Euphytica (2021) 217:114
https://doi.org/10.1007/s10681-021-02852-6

Seed generation effect on quality of genetic information from maize (*Zea mays* L.) diallel cross for maize weevil (*Sitophilus zeamais* Motschulsky) resistance

Lwanga Charles Kasozi · John Derera · Pangirayi Tongoona · Edmore Gasura

Received: 27 March 2018 / Accepted: 10 May 2021 / Published online: 20 May 2021

Abstract Maize weevil (*Sitophilus zeamais* Motschulsky) is a common insect pest affecting stored maize (*Zea mays* L.) worldwide and can be controlled by breeding for host resistance. Information on combining ability and gene effects conditioning maize weevil resistance would be required to devise breeding strategies. However, there are disagreements regarding the seed generation to subject to maize weevil resistance evaluation. This study determined the seed generation effect on the quality of genetic information obtained from a maize diallel cross. Eight weevil-resistant and two susceptible maize inbred lines from eastern and southern Africa were crossed in a 10-parent diallel scheme. The resulting F_1 hybrid seed, F_2 full-sib grain from controlled pollination, and F_2 half-sib grain from open pollination were evaluated for maize weevil resistance and responses were determined using the number of F_1 weevil emergence from the seed (FWE), median development period (MDP), Dobie's index of susceptibility (DIS), and parental weevil mortality (PWM). General combining ability (GCA) and specific combining ability (SCA) effects were significant for the FWE, MDP, and DIS in all seed categories. Results revealed that reciprocal effects were predominant in F_1 hybrid seed, GCA effects were predominant in F_2 full-sib grain, while SCA effects were more important in the F_2 half-sib grain. The F_2 full-sib generation exhibited superiority in providing genetic information required for parental line selection when breeding for weevil resistance, compared to F_1 hybrid and F_2 half-sib grain. Resistant inbred lines MV170 and MV142, produced hybrids that exhibited high levels of maize weevil resistance across all the three seed categories thus, qualifying as suitable materials for breeding weevil resistant maize hybrids.

Keywords Combining ability · Gene effects · Maize · Maize weevil (*Sitophilus zeamais* Motschulsky) · Maize weevil resistance genetics

Abbreviations

CIMMYT	International Maize and Wheat Improvement Center
DSI	Dobie's index of susceptibility

L. C. Kasozi (✉) · J. Derera · P. Tongoona · E. Gasura
School of Agricultural, Earth and Environmental Sciences, University of KwaZulu-Natal, P. Bag X01, Scottsville 3209, South Africa
e-mail: kclwanga@gmail.com

L. C. Kasozi
National Agricultural Research Organisation (NARO), P.O. Box 295, Entebbe, Uganda

J. Derera
International Institute of Tropical Agriculture (IITA), PMB 5320, Oyo Rd, Ibadan, Nigeria

E. Gasura
Department of Plant Production Sciences and Technologies, University of Zimbabwe, MT Pleasant, P.O Box MP167, Harare, Zimbabwe

ENV	Environment
F_1	First filial generation
F_2	Second filial generation
GCA	General combining ability
FWE	Number of F_1 weevil emergence
MAT	Maternal effects
MDP	Median development period
NaCRRI	National Crops Resources Research Institute
NMAT	Non-maternal effects
REC	Reciprocal effects
SCA	Specific combining ability

Introduction

Maize weevil (*Sitophilus zeamais* Motschulsky) is one of the most destructive storage pests of maize, prevalent in all maize growing zones worldwide (Mutambuki and Likhayo 2021). Losses in grain weight associated with the maize weevil are not well documented in Uganda; however, Ngatia and Kimondo (2011) reported a cumulative grain weight loss of up to 20% under crib conditions and more than 25% under house conditions in Kenya. The weevils do not only cause grain weight losses but also reduce grain quality by causing bad odours and secondary infections by moulds especially *Aspergillus* (Forbanka 2021). Improper grain handling and management through the mixing of well-dried and poorly dried grains, mixing old maize batches with new ones are responsible for the survival of the maize weevil from one cropping season to another (Sserumaga et al. 2021). From the storage facilities, the maize weevil initiates infestation of the new maize crop in the field (Sserumaga et al. 2021). Thus, weevil prevalence both in the field and under storage complicates its control.

