African Crop Science Journal, Vol. 9. No. 2, pp. 441-450, 2001
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ISSN 1021-9730/2001 $ 4.00

RESISTANCE OF MAIZE TO THE MAIZE WEEVIL: II. NON-PREFERENCE

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(Received 9 June, 2000; accepted 14 December, 2000)

ABSTRACT

Although there have been significant advances in improving maize for grain yield, progress in developing varieties resistant to the maize weevil *(Sitophilus zeamais* Motsch.) has been limited. In this study, fifty-two hybrids were evaluated against the maize weevil for non-preference in free choice experiment to study gene action determining inheritance of this mechanism of resistance. Eighteen inbred lines, six each from southern Africa, Mexico and CIMMYT-Zimbabwe were used to make the hybrids. Lines were mated among sub-groups of three each, according to a North Carolina Design II scheme. F_2 grain of the hybrids was evaluated for non-preference resistance under controlled temperature and relative humidity conditions. Maize weevil preferred some hybrids, and caused grain weight losses ranging from 0.85 to 8.45% after 70 days of feeding in a free-choice environment with equal access to all maize genotypes. The maize weevil preferred 'SR52', a local commercial hybrid that we used as the susceptible check (6.62% weight loss), and other local hybrids (6.02 to 6.80% weight loss), to 'Oaxaca 179' (the resistant check), which incurred a weight loss of 3.50%. Four percent of the experimental hybrids incurred less than 2.0% grain loss and were classified as resistant, while a further 29% of hybrids were moderately resistant to weevil attack. General combining ability effects (GCA) of lines used as male and female parents were significant ($P<0.01$) and had similar variance, indicating that, on average, both parents of each hybrid contributed equally to non-preference resistance to weevil. Significant specific combining ability (SCA) effects signalled the importance of non-additive gene action for this trait. Results suggest that it is possible to develop hybrids with improved non-preference resistance of F_2 grain to maize weevil.

Key Words: Maize, maize weevil, insect resistance, non-preference, *Sitophilus zeamais*

RÉSUMÉ

Bien qu'il y a eu des progrès significatifs dans l'amélioration des rendements grains du mais, le développement des variétés résistantes au charançon du maïs (*Sitophilus zeamais* Motsch.) a été limitée. Cinquante deux hybrides ont été évalués pour la non-préference au charançon du maïs dans des essais libres pour étudier l'action du gène déterminant l'héritage de ce mécanisme de résistance. Dixuit lignées de familles, dont six chacuns sont de l'Afrique du sud, du Mexique et CIMMYT-Zimbabwe ont été utilisés pour former des hybrides. Les lignéens ont été croisées entre les sous-groupes pour chacun des trois, selon le plan de protocole II de Corolina Nord. Les grains F2 des hybrides ont été évalués pour la résistance à la non-préference sous conditions contrôllées de températures et d'humidité relative. Les charançons du maïs ont préferré certains hybrides et ont causé des pertes de poids variant entre 0.85 et 8.45% après 75 jours d'alimentation dans un environnement libre ayant même access à tous les génotypes. Le charançon du maïs a préferré 'SR52', un hybride commercial local, qui a été utilisé comme témoin susceptible (6.62% de perte de poids), et un autre hybride local (6.02 a 6.50% de perte de poids) et l''Oaxaca 179' (témoin résistant) qui a encouru une perte de poids de 3.50%. Quatre pourcent des hybrides des essais ont subi moins de 2% de perte de grains et ont été clasifiés résistants, alors que 29% des hybrides ont été modérement résistants à l'attaque du charançon du maïs. Des effets d'habitude à la combinaison (GCA) des lignées utilisées comme des parents mâles et femelles ont été significatifs (P<0.01) et avaient des variances semblables, suggérant qu'en moyenne, les deux parents ont contribué de façon égale à la résistance de non-préference au charançon. Des effets significatifs d'habitude spécifique à la combinaison (SCA) ont indiqué une action des gènes non-additive pour le caractère. Des résultats suggèrent qu'il est possible de développer des hybrides améliorés avec resistance de non-préference de grains F_2 au charançon du maïs.

