Original Paper **Open Access**

Genetic analysis of grain yield performance and weevil [*Sitophilus zeamais* (Motschulsky)] resistance in southern African maize hybrids

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Abstract

Maize (*Zea mays* L) grain losses due to grain weevils threaten food security in poor rural communities where grain is stored on farm without any chemical treatment in developing countries. Progress in developing high-yielding and weevil-resistant maize varieties is scarcely reported in the literature. Knowledge of the mode of inheritance for both grain yield and weevil resistance in elite maize germplasm would be crucial in designing viable breeding strategies. Therefore hybrids that were generated in a North Carolina design II mating scheme were evaluated for grain yield over three environments. Hybrids were also evaluated for maize weevil (*Sitophilus zeamais* Motsch) resistance under controlled temperature and relative humidity in the laboratory. Results revealed that only a few hybrids combined high grain yield potential and maize weevil-resistance reflecting the challenges which may be encountered in developing productive hybrids. However, highly significant differences between hybrids for both grain yield and weevil resistance indicated opportunities for selection. Furthermore, weevil resistance was found in at least four major heterotic groups suggesting that development of weevil-resistant hybrids could be created by crossing complementary lines from these heterotic groups. Significance of GCA and SCA effects suggested that genes with both additive and non-additive effects, respectively, were important for grain yield. The SCA effects were not significant ($P > 0.05$) for grain weevil resistance parameters, suggesting that genes with additive effects played a predominant role in governing the resistance in hybrids. Generally the baseline resistance to maize weevil could be improved through selection, while procedures that emphasize both GCA and SCA would be exploited to enhance grain yield in this set of maize germplasm.

Keywords: maize, combining ability, maize weevil, resistance, post-harvest losses

Introduction

Post-harvest losses to storage insect pests such as the maize weevil (*Sitophilus zeamais* Motsch) are a serious problem to smallholder farmers in developing countries. These losses have been further worsened by the replacement of traditional varieties with high yielding, but more susceptible varieties (Fortier et al, 1982). Most of the new varieties and hybrids possess improved agronomic performance and tolerance to biotic stresses. However, this has been achieved at the expense of traits that improve post-harvest storage (Mihm, 1994), a characteristic particularly important in developing countries, where grain is stored under adverse conditions on farm. Mutiro et al (1992) estimated up to 80% loss in on-farm stores in tropical countries, and storage losses of 20–90% have been reported for untreated maize due to weevil attack in southern Africa (Giga and Mazarura, 1991). Studies in Malawi and Zimbabwe (Giga and Mazarura, 1991) have shown increased susceptibility of the hybrid maize to weevil attack, with losses of > 80% as compared to the unimproved varieties. Approximately, 95% of the maize produced in Africa is grown by smallholder farmers who cultivate ≤ 10 ha of land, with low yields averaging 1.2 t ha^{-1} (CIMMYT, 2001). As a result, any post-harvest storage losses are serious problems for farmers. Grain is most susceptible to weevil damage when stored at moisture contents > 15% (CIMMYT, 2001). In general, weevils thrive in hot humid conditions, hence infestation of new maize usually occurs in late summer or fall before the crop is harvested (Painter, 1968). Damage by weevils not only jeopardizes food security throughout the developing world, but also affects the seed bank since most farmers retain grain for use as seed. Seed retained on-farm is used to plant up to 70% of maize in eastern and southern Africa (CIMMYT, 1994; Pingali and Pandey, 2001).

Appropriate control measures have to be applied to reduce losses due to weevil damage. Chemical protectants are effective, but only for shelled grain in closed containers (Perez-Mendoza, 1999). Unfortunately, however, most smallholder farmers have no access to shelling devices and if they use chemicals

RECEIVED 9/28/2015

these can cause health hazards since the farmers may not have necessary training on their safe use. The increasing occurrence of insecticide resistance in the weevils, and environmental concerns over the use of chemical insecticides means that alternative control measures should be found. Integrated pest management practice is an alternative control measure to reduce grain postharvest losses caused by maize weevils and a major component of this strategy is the use of host plant resistance to reduce losses and minimize the impact on grain quality (Bergvinson, 2001). According to Boxall et al (1997), early harvesting, sun drying, oil treatments, and smoking are some practices that can be used with integrated pest management.

