Combining Ability in Maize Lines for Agronomic Traits and Resistance to Weevil (*Sithophilus zeamais* Motschulky)

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Abstract

In Ethiopia, heavy losses to stored maize are inflicted by various insect pests including Sitophilus weevils and Sitotroga cereallela. This study was conducted to determine the combining ability of five introduced inbred lines in agronomic traits and maize weevil resistance by crossing them with three testers using line × tester mating system. These crosses were then evaluated in tri-plicated randomized complete blocks at Bako Agricultural Research Center in 2003. Samples (50 g) of the F_2 full-sib grain of the genotypes were further tested for weevil resistance under a no-choice laboratory environment. Mean squares due to general (GCA) and specific (SCA) combining ability were significant for most of the agronomic traits. However, GCA mean squares predominated in all weevil resistance traits. The lines varied in their GCA effects for the various agronomic traits considered. However, all of them were found to be poor general combiners for grain yield, although certain crosses gave acceptable yield. The lines SZSYNA99-F_2-133-2-3, SZSYNA99-F_2-33-4-1, SZSYNA99-F_2-33-4-2 and SZSYNB99-F_2-98-4-3 exhibited desirable GCA effects for most of the resistance traits. Overall, this study suggested the existence of heritable weevil resistance quantitative traits that can be used in weevil resistance breeding programs.

Key words: insect resistance, maize, maize weevil, *Sitophilus zeamais,* storage pests

Introduction

Many insect pests are known to cause heavy losses to stored maize in Ethiopia. Of these, *Sitophilus* weevils and *Sitotroga cereallela* are predominant. Surveys of damage caused by storage pests to stored maize in Ethiopia revealed average grain damage of 29.3% and mean grain weight loss of 5.6% during the survey season of 2002 (Tadesse and Basedow, 2004). Farmers have been using insecticides to reduce storage losses since long ago. The high cost of pesticides, the risk of pest resistance build-up and the potential hazard of pesticides in the hand of unskilled users make alternative control measures highly important. Considering these issues and the need for an integrated pest management system, the incorporation of resistant varieties into the system for the protection of stored maize would, thus, be an important long-term goal. Once such resistant varieties are availed, insect pest control requires no extra skill and labor, and would, therefore, be economical.

In spite of all these advantages, resistance to post-harvest pests, however, has not so far been incorporated into the breeding programs. Consequently, high-yielding cultivars became susceptible to attack by storage pests even more so than the local varieties they are intended to replace

(Arnason *et al*., 1994). Therefore, it is imperative to identify sources of resistance and develop resistant varieties that represent one of the simplest, economical and most convenient methods of storage pest control. This process of breeding for resistance, in turn, requires information about the source germplasm.

To that effect, knowledge on the combining ability of maize germplasm is of great value to maize breeders. GCA and SCA effects are important indicators of the potential value of inbred lines in hybrid combinations and subsequent hybrid development (Sprague and Tatum, 1942; Hallauer and Miranda, 1988). Using the concept of combining ability, genetic variance is partitioned into componentsdue to GCA and due to SCA (Hallauer and Miranda, 1988). Besides, combining ability studies allow classification of selected parental materials with respect to breeding behavior (Hallauer and Miranda, 1988; Sleper and Poehlman, 2006). This study was, therefore, conducted to assess the general and specific combining abilities of five introduced inbred lines in agronomic traits and maize weevil resistance using crosses of line × tester mating scheme.

Materials and Methods

The experiment was conducted in two phases at the Bako Agricultural Research Center. The first phase of the experiment was a fieldwork, where maize genotypes were evaluated for yield performance and other agronomic traits. In the second phase, the genotypes evaluated under field conditions were further tested in the laboratory for their resistance to maize weevil.

Plant materials

The maize hybrids used in this study were derived from six introduced lines (CIMMYT-Zimbabwe) and two parental materials, an inbred line and a population of local sources. Five of the six introduced materials were S_3 lines, chosen on the basis of above average weevil resistance in evaluations conducted by CIMMYT, Zimbabwe. A base-line test of weevil resistance of the eight parental genotypes was done at Bako Agricultural Research Center (Table 1). In addition, since these lines were at their early generations, it was required to evaluate them through test crosses for their adaptability and performance both for agronomic and weevil resistance traits using locally adapted lines and genetically broad-based testers. Hence, crosses were made according to a line × tester mating scheme whereby Gutto $LMS_{5,}$ SC_{22} and CML 197 were utilized as testers in the 2002/2003 off-season at Bako. Reciprocal crosses were also made along with the direct crosses.