Mots Clés: Maïs, charançon du maïs, résistance de l'insecte, non-préference, *Sitophilus zeamais*

INTRODUCTION

The maize weevil (*Stophilus zeamais* Motsch.) is the most destructive pest of stored maize in southern Africa. A survey of literature indicates that there is much variation in maize for resistance to the maize weevil. Exceptional grain resistance to maize weevil has been reported in indigenous landraces from Mexico, Belize and some CIMMYT genotypes (Arnasson *et al.*, 1994), while Giga and Mazarura (1991) found significant variation among genotypes from Malawi and Zimbabwe. Despite this, no significant attempts have been made towards developing maize germplasm with improved resistance to storage pests. The high levels of damage caused by insects in small farmer storage makes it imperative that breeders identify sources of resistance and select for traits that confer resistance (Smale *et al.*, 1993).

Three resistance components of plants: antibiosis, non-preference and tolerance to insect pests were reported by Painter (1951) and have been studied and found to be important bases of grain resistance to maize weevil (Gomez *et al.*, 1982, 1983; Horber, 1989; Arnasson *et al.*, 1997). Non-preference is the heritable feature of the grain, which discourages insects from feeding, colonising and oviposition or a combination of the three. Tipping *et al.* (1986, 1987) reported large differences in attractiveness of maize grain to attack by the maize weevil. Grain texture has been suggested (Tipping *et al.*, 1988) as the basis of non-preference resistance, because the smooth pericarp may deter weevils from feeding and oviposition. Thus, these studies suggest that the improvement of grain resistance to weevil should focus mainly on antibiosis and non-preference mechanisms.

Small-scale farmers grow different maize varieties to reduce the risk of grain losses due to several factors including drought and damage by storage pests such as the maize weevil. Schulten (1975) reported that farmers in Malawi grew both local varieties and commercial hybrids and that local varieties were resistant, while improved varieties and hybrids were very prone to attack by the maize weevil. Dobie (1974) also reported that the maize weevil, which is a strong flier, is capable of exercising choice of grain among hybrids. Whereas Kang *et al.* (1995) reported that the maize weevil preferred some crosses for feeding, there is still limited genetic information on the basis of non-preference resistance in maize grain. Knowledge of inheritance of non-preference resistance to weevil feeding and oviposition would be helpful in designing breeding strategies to develop resistant maize. Previous studies have been mainly confined to studying grain resistance in no-choice tests in the laboratory, yet in the field insects would select grain to feed on and for oviposition.

The objectives of this study were to evaluate non-preference resistance to weevil in free-choice trials using F_2 grain of experimental maize hybrids and to study the gene action determining inheritance of this trait. A companion paper (Derera *et al.*, 2001, this volume) report results of no-choice experiments studying inheritance of antibiosis type of weevil resistance for the same hybrids.

MATERIALS AND METHODS

Formation of hybrids. Fifty-four experimental hybrids from 18 inbred lines, six each from southern Africa, CIMMYT-Mexico and CIMMYT-Zimbabwe (Table 1) were formed. The six inbred lines from CIMMYT-Mexico were derived from four populations, which are adapted to lowland tropics, but could be grown in Harare, Zimbabwe. These were previously screened and classified as resistant to maize weevil at CIMMYT-Mexico, and therefore selected for our study. The southern African lines were selected because of their adaptation in the region and importance in regional breeding programmes. These lines have not previously been screened for resistance to the maize weevil. The CIMMYT-Zimbabwe lines, which were derived from populations with good yield and agronomic characteristics, were selected because of their tolerance to maize streak virus disease, an economically important disease in southern Africa.