Various measures are used to control weevil infestations and ultimately damage to the maize grain. The most used control measure is the commercial insecticides. However, the cost implications associated with chemicals especially for small scale farmers, development of insecticide resistance by the maize weevils, and their eco-unfriendliness render chemicals unsustainable (Corrêa et al. 2011). Other weevil control measures tested include the use of biological control agents especially *Beauveria* spp. (Akmal et al. 2020; Zaman et al. 2020) and botanical extracts and indigenous technical knowledge but their application is limited to subsistence scale. Accordingly, host plant resistance would provide a cheap, environmentally sound and sustainable alternative weevil control measure. The weevil resistant maize germplasm has been reported and genotypes with enhanced weevil resistance have been developed (Dhliwayo and Pixley 2003; Dari et al. 2010; Mwololo et al. 2012). However, no weevil resistant maize varieties have been identified and deployed in Uganda, except for the few inbred lines being evaluated for the weevil resistance in this study.

Introduction of new sources of weevil resistance from exotic maize germplasm would enhance the development of the adapted weevil resistant maize cultivars. Generation of more information on combining ability for yield and weevil resistance, heritability, and gene effects conditioning weevil resistance in maize would guide breeders in germplasm selection and designing appropriate breeding strategies when breeding for weevil resistance.

Genetic studies are usually conducted on F_1 hybrid seed which is planted by farmers to obtain F_2 grain that is stored for home consumption or for sale (Dari et al. 2010). Therefore, it is F_2 grain which is prone to weevil damage and thus requiring adequate resistance. However, the type of generation to use for screening germplasm for maize weevil resistance is not clear (Dari et al. 2010; Dhliwayo and Pixley 2003). For the purpose of integrating the seed categories usually utilized at research and farmer levels, the study involved determining the genetics of weevil resistance in three maize seed categories. The first category was the F_1 hybrid seed which was basically parental inbred line seed obtained by crossing with another inbred line parent (single crosses). The second category was F_2 full-sib grain that was obtained through sib-mating of F_1 hybrid plants that were generated by planting F_1 hybrid seed. The third category was F_2 half sib grain derived from open pollination that was generated by outcrossing F_1 hybrid plants derived from F_1 hybrid seed. Existence of genetic correlation among the three seed categories would be desirable; because it would justify the evaluation of only one seed generation to obtain adequate genetic information, required for decision making. This would save time and costs involved in conducting more than one study. Therefore, the objective of the current study was to determine the seed generation effect on the quality of genetic information that is obtained from a maize diallel cross. In addition, the combining ability and gene effects conditioning maize weevil resistance in the selected set of maize germplasm lines from the eastern and southern Africa region was determined.

Materials and methods

Germplasm

The study materials comprised of ten parental lines from the eastern and southern Africa maize germplasm (Table 1). Germplasm was acquired from three sources namely: The National Crops Resources Research Institute (NaCRRI), based at Namulonge 30 km north of Kampala, Uganda and the International Maize and Wheat Improvement Center (CIMMYT-Kenya). These two sources contributed the eastern Africa germplasm; while parental lines from the University of KwaZulu Natal, South Africa constituted germplasm from southern Africa. Table 1 shows the list of experimental inbred lines together with resistant and susceptible checks which were used in the study. Preliminary evaluation of inbred lines was first conducted at NaCRRI, Namulonge to select the best 10 inbred lines with superior agronomic performance. NaCRRI is 1200 masl, 0°32′N and 32°34′E, with mean rainfall of 1300 mm distributed in a bimodal pattern. The Smith-Hazel selection index was used to select the best performing inbred lines

Table 1 Code names, pedigrees, origin and characteristics of the parental lines used in the 10-parent full diallel cross, and the local checks used in the experimental hybrid evaluation

Genotype code	Pedigree/parents	Origin	Response to Weevil infestation
MV13	CKL05019	CIMMYT-Kenya	Resistant
MV21	CML507	CIMMYT-Kenya	Resistant
MV31	[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-B//EV7992/EV8449…-3-2-2-1-BBBBB-B-B-B	CIMMYT-Kenya	Resistant
MV44	[(CML395/CML444)-B-4-1-3-1-B/CML444//[[TUXPSEQ]C1F2/MV449-SR]F2-45-7-1-2-BBB]-2-1-2-2-BBB-B-B-B	CIMMYT-Kenya	Susceptible
MV63	09MAK17-15-1	South Africa	Resistant
MV75	09MAK17-28-1	South Africa	Resistant
MV102	09MAK9-157	South Africa	Susceptible
MV142	WL-118-3	Uganda	Resistant
MV154	WL429-27	Uganda	Resistant
MV170	WL118-9	Uganda	Resistant
Check 1	Longe5 (OPV)	Uganda	Susceptible
Check 2	[weevil/CML312]-B-13-2-1-BBB/[weevil/CML387]-B-9-1-1	CIMMYT-Zimbabwe	Resistant
Check 3	07WEEVIL	CIMMYT-Zimbabwe	Resistant
Check 4	Longe10H (hybrid)	Uganda	Susceptible
Check 5	Popcorn (local OPV)	Uganda	Susceptible
Check 6	Longe6H (hybrid)	Uganda	Susceptible
Check 7	CML312/CML442 (Heterotic group A tester -hybrid)	CIMMYT-Kenya	Susceptible
Check 8	CML202/CML395 (Heterotic group B tester-hybrid)	CIMMYT-Kenya	Susceptible

