

## RESISTANCE OF MAIZE TO THE MAIZE WEEVIL: I. ANTIBIOSIS

J. DERERA, K.V. PIXLEY<sup>1</sup> and P. DENASH GIGA<sup>2</sup>

Department of Research & Specialist Services, P. O. Box CY550, Causeway, Harare, Zimbabwe

<sup>1</sup>CIMMYT-Zimbabwe, P. O. Box MP 163, Mt. Pleasant, Harare, Zimbabwe

<sup>2</sup>University of Zimbabwe, P. O. Box MP 167, Mt. Pleasant, Harare, Zimbabwe

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### ABSTRACT

Resistance to damage by maize weevil (*Sitophilus zeamais* Motsch.) is critically important to subsistence farmers who typically store maize grain on-farm. To evaluate grain's antibiosis effects to weevil, 18 inbred lines, six each from Southern Africa, Mexico and CIMMYT-Zimbabwe were mated in sets, according to a North Carolina Design II. Hybrids were advanced to F<sub>2</sub> by controlled full-sib matings. Tests of weevil antibiosis of grain were conducted under controlled temperature and relative humidity. Fifty-gram samples of each hybrid and line were infested with 32 unsexed weevils for 10 days. F<sub>1</sub> progeny were counted at 2-day intervals until all progeny had emerged. Some hybrids had detrimental effects to weevil-biology (antibiosis), as hybrids differed significantly for adult mortality (0 to 89%), progeny emergence (1 to 188 weevils), development period (29 to 44 days) and relative index of susceptibility (0.3 to 11.7). Variation for index of susceptibility (antibiosis) among hybrids was more in F<sub>1</sub> than F<sub>2</sub> generation. Additive, non-additive, and maternal effects were significant in determining weevil resistance for F<sub>1</sub> seed and F<sub>2</sub> grain. Variance of GCA effects for lines used as females was larger than that for lines used as males, suggesting that breeders developing weevil resistant hybrids should place greatest emphasis on choice of the female parent. Results indicate that it is essential to evaluate weevil resistance of F<sub>2</sub> grain, because we generally found no relationship between performance in F<sub>1</sub> and F<sub>2</sub>, and because it is weevil resistance in F<sub>2</sub> that is of practical significance to farmers and grain merchants.

*Key Words:* Antibiosis, insect resistance, maize, *Sitophilus zeamais*

### RÉSUMÉ

La résistance aux dégâts des charançons du maïs (*Sitophilus zeamais* Motsch.) est très importante aux agriculteurs de subsistance qui stoquent leur maïs aux champs. Pour évaluer les effets d'antibiose des grains sur les charançons, 18 lignées de familles, dont six chacune provenait de l'Afrique du Sud, du Mexique, et du CIMMITY-Zimbabwe ont été mises en groupes selon le protocole II du Carolina Nord. Les hybrides ont été avancés à F<sub>2</sub> par croisement contrôlé des vraies soeurs. Les tests d'antibiose des charançons des grains ont été conduits dans les conditions de température et d'humidité relative contrôlées. Des échantillons de 55 g de chaque hybride et lignées ont été infestées avec 32 charançons sans sexes pour 10 jours. La progéniture F<sub>1</sub> a été comptée à un intervalle de deux jours jusqu'à ce que toute la progéniture ait émergé. Certains hybrides à effets néfastes sur la biologie des charançons (antibiose), comme des hybrides ont été différents significativement pour la mortalité des adultes (0 à 89%), l'émergence de la progéniture (1 à 188 charançons), la période de développement (29 à 44 jours) et pour l'indice de sensibilité (0.3 à 11.7). La variation de l'indice de sensibilité (antibiose) parmi les hybrides était plus importante chez les F<sub>1</sub> que les F<sub>2</sub>. Des effets additifs, non additifs et effets maternels étaient significatifs dans la détermination de la résistance au charançon pour F<sub>1</sub>, les semences et les grains F<sub>2</sub>. La variation des effets de GCA pour des lignées utilisées comme femelles était large plus que celles utilisées comme mâles, suggérant que les sélectionneurs qui développent des hybrides résistants aux charançons devraient mettre de l'importance sur le

choix des parents femelles. Des résultats montrent qu' il est essentiel d'évaluer la résistance au charançon des grains  $F_2$ , parce que nous avons trouvé généralement qu'il n'y a pas de relation entre les performances de  $F_1$  et  $F_2$ , et c'est la résistance au charançon de  $F_2$  qui a de l'importance pratique aux agriculteurs et les marchands des grains.

*Mots Clés:* Antibiose, résistance des insectes, maïs, *Sitophilus zeamais*

## INTRODUCTION

Genetic resistance of maize grain to storage insects is an important component of integrated control for use in rural storage, but progress towards finding and using such resistance has been limited. Farmers in Zimbabwe have been demanding maize with good storability (Jayne, T. personal communication, cited in Blackie, 1994), because most of the available hybrids are susceptible to maize weevil (*Sitophilus zeamais* Motsch.) (Giga and Mazarura, 1991). Pesticides, especially Malathion (O,O-dimethyl-s-1,2-di(carboethoxy) ethyl phosphorodithioate), have for many years been providing effective control of maize weevil in rural areas of Zimbabwe (Giga and Mazarura, 1990). However, continued use of insecticides may lead to breakdown in their effectiveness and is hampered by potential hazard to users and consumers.

