplication as their seed production was gradually reduced. Parents TZISTR1181, TZISTR1198, CML312, 1368STR and TZISTR1132 had very high GCA effects for area under *Striga* number progressive curve indicating susceptibility, while TZISTR1199, TZISTR1192, TZISTR1174 and TZISTR1162 had low GCA effects indicating good resistance to *Striga hermonthica.* Similarly, GCA effect for area under *Striga* severity progressive curve and *Striga* vigor were generally low.

The least values were recorded in TZISTR1199, TZISTR1192, TZISTR1174 and TZISTR1162 indicating good resistance to *Striga hermonthica*, hence higher resistance level in the parents. Kim (1994) reported low GCA effects for *Striga hermonthica* emergence and host-plant response for most resistant maize inbred lines and high GCA effects for the susceptible. Omanya *et al.*, (2004) and Hausmann *et al.*, (2000b) reported strong genetic control for AUSNPC and AUSVPC in the field. They observed that the two parameters were useful measures of progressive *Striga* development in the field. However, Hausmann *et al.*, (2000a) additionally found that individual *Striga* emergence count was also under genetic control from experiments conducted in pots.

The findings of the present study add to the observations of Omanya *et al.*, (2004) and Hausmann *et al.*, (2000b) suggesting that *Striga* vigour was under strong genetic control. Significant genotypic differences were observed in AUSNPC, AUSVPC and *Striga* vigour in the single crosses with their average contributions being 79.6%, 90.4% and 60.4%, respectively, suggesting that additive gene action was more important than the non-additive gene action in controlling resistance to*Striga*in the present maize populations.

Specific combining ability effectsfor Striga traits

The results of specific combining ability of single cross hybrids for *Striga* related traits are presented in Table 4.

Table 4. SCA effects for Striga traits across locations.