Field experiment

The F_1 single crosses including reciprocals and two commercial hybrids were grown on four-row plots arranged in randomized complete block design with three replications at Bako during the 2003 main season. The two middle rows were used to collect agronomic data and eventually harvested for yield evaluation, and the border rows were reserved for full-sib pollination within each plot to obtain F_2 seed for each hybrid.

The plot size was 15.3 m^2 (row length of 5.1 m spaced 0.75 m apart). Two seeds were planted per hill and later thinned out to one plant with 30 cm spacing between hills. Nitrogen fertilizer at the rate of 92 kg N ha^{-1} was used in split application, while 69 kg P_2O_5 ha^{-1} was applied at planting. All other management practices were performed as per the research recommendations for the location.

Table 1. Parental lines used for the experiment

Code	Pedigree	Origin	Source	Weevil resistance*	Grain texture
T1	Tuxpeno C_{18} (Gutto LMS_5)♠	Tuxpeno-1	CIMMYT	Susceptible	Semi-flint
T2	SC_{5522} (SC_{22})	Kitale	E. Africa	Highly susceptible	Dent
T3	MSR 270-253-5-1-B-B (CML 197)	-----	CIMMYT	Susceptible	Flint
L1	SZSYNA99-F_2 -79-4-3	HA01A-183-207-3	CIMMYT	Resistant	Flint
L2	SZSYNA99-F_2 133-2-3	HA01A-183-308-3	CIMMYT	Resistant	Flint
L3	SZSYNA99- F_2 -33-4-1	HA01A-183-84-1	CIMMYT	Resistant	Flint
L4	SZSYNA99- F_2 -33-4-2	HA01A-183-84-2	CIMMYT	Resistant	Flint
L5	SZSYNB99-F_2 -98-4-3	HA01A-184-245-3	CIMMYT	Resistant	Dent

* *Based on arbitrary scale of susceptibility indices 0-5 as resistant, 6-10 as susceptible and above 11 as highly susceptible.* ♠ *= Population.*

Laboratory evaluation of weevil resistance

The kernel samples were first kept in a deep freezer at -20 °C for 14 days to avoid any field infestation by weevil or any other pests. Kernel samples of 50 g each from the F_2 seeds of the 40 genotypes (30 single crosses, two commercial hybrids and eight parents) were put in a 250 cm^3 glass jar with brass screen lids which permitted adequate ventilation, and were placed in the laboratory which was maintained at 25±5 °C and 70±5% relative humidity for a three week acclimatization period. This helped maintaining uniform grain temperature and moisture content among all samples. The samples having moisture content of 12-13% were then infested in a no-choice test environment with 30 unsexed weevils aged 10 to 14 days. The jars were set in a randomized complete block design with three replications. After an oviposition period of 10 days, the weevils were removed and the numbers of dead and living weevils were recorded. The samples were then left in the laboratory for 40 days after which the number of progeny weevils that had emerged from each sample were recorded every two days until all progeny had emerged. Emergents were removed from the jars at each count. Finally, the grains in each jar were weighed and grain weight loss was calculated after all progeny had emerged.

Observations

From field experiments, data were collected on agronomic traits including days to mature, ear and plant height, bare-tipness, grain yield and 100-kernel weight. In the laboratory weevil resistance assessment, observations were made on adult weevil mortality, progeny weevil count, median development period (the number of days from day five of infestation until the first progeny emergence), Dobie index of susceptibility (Dobie, 1974), damaged kernel count and weight loss percentage.

Data analyses

Analysis of variance was first carried out to see whether there are significant differences among the genotypes or not for both agronomic and weevil resistance parameters collected from 32 and 40 genotypes, respectively. However, only the 15 direct cross hybrids were subjected to line × tester analysis without parents for the agronomic and weevil resistance parameters. Prior to analysis, data on some of the traits were transformed using either arcsine (percentage of bare-tipped plants) or square root (weight loss % and all count data) transformation. Values of general combining ability (GCA) and specific combining ability (SCA) effects and the standard error for these effects were calculated from the actual values for easy comparisons. For the traits that showed significant differences among crosses, general and specific combining ability effects were computed following line × tester analysis of variance (Kempthorne, 1957) for fixed effects model involving only crosses using AGROBASE 98 computer program. Mean squares due to crosses were partitioned into GCA and SCA effects for the inbred parents and their F_1 crosses, respectively.