The lines were grouped according to their origin as Mexico (Resistant; CIMMYT-Mexico), Regional (southern Africa) and CIMMYT (CIMMYT-Zimbabwe). Further, the lines in each group were split into two sub-groups of three each, using previous information on their pedigrees to allocate lines of the same heterotic orientation into each sub-group. Inbred lines were numbered 1 to 18, for convenience (Table 1), and hereafter, the lines and hybrids formed among them are referred to and identified by these numbers plus abbreviated pedigrees.

Lines were crossed among sub-groups of three each according to a North Carolina design II mating scheme (Comstock and Robinson, 1952), to form nine crosses in each of the six sets, during winter of 1996 at Muzarabani. Each inbred line was used as a male in one set (for three crosses) and as a female for another set of crosses (for three different crosses), thus resulting in a balanced mating design. The crossing of lines among sub-groups with different heterotic orientation was conducted to maximise the likelihood of obtaining high-yielding hybrids and to minimise the chance that any of the hybrids might lack vigour (inbreeding). The 54 F_1 experimental hybrids, plus local commercial hybrids were full-sib mated to advance the seed to F_2 grain, during summer (1996/97), at CIMMYT station near Harare. We failed to obtain adequate F_2 grain for two hybrids (8x10 and 9x12), hence grain of 52 experimental hybrids was available for the resistance screening.

Resistance screening (Free-choice test). The F_2 grain was used to evaluate non-preference resistance because this represents the generation that is stored by farmers and will be vulnerable to attack by the weevil. In addition to the 52 experimental hybrids, we included F_2 grain of five local commercial hybrids as reference entries.

TABLE 1. Pedigree and origin of inbred lines, and groups and sub-groups of the lines used to form hybrids in a North Carolina Design II mating

Group	Sub-group	Inbred No.	Pedigree	Origin
Mexico	1	1	Rattray Arnold 8149 1-6-2-1-1-b-B	CIMMYT-Mexico
(Resistant)		2	Rattray Arnold 8149 1-7-1-1-1-b-B	CIMMYT-Mexico
		3	Pool 23QPM 5-9-5-2-1-b-B	CIMMYT-Mexico
	2	4	Poza Rica 8121 7-12-1-1-1-b-B	CIMMYT-Mexico
		5	Poza Rica 8121 7-2-5-1-1-b-B	CIMMYT-Mexico
		6	Muneng 8128 14-11-2-1-1-b-B	CIMMYT-Mexico
Southern	3	7	M162W-X	South Africa
Africa		8	SC Malawi (95A)-x-B	Malawi/Zimbabwe
(Regional)		9	NAW5867-X	Zimbabwe
	4	10	M37W-X-X-6-X	South Africa
		11	N3 Malawi (95A)-X-B	Malawi/Zimbabwe
		12	I137TN-X-X-1-X	South Africa
CIMMYT-	5	13	CML202	CIMMYT-Zimbabwe
Zimbabwe		14	CML216	CIMMYT-Zimbabwe
(CIMMYT)		15	FR810/TZMSRW-5-2-1-X-1-B	CIMMYT-Zimbabwe
	6	16	CML206	CIMMYT-Zimbabwe
		17	[M37W/ZM6073#bF37sr-2-3sr-6-2X]-8-2-X-1-B	CIMMYT-Zimbabwe
		18	[MSRXPOOL9]C1F2-176-4-1-4-X-X-B	CIMMYT-Zimbabwe

The commercial hybrid 'SR52' and a Mexican composite 'Oaxaca 179' were used as the susceptible and resistant checks, respectively. The maize weevils were obtained from CIMMYT-Zimbabwe's laboratory culture; these were F_1 progeny of a field population collected from the University of Zimbabwe farm, near Harare.

Two hundred grams of undamaged grain of each hybrid were kept for 14 days in a freezer at −20°C to disinfest the grain of any prior field infestations (Horber, 1989). Maize samples were then conditioned for six weeks in a controlled temperature and humidity (CTH) room, which was maintained in darkness at 28±2°C and 70±5% relative humidity.