Assessment of the intrinsic levels of weevil resistance in maize grain has shown large variation among maize genotypes from Eastern, Southern and Western Africa and Latin America (Wright *et al.*, 1989; Giga and Mazarura, 1991; Kossou *et al.*, 1993; Tadesse *et al.*, 1995). Inheritance of grain resistance to maize weevil has been reported to involve maternal effects, additive and non-additive gene action (Widstrom *et al.*, 1975).

The basis of grain resistance to weevil has been explained according to Painter's (1951) three-fold resistance mechanism as antibiosis, non-preference and tolerance. Antibiosis resistance is the ability of a host to injure the pest, reduce reproduction potential, retard rate of development and or kill the pest (Dent, 1991). Schoonhoven *et al.* (1975) reported antibiosis resistance of grain to weevil, while Kang *et al.* (1995), Schoonhoven *et al.* (1976) and Gomez *et al.* (1982; 1983) have reported non-preference. Horber (1989) argued that host tolerance was inapplicable or not useful in the case of stored grain, because grain is dormant and damage incurred is terminal. Thus, selection

of grain for weevil-resistance should focus on antibiosis and non-preference resistance types. This paper will discuss antibiosis, while a companion paper focuses on non-preference type of resistance to weevil (see Derera *et al.*, 2001, this volume).

Recent studies have shown that hydroxycinnamic acids (phenolics) play an important role in grain resistance to weevil through mechanical and antibiosis resistance types (Serratos *et al.*, 1987; Classen *et al.*, 1990; Arnasson *et al.*, 1992, 1997; Sen *et al.*, 1994;). Classen *et al.* (1990), Sen *et al.* (1994), and Arnasson *et al.* (1997) reported that kernel hardness was correlated to phenolics, because phenolic acids esterified to carbohydrates form dimers, feruloyl and p-coumaroyl arabinoxylaus, which result in a mechanical cross-link in the cell wall; hence these dimers make tissues hard and limit biodegradability of the cellwall polysaccharides by the insects. Resistant hybrids have higher levels of phenolic acids, which cause adverse effects to weevil feeding and survival, hence biochemical screening may be used as a first step towards selection of genotypes for resistance. However, we are not aware of any published attempts to develop protocols for biochemical screening of maize for resistance to the maize weevil, despite their apparent advantages compared to timely and costly conventional methods using live insects and long evaluation periods in controlled environment rooms.

Most published studies about weevil resistance have evaluated grain resistance in  $F_1$  crosses, yet farmers store  $F_2$  grain. We evaluated weevil resistance of both  $F_1$  seed and  $F_2$  grain to enable us to study inheritance of weevil resistance while also obtaining results relevant to farmers. This research was designed to study the levels of antibiosis effects and the genetic basis of resistance in  $F_1$  and  $F_2$  hybrids. A companion paper (Derera *et al.*, 2001) presents an analysis of non-preference type of resistance to weevil for the same hybrids. An understanding of the genetic basis and

mechanisms of resistance is essential to develop maize with improved levels of resistance.

## MATERIALS AND METHODS

**Formation of hybrids.** The maize hybrids used in this study were derived from 18 inbred lines, 6 of each from southern Africa, Mexico and CIMMYT-Zimbabwe, respectively (Table 1). The lines from Mexico were reported to be resistant to maize weevils at CIMMYT-Mexico (D. Bergvinson, personal communication), while resistance of southern African and CIMMYT-Zimbabwe lines had not been previously evaluated. Two subgroups of 3 lines were formed within each group, and crosses were made according to a North Carolina design II mating scheme with six sets (Comstock and Robinson, 1952). The lines of the same heterotic orientation were assigned to

the same subgroup, such that crosses were formed between lines with different heterotic orientation. Sets, consisting of 9 hybrids each, were formed among subgroups of lines (Table 1): resistant x regional (subgroup 1 x 3), resistant x resistant, (2 x 1), regional x regional (3 x 4), CIMMYT x resistant (6 x 2), regional x CIMMYT (4 x 5) and CIMMYT x CIMMYT (5 x 6). The sets were balanced, meaning that each line was used once as male (3 hybrids) and once as female (3 hybrids) in different sets; lines used as females are always listed first, and males second (e.g. Set 1 x 3 used lines 1, 2 and 3 as females for lines 7, 8 and 9 as males). The single crosses from the Design II mating, plus reference entries, including commercial hybrid 'SR52' were grown at Harare during summer of 1996/97. Plant to plant, full-sib pollination within each plot was conducted to form F<sub>2</sub> grain for each hybrid. Pollination for two

TABLE 1. Pedigree, origin, and relative index of susceptibility to weevil for 18 inbred maize lines and four reference entries, and groups and sub-groups of the lines used to form hybrids in a North Carolina Design II mating