Results and Discussion

Yield and other agronomic traits

The analyses of variance showed that mean squares for genotypes were significant for the various traits indicating the possibility of running genetic analysis (Table 2). Accordingly, line × tester analysis of variance for grain yield and related agronomic traits indicated that mean squares of GCA and SCA for the inbred parents and crosses were significant (Table 3) suggesting both additive and non-additive gene actions. Similar to the presemt results, various workers (Hallauer *et al*., 1988; Mandefro, 1998; Habtamu, 2000; Dagne, 2002) have reported the importance of either additive or non-additive or both types of gene actions in the inheritance of agronomic traits.

Highly significant ($P< 0.01$) GCA mean squares of lines were observed for some traits, *viz*., days to maturity, ear height, plant height, percent1 bare tip plants while significant ($P< 0.05$) GCA of lines was noted for 100-kernel weight (Table 3). In contrast, the mean squares for GCA of lines were not significant for grain yield. On the other hand, the GCA mean squares for yield and all other agronomic traits were both highly significant and much greater than the GCA mean squares of lines. This might be because of different genetic bases and origin of the testers used in this study. Two of them were of narrow genetic background (SC-22 and CML-197) and the remaining one (Gutto LMS_5) was broad- based.

The SCA mean squares of crosses were highly significant for days to mature, plant height and hundred-kernel weight, and significant for ear height and percent bare tip plants (Table 3). In contrast grain yield did not show significant SCA mean squares. Similar to the present findings, Habtamu (2000) found significant GCA and SCA effects for days to maturity. But Mandefro (1998) reported no significant differences due to SCA for days to maturity. In general, the GCA mean squares of all traits were higher for testers than for lines, but the contributions of the latter were also considerable.

Table 2. Mean squares from the analysis of variance of F_1 direct crosses and reciprocals for yield and other agronomic traits

Traits	Genotypes (df = 31)	Error (df = 62)
Days to maturity	112.916^{**}	1.625
Ear height	646.181^{**}	61.449
Plant height	1064.891^{**}	101.500
Bare-tip plants (%)	446.707^{**}	21.515
10-kernel weight	46.460^{**}	2.670
Yield	4977295.492^{**}	1259673.533

df = degrees of freedom, ** = Significant at $P\leq0.01$

Table 3. Mean squares from the line × tester analysis of variance of F_1 crosses for yield and other agronomic traits

Traits	GCA for lines (df = 4)	GCA for testers (df = 2)	SCA (Line × Tester) (df = 8)	Error (df = 28)	CV (%)
Days to mature	79.24**	347.82**	95.29**	1.94	0.92
Ear height	657.47**	3352.69**	228.05*	75.89	8.31
Plant height	680.00**	6096.87**	463.78**	111.92	5.10
Bare tip plants (%)	289.50**	3760.05**	65.72**	40.23	23.19
100-kernel weight	8.73*	148.06**	42.32**	2.77	5.09
Yield	96329.90	37281817.10**	1630611.60	1688551.00	15.74

df = degrees of freedom

For days to mature, negative and highly significant ($P< 0.01$) estimates of GCA effects were noted for line L1, L3 and Gutto LMS_5 while L2, L5 and CML-197 exhibited positive and significant GCA values (Table 4). Although not significant, Line-4 and SC-22 also revealed negative GCA effects on days to mature. However, Dagne (2002) reported positive and significant GCA effects on days to mature for Gutto LMS_5, SC-22 and CML-197. The present results also suggested the possibility of developing both early maturing varieties using inbred parents such as lines L1, L3 and Gutto LMS_5, and late maturing varieties using parents like line L2, L5 and CML-197. To this effect, inbred parents with early maturity can be best combiners to develop early maturing hybrids that could be used for hunger breaking when utilized as green cob during the months of food shortage, and also escape drought during seasons of short rainy periods. Despite the fact that the increase in days to maturity observed in some parents is not desirable, this trait has direct association with yield (Hallauer *et al., 1988;* Mandefro, 1998). Therefore, these parents with the undesirable late maturity trait can be used to develop high yielding and agronomically acceptable hybrids by crossing them with early maturing parents.