Weevil resistance can be used as a criterion for selecting inbred lines for use in developing hybrids for deployment in the subsistence sector where grain is stored on farm. The goal of breeding programs should be to deliver high-yielding and weevil resistant maize hybrids and open pollinated varieties Dari et al (2010) to reduce the levels of postharvest grain losses in tropical environments. Understanding the mode of gene action controlling weevil resistance of experimental maize hybrids would be helpful in choosing an effective breeding strategy. Maize weevil resistance inheritance has been studied in both temperate and tropical maize (Garcia-Lara et al, 2009). Widstrom et al (1975) reported dominant maternal effects but no cytoplasmic effects for maize weevil resistance. Tipping et al (1989) found general combining ability to be more important than specific combining ability. Derera et al (2001a), Kim and Kossou (2003), Dhliwayo and Pixley (2003) and Dhliwayo et al (2005) also confirmed the polygenic (quantitative) inheritance of maize weevil resistance, the importance of maternal effects and additive, and nonadditive gene action; but the relatively low broad-sense heritability implied relatively slow progress in moving this trait into elite germplasm via phenotypic selection.

Despite the progress made in understanding weevil resistance in maize and identifying weevil resistant sources we are not aware of any commercial maize breeding program that is addressing this objective.

The specific objectives of the current study were to determine feasibility of developing new hybrids that combine high grain yield with maize weevil resistance. Therefore, southern African experimental maize hybrids were evaluated for grain yield and weevil resistance, and the nature of the gene action governing these traits were determined.

Materials and Methods

Plant materials

Parental inbred lines used in this experiment represented a sample of the eight major heterotic groups and their derivatives (Table 1) that are widely used in breeding programs in southern Africa as reported by Gevers and Whythe (1987) and Mickelson et al (2001). Inbred lines were divided into eight subgroups of three each; hence, three inbred lines in one subgroup were used as females and crossed with three lines from another subgroup, used as male parents, to form hybrids, according to a North Carolina Design II mating scheme (Comstock and Robinson, 1948; 1952). A complete set had nine hybrids. Each inbred line was used once as a female parent in one set and once as a male parent in another set. Seventy two F_1 hybrids were generated at Rattray Arnold Research

Table 1 - Pedigrees of 18 inbred lines used in a design II mating scheme which formed the four complete sets evaluated for grain yield and weevil resistance.

Inbred	Heterotica Group[$]	Pedigrees for the non-priorietary inbred lines (Property lines are coded in brackets)
CML312	A	S89500F2-2-2-1-1-B*5
B16	I	[MSR123X1137TN 9-2-4-X-3/LZ95644]-B-1-5-5-B-4-B-B-B-B
A13	A	[[EV7992]C1F2-430-3-3-3-X-B-B/CML202-6-2-2-3-B-B
A14	A	Z97SYNGLS(A)F2-97-1-1-1-B
CML442	A	[M37W/ZM607#bF37sr-2-3sr-6-2-X]-8-2-X-1-BBB
B17	B	[LZ956441/LZ966295]-B-3-4-4-B-5-B-B-B-B
CML395	B	90323(B)-1-B-1-B*4
CML444	B	P43C9-1-1-1-1-1-BBB
CML488	B	DTPWC8F31-4-2-5-BBB
A15	N3	[CML197/N3//CML206]-X-32-1-4-B-B-B-B
CML445	AB	[[TUXPSEQ]C1F2/P49-SR]F2-45-7-5-1-BBB
B18	B	Z97SYNGLS(B)-F2-188-2-1-3-B
C11	H	(L48 X L92)
C12	W	(L89 X L42)
C14	W	(L32 X L16)
C18	H	(L46 X L96)
C20	H	(L52 X L30)
C21	P	(L29 X L82)

[$] Heterotic group A includes materials related to N3 (Salisbury white), NAW, Tuxpeno, Kitale and B73; heterotic group B consists of materials related to SC (Southern Cross), H and K (pride of saline), Eto, Ecuador , Mo17, P Potchefstroom Pearl and W is M37W.

Station near Harare during the summer 2002-3 but due to inadequate seed for some of the hybrids, only 58 hybrids were evaluated for grain yield. For weevil screening, F_2 seed was produced by advancing the F_1 hybrids to F_2 generation by full-sib mating in winter 2003 at Muzarabani, Zimbabwe.