Group	Sub-group	Inbred line	Pedigree	Origin	Relative index of susceptibility	Resistance category
CIMMYT-Mexico (Resistant)	1	1	Ratray Arnold 8149 1-6-2-1-1-b-B	C-Mex†	5.4‡	MR#
		2	Ratray Arnold 8149 1-7-1-1-1-b-B	C-Mex	6.7	MR
		3	Pool 23QPM 5-9-5-2-1-b-B	C-Mex	7.5	S
	2	4	Poza Rica 8121 7-12-1-1-1-b-B	C-Mex	8.5	S
		5	Poza Rica 8121 7-2-5-1-1-b-B	C-Mex	5.5	MR
		6	Muneng 8128 14-11-2-1-1-b-B	C-Mex	5.9	MR
Southern Africa (Regional)	3	7	M162W	RSA	7.4	S
		8	SC (Malawi 95A)	Mal/Zim	7.6	S
		9	NAW5867	RSA	8.0	S
	4	10	M37W-X-X-6-X	RSA	7.6	S
		11	N3 (Malawi 95A)	Mal/Zim	9.7	S
		12	I137TN-X-X-1-X	RSA	8.4	S
CIMMYT-Zimbabwe (CIMMYT)	5	13	CML202	C-Zim	7.8	S
		14	CML216	C-Zim	6.7	MR
		15	FR810/TZMSRW-5-2-1-X-1-B	C-Zim	6.7	MR
	6	16	CML206	C-Zim	8.7	S
		17	[M37W/ZM6073#bF37sr-2-3sr-6-2X]-8-2-X-1-B	C-Zim	4.5	MR
		18	[MSRXPOOL9]C1F2-176-4-1-4-X-X-B	C-Zim	8.5	S
Reference Entries			Kayile (local, open-pollinated)	Zimbabwe	9.9	S
			Oaxaca 179 (composite resistant check)	Mexico	8.8	S
			Popcorn (susceptible check)	Zimbabwe	11.4	HS

† C-Mex: CIMMYT, Mexico; RSA: Republic of South Africa; Mal/Zim: Malawi and Zimbabwe; C-Zim: CIMMYT, Zimbabwe

‡ Relative index of susceptibility is the weevil susceptibility relative to SR52, the susceptible hybrid check

# MR: moderately resistant; S: susceptible; HS: highly susceptible

hybrids in the regional x regional set failed to produce seed; hence 52 of the possible 54 hybrids were screened for maize weevil resistance.

**Resistance tests.** After harvest, all grain samples were frozen at  $-20^{\circ}\text{C}$  for 10 days to kill any insects or eggs that may have been present on grain due to natural, random insect attack in the field. Grain samples were then conditioned in a constant temperature and humidity (CTH) room at  $28\pm 2^{\circ}\text{C}$  and  $70\pm 5\%$  relative humidity for 42 days before being subjected to weevil infestation. The local commercial hybrid SR52 was used as a susceptible control, while Mexican composite 'Oaxaca 179' was included as a resistant check. The local open pollinated variety 'Kayile', and a local popcorn obtained from the University of Zimbabwe Farm were also used as standard checks.

After removing damaged kernels, each sample was divided into four 50 g sub-samples (replications). Each 50g sub-sample was placed in a glass jar ( $500\text{ cm}^3$ ) that was closed with a mesh screen lid. The jars were arranged in the CTH room as a randomised complete block design having four replications. Each jar was infested with 32 unsexed weevils, aged 21 to 28 days, from a laboratory culture. The weevils were removed and the numbers of dead and live insects were recorded after a 10-day oviposition period in the CTH room. The maize sub-samples were then incubated in the CTH room. Progeny emergence counts were made every two days beginning 25 days after the removal of the parent insects and ending when all progeny ( $F_1$ ) had emerged. Emerged progenies were removed from the jars at each count.

The total number of progeny that emerged and their mean development period were derived for each replicate and subjected to an analysis of variance. Median development period was calculated as the number of days from day-5 of oviposition to 50% emergence of progeny. An index of susceptibility (Equation 1) was calculated for each hybrid and parent inbred lines according to Dobie (1977): Equation 1:

$$\text{Index of susceptibility} = 100 \times \left[ \log_e(\text{total number of } F_1 \text{ adults emerged}) / (\text{median development period}) \right]$$

A relative index of susceptibility for each genotype was also calculated as the index of susceptibility expressed as a proportion of the index of susceptibility for the susceptible check, SR52 (Dobie, 1977) and multiplied by 10 for convenience (Giga and Mazarura, 1991).

**Statistical analyses.** A random-effects model was used for analyses of variance (ANOVA) for adult weevil mortality, number of progeny emerged, mean development period and index of susceptibility data of inbred lines and hybrids. Mean square expectations for the sources of variation for index of susceptibility of hybrids ( $F_1$  and  $F_2$ ) were calculated as described by Hallauer and Miranda (1988). The variation due to entries was partitioned into sources due to sets and hybrids-within-sets. Further, hybrids-within-sets was partitioned into variation due to females within sets, males within sets and female x male interaction within sets. Throughout this paper, variation due to females within sets, males within sets and males x females within sets are referred interchangeably as  $GCA_f$  (general combining ability effects for females within sets),  $GCA_m$ , and SCA (specific combining ability effects for hybrids within sets), respectively (Hallauer and Miranda, 1988). GCA and SCA effects were fixed, while replications-within-sets were considered random sources of variation.

## RESULTS AND DISCUSSION

**Grain resistance.** Antibiosis resistance, or significant detrimental effects to the biology of weevil was identified among inbred lines and hybrids. Significant differences were recorded for adult weevil mortality, progeny emergence, development period and the index of susceptibility of maize genotypes (Table 2). In general, hybrids exhibited higher levels of antibiosis effects in  $F_1$  than  $F_2$  generation.