For ear height, the inbred lines L1 and L2 exhibited significant ($P<0.05$) positive and negative GCA effects, respectively, while L4 and L5 similarly showed highly significant ($P< 0.01$) positive and negative GCA effects, respectively (Table 4). Among the inbred parents, only one line (L3) showed no significant positive GCA value for ear height. While only Gutto LMS_5 with a highly significant GCA effect gave a negative value, the two remaining testers (SC-22 and CML-197) showed highly significant GCA and positive effects on ear height. On the other hand, L5 and Gutto LMS_5 showed highly significant GCA and negative effects for plant height. In contrast, highly significant and positive GCA values for plant height were noted for the other two testers. From the three lines (L1, L3 and L4 (that depicted positive GCA effects on plant height, the effect of only L1 was significant, while the negative GCA effect on plant height noted for L2 was also not significant (Table 4).

Table 4. Estimates of general combining ability (GCA) effects for yield and other agronomic traits

GCA effects due to lines (L) & testers (T)	Days to mature	Ear height	Plant height	Bared tipped plants (%)	100-kernel weight	Yield[a]
L1	-2.58**	7.36*	8.22*	-9.99**	-0.77	__
L2	1.64**	-6.87*	-4.67	4.04	0.83	__
L3	-2.58**	1.47	2.22	2.29	-0.57	__
L4	-0.80	8.69**	6.89	-5.89*	1.29*	__
L5	4.31**	-10.64**	-12.67**	9.55**	-0.77	__
SE (g_i)±	0.46	2.90	3.53	2.76	0.56	__
SE (g_i-g_j)±	0.66	4.10	4.99	3.90	0.79	__
T1	-4.58**	-17.16**	-23.20**	9.36**	-3.46**	-1815.26**
T2	-0.44	6.91**	13.27**	11.87**	2.68**	788.98*
T3	5.02**	10.24**	9.93**	-21.22**	0.77	1026.28**
SE (g_j)±	0.36	2.25	2.11	2.14	0.43	335.52
SE (g_j-g_k)±	0.51	3.18	3.86	3.02	0.61	474.49

[a] For yield GCA effects for lines were not analyzed because the GCA mean squares from the ANOVA were not significant; * and ** = significant at $P \leq 0.05$ and $P \leq 0.01$, respectively

The significant differences due to GCA and SCA effects for plant and ear height noted in this study are congruent with the findings of Mandefro (1998), Revilla *et al.* (1999) and Dagne (2002). But Leta *et al.* (1999) found significant GCA effects and no significant SCA effects for plant and ear height. Therefore, if the interest is to breed for short stature, L2, L5 and GuttoLMS$_5$ would be good combiners, while inbred parents (L1 and L4, SC-22 and CML-197) having positive and high GCA values can be used to develop tall varieties. It is also good to note from our results that significant GCA or SCA values of ear height either for parents or crosses does not necessarily mean significant value for plant height.

Highly significant negative GCA estimates from lines L1 and CML-197 and significant negative estimates from L4 were obtained for percentage of bare tipped plants, suggesting that they were carrying desirable gene(s) of this trait as far as breeding for weevil resistance is concerned. Conversely, L5, Gutto LMS$_5$ and SC-22 had highly significant positive GCA effects for the same trait. Though not significant, L2 and L3 also had positive GCA values for bare-tippedness (Table 4). Most lines with flint grain texture have higher numbers of husk leaves and subsequently have tighter husk cover which makes them less prone to weevil damage (Kim, 1994).

When lines were compared for hundred-kernel weight, only L4 significantly increased this trait, whereas three of the lines (L1, L3 and L5), although not significantly, reduced the trait in that they had a negative GCA value (Table 4). Likewise, Gutto LMS$_5$ also significantly reduced this trait while SC-22 proved to be best combiner for the same trait since it had a highly significant and positive GCA value.

For yield, none of the lines differed significantly in terms of either enhancing or hindering the trait (Table 4). This implies that the lines must not have been bred as best combiner for yield considering the fact that all of them exhibited no significant GCA effect estimates. On the contrary, as it was expected, the testers showed highly significant GCA effects (Gutto LMS_5 and CML-197) for yield, although the effect was negative for Gutto LMS_5 and it was positive and significant for SC-22. CML-197 proved best qualified combiner for yield followed by SC-22.