Using a standard hole-puncher (for preparing paper for insertion in a ring-binder notebook), we made four 3cm-diameter holes through both sides of the small paper envelopes for the experiment. Fifty grams of conditioned grain were placed inside, and the envelopes were then sealed, except for the holes, which would allow weevil entry and exit. These envelopes were randomly placed in an ovoid plastic container full of grain of a very weevil-susceptible commercial hybrid. This grain had previously been infested with 500 weevils. The envelopes were adequately spaced from each other to allow free movement of weevils, and were held in approximately vertical (standing) position by the grain of the susceptible hybrid filling the bottom of the container. This set-up was replicated four times, with each replicate forming a randomised complete block including the entire test hybrids and checks. Weevil-infested grain in each replication (large plastic container) provided the source of insects for the free-choice test. Grain samples had an equal chance of being infested, because insects were randomly distributed in the grain bulk and all envelopes were spaced within the container to allow ready access by insects. The containers were randomly placed on the shelves in a CTH room and examined after 70 days.

This period allowed insects to feed and produce at least two generations of progeny; the average development period of the maize weevil being 35 days, at optimal conditions (Gewinner *et al.*, 1996). At the end of the 70-day incubation period, the grain in each envelope was sieved, weighed and the number of insects counted. The percentage grain weight loss in each sample was calculated and Pearson phenotypic correlation coefficients between grain loss, grain texture, and 100-seed weight were calculated.

For discussion purposes, the maize hybrids were classified into five categories of resistance based on weight loss incurred by the susceptible and resistant checks:

Resistant:	grain weight loss ≤ 2.0% (less than the resistant check).
Moderately resistant:	grain weight loss between 2.1 and 4.0% (similar to the resistant check).
Moderately susceptible:	grain weight loss between 4.1 and 6.0% (less than susceptible check).
Susceptible:	grain weight loss between 6.1 and 8.0% (similar to susceptible check).
Highly susceptible:	grain weight loss greater than 8.1% (greater than the susceptible check).

Statistical analyses. General analysis of variance (ANOVA) for random effects model was conducted for grain weight loss data using the SAS (1990) statistical package. The grain weight loss data were subjected to the Design II analysis (Hallauer and Miranda, 1988), to estimate general (additive) and specific combining ability (non-additive) effects for the hybrids within and across sets. Variance of GCA effects was calculated for male (GCA_m) and female lines (GCA_f). GCA effect for each line as male and female within its respective sets of crosses, and SCA effect for each hybrid within its set of crosses, were calculated as appropriate (i.e., when ANOVA indicated that variance was statistically significant). Combining ability effects were fixed, while replication effects were treated as random.

RESULTS AND DISCUSSION

Resistance screening. There were significant ($P<0.01$) differences among hybrids for grain weight loss due to weevil damage during the 70-day free choice exposure to weevils in the CTH room (Table 2). Weight loss suffered by the experimental hybrids ranged from 0.85 to 8.45%. As expected, the resistant check (Oaxaca 179) incurred significantly lower weight loss than the susceptible check (SR52). The four commercial hybrids incurred weight losses similar to SR52 (Table 2). When averaged for all hybrids within each set of the Design II mating, weight loss ranged from 2.74% in the "resistant x resistant" to 5.98% in the "regional x CIMMYT" set (Table 3).

The significant differences we recorded among hybrids for weevil damage during this free choice experiment indicated that the maize weevil preferred some hybrids relative to others. Small-scale farmers in Africa and Latin America grow a combination of higher-yielding, improved maize varieties as well as a wide range of traditional varieties. There is much anecdotal evidence that

TABLE 2. Grain weight loss of the 10 most resistant and 10 most susceptible experimental hybrids from a Design II mating among 18 inbred maize lines, and for 6 reference entries