Parent weevil mortality was almost always below 10%, but ranged from 0 to 89% in  $F_1$ , and from 0 to 42% in  $F_2$  hybrids (Table 2).  $F_1$  hybrids 5x1, 5x3 and 6x2 had very high adult weevil mortality, suggesting they contained antibiosis factors, which were lethal to weevil. Progeny ( $F_1$ ) emergence ranged from 1 to 169 in  $F_1$  and from 18 to 188 in  $F_2$  hybrids (Table 2). Similar results,

TABLE 2. Parent mortality, F<sub>1</sub> weevils emerged, relative index of susceptibility (RI) and rank of RI for F<sub>1</sub> and F<sub>2</sub> hybrids from a North Carolina Design II mating among 18 maize lines

Hybrid	Set	Parent mortality (%)	F <sub>1</sub> hybrids		Rank	Parent mortality (%)	F <sub>2</sub> hybrids		Rank*
			F weevils <sup>1</sup> (No.)	Relative index of suscept.			F weevils <sup>1</sup> (No.)	Relative index of suscept.	
1 x 7†	Res x Reg‡	0.8	127	10.4	42	4.7	101	9.6	28
1 x 8	Res x Reg	1.0	45	8.0	6	4.7	105	8.9	12
1 x 9	Res x Reg	0.0	104	10.1	35	1.6	103	9.0	13
2 x 7	Res x Reg	0.0	154	10.9	48	8.6	79	8.4	5
2 x 8	Res x Reg	7.8	69	9.0	13	2.4	120	9.7	32
2 x 9	Res x Reg	6.3	84	9.5	24	0.8	100	9.1	15
3 x 7	Res x Reg	7.8	125	10.2	37	2.4	167	10.4	47
3 x 8	Res x Reg	0.0	79	8.6	9	0.0	156	10.5	49
3 x 9	Res x Reg	2.1	87	9.3	18	7.0	118	9.4	25
4 x 1	Res x Res	0.8	68	8.5	8	2.4	79	8.5	6
4 x 2	Res x Res	2.3	85	9.5	24	7.8	79	8.5	6
4 x 3	Res x Res	0.0	83	9.4	21	10.9	105	9.2	17
5 x 1	Res x Res	88.3	2	1.32	10.9	96	8.9	9	
5 x 2	Res x Res	0.0	161	11.0	49	3.9	91	9.2	17
5 x 3	Res x Res	89.1	1	0.3	1	1.6	117	10.5	49
6 x 1	Res x Res	3.9	84	9.5	24	16.4	51	7.9	4
6 x 2	Res x Res	48.4	21	5.6	4	4.7	62	7.9	3
6 x 3	Res x Res	9.4	79	9.0	13	42.2	18	4.4	1
7 x 10	Reg x Reg	5.0	129	10.6	44	3.1	121	9.9	37
7 x 11	Reg x Reg	5.5	121	10.6	44	3.1	101	9.0	13
7 x 12	Reg x Reg	24.0	118	10.3	39	0.0	155	10.4	46
8 x 10	Reg x Reg	40.6	32	5.1	3	-	-	-	-
8 x 11	Reg x Reg	25.0	38	5.7	5	1.6	131	9.7	32
8 x 12	Reg x Reg	4.2	88	8.8	11	3.1	140	9.8	35
9 x 10	Reg x Reg	4.7	110	10.0	32	13.3	81	8.7	8
9 x 11	Reg x Reg	1.6	119	10.1	35	9.4	140	10.1	41
9 x 12	Reg x Reg	2.1	101	10.0	32	-	-	-	-
10 x 13	Reg x CIM	2.4	98	9.8	30	0.8	103	9.4	23
10 x 14	Reg x CIM	2.4	99	9.7	28	2.4	123	9.7	32
10 x 15	Reg x CIM	13.3	69	9.1	16	2.4	128	9.9	39
11 x 13	Reg x CIM	0.0	110	10.0	32	1.6	144	10.5	49
11 x 14	Reg x CIM	1.0	110	8.9	12	3.1	117	9.2	17
11 x 15	Reg x CIM	3.1	99	9.4	21	0.0	154	10.3	45
12 x 13	Reg x CIM	3.1	139	10.2	38	3.9	141	9.9	37
12 x 14	Reg x CIM	0.0	109	9.9	31	0.8	115	9.3	20
12 x 15	Reg x CIM	1.6	132	10.3	39	3.1	128	9.5	27
13 x 16	CIM x CIM	3.1	78	9.4	19	3.1	188	10.6	52
13 x 17	CIM x CIM	4.2	61	8.6	9	0.8	148	10.2	43
13 x 18	CIM x CIM	4.7	61	8.37	1.6	116	9.6	28	
14 x 16	CIM x CIM	1.6	128	10.3	39	4.7	172	10.2	43
14 x 17	CIM x CIM	0.0	151	10.5	43	8.9	60	7.8	2
14 x 18	CIM x CIM	3.9	89	9.2	17	2.4	154	10.4	47
15 x 16	CIM x CIM	0.0	169	11.7	54	1.6	96	9.3	20
15 x 17	CIM x CIM	3.1	167	11.4	53	3.1	136	10.1	41
15 x 18	CIM x CIM	6.3	163	11.3	52	0.8	93	8.9	9
16 x 4	CIM x Res	3.1	102	9.6	27	1.6	111	9.4	25
16 x 5	CIM x Res	2.4	94	9.4	19	0.8	124	9.8	35
16 x 6	CIM x Res	0.0	136	10.6	44	2.4	112	9.4	23
17 x 4	CIM x Res	2.4	150	11.0	49	1.6	130	9.6	31
17 x 5	CIM x Res	0.8	133	10.6	44	0.0	110	9.3	20
17 x 6	CIM x Res	1.6	152	11.2	51	2.4	92	8.9	9
18 x 4	CIM x Res	4.2	90	9.4	21	6.3	94	9.1	16
18 x 5	CIM x Res	0.0	98	9.7	28	2.4	117	9.6	28
18 x 6	CIM x Res	4.7	74	9.0	13	3.1	113	9.9	39
SR52 (Susceptible)		3.1	95		7.8	129			
F (Sig.)		**	**	**	**	**	**	**	
Std. Error of a difference		5.5	25	1.1		5.4	24	0.9	