Estimates of specific combining ability (SCA) effects for the agronomic traits showing significant SCA mean squares in the analyses of variance are presented in Table 5. Crosses such as L1 × SC-22, L2 × Gutto LMS_5, L3 × SC-22 and L5 × CML-197 had significant negative SCA values for days to maturity followed by crosses L3 × Gutto LMS_5, L4 × Gutto LMS_5 and L4 × CML-197 having negative but not significant SCA effects. This indicates that these combinations of parents imparted early maturity. Other crosses like L1 × CML-197, L2 × SC-22, L3 × CML-197 and L5 × Gutto LMS_5 had the highest and highly significant positive SCA value, except for the first cross which was significant for days to maturity. This showed that these parental combinations exhibited increased lateness in maturity. Dagne (2002) also found that cross combinations involving the three testers used in this study had the highest and positive SCA estimates for days to maturity.

Only one cross (L3 × Gutto LMS_5) exhibited significantly reduced height for ear placement as reveled by highly significant and negative SCA estimates. All the remaining crosses were not significant in either maximizing or minimizing ear height. Likewise, highly significant negative and positive SCA estimates for plant height were noted only for the two crosses L2 × Gutto LMS_5 and L1 × Gutto $LMS_{5,}$ respectively. This suggests that these crosses in that order had shorter and taller plant height than the means of their respective parents.

The only cross having negative and significantly low SCA value for bare-tippedness was L5 × CML-197, which comprised a highly significant positive GCA parent (L5) and a highly significant negative GCA parent (CML-197) for this trait (Table 5). Also, crosses such as L1 × SC-22, L2 × SC-22, L4 × Gutto LMS_5, L3 × CML-197 and L1 × Gutto LMS_5 gave lower SCA values for bare-tippedness; while all the remaining crosses gave higher but not significant SCA values. Hence, some of the parental combinations such as L5 × CML-197 comprised desirable gene(s) for good husk cover, which may be the first target in breeding for weevil resistance against field infestation of maize by *sitophilus* weevils. Kim and Kossou (2003), in discussing weevil resistance in maize varieties, reported that field infestation by weevils depended primarily upon the length and tightness of the husk cove on the maturing ear. However, our study revealed that certain of the genotypes identified for having good husk cover in the field did not show acceptable levels of resistance under laboratory evaluations, and this implies that husk cover is not the only factor to be considered in weevil resistance breeding.

The crosses that exhibited high estimates of SCA effects on 100-kernel weight were L2 × Gutto LMS_5 and L4 × CML-197 (Table 5). Conversely, crosses L2 × CML-197 and L4 × Gutto LMS_5 were found to be poor combinations for this trait. Other than the above four crosses, all the remaining crosses showed no significant SCA effects on 100-kernel weight. On the other hand, though SCA mean squares for yield were not significant, crosses such as L1 × CML-197 (10287 kg ha^{-1}) and Line-3 × SC-22 (9937 kg ha^{-1}) gave relatively high average yield (data not shown). Several investigators reported the inheritance of both additive and non-additive gene actions for seed weight and grain yield. Dagne (2002) and Habtamu (2000) found significant mean squares due to GCA and SCA for both traits. Their result is in concordance with our result except that GCA of lines and SCA of crosses were not significant for yield in our case. Nevertheless, Vassal *et al.* (1993) reported that grain yield was controlled by additive gene action. On the other hand, Gamble (1962) reported the importance of non- additive gene action while Revilla *et al*. (1999) reported the importance of additive gene action for the control of seed weight.

Weevil resistance

The analysis of variance revealed significant genotype variation for most of weevil resistance parameters (Table 6). From the line × tester analysis of variance (Table 7), it is particularly interesting to note that the GCA mean squares when tested against the SCA mean squares gave a very high F value indicating a very large contribution of GCA effects (additive) to the total genetic effects. These results are concurrent with the findings that resistance to maize weevil is largely additive with non-additive gene action playing a minor role (Kim, 1994). However, other studies (e.g. Kim and Kossou, 2003) have reported additive, non-additive and maternal effects to be important in determining inheritance of maize weevil resistance in maize genotypes.