Hybrid	Abbreviated pedigree†	Hybrid set	Grain weight loss (%)	Rank‡
Experimental hybrids				
6 x 2	Muneng8128 x RA8149 1-7	Res x Res#	0.85	1
6 x 1	Muneng8128 x RA8149 1-6	Res x Res	1.77	2
5 x 1	PR8121 7-2 x RA8149 1-6	Res x Res	2.07	3
5 x 2	PR8121 7-2 x RA8149 1-7	Res x Res	2.37	4
4 x 2	PR8121 7-12 x RA8149 1-7	Res x Res	2.49	5
4 x 1	PR8121 7-12 x RA8149 1-6	Res x Res	2.81	6
16 x 6	CML206 x Muneng8128	CIM x Res	2.88	7
7 x 11	M162W x N3	Reg x Reg	3.11	8
2 x 9	RA8149 1-7 x NAW5867	Res x Reg	3.12	9
9 x 11	NAW5867 x N3	Reg x Reg	3.33	10
18 x 6	MSRXPOOL9 x Muneng8128	CIM x Res	6.32	44
13 x 18	CML202 x MSRXPOOL9	CIM x CIM	6.43	45
12 x 15	I137TN x FR810/TZMSRW	Reg x CIM	6.79	49
3 x 8	Pool23QPM x SC	Res x Reg	6.95	51
18 x 5	MSRXPOOL9 x PR8121 7-2	CIM x Res	7.20	52
11 x 14	N3 x CML216	Reg x CIM	7.93	53
16 x 4	CML206 x PR8121 7-12	CIM x Res	7.95	54
7 x 12	M162W x I137TN	Reg x Reg	7.95	55
10 x 14	M37W X CML216	Reg x CIM	8.29	56
8 x 11	SC x N3	Reg x Reg	8.45	57
Reference entries				
PAN695			6.72	48
CX5005			6.80	50
CX5003			6.02	41
SC501			6.43	46
Oaxaca 179 (Resistant)			3.50	11
SR52 (Susceptible)			6.62	47
Mean			4.90	
Significant (F)			**	
LSD (5%)			1.34	

† Refer to Table 1 for complete pedigree and origin of each line

‡ Note that ranks are not continuous because only the 10 most resistant and the 10 most susceptible experimental hybrids and the 6 reference entries are presented

Res = resistant; CIM = CIMMYT-Zimbabwe; Reg = regional

** Significant at 1% probability level

"local" maize varieties, which are stored for planting from one season to the next, bartered or shared among neighbours and handed-down from one generation to the next of farmers, are generally less susceptible to weevil than "improved" maize varieties. This might in fact be expected, because farmers inadvertently (or deliberately) effect recurrent selection for weevil resistance, since each season it is the undamaged grain that survives to germinate and produce the next crop of grain and "seed". Giga and Mazarura (1991) have reported preference of commercial hybrid grain by the maize weevil. Schulten (1975) and Wright *et al.* (1989) have reported that farmers grow improved varieties specifically for sale while the traditional maize, which is less prone to weevil damage, is stored for home consumption. Although it was too small a sample to justify conclusions about general weevil susceptibility of commercial or "improved" varieties, the four commercial hybrids we evaluated were susceptible and similar to the susceptible check for damage by weevil (Table 2).

Based on our classification, hybrids 6x1 and 6x2 were classified as resistant, while 10x14 and 8x11 were highly susceptible to the maize weevil (Table 2). Frequency distribution of the 52 experimental hybrids for weight loss was approximately normal, with 4% resistant, 29% moderately resistant, 44% moderately susceptible, 19% susceptible and 4% highly susceptible hybrids. This wide variation of genotypes for resistance to maize weevil indicated segregation of resistance genes in the F_2 generation hybrids. This result is similar to Dobie's (1977) categorisation of 217 genotypes, which showed normal distribution with 20% of the genotypes at the lower end of the weevil susceptibility index scale (resistant), 30% moderately resistant/susceptible, 30% susceptible and 20% highly susceptible.