Yield evaluations for F_1 hybrids

Hybrids were evaluated for grain yield at Cedara in South Africa (1,076 m altitude), Rattray Arnold Research Station (RARS): 1,350 m altitude and Kadoma Research Centre (KRC): 1,162 m altitude, in Zimbabwe. Fifty eight hybrids and six hybrid checks: 64 genotypes were evaluated for yield performance in an 8x8 simple lattice design, during the 2003/4 season. Hybrids were planted in 4 m rows with 0.80 m between adjacent rows and 0.50 m between plants within rows (to give a plant population of ≈ 44,000 plants ha^{-1}) at Cedara. At RARS and KRC, hybrids were spaced at 0.75 m between adjacent rows and 0.25 m between plants within a row resulting in plant population of ≈ 53,000 plants ha^{-1}. Standard agronomic cultural practices were applied in all the trials. Data was recorded for grain yield (GYD): shelled grain weight was adjusted to 12.5% moisture and converted to tons per hectare; and ears per plant (EPP): number of ears with at least one fully developed grain divided by number of harvested plants.

Weevil resistance evaluation for the experimental hybrids

The F_2 grain for weevil evaluations was produced in a single environment: at Muzarabani under optimum conditions, because of the prohibitive cost of replicating this effort at multiple sites, and is justified by reports of non-significant genotype x environment (site or year) interaction for resistance to the maize weevil (Tipping et al, 1988; Kang et al,1995). Moreover, comparing weevil resistance of grain produced in the same season and site is important because environmental effects on weevil resistance can be large (Dhliwayo and Pixley, 2003). Thirty six F_2 hybrids which constituted four complete sets of nine hybrids were evaluated for weevil resistance together with popcorn (*Zea mays* subsp *mays*) as the resistant check. The screening protocol used was a modified Dobie method (Dobie, 1974; 1977), which is used at CIMMYT-Zimbabwe (Derera et al, 2010; Derera et al, 2001b; Dhliwayo and Pixley, 2003).

Four replications of grain samples of 50 ± 0.1 g of the hybrids and popcorn were disinfested in a freezer at –20°C for 14 days to eliminate field infestations (live insects or eggs) of weevils or any other pests. Each sample was then put in a 250 ml glass jar with brass screen lid that allowed adequate ventilation and then placed in the controlled temperature and humidity (CTH) room for 3 weeks to equilibrate grain moisture content to ≈ 13% (Derera et al, 2001a). The grain samples were infested with 32 unsexed (i.e. of unknown gender) 7–14-day old weevils for an oviposition period of 10 days in the CTH room, after which all the weevils were removed and the number of living and dead weevils recorded to determine parent weevil mortality during the oviposition period. The grain in the jars was then left in the CTH room for about 35 days, which was the weevil incubation period.

The primary measure of resistance to the weevils was the Dobie Index of susceptibility (DI). The number of F_1 weevil progeny that emerged was counted every two days after the oviposition period until day 71: the end of experimental period. The Median Development Period (MDP) of the weevils and Dobie index of susceptibility were calculated as:

MDP = (N° of days from day-5 to 50% weevil progeny emergence) and

Dobie index = [100 × loge (total progeny emerged)]/MDP.

The Relative Dobie Index of susceptibility (RDI) was then calculated as a ratio of the Dobie index of susceptibility of each hybrid in relation to the Dobie index of popcorn (the susceptible check).

At the end of the experiment the samples were weighed to determine weight loss: calculated as the difference between initial grain weight and final grain

Table 2 - Mean squares from the analysis of variance of grain yield of hybrids pooled over sets across three locations during the 2003-2004 season, and weevil resistance data.

		Mean squares Grain yield data	
Source of variation$^{\$}$	df	Grain yield(t ha^{-1})	EPP$^{\#}$
Location	2	243.40***	1.42***
Sets	3	2.94***	0.032*
Location x sets	6	3.24**	0.017***
Replication/sets/location	12	1.096***	0.023**
Block/replication/site	45	2.082***	0.027***
Hybrids/sets	31	4.31***	0.056***
GCAf/sets	8	5.14***	0.12***
GCAm/sets	8	5.76***	0.067***
SCA/sets	15	3.097***	0.016***
Hybrids x location/sets	62	1.15*	0.028***
Location x GCAf/sets	16	1.23***	0.049***
Location x GCAm/sets	16	2.10***	0.037***
Location x SCA/sets	30	0.61***	0.012***
Pooled Error	105	0.91	0.0085

			Mean squares Weevil data	
Source of variation	df‡	F_1 progeny $Log_{10}(n+1)$	Dobie Index	RDI§
Sets	3	0.20*	17.32**	3231.49**
Replication/sets	15	0.35***	14.73***	2753.76***
Genotypes/sets	34	0.16***	8.33***	1560.60***
GCAf/sets	11	0.20 **	11.92***	2248.73***
GCAm/sets	11	0.19***	9.89**	1841.51**
SCA/sets	12	0.095	3.61	672.31
Error	88	0.064	3.49	655.83

*, **, ***significant at the 0.05, 0.01, and 0.001 probability level. $^{\$}GCA_m$, general combining ability due to males within sets; GCA_f, general combining ability due to females within sets; SCA, specific combining ability. $^{\#}$EPP is number of ears per plant. ‡Error degrees of freedom for Dobie index and RDI = 82. §RDI is the Relative Dobie Index of susceptibility: ratio of the susceptibility of each hybrid in relation to popcorn, the susceptible check.

weight after thorough sieving to remove floury products left by weevils after feeding (Dari et al, 2010).