The analysis of variance for combining ability effects (Table 7) also showed that the variances due to GCA of lines were highly significant ($P < 0.01$) for adult weevil mortality and number of damaged kernels, and significant ($P < 0.05$) for weight loss percentage. Likewise, the mean squares due to testers were highly significant for number of damaged kernels and index of susceptibility (IS), and significant for progeny emergence and median development period (Table 7). No significant SCA mean squares were observed for all weevil resistance traits considered in the study. Mean squares for GCA of lines were also not significant for progeny weevil emergence. In addition, the mean squares were also not significant for GCA of testers for adult weevil mortality and grain weight loss percentage, and for GCA of lines for median development period and susceptibility index.

Table 5. Estimates of specific combining ability analysis (SCA) for yield and other agronomic traits

SCA effects due to crosses	Days to male flowering	Days to mature	Ear height	Plant height	Bare tipped plants (%)	100-kernel weight
L1XT1	-1.80	0.91	8.38	16.98^{**}	-1.68	0.00
L1XT2	2.93^{*}	-2.89^{**}	-4.69	-11.49	-5.89	-0.01
L1XT3	-1.13	1.98^{*}	-3.69	-5.49	7.57	0.01
L2XT1	-0.47	-6.31^{**}	-4.73	-17.13^{**}	6.02	6.73^{**}
L2XT2	0.27	4.89^{**}	6.20	12.07	-8.15	-1.87
L2XT3	0.20	1.42	-1.47	5.07	2.13	-4.86^{**}
L3XT1	-1.24	-1.42	-12.73^{**}	-10.36	0.47	-0.63
L3XT2	-0.51	-3.89^{**}	6.20	6.18	2.43	-0.37
L3XT3	1.76	5.31^{**}	6.53	4.18	-2.90	1.01
L4XT1	1.09	-0.53	3.04	0.31	-6.88	-4.27^{**}
L4XT2	-1.18	0.67	2.31	-1.16	3.31	0.53
L4XT3	0.09	-0.13	-5.36	0.84	3.57	3.74^{**}
L5XT1	2.42	7.36^{**}	6.04	10.20	2.07	-1.83
L5XT2	-1.51	1.22	-10.02	-5.60	8.30	1.73
L5XT3	-0.91	-8.58^{**}	3.98	-4.60	-10.38^{*}	0.11
SE (S_{ij})±	1.23	0.80	5.03	6.11	4.78	0.96
SE (S_{ij}-S_{kl})±	1.74	1.14	7.11	8.64	6.76	1.36

*and ** = significant at $P \leq 0.05$ and $P \leq 0.01$, respectively

Table 6. Mean squares from the analysis of variance of weevil resistance traits for F_1 crosses including reciprocals and parents

Traits	Genotypes (df = 39)	Error (df = 78)
Dead parent weevil count	0.343**	0.158
Progeny count	1.527**	0.157
Median development period	423.513**	56.122
Number of damaged grain	2.384**	0.252
Index of susceptibility	15.842**	1.768
Weight loss percentage	0.107**	0.012

df = degrees of freedom; ** = Significant at P≤0.01

Table 7. Mean squares for Line × Tester analysis of variance of F_1 crosses for weevil resistance traits

Source of variation	Degrees of freedom	No. of dead adult weevils	Weevil progeny emergence	Median development period	No. of damaged kernels	Suscepti-bility Index	Grain weight loss (%)
GCA of Lines	4	1.15**	0.36	122.11	1.41**	1.87	0.07*
GCA of Testers	2	0.30	1.07*	476.96*	2.04**	11.59**	0.01
SCA of Line × Tester	8	0.14	0.15	135.93	0.22	1.85	0.01
Error	28	0.20	0.17	116.57	0.23	1.58	0.02
CV (%)♠	-	8.65	23.45	29.90	26.39	65.36	11.8

♠ = CV calculated from the transformed values; *and ** = significant at P≤0.05 P≤0.01, respectively

Estimates of GCA effects for adult weevil mortality were highly significant in lines L2, L3 and L4 but such effects, though highly significant, were negative in case of lines L1and L5 (Table 8). The three resistant lines (*viz,,* L2, L3 and L4) possessed highly significant positive and desirable GCA effects which were at par with each other for this trait. GCA estimates of the five parental inbreds for the trait ranged from -5.22 (L1) to 2.89 (L4). Among the five lines, only L5 is dent-grained inbred and the other four are flint-grained inbreds. For progeny emergence and median development period, SC-22 and CML-197 showed positive and non-significant GCA effects, but the GCA effect was negative and significant in case of the semi-flint textured line Gutto LMS$_5$ suggesting that this inbred parent significantly prolonged progeny emergence than the two other testers.