† Refer to Table 1 for pedigree and descriptions for each line

‡ Res=resistant; Reg=regional; CIM=CIMMYT (see Table 1 for details)

Phenotypic correlation coefficient between F<sub>1</sub> and F<sub>2</sub> for RI = -0.01; rank correlation coefficient = -0.09

\*

namely, 3 to 143 progeny emerged among 25 maize genotypes, were reported by Tadesse *et al.* (1995). Progeny development period ranged from 29 to 44 days in  $F_1$ , but did not differ among  $F_2$  hybrids (mean of 36 days), suggesting reduced antibiosis effects in  $F_2$  generation (data not presented). Gomez *et al.* (1982) reported significant differences in number of days to pupation, ranging from 30 to 38 days among maize genotypes.

Relative index of susceptibility ranged from 0.3 to 11.7 in  $F_1$ , and from 4.4 to 10.6 among  $F_2$  hybrids (Table 2). These results are not very different from relative index of susceptibility ranging from 4 to 12 among 217 materials, reported by Dobie (1977), and relative index from 6.5 to 12.1 among 84 materials reported by Giga and Mazarura (1991). The mean relative index of susceptibility for sets of hybrids ranged from 7.4 to 10.2 for  $F_1$ , and 8.3 to 9.7 for  $F_2$  hybrids (Table 3). The resistant x resistant set of hybrids was significantly more resistant to weevil than all other sets both for  $F_1$  and  $F_2$  hybrids; there were no significant differences for weevil resistance among any of the remaining five sets of hybrids. This result suggests that significant weevil resistance was generally obtained only for hybrids with both parent lines being resistant to weevil.

We classified materials with relative index of susceptibility  $\leq 4$  as resistant, 4.1 to 6 moderately resistant, 6.1 to 8.0 moderately susceptible, 8.1 to 10.0 susceptible, and  $\geq 10.1$  highly susceptible. To provide a basis for comparisons across experiments, we defined the relative index of susceptibility of hybrid SR52 to be 10.0. Hence, genotypes in the susceptible group were similar to

SR52. Four percent of the hybrids were classified resistant in  $F_1$ , but none were resistant in  $F_2$  (Table 2). A local popcorn variety was highly susceptible, while the open-pollinated local variety (Kayile) and the Mexican check (Oaxaca179) were susceptible and similar to SR52 (Table 1). The parent inbred lines for the North Carolina Design II ranged from moderately resistant to susceptible. A less conservative classification method might put all materials that were significantly less susceptible than SR52 in the resistant category. Presently, there is no agreed method for classifying genotypes for resistance to weevil. In addition, conclusions are strongly influenced by choice of susceptible check for use in calculating relative index of susceptibility. Dobie (1977) recommended the use of the Mexican variety 'Cacahuacintle' as a reliable susceptible check. We used SR52 as a susceptible check in the current study, because previous researchers (Giga and Mazarura, 1991; Dobie, 1977) classified it susceptible, relative to Cacahuacintle.

**Genetics of weevil resistance.** Genetic analyses were performed only for the index of susceptibility because it incorporates all resistance parameters (Equation 1). Variance of general combining ability effects of female lines ( $GCA_f$ ) was significant for both  $F_1$  and  $F_2$ , while that of  $GCA_m$  ( $GCA$  effects of male lines) was significant only for  $F_1$  hybrids (Table 4).  $GCA$  (additive) and  $SCA$  (non-additive) effects were of similar importance in explaining differences in antibiosis among hybrids. Greater importance of  $GCA_f$  relative to  $GCA_m$ , however, indicated importance of additive maternal effects determining antibiosis type of

TABLE 3. Mean index and relative index of susceptibility to weevils for sets of  $F_1$  and  $F_2$  maize hybrids for a North Carolina Design II mating among 18 maize lines

Hybrid sets	Index of susceptibility		Relative index to susceptibility	
	$F_1$	$F_2$	$F_1$	$F_2$
CIMMYT x CIMMYT	12.9 (6) <sup>†</sup>	13.5 (4)	10.2 (6)	9.6 (4)
CIMMYT x Resistant	12.8 (5)	13.2 (2)	10.1 (5)	9.4 (2)
Regional x CIMMYT	12.4 (4)	13.6 (6)	9.8 (4)	9.7 (6)
Regional x Regional	11.9 (2)	13.5 (4)	9.4 (2)	9.6 (4)
Resistant x Regional	12.2 (3)	13.2 (2)	9.6 (3)	9.4 (2)
Resistant x Resistant	9.4 (1)	11.6 (1)	7.4 (1)	8.3 (1)
Sig. (F)	**	**	-	-
Std. err. of a difference	0.4	0.3	-	-

<sup>†</sup> Ranks within column are shown in brackets. \*\* Significant at 1% probability level

resistance to weevil in both  $F_1$  and  $F_2$  grain, and that differences for additive effects were contributed primarily by the female parent involved in each hybrid. These results mean that: 1) SCA effects, which are unpredictable from parent resistance *per se*, are important for weevil resistance, and 2) in as far as hybrid performance is predictable, resistant hybrids are most likely to be obtained when the more resistant parent is used as the female in producing the hybrid.