For discussion purposes, the maize hybrids were classified into six categories based on their RDI: very resistant (RDI < 50%), resistant (50-60%) and moderately resistant (61-71%) hybrids. Moderately susceptible, susceptible and very susceptible hybrids had RDI values of 72-79%, 80-96%, and 97-160% respectively.

Statistical analysis

General analyses of variance for grain yield and weevil resistance parameters were performed for the experimental maize hybrids including checks. Thirty six hybrids: four complete sets of nine hybrids per set were used in the analysis. The weevil screening laboratory experiments used a randomized complete block design with four replications. Each replication formed a complete block and occupied a different shelf and position in the CTH room. Grain weight loss data was angular-transformed (arcsine√proportion), while weevil progeny data were transformed by the logarithm transformation in order to stabilize the variance (Abebe et al, 2009; Dari et al, 2010) before analysis by the general linear model (GLM) of SAS (SAS Institute, 2003). The genetic analysis for yield and weevil resistance data was performed as described by Hallauer and Miranda (1988) using North Carolina design II in SAS. For grain yield, the analysis followed a fixed effects model for the experimental hybrids across locations for the individual sets and pooled over sets. For weevil screening, the analysis followed the same model but hybrids were analyzed as individual and pooled sets with no environmental effects/interactions (since hybrids were produced in a single environment). The sources of variation in the analysis were males, females and their interaction. The expectations of males and females for the design are equivalent to the general combining ability (GCA), and the male and female interaction to the specific combining ability (SCA) of a diallel analysis (Hallauer and Miranda, 1988). Because there were two sets of parents in the North Carolina Design II, there were two independent estimates of GCA: GCA due to male parents (GCAm), and GCA due to female parents (GCAf). Pearson phenotypic correlation coefficients were calculated among all traits measured using least squares means for grain yield and weevil resistance parameters of the hybrids.

Results and Discussion

Combining ability effects for yield

Hybrids showed highly significant (P < 0.001) variation for grain yield and weevil resistance (Table 2). Analyses pooled over sets showed significant variation among sets, GCA due to males within sets (GCA_m), and GCA due to females within sets (GCA_f) for both grain yield and weevil resistance parameters, while SCA within sets was highly significant (P < 0.001) for grain yield parameters only. Thus, both additive and nonadditive gene action were important for controlling grain yield; while only the additive gene action was significant in determining weevil resistance in these hybrids. However, GCA effects were greater than SCA effects: 65% versus 35% and 86% versus 14% of the cross sum of squares for grain yield and ears per plant (prolificacy), respectively. This indicated the predominance of additive over nonadditive gene action for these traits. Beck et al (1990) also reported the importance of additive gene action to nonadditive gene action for grain yield. The GCA due to male (GCA_m) effects were equally important as the GCA due to female lines (GCA_f) effects for grain yield, because the GCA_m sum of squares contributed 34% of the total variance while the GCA_f sum of squares contributed 31% of the total variance suggesting that maternal effects were not significant for grain yield in these hybrids. Significant maternal

Table 3 - Mean squares from the analysis of variance of grain yield of four hybrid sets across three locations during the 2003-2004 season.