Of only two of the lines (L1 and L4) that depicted significant GCA effects on the number of damaged kernels, L1 that had highly significant and positive estimates of GCA (2.76) while L4 in contrast had significant and negative GCA effects (Table 8). The range of GCA values varied between 2.76 (L1) and –1.69 (L4). The negative GCA for number of damaged kernel in our study is desirable character though it is difficult to verify the chemical basis of such kind of resistance mechanism in the present study. Nevertheless, some reporters (Tipping *et al*., 1988) concluded that most of the resistance resides in the pericarp and the maternal genotypes and endosperm are important in determining seed resistance. Furthermore, Arnason *et al*. (1994) have also noted that biochemical characteristics are highly correlated with insect resistance and it should be possible to introduce this resistance into improved maize such that selection resulting in moderate increases in pericarp and aleurone layer phenolic acid carbohydrate complexes and diphenolic cross links, should provide greater mechanical resistance to stored product insects.

Considering index of susceptibility, the lines were not significantly different from each other. However, Gutto LMS$_5$ from testers was found to be a promising combiner because of its highly significant negative GCA estimate for index of susceptibility (Table 8). In contrast, although the effects were not statistically significant, SC-22 (dent-grained) and CML-197 (flint-grained) had positive GCA values for susceptibility index, thus, exhibiting poor performance for weevil resistance. On the other hand, negative GCA estimate for grain weight loss indicates resistance, whatever the mechanism might be, while positive GCA indicates preference of a given line by the weevil. Accordingly, highly significant and positive GCA effects were noted for L1 (0.40) but the effects, although not significant, were negative for the remaining lines. Thus, the four lines (i.e. L2, L3, L4 and L5) had reduced damage that in effect led to very minimum potential loss by the weevils (Table 8).

Based on the overall results, it may be advisable to develop a breeding population using the four resistant inbred lines (L2, L3, L4 and L5) as source materials for maize weevil resistance.To this end, recurrent selection can be utilized in concentrating genes for resistance. Other selected inbred lines (CML-197 and SC-22) or populations would be used as sources of high grain yield. Another option would be to use adapted lines that had good combining ability for weevil resistance as the recurrent parent in back crosses with resistant lines lacking adaptation. However, further evaluations of the resistant materials both in the laboratory and under field conditions at several locations are necessary for confirmation of the present results.

In conclusion, the present study suggests that there are heritable quantitative traits controlling weevil resistance and these can be exploited in thebreeding program. Cognizant of the fact that genetic information on weevil resistance of maize in Ethiopia is scanty, further studies are worth for understanding the underlying mechanisms of resistance and for identifying desirable parents that can be used to develop populations for molecular tagging in resistance breeding programs.

Table 8. Estimates of general combining ability analysis (GCA) for weevil resistance traits

GCA effects due to Lines (L) & Testers (T)	No. of dead weevils	Weevil progeny emergence	Median development period	No. of damaged kernels	Susceptibility index	Grain weight loss (%)
L1	-5.2222^{**}	—	—	2.7556^{**}	—	0.3998^{**}
L2	2.5556^{**}	—	—	-0.5778	—	-0.1713
L3	0.6667^{**}	—	—	-0.0222	—	-0.0669
L4	2.8889^{**}	—	—	-1.6889^{*}	—	-0.1024
L5	-0.8889^{**}	—	—	-0.4667	—	-0.0591
SE (gi)±	0.1488	—	—	0.7853	—	0.1202
SE (g_i -g_j)±	0.2104			1.1106		0.1700
T1	—	-1.1333^{*}	-6.5111^{*}	-1.6222^{*}	-1.0036^{**}	—
T2	—	0.4000	3.2222	0.3778	0.3711	—
T3	—	0.7333	3.2889	1.2444	0.6324	—
SE (gj)±	—	0.4440	2.7877	0.6083	0.3247	—
SE (g_j-g_k)±		0.6279	3.9424	0.8603	0.4592	

Dashes (**-**) indicate GCA effects not analyzed because the mean squares of the GCA of lines and testers were not significant; * and ** = significant at P≤0.05 and P≤0.01, respectively

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