Other researchers have also reported significant additive, non-additive and maternal effects determining maize weevil resistance in maize grain (Schoonhoven *et al.*, 1975; Widstrom *et al.*, 1975 and 1983; Tipping *et al.*, 1989). Widstrom *et al.* (1975) found that dominance effects were important for seed resistance to weevil among sources segregating for maternal and endosperm genotypes.

Negative GCA and SCA effects indicated good

TABLE 4. Mean squares from analysis of variance for Dobie index of susceptibility to maize weevil for  $F_1$  and  $F_2$  generations of hybrids from a North Carolina Design II mating among 18 maize inbred lines

Source of Variation	degrees of freedom	Mean square	
		$F_1$	$F_2$
Sets(S)	5	54.93**	19.94**
Replication/S	18	5.87*	2.96*
Hybrids/S	48	19.81**	6.40**
GCA <sub>f</sub> /S	12	34.69**	10.56**
GCA <sub>m</sub> /S	12	9.38**	1.72
SCA/S	24	18.08**	6.62**
Error	144	2.90	1.73

\*, \*\* = Significant at  $P < 0.05$  and  $P < 0.01$ , respectively

TABLE 5. Estimates of general combining ability effects for index of weevil susceptibility calculated for  $F_1$  and  $F_2$  hybrids of lines used as females (GCA<sub>f</sub>) or males (GCA<sub>m</sub>) in a North Carolina Design II mating scheme

Line <sup>†</sup>	Set of hybrids	$F_1$		$F_2$		Set of hybrids	$F_1$ <sup>‡</sup>	
		GCA <sub>f</sub>	SE (±)	GCA <sub>f</sub>	SE (±)		GCA <sub>m</sub>	SE (±)
1	Res x Reg <sup>#</sup>	0.0	0.3	-0.4*	0.2	Res x Res <sup>#</sup>	-0.6*	0.3
2	Res x Reg	0.5	0.3	-0.5*	0.2	Res x Res	1.9**	0.3
3	Res x Reg	-0.3	0.3	0.9*	0.2	Res x Res	-1.3**	0.3
4	Res x Res	2.7**	0.3	0.6	0.5	CIM x Res	0.0	0.3
5	Res x Res	-3.7**	0.3	1.7**	0.5	CIM x Res	-0.2	0.3
6	Res x Res	1.0**	0.3	-2.3**	0.5	CIM x Res	0.2	0.3
7	Reg x Reg	2.4*	0.6	0.2	0.2	Res x Reg	1.1**	0.3
8	Reg x Reg	-3.3**	0.6	0.2	0.2	Res x Reg	-1.4**	0.3
9	Reg x Reg	0.9	0.6	-0.4	0.2	Res x Reg	0.3	0.3
10	Reg x CIM	-0.3	0.3	-0.1	0.3	Reg x Reg	0.1	0.6
11	Reg x CIM	0.0	0.3	0.4	0.3	Reg x Reg	-0.4	0.6
12	Reg x CIM	0.3	0.3	-0.3	0.3	Reg x Reg	0.3	0.6
13	CIM x CIM	-1.7**	0.3	0.6	0.3	Reg x CIM	0.4	0.3
14	CIM x CIM	-0.2	0.3	-0.3	0.3	Reg x CIM	-0.2	0.3
15	CIM x CIM	1.9**	0.3	-0.3	0.3	Reg x CIM	-0.2	0.3
16	CIM x Res	-0.4	0.3	0.1	0.3	CIM x CIM	0.5	0.3
17	CIM x Res	1.3**	0.3	-0.2	0.3	CIM x CIM	0.2	0.3
18	CIM x Res	-0.9**	0.3	0.1	0.3	CIM x CIM	-0.7	0.3

<sup>†</sup> Refer to Table 1 for pedigree and descriptors for each line. <sup>‡</sup> Estimates of GCA<sub>m</sub> are only presented for  $F_1$  hybrids because there was no significant variance for GCA<sub>m</sub> among  $F_2$  hybrids. <sup>#</sup> Res=resistant; Reg=regional; CIM=CIMMYT (see Table 1 for details). \*, \*\* Significant at 5% and 1% probability level, respectively; SE = standard error

(favourable) combining ability for grain's antibiosis effects. Estimates of combining ability effects for each line are only relative to the other lines included in the same set with the line. For example, regional line 8 (SC) showed negative GCA as female in  $F_1$  hybrids for set "Regional x Regional" and as male in  $F_1$  hybrids for set "Resistant x Regional" (Table 5). This result indicates that line 8 was relatively better than lines 7 and 9 when crossed as female for lines 10, 11 and 12, and as male for lines 1, 2 and 3. Estimates of GCA effects were generally not consistent from  $F_1$  to  $F_2$ , suggesting that maternal effects of lines affect resistance in  $F_1$  but are dissipated in  $F_2$  generation hybrids. The lack of consistency of GCA effects for lines used as female or male may reflect the lesser importance of male contribution to GCA effects, or it might be a consequence of the experimental design, which paired sub-groups of lines differently as female and male (as opposed to a diallel design, where each line would have been crossed to all other lines).