		Grain yield (t ha^{-1})				EPP[‡]			
Source of variation[$]	df[#]	Set1	Set 2	Set 3	Set 4	Set 1	Set 2	Set 3	Set 4
Location	2	84.61***	55.82***	64.74***	50.61***	0.56***	0.38***	0.33***	0.20***
Replication/location	2	0.72	0.90	0.91	0.36	0.0037	0.015**	0.011	0.0057
Block/replication	14	0.81	0.98	0.64	1.36	0.0077	0.0053	0.017	0.0075
Hybrids	8	2.88**	11.054***	1.00	3.15*	0.12***	0.034***	0.023	0.039***
GCA_f	2	5.24**	11.14***	0.33	6.74**	0.35***	0.018*	0.056*	0.040*
GCA_m	2	4.91**	18.58***	0.23	2.21	0.082***	0.086***	0.025	0.067**
SCA	4	0.69	7.92***	1.71	1.83	0.031**	0.0039	0.0066	0.024*
Hybrids x location	16	1.18	1.61	0.30	1.58	0.037***	0.033***	0.022	0.021**
Location x GCA_f	4	0.64	0.67	0.42	3.21*	0.11***	0.014*	0.024	0.044**
Location x GCA_m	4	2.45*	4.65**	0.44	0.87	0.014	0.066***	0.029	0.028*
Location x SCA	8	0.81	0.23	0.18	1.11	0.013	0.019**	0.017	0.0052
Pooled Error	27	0.85	0.94	0.73	1.12	0.0065	0.0048	0.015	0.0074
CV		10.61	11.19	10.26	9.93	6.52	3.41	9.41	8.10
Mean		9.22	8.73	8.85	9.17	1.11	1.11	1.074	1.063
R^2		0.95	0.96	0.94	0.83	0.98	0.99	0.92	0.84
GCA_f/GCA_m		1.067	0.60	1.41	3.05	4.33	0.21	2.26	0.60

*, **, ***significant at the 0.05, 0.01, and 0.001 probability level. [$]$GCA_m$, general combining ability due to males within sets; GCA_f, general combining ability due to females within sets; SCA, specific combining ability. [#]Degrees of freedom in set 2 are adjusted for missing values: Genotypes = 7, SCA = 3, Location x SCA = 6 and error degrees of freedom = 24. [‡]EPP is number of ears per plant.

differences for yield have been scarcely reported in the literature. Khehra and Bhalla (1976) examined reciprocal differences under non-drought conditions and reported non-significant cytoplasmic effects for grain yield, which is consistent with our observations herein. However, GCA_f effects were 1.8 times larger than GCA_m effects for prolificacy and the GCA_f sum of squares contributed more (55% of the total variance) than GCA_m sum of squares (31% of the total variance) suggesting the significance of maternal or cytoplasmic effects for the trait. On the contrary, Bhat and Dhawan (1971) reported non-significant cytoplasmic effects for prolificacy and significant cytoplasmic effects for grain yield in F_1 and backcross populations of varietal crosses under normal conditions. The differences between findings could be explained by the different germplasm used (Derera et al, 2008) and could be a result of the cytoplasm interacting with genotypes (Khehra and Bhalla, 1976).

Analysis of the individual sets showed that GCA_f effects were significantly larger than GCA_m effects in three sets: set 1, set 2, and set 4 (Table 3) for grain yield, thus suggesting that maternal effects were important for grain yield in these sets. This was consistent with previous findings by Derera et al (2008) who found significant maternal effects for inheritance of yield in three sets of southern African maize germplasm evaluated for grain yield and gray leaf spot resistance. In contrast, a survey of the literature indicated that maternal effects have not been reported to be important for yield in maize, except for some quality traits and seed size (Singh, 1993) and days to silk emergence (Khehra and Bhalla, 1976).

Combining ability effects for weevil resistance

For F_1 progeny emerged, Dobie index and Relative Dobie index of susceptibility, GCA effects were greater than SCA effects indicating a preponderance of additive over nonadditive gene action. In total, GCA effects (i.e. GCA_m plus GCA_f) accounted for 79% and 85% of the cross sum of squares for F_1 progeny emerged and Relative Dobie index, respectively. Thus, GCA effects were more important than SCA effects in explaining differences among hybrids for these traits. Additive gene action was, therefore, more important than non-additive gene action in determining weevil resistance. Breeding for weevil resistance can be made effective by selecting resistance lines during inbreeding. In contrast, Dari et al (2010) reported that additive and nonadditive gene action were important in determining weevil resistance of early generation maize inbred lines and their hybrids and concluded that breeding for weevil resistance can be made more effective by selecting during inbreeding, followed by evaluating specific hybrid combinations among the best lines. Slightly more GCA_f effects (40% for F_1 progeny emerged and 47% for Relative Dobie index) compared to GCA_m effects (39% for F_1 progeny emerged and 38% for Relative Dobie index) could indicate the importance of maternal effects in determining resistance of hybrids to the maize weevil. The results were similar to findings by Kang et al (1995), showing significant maternal effects for non-preference of F_2 hybrids by the maize weevil in free-choice tests. Thus, breeders have to make a critical decision about parents which should be used as females when developing hybrids. However, Dari et al (2010) concluded that both parents should be resistant to achieve the greatest weevil resistance in a hybrid, which is consistent with the observation of additive gene effects in conditioning the resistance. Another implication for significant maternal effects for weevil resistance in F_2 maize hybrids is that, if unchecked, maternal effects would inflate GCA variance for weevil resistance and secondary traits causing an overestimation of heritability which might mislead breeders in adopting wrong selection strategies for developing weevil resistant maize varieties. However the role of maternal effects require further investigation by performing reciprocal crosses to check the role of different cytoplasm on weevil resistance.