TABLE 3. Mean grain weight loss incurred by hybrids within each set of a Design II mating among 18 inbred maize lines

Set	Grain weight loss %	Rank
CIMMYT x CIMMYT	4.69	3
CIMMYT x resistant	5.24	4
Regional x CIMMYT	5.98	6
Regional x regional	5.63	5
Resistant x regional	4.69	2
Resistant x resistant	2.74	1
Mean	4.82	
LSD (0.05)	0.47	

Genetic basis of weevil resistance. Mean squares of GCA for lines used as males (GCA_m), lines used as females (GCA_f) and SCA of hybrids for grain weight loss across sets were highly significant ($P<0.01$) (Table 4). GCA and SCA effects were of similar importance for explaining differences of grain weight loss among hybrids, accounting for 47 and 53% of sum of squares for hybrids, respectively. GCA_m (25%) and GCA_f (22%) effects across sets were of similar magnitude.

The significant GCA for weight loss indicates that additive gene action was important in determining non-preference resistance to maize weevil. Equal importance of GCA_m and GCA_f indicated that maternal effects were not important in determining non-preference. Thus both parents were contributing similar levels of resistance to these hybrids. Furthermore, significant SCA for grain weight loss among hybrids indicated that non-additive gene action was important in determining non-preference of some hybrids. However, similar male and female additive effects for non-preference were in contrast with Kang *et al.*'s (1995) findings in which maternal effects were significant for non-preference of F_2 hybrids by the weevil in free-choice tests.

Negative GCA for grain weight loss indicates non-preference, while positive GCA indicates preference of hybrids of a given line by the weevil (Table 5). Inbred lines 2 and 9 had significant negative GCA for weight loss as both male and female, indicating that these inbred lines contributed more than average levels of non-preference type of resistance to maize weevil as both pollen sources and seed parents. It is important to remember that performance of lines in this experiment is only relative to the other lines used within the same set of hybrids; therefore, inferences about the broader value of lines in breeding programmes should be made with caution.

Regional inbred lines (9 and 12) that had negative GCA for non-preference resistance to weevil as male or female might be directly useful in regional

TABLE 4. Mean squares from analysis of variance across sets, and for each set of a Design II mating among 18 inbred maize lines for grain weight loss (%) of hybrids caused by weevils during a non-preference experiment

Source of Variation	Across sets			Res[†] x Reg	CIM x Res	Res x Res	Reg x CIM	Reg x Reg	CIM x CIM
	df	MS	df	Mean square					
Sets	5	45.96**							
Replication	18	17.68**	3	11.90**	12.40**	8.83**	38.30**	17.30**	17.40**
F2 Hybrids	46	7.69**	8	5.91**	10.80**	5.58**	7.70**	15.30**[‡]	2.79**
GCA female	12	6.21**	2	13.80**	3.99	1.63**	4.03*	11.70*	2.10
GCAmale	12	7.11**	2	2.73**	1.59	17.00*	7.46**	7.36	6.53**
SCA	22	8.05**	4	3.55**	18.70**	1.85**	9.66**	18.40**	1.26
Error	138	1.03	24	0.44	1.51	0.30	1.11	2.34[‡]	0.82

[†] Res = resistant; CIM = CIMMYT-Zimbabwe; Reg = regional

[‡] F_2 Hybrid and error d.f = 6 and 18 respectively

*, ** Significant at 5% and 1% probability level, respectively

TABLE 5. Estimates of general combining ability effects (GCA) for grain weight loss (%) for lines with significant GCA as females or males within sets of Design II mating among 18 inbred maize lines

Inbred No.	Abbreviated pedigree[†]	Hybrid set	GCA (%)	S.E(±)[‡]
Lines used as females				
2	RA8149 1-2	Res x Reg#	-1.1**	0.2
3	Poo123QPM	Res x Reg	1.1**	0.2
6	Muneng 8128	Res x Res	-0.4**	0.1
8	SC	Reg. X Reg	1.7**	0.4
9	NAW 5867	Reg. Reg	-1.5**	0.4
12	1137TN	Reg x CIM	-0.6*	0.3
Lines used as males				
1	RA8149 1-6	Res x Res	-0.5**	0.1
2	RA8149 1-7	Res x Res	-0.8**	0.1
3	Poo123QPM	Res x Res	1.3**	0.1
7	M162W	Res x Reg.	0.3*	0.2
9	NAW5867	Res x Reg.	-0.5**	0.2
13	CML202	Reg. x CIM	-0.7*	0.3
14	CML216	Reg. x CIM	0.9**	0.3
17	M37W/ZM607	CIM x CIM	0.5**	0.2
18	MSRXPOOL9	CIM x CIM	0.8**	0.2

[†] Refer to Table 1 for complete pedigree and origin of each line

[‡] S.E = standard error

#Res = resistant; CIM = CIMMYT-Zimbabwe; Reg = regional.