Single crosses	Striga count				Striga severity		Striga vigor		
	SC/m^2 (8wap)	SC/m^2 (10wap)	SC/m^2 (12wap)	AUSNPC (m^2)	SS (10wap)	SS (12wap)	SV (10wap)	SV (12wap)	AUSVPC (m^2)
TZISTR1199 x TZISTR1192	2.28	2.08	7.39	170.91	40.30	38.70	0.76	-0.63	2371.26
TZISTR1199 x TZISTR1132	0.96	-6.21	-8.06	-295.06	-74.40	-43.60	0.35	0.59	-3539.78
TZISTR1199 x TZISTR1174	-2.36	17.93	6.35	666.33	100.80	29.40	1.31*	0.27	3906.64
TZISTR1199 x 1368STR	7.58	23.18	10.94	961.67	255.02*	84.70	0.66	0.69	10191.22*
TZISTR1199 x TZISTR1162	6.16	-7.42	-5.91	-236.10	-70.20	-22.20	-1.20*	-0.70	-2772.61
TZISTR1199 x TZISTR1181	-7.45	-26.61*	-12.58	-1058.28	-165.30	-81.90	-2.26**	-1.53**	-7414.90
TZISTR1199 x TZISTR1198	-1.20	2.45	3.35	104.66	-48.60	-19.40	-0.72	-0.08	-2039.74
TZISTR1199 x CML312	-2.10	-10.72	-1.26	-391.69	-38.00	14.40	1.26	0.99*	-710.24
TZISTR1199 x CML442	-3.86	5.32	-0.22	77.56	0.40	-0.10	-0.15	0.41	8.14
TZISTR1192 x TZISTR1132	9.86	5.95	-12.34	170.77	-51.30	-70.80	-0.91	-0.85	-3664.07
TZISTR1192 x TZISTR1174	-7.34	-7.04	-5.58	-4100.00	-35.80	-15.80	-0.61	0.51	-1547.65
TZISTR1192 x 1368STR	-8.79	-23.72	-13.13	-1053.57	-175.30	-99.80	-1.09	-0.84	-8252.40
TZISTR1192 x TZISTR1162	-1.53	-7.28	4.40	-171.39	-38.60	-11.20	-0.53	-0.47	-1494.57
TZISTR1192 x TZISTR1181	-3.44	-4.43	-10.64	-375.22	-104.90	-63.70	-0.65	-0.46	-5058.86
TZISTR1192 x TZISTR1198	12.00*	14.82	2.31	648.83	18.90	5.20	-0.66	0.33	720.97
TZISTR1192 x CML312	-8.65	5.80	12.03	233.93	148.80	100.90	0.25	-0.14	7489.47
TZISTR1192 x CML442	5.61	13.82	15.56	785.74	197.90*	116.60	3.44**	2.55***	9435.85*
TZISTR1132 x TZISTR1174	-2.77	-18.19	-16.09	-842.02	-102.90	-94.00	-0.22	-0.33	-5907.36
TZISTR1132 x 1368STR	-5.09	3.80	14.11	215.41	58.50	113.70	0.20	0.31	5166.56
TZISTR1132 x TZISTR1162	2.66	18.18	3.89	684.60	124.90	45.50	-0.04	-0.43	5112.06
TZISTR1132 x TZISTR1181	-1.90	9.63	7.61	341.71	13.80	24.70	0.01	-0.57	1157.76
TZISTR1132 x TZISTR1198	12.78*	14.83	25.80*	1012.09	274.50	179.80*	3.00.***	2.05***	13627.26*
TZISTR1132 x CML312	-10.71*	-18.08	-15.8	-968.50	-214.70*	-139.60*	-2.33**	-0.54***	-10629.24*
TZISTR1132 x CML442	-5.79	-9.90	0.87	-319.00	-28.30	-15.80	-0.06	-0.23	-1323.19
TZISTR1174 x 1368STR	12.33*	16.86	18.87*	1000.14	129.30	139.10*	0.12	0.33	8051.31
TZISTR1174 x TZISTR1162	-0.47	-9.01	-7.37	-414.02	-75.10	-48.70	-0.59	-0.29	-3713.86
TZISTR1174 x TZISTR1181	-5.09	0.36	5.80	3.53510	2.40	11.30	1.08	0.88	413.18
TZISTR1174 x TZISTR1198	-5.86	-14.35	-18.18*	-808.25	-155.50	-113.10	-1.84**	-1.40*	-8057.65
TZISTR1174 x CML312	10.32	20.55	25.47*	1179.60*	203.20*	147.50*	1.84**	0.79	10521.85*
TZISTR1174 x CML442	1.24	-7.12	-9.27	-375.31	-66.50	-55.70	-1.08	-0.75	-3666.44
1368STR x TZISTR1162	-3.18	-6.78	-4.12	-318.94	-31.40	-24.50	0.86	0.82	-1675.61
1368STR x TZISTR1181	-3.75	-8.17	-17.21*	-507.23	-91.50	-155.70*	-1.21*	-1.64**	-7414.24
1368STR x TZISTR1198	0.93	11.29	-3.01	352.70	-54.90	-42.90	-1.13	-1.13*	-2933.40
1368STR x CML312	3.35	-5.95	4.42	-83.26	34.80	68.30	1.41*	1.69**	3094.43
1368STR x CML442	-3.36	-10.50	-10.89	-566.94	-124.60	-83.00	0.18	-0.23	-6227.86
TZISTR1162 x TZISTR1181	-0.34	12.76	21.24*	669.54	162.80	168.90*	1.46*	1.21*	9952.26*
TZISTR1162 x TZISTR1198	-18.15**	-29.41*	-19.13*	-1453.19*	-172.70	-90.90	-0.16	0.49	-7909.57
TZISTR1162 x CML312	11.69*	30.55*	7.58	1228.73*	116.30	7.50	0.15	-0.03	3713.60
TZISTR1162 x CML442	3.16	-1.58	-0.59	10.76	-15.90	-24.50	0.06	-0.60	-1211.69
TZISTR1181 x TZISTR1198	16.27*	6.72	13.39	653.90	206.6*	110.30	2.60***	1.10*	9507.47*
TZISTR1181 x CML312	2.30	0.81	-10.35	-40.24	-39.70	-52.50	-0.52	-0.06	-2767.03
TZISTR1181 x CML442	3.40	8.93	2.75	312.27	15.70	38.40	-0.49	1.07*	1624.35
TZISTR1198 x CML312	-11.28*	-15.17	-14.22	-872.11	-150.0	-99.80	-0.62	-0.93	-7494.53
TZISTR1198 x CML442	-5.48	8.82	9.68	361.36	81.90	70.80	-0.47	-0.44	4579.18
CML312 x CML442	5.09	-7.79	-7.89	-286.45	-60.60	-46.70	-1.42*	1.77**	-3218.32

Continued.

Significant SCA effects recorded for some *Striga* related characters indicated differential response of the crosses to these *Striga* traits. Non-additive gene action played significant role in the inheritance of resistance to *Striga* in most of the crosses.

Inbred lines TZISTR1199, TZISTR1192, TZISTR1174 and TZISTR1162 were identified as good combiners whose crosses had the lowest SCA making them useful in resistance to *Striga* breeding of maize. Kim (1991) reported that the highest level of resistance to *Striga hermonthica* was obtained from crosses involving two resistant parents.

The results also suggested that the genes for resistance might be recessive since *Striga hermonthica* resistance appeared more common in resistant x resistant crosses compared with resistant x susceptible crosses. Kim (1994) reported a negative SCA effect of -1.0 for *Striga* tolerant rating while studying the genetics of *S. hernonthica* tolerance in maize.

Conclusion

The mode of inheritance of resistance to *Striga hemonthica* in maize is mainly additive indicating that resistance could be effectively improved through selection. Parental lines TZISTR1199, TZISTR1192, TZISTR1174 and TZISTR1162 displayed negative GCA effects for resistance to *Striga* hence could be used as sources of resistance genes to *Striga*.

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