Weevil Resistance and Grain Yield

Based on our categorization of the hybrids (Table 5), 26% of the 36 hybrids were highly susceptible, 40% were susceptible, 17% were moderately susceptible, 11% were moderately resistant, and 6% were in the resistant to very resistant category. The

Table 4 - Mean squares from the analysis of variance of weevil resistance parameters of four hybrid sets.

Source of variation$^{\$}$	df$^{\#}$	F1 progeny log10(n+1) Set 1	Set 2	Set 3	Set 4	Dobie index Set 1	Set 2	Set 3	Set 4	Relative Dobie index(%) Set 1	Set 2	Set 3	Set 4
Replication	3	0.34*	0.86***	0.18*	0.18	3.74	31.15*	13.25**	12.39**	703.07	5821.74*	2456.61	1988.77*
Hybrids	8	0.27*	0.15*	0.053	0.15	7.51*	14.78*	2.63	5.59*	1414.028*	2760.71*	480.31	1060.59*
GCA_f	2	0.57**	0.13	0.10	0.043	22.45**	15.36	3.71	0.63	4232.18	2985.48	669.90	115.17
GCA_m	2	0.17*	0.19*	0.064	0.28	1.03	16.94	4.50	8.060*	198.033*	3124.47	814.99	1426.83*
SCA	4	0.17*	0.14*	0.023	0.15	2.55	14.55	0.69	7.26*	480.94*	2677.11	133.92	1368.45*
Error	23	0.097	0.045	0.041	0.089	3.29	7.84	1.85	2.17	615.26	1478.67	343.75	404.28
CV		28.00	17.84	17.92	29.42	29.42	37.67	21.32	25.68	29.35	37.74	21.20	25.54
Mean		1.077	1.19	1.14	1.013	6.16	7.43	6.39	5.73	84.52	101.89	87.44	78.73
R^2		0.58	0.77	0.50	0.47	0.51	0.52	0.60	0.65	0.51	0.52	0.60	0.65
GCA_f/GCA_m		3.37	0.69	1.63	0.15	21.76	0.91	0.82	0.078	21.37	0.96	0.82	0.081

*, **, ***significant at the 0.05, 0.01, and 0.001 probability level. $^{\$}GCA_m$, general combining ability due to males within sets; GCA_f, general combining ability due to females within sets; SCA, specific combining ability. $^{\#}$Degrees of freedom in set 2 are adjusted for missing values: Genotypes = 7, SCA = 3, Location x SCA = 6 and error degrees of freedom = 24. ‡EPP is number of ears per plant.

frequency distribution of the experimental hybrids for weevil resistance was approximately normal (plot not shown). The wide variation in genotypes for resistance to maize weevil indicated segregation for resistance genes in the F2 hybrids (Derera et al, 2001b). Although the sample of 18 lines was small these results were similar to the categorization of 217 genotypes by Dobie (1977), which showed a normal distribution with 20% of the genotypes showing high resistance, 30% being moderately resistant/susceptible, 30% susceptible and 20% highly susceptible.

The highly significant ($P < 0.001$) differences among hybrids for weevil resistance (Table 2) were in line with findings from several studies which reported genetic variation for resistance to weevil damage. Tadesse et al (1995) reported significant variation for the numbers of F_1 weevil progeny emerged among 25 local maize varieties. Resistance of maize to the maize weevil was reported in Mexican landraces, notably Sinaloa 35 and Yucatun 7 (Arnason et al, 1994), and in temperate inbred lines B37, B68, R805 and T220 (Tipping et al, 1988). Differences in progeny emerged between genotypes have also been reported by Dhliwayo and Pixley (2003) in a divergent selection study of two synthetic populations and four biparental maize populations. Similarly, Derera et al (2001b) reported significant differences among inbred lines for F_1 weevil progeny emerged in the evaluation of the F_2 maize hybrids formed from inbred lines from southern Africa, CIMMYT-Mexico, and

Table 5 - Means for weevil resistance parameters for the maize hybrids and classification of the hybrids based on the relative Dobie index of susceptibility.