*, ** Significant at 5% and 1% probability level, respectively

programmes because they are adapted to southern Africa. Moreover, Mexican weevil-resistant lines that showed good GCA for non-preference resistance could be used as sources in breeding projects to improve regionally adapted and elite lines. Negative (favourable) SCA effects indicated that some hybrids had unexpectedly good performance for non-preference by the maize weevil (Table 6). The significant negative SCA effects for weight loss imply that greatest non-preference resistance to weevil will be obtained in hybrids that are combinations of lines that exploit non-additive gene action, or heterosis for this trait.

Our results concur with the findings of Kang *et al.* (1995) that additive and non-additive gene action are important in conditioning non-preference resistance of grain to maize weevil. Whereas our study did not investigate the chemical basis for grain's non-preference resistance, Schoonhoven *et al.* (1976) suggested that non-preference was based on the lack of feeding stimulants in resistant kernels. Furthermore, Gomez *et al.* (1982, 1983) reported that the inbred line 'A619' attracted more weevils for oviposition, and contained higher ethanol content, which was suggested to be a weevil stimulant. Our results suggest that it is possible to develop hybrids with improved non-preference resistance of F_2 grain to maize weevil. Practical considerations, such as the substantial time and money costs of implementing a weevil resistance selection scheme within an applied maize breeding programme, are likely to result in hesitation among maize breeders to pursue this goal. We believe that more research is needed to confirm these results using a broader spectrum of maize germplasm, and that this research is most suitably conducted within the public sector, at institutions such as ours (CIMMYT and the University of Zimbabwe).

TABLE 6. Estimates of specific combining ability effects (SCA) for grain weight loss (%) for hybrids with significant SCA within sets of a Design II mating among 18 inbred maize lines

Hybrid	Abbreviated Pedigree[†]	Hybrid set	SCA (%)	S.E.(±)[‡]
1 x 8	RA8149 1 – 6 x SC	Res x Reg#	-1.5**	0.2
1 x 9	RA8149 1-6 x NAW5867	Res x Reg.	0.8*	0.2
3 x 8	Poo123QPM x SC	Res x Reg	1.0*	0.2
3 x 9	Poo123QPM x NAW5867	Res x Reg	-0.9**	0.2
4 x 1	PR8121 7-12 x RA8149 1-6	Res x Res	0.4*	0.2
4 x 2	PR8121 7 –12 x RA8149 1-7	Res x Res	0.4*	0.2
4 x 2	PR8121 7-12 x P99123QPM	Res x Res	-0.7**	0.2
6 x 2	Muneng8128 x RA8149 1-7	Res x Res	-0.6**	0.2
6 x 3	Muneng 8128 x Poo123QPM	Res x Res	0.4*	0.2
8 x 11	SC x N3	Reg x Reg	1.4*	0.5
8 x 12	SC x 1137TN	Reg x Reg	02.3**	0.5
9 x 10	NAW5867 x M37W	Reg. x Reg	1.4*	0.5
10 x 14	M37W x CML216	Reg x CIM	1.2**	0.4
10 X 15	M37W x FR810/TZMSRW	Reg x CIM	-0.9*	0.4
12 x 15	I137TN x R810/TZMSRW	Reg x CIM	1.6**	0.4
16 x 4	CML206 x PR8121 7-12	CIM x Res	2.7**	0.4
16 x 5	CML206 x PR8121 7-2	CIM x Res	-0.9*	0.4
16 x 6	CML206 x Muneng8128	CIM x Res	-1.8**	0.4
18 x 4	MSRXPOOL9 x PR8121 7-12	CIM x Res	-2.7**	0.4
18 x 5	MSRXPOOL9 x PR8121 7-2	CIM x Res	1.2*	0.4
18 x 6	MSRXPOOL9 x Muneng 8128	CIM x Res	0.9*	0.4