Variance of SCA effects was significant only for  $F_1$  hybrids in one set and  $F_2$  hybrids in two sets (Table 6). Only the "Resistant x Resistant" set had significant SCA effects in both  $F_1$  and  $F_2$ , and these were not consistent between the two generations. For example, hybrid 5x3 had the best SCA effect in  $F_1$ , but showed a reversal to unfavourable SCA effect in  $F_2$ . By contrast, hybrid 6x3 had positive SCA in  $F_1$  and negative SCA in  $F_2$ . These results are difficult to interpret. We can conclude that: 1) SCA effects were not significant for most hybrids, and 2) it is essential to assess weevil resistance for  $F_2$  grain because  $F_1$  is generally not a reliable predictor of  $F_2$  performance. It is resistance shown in  $F_2$  which is of practical significance, because farmers store and merchants trade  $F_2$  grain.

## CONCLUSION

We can only speculate whether our results would have been different from those reported herein if we had worked with hybrids exhibiting higher

TABLE 6. Estimates of SCA effects (for sets of hybrids where these were significantly different from zero) for index of susceptibility of  $F_1$  and  $F_2$  hybrids within sets of a North Carolina Design II mating among 18 maize inbred lines

Hybrid	Set	$F_1$		$F_2$	
		SCA	SE ( $\pm$ )	SCA	SE ( $\pm$ )
4 x 1 <sup>†</sup>	Res x Res <sup>‡</sup>	0.3	0.5	-0.5	0.7
4 x 2	Res x Res	-1.6**	0.5	-0.6	0.7
4 x 3	Res x Res	1.4*	0.5	1.1	0.7
5 x 1	Res x Res	-2.8**	0.5	-1.1	0.7
5 x 2	Res x Res	6.6**	0.5	-0.7	0.7
5 x 3	Res x Res	-3.8**	0.5	1.8*	0.7
6 x 1	Res x Res	2.5**	0.5	1.6*	0.7
6 x 2	Res x Res	-5.1**	0.5	1.3	0.7
6 x 3	Res x Res	2.5**	0.5	-2.9**	0.7
13 x 16	CIM x CIM	#	-	0.1	0.4
13 x 17	CIM x CIM	-	-	0.5	0.4
13 x 18	CIM x CIM	-	-	-0.7	0.4
14 x 16	CIM x CIM	-	-	0.6	0.4
14 x 17	CIM x CIM	-	-	-1.9*	0.4
14 x 18	CIM x CIM	-	-	1.4*	0.4
15 x 16	CIM x CIM	-	-	-0.7	0.4
15 x 17	CIM x CIM	-	-	1.4*	0.4
15 x 18	CIM x CIM	-	-	-0.7	0.4

<sup>†</sup> Refer to Table 1 for pedigree and descriptors for each line. <sup>‡</sup> Res=resistant; CIM=CIMMYT (see Table 1 for details). # Values are not shown because these were not significantly different from zero. \*, \*\* Significant at 1 and 5% probability level, respectively; SE = standard error



levels or greater variation for weevil resistance. Clearly, most of the hybrids in this study were susceptible to weevil and not very different from each other for this trait. Nevertheless, we found that hybrids had significant levels of antibiosis, and that variation for antibiosis among hybrids was larger in  $F_1$  than  $F_2$  generation. Additive, non-additive, and maternal effects played significant roles in determining antibiosis in  $F_1$  seed and  $F_2$  grain. Variance of GCA effects for lines used as females was generally more important than that for lines used as males, suggesting that breeders developing weevil resistant hybrids should place greatest emphasis on choice of the female parent. Our results indicate it is essential to evaluate weevil resistance of  $F_2$  grain, because we generally found no relationship between performance in  $F_1$  and  $F_2$ , and because it is weevil resistance in  $F_2$  that is of practical significance.