Set	Hybrid	Grain yield (t ha^{-1})	Ears plant^{-1}	F_1 progeny	LogF_1 progeny	Dobie index	RDI (%)	Class$^{\$}$
2	CML312/C12	9.23	1.13	17.75	1.24	11.68	160.00	Vs
1	CML395/C18	9.90	0.98	46.25	1.62	8.50	116.50	Vs
2	CML442/C14	7.80	1.15	38.75	1.53	8.48	116.00	Vs
1	CML395/C11	8.78	0.98	26.25	1.39	7.65	104.75	Vs
2	CML445/C12	7.07	1.15	21.25	1.26	7.50	102.25	Vs
2	CML312/C14	.	.	22.50	1.25	7.30	100.75	Vs
3	C14/A15	9.00	1.15	19.00	1.24	7.33	100.00	Vs
2	CML442/C21	9.70	1.07	26.75	1.22	7.15	97.75	Vs
3	C12/A15	8.43	1.15	18.50	1.26	7.08	97.00	Vs
3	C14/A14	8.65	1.03	19.50	1.31	7.05	96.25	S
4	B16/CML442	9.13	1.00	18.00	1.27	6.85	94.00	S
3	C12/A14	8.50	1.12	13.25	1.12	6.75	92.50	S
4	B16/CML312	10.75	1.08	22.25	1.12	6.71	92.27	S
1	CML395/C20	8.87	0.97	10.75	0.95	6.68	91.93	S
4	B18/CML442	8.97	1.03	14.50	1.15	6.58	90.25	S
3	C14/A13	9.20	1.10	13.25	1.12	6.55	89.75	S
2	CML312/C21	10.00	0.98	15.75	1.17	6.35	87.50	S
2	CML445/C14	10.40	1.17	22.25	1.16	6.38	87.25	S
2	CML442/C12	6.82	1.22	12.25	1.08	6.13	84.00	S
1	CML444/C18	10.63	1.18	16.75	1.05	6.08	83.60	S
3	C21/A14	9.58	1.02	11.76	1.07	6.07	83.05	S
4	B17/CML442	9.23	1.03	11.75	1.05	5.95	81.75	S
4	B17/CML445	8.70	1.05	11.75	1.10	5.90	81.25	S
3	C21/A15	8.72	1.05	9.75	1.01	5.78	79.00	Ms
1	CML488/C11	8.45	1.12	11.25	1.01	5.68	78.00	Ms
4	B18/CML445	8.33	1.10	6.00	0.77	5.34	72.86	Ms
4	B18/CML312	8.43	1.05	9.50	0.95	5.23	72.00	Ms
1	CML488/C20	8.78	1.28	9.00	0.95	5.25	71.75	Ms
3	C21/A13	8.40	0.97	12.00	1.01	5.20	71.50	Ms
3	C12/A13	9.15	1.08	11.25	1.01	5.15	70.75	Mr
1	CML444/C20	9.58	1.03	7.50	0.90	5.08	69.50	Mr
2	CML445/C21	8.82	1.05	7.00	0.80	4.84	66.60	Mr
1	CML444/C11	9.10	1.03	11.43	0.88	4.71	64.27	Mr
1	CML488/C18	8.85	1.37	6.75	0.83	4.28	58.75	R
4	B16/CML445	9.52	1.25	4.75	0.70	3.13	42.75	Vr
	Popcorn			35.50	1.56	7.33	100.50	
	Mean value	9.00	1.09	16.63	1.12	6.48	88.91	
	P value	***	***	***	***	**	**	
	LSD	2.089	0.24	14.78	0.36	2.76	37.86	
	Heritability	0.74	0.71	0.63	0.58	0.53	0.53	
	R^2	0.77	0.63	0.60	0.60	0.52	0.53	

**, ***significant at the 0.01 and 0.001 probability level. $^{\$}$Hybrid classified as very susceptible (Vs), susceptible (S), moderately susceptible (Ms), moderately resistant (Mr), resistant (R), and very resistant (Vr).

CIMMYT-Zimbabwe. Dari et al (2010) also found significant genotypic variation among lines and hybrids for F_1 progeny emerged. Findings in the current and previous studies underscore that breeding for weevil resistance would be feasible through selection from the variation observed.