[†] Refer to Table 1 for complete pedigree and origin of each line

[‡] S.E. = standard error

#Res = resistant; CIM=CIMMYT-Zimbabwe; Reg=regional

*, ** Significant at 5% and 1% probability level, respectively

ACKNOWLEDGEMENT

We gratefully acknowledge The Rockefeller Foundation for funding this project.

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 Centre (CIMMYT)* 27 November -3. December, 1994. Mihm, J.A. (Ed.), pp. 91-95. Mexico, D.F.: CIMMYT.

Arnasson, J. T., Baum, B., Gale, J., Lambert, J. D. H., Bergvinson, D., Philogene, B. J. R., Serratos, J. A., Mihm, J. and Jewel, D.C. 1994. Variation in resistance of Mexican landraces of maize to maize weevil, *Sitophilus zeamais*, in relation to taxonomic and biochemical parameters. *Euphytica* 74:227-236.

Comstock, R. E. and Robinson, H.F. 1952. Estimation of average dominance of genes. In: *Heterosis*. Gowen, J.W. (Ed.), pp. 494-516 . Iowa State University Press Ames, Iowa, USA.

Derera, J., Pixley, K.V. and Giga, D. P. 2001. Resistance of maize to the maize weevil: 1. Antibiosis. *African Crop Science Journal* 9:431-440.

Dobie, P. 1974. The laboratory assessment of the inherent susceptibility of maize varieties to post harvest infestation by *Sitophilus zeamais*. *Journal of Stored Product Research* 10:183-197.

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.

Gewinner J., Harnisch, R. and Muck, O. 1996. *Manual of the Prevention of Post-Harvest grain losses*. Post-Harvest Project. GTZ, Eschborn. 330 pp.

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 Universitiy Press, Ames, Iowa, USA.

Horber, E. 1989. Methods to dect and evaluate resistance in maize to grain insects in the field in storage. In: *Towards 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.

Painter, R. H. 1951. *Insect resistance in Crop Plants*. McMillian, New York. 520 pp.

SAS Institute Inc., 1990. *SAS Procedures Guide Version 6, Third Edition*, Cary, North Carolina, USA.

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.

Schulten, G.C. 1975. Losses in stored maize in Malawi (C. Africa) and work undertaken to prevent them. *Eppo. Bulletin* 5:113-120.

Smale, M., Kaunda, Z.H.W., Makina, H.L. and Mkandawire, M.M.M.K. 1993. *Farmers' evaluation of newly released maize cultivars in Malawi: A comparison of local maize, semi-flint and dent hybrids*. CIMMYT-Malawi & Zimbabwe.

Tipping, P. W., Legg, D. E., Rodriguez, J. G. and Poneleit, C. G. 1988. Influence of maize pericarp surface relief on resistance to the maize weevil (Coleoptera: Curculionidae). *Journal of Kansas Entomological Society* 61: 237-241.

Tipping, P. W., Mikolajczak, K. L., Rodriguez, J. G., Poneleit, C. G. and Legg, D. E. 1987. Effects of whole corn kernels and extracts on behaviour of maize weevil (Coleoptera: Curculionidae). *Journal of Economic Entomology* 80:1010-1013.

Tipping, P. W., Mikolajczak, K. L., Rodriguez, J. G., Zilkowski, B. W. and Legg, D. E. 1986. Attraction of *Sitophilus oryzae* (L.) and *S. zeamais* Motsch. (Coleoptera: Curculionidae) to extracts from two corn genotypes. *Journal of the Kansas Entomological Society* 59:190-194.

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.