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#### REFERENCES

- Arnasson, J. T., Conilh de Beyssac, B., Philogene, B. J. R., Bergvinson, D., Serratos, J. A. and Mihm, J. A. 1997. Mechanisms of resistance in maize grain to the maize weevil and the larger grain borer. In: *Insect resistant maize: Recent advances and utilisation*. Proceedings of an International Symposium held at the International Maize and Wheat Improvement Center (CIMMYT), 27 November-3 December, 1994. Mihm, J. A. (Ed.), pp. 91-95. Mexico, D.F.: CIMMYT.
- Arnasson, J. T., Gale, J., Conilh de Beyssac, B., Sen, A., Miller, S. S., Philogene, B. J. R., Lambert, J. D. H., Fulcher, R. G., Serratos, A. and Mihm, J. 1992. Role of phenolics in resistance of maize grain to the stored grain insects, *Prostephanus truncatus* (Horn) and *Sitophilus zeamais* (Motsch.). *Journal of Stored Products Research* 28:119-126.
- Blackie, M. J. 1994. In: *Realising smallholder agricultural potential*. Rukuni, M. and Carl, E. (Eds.), pp. 335-347. Zimbabwe's *Agricultural Revolution*. University of Zimbabwe Publications. Harare.
- Classen, D., Arnasson, J. T., Serratos, J. A., Lambert, J. D. H., Nozzolillo, C. and Philogene, B. J. R. 1990. Correlation of phenolic acid content of maize to resistance to *Sitophilus zeamais*, the maize weevil in CIMMYT's collections. *Journal of Chemical Ecology* 16: 301-315.
- Comstock, R. E. and Robinson, H. F. 1952. Estimation of average dominance of genes. In: *Heterosis*. Gowen, J.W. (Eds.), pp. 494-516. Iowa State University Press, Ames, Iowa, USA.
- Dent, D. 1991. *Insect pest management*. CAB International, United Kingdom. 604 pp.
- Derera, J., Giga, D.P. and Pixley, K.V. 2001. Resistance of maize to the maize weevil: II. Non-preference. *African Crop Science Journal* 9:
- Dobie, P. 1977. The contribution of the Tropical Stored Products Centre to the study of insect resistance in stored maize. *Tropical Stored Products Information* 34:7-21.
- Giga, D. P. and Mazarura, U. M. 1990. Malathion resistance in *Sitophilus zeamais* (Motsch.) in Zimbabwe. *Tropical Pest Management* 36: 320.
- Giga, D. P. and Mazarura, U. W. 1991. Levels of resistance to the maize weevil, *Sitophilus zeamais* (Motsch.) in exotic, local open-pollinated and hybrid maize germplasm. *Insect Science and its Applications* 12:159-169.
- Gomez, L. A., Rodriguez, J. G., Poneleit, C. G. and Blake, D. F. 1982. Preference and utilisation of maize endosperm variants by the rice weevil. *Journal of Economic Entomology* 75:363-367.
- Gomez, L. A., Rodriguez, J. G., Poneleit, C. G., Blake, D. F. and Smith, C. R. Jr. 1983. Chemosensory responses of the rice weevil (Coleoptera: Curculionidae) to a susceptible and a resistant corn genotype. *Journal of Economic Entomology* 76:1044-1048.
- Hallauer, A. R. and Miranda, J. B. 1988. *Quantitative genetics in maize breeding*. 2nd edition. Iowa State University Press, Ames, Iowa, USA. pp. 64-74.
- Horber, E. 1989. Methods to detect and evaluate

- resistance in maize to grain insects in the field and in storage. In: *Toward insect resistance maize for the Third World. Proceedings of the International Symposium on methodologies for developing host plant resistance to maize insects*. Mexico, D.F. CIMMYT. 327 pp.
- Kang, M. S., Zhang, Y. and Magari, R. 1995. Combining ability for maize weevil preference of maize grain. *Crop Science* 35:1556-1559.
- Kossou, D. K., Mareck, J. H. and Bosque-Perez, N. A. 1993. Comparison of improved and local maize varieties in the Republic of Benin with emphasis on susceptibility to *Sitophilus zeamais* Motschulsky. *Journal of Stored Product Research* 29:333-343.
- Painter, R. H.: 1951. *Insect Resistance in Crop Plants*. McMillan, New York. 520 pp.
- Schoonhoven, A. V., Horber, E. and Mills, R. B. 1976. Conditions modifying expression of resistance of maize kernels to the maize weevil. *Environmental Entomology* 5:163-168.
- Schoonhoven, A. V., Horber, E., Wassom, C.E. and Mills, R.B. 1975. Selection for resistance to the maize weevil in kernels of maize. *Euphytica* 24:639-644.
- Sen, A., Bergvinson, D., Miller, S. S., Atkinson, J., Fulcher, G. R. and Arnason, J. T. 1994. Distribution and micro-chemical detection of phenolic acids, flavonoids, and phenolic acid amides in maize kernels. *Journal of Agricultural and Food Chemistry* 42:1879-1883.
- Serratos, A., Arnason, J. T., Nozzolillo, C., Lambert, J.D.H., Philogene, B.J.R., Fulcher, G., Davidson, K., Peacock, L., Atkinson, J. and Morand, P. 1987. Factors contributing to resistance of exotic maize populations to maize weevil, *Sitophilus zeamais*. *Journal of Chemical Ecology* 13:751-761.
- Tadesse, A., Medhin, T. G. and Hulluka, M. 1995. Comparison of some maize genotypes for resistance to the maize weevil, *Sitophilus zeamais* Motsch. (Coleoptera: Curculionidae) in Ethiopia. In: *Maize Research for stress environments. Proceedings of the Fourth Eastern and Southern Africa Regional Conference, held at Harare, Zimbabwe, 28 March -1 April 1994*. Jewell, D. C., Waddington, S.R., Ransom, J. K. and Pixley, K. V. (Eds.), pp. 198-201. Mexico D.F. CIMMYT.
- Tipping, P. W., Cornelius, P. L. and Legg, D. E. 1989. Inheritance of resistance in whole kernel maize to oviposition by the maize weevil (Coleoptera: Curculionidae). *Journal of Economic Entomology* 82:1466-1469.
- Widstrom, N. W., Hanson, W. D. and Redlinger, L. M. 1975. Inheritance of maize weevil resistance in maize. *Crop Science* 15:467-470.
- Widstrom, N. W., McMillian, W. W., Redlinger, L.M. and Wiser, W.J. 1983. Dent corn inbred sources of resistance to the maize weevil (Coleoptera: Curculionidae). *Journal of Economic Entomology* 76:31-33.
- Wright, V. F., Mills, R. B. and Willcutts, B. J. 1989. Methods for culturing stored grain insects. In: *Toward insect resistance maize for the Third World. Proceedings of the International Symposium on methodologies for developing host plant resistance to maize insects*. Mexico, D.F. CIMMYT. 302 pp.