An important goal in any breeding program aimed at increasing food security is producing maize hybrids that combine both high yields and post harvest insects loses resistance e.g. weevil resistance. In this study, experimental hybrids in sets 1 and 4 with the highest average grain yield also had the lowest Relative Dobie index and least number of F_1 progeny emerged: were also weevil resistant (Table 4). Thus, parental lines that constituted hybrids in these two sets combined favorable alleles for high grain yield and high weevil resistance. Hybrids in set 2 had the highest mean F_1 progeny emerged, Dobie index and Relative Dobie index of susceptibility: were susceptible to weevil attack. Inbred lines CML488, CML444, B18 (all from heterotic group B), CML445 (heterotic group AB), C20 (heterotic group H), and B16 (heterotic group I) contributed high levels of weevil resistance in their respective sets, while inbred lines CML395 (heterotic group B) and CML312 (heterotic group A) contributed less to weevil resistance (data not shown). The fact that resistance was found in at least four major heterotic groups suggests that development of weevil resistant hybrids would be easy when lines from complementary heterotic groups are crossed. Unsurprisingly, the most resistant hybrids: B16/CML445 and CML488/C18 (Table 5) were constituted by lines with high GCA effects for weevil resistance whilst the most susceptible hybrids: CML312/C12 and CML395/C18 were made up of lines with low GCA effects for weevil resistance.

A few inbred maize lines such as CML444 combined high weevil resistance with high grain yield. Lines with such attributes would be desirable to ensure food security as high yields are complemented by reduced post harvest losses in storage. However, some lines had high levels of weevil resistance and contributed less to grain yield e.g. lines C20 and CML445, and some lines had low levels of weevil resistance but contributed to high grain yield in hybrids e.g. line CML312. Yield potential and weevil resistance are complex traits that result from the combination of many traits and no work has been done to introduce both traits into southern Africa germplasm. The fact that genetic variance for grain yield and weevil resistance are highly significant means that we can effectively select and simultaneously improve breeding populations for these traits, in a recurrent selection programme.

Phenotypic correlations and heritability

Although significant, the phenotypic correlations between grain yield and ear count (r = 0.25**), and between grain yield and prolificacy (r = 0.20**) were too weak to explain the yield differences among hybrids. The correlation between F_1 progeny emerged and Dobie index/ RDI were highly significant (r = 0.57***) implying that the parameters are equally important indicators of weevil resistance in maize. However, there was no significant correlation between grain yield and weevil resistance parameters (r = 0.13; P = 0.48 for F_1 progeny emerged and r = -0.020; P = 0.91 for RDI) and this could partly be explained by the fact that there was a group of hybrids that combined high weevil resistance with high yield, and another group that showed high yield but were susceptible to weevil attack and/or that showed low yield but were resistant to weevil damage.

Broad sense heritabilities (calculated as 1-1/F) were 74%, 71%, 58%, and 53% for grain yield, prolificacy, log-transformed number of weevils emerged, and Relative Dobie index of susceptibility (Table 5). Dari et al (2010) reported broad sense heritabilities of 62% and 50% for F_1 progeny emerged among early generation inbred lines and their corresponding test cross hybrids. In a divergent selection study, Dhliwayo and Pixley (2003) reported low heritability estimates for weevil resistance in the F_3:F_4 maize populations. The moderate to high estimates for heritability in this study reflected high GCA variance for yield performance and weevil resistance and suggest that the traits could be improved by selection

Conclusions

Our results concur with the findings of Derera et al (2008), who found that additive and non-additive gene action were important in determining grain yield. Additive gene action was significant for controlling weevil resistance implying that the greatest effectiveness in breeding for this trait can be made by selecting during inbreeding in this set of regional maize germplasm. The moderate to high estimates of broad-sense heritability for weevil resistance and grain yield reflected high genetic variance, thus, the traits could be improved by selection. More so, the variation among hybrids for both weevil resistance and yield potential showed that selection for lines, which combine both high weevil resistance and grain yield can be effective. The fact that parental lines used in crosses in this study were a representative sample of the major heterotic groups used in regional breeding programs and that, among these, only a few lines were both weevil resistant and high-yielding; poses a challenge to southern African breeders to incorporate both traits into their germplasm. However, practical considerations when implementing weevil-resistance selection schemes and the complications associated with incorporating two complex traits: weevil resistance and grain yield, into germplasm might be challenges that hamper breeding progress. Unless improvement for weevil resistance can be effectively integrated within routine breeding programs at acceptable costs, breeders are likely to be reluctant in incorporating weevil-resistance-breeding into their programs.

Acknowledgements

Financial support of laboratory evaluation by CIMMYT is gratefully acknowledged. The development of crosses and field evaluation of the hybrids study was funded by the Rockefeller Foundation and Seed Co Ltd. Germplasm lines were obtained from Seed Co Ltd and CIMMYT.

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