from the respective sources, with grain yield and weevil resistance being given the first and second priority in the selection index, respectively (Crispim-Filho et al. 2020). Selections were carried out in the first rainy season of 2010 (2010A). The first season usually occurs from March to July of each year. Seed for selected inbred lines was increased in the second season of 2010 (2010B), which ran from August to December.

Nursery establishment

The nurseries for the 10-parent diallel cross were planted twice that is in March and September 2011 that formed the 2011A and 2011B seasons, respectively, at NaCRRI, Namulonge. The row length was 5 m with an inter-row spacing of 0.75 m, while the intra row spacing was 0.3 m. Twenty rows of each inbred line parent were planted in an alternating arrangement, in such a way that each inbred line was crossed with the remaining nine parental lines. Di-ammonium phosphate (18% P) was applied at a rate of 120 kg P ha^{-1}, at planting; while urea (46% N) was applied at a rate of 120 kg N ha^{-1}, 21 days after planting. To provide for cultivar differences in flowering periods, three staggered plantings of each inbred line were made at intervals of five days between each planting. This improved synchronization of silk emergence and pollen shedding among the parental lines. Other growing practices were done as recommended for commercial maize grain production in the area.

Seed harvesting and development of subsequent generations of grain

The early nurseries that were established in March 2011 (2011A season) were harvested in July 2011. These were used in the development of other grain generations (F_2-full sib and F_2 derived from open pollination) at NaCRRI, during September 2011 (2011B season). The late planted nurseries that were established in September 2011 (2011B season) were harvested in January 2012. All seed generations were processed for maize weevil resistance screening that commenced in March 2012 (2012A season). The 45 experimental hybrids, together with the 45 reciprocal crosses obtained from a 10-parent diallel mating design and eight local checks (two weevil-resistant and six susceptible) were planted along with the ten inbred lines. The ten inbred line parents were planted in a separate trial nearby, to avoid competition with the taller hybrids. In the field, the hybrids were arranged in a 7 × 14 alpha lattice design with two replications; while the parents were in a randomized complete block design, with two replications. Two-row plots of length 5 m, inter-row spacing 0.75 m, and intra-row spacing 0.30 m were planted, giving a plant population of 44,444 plants per hectare. The same fertilizer rate used in the inbred line nursery was also used in this trial. For comparison of the influence of full-sib mating and open-pollinated mating on gene effects and combining ability for weevil resistance, at least five plants in the second row of each plot were sib-mated. Sib-mating (generation of F_2 full-sib grain) was achieved by collecting pollen from within each row, bulking it, and pollinating plants with receptive silks within each row. The silks and tassels of the sib-mated plants were protected from contamination with unwanted pollen, using shoot bags and tassel bags, respectively. The rest of the plants were left to outcross, and as a result, generated F_2 grain derived from open pollination. The plants were harvested at maturity and the grain moisture content (%) of each genotype was determined. All ears from each plot were then weighed to establish their field weight (kg plot^{-1}), after which they were dried, shelled, and grain prepared for screening against the maize weevil in the laboratory.

Weevil rearing

Prior to the screening exercise, weevils were first reared to provide an adequate supply of weevils that were ≤ 7 days. This represented the first generation of laboratory-reared weevils with known age. Weevil rearing was achieved by obtaining adult weevils from infested maize grain from nearby maize storage facilities. About 300 unsexed weevils were introduced into 1500 g of maize variety Longe 5, one of the most susceptible maize varieties in Uganda, into large plastic jars of volume 3000 cm^3. To provide for proper ventilation, the lids of the plastic jars were a perforated and gauze-wire mesh of pore size less than 1 mm stuck on them (lids) to prevent the weevils from escaping. The weevil-maize culture was incubated for 14 days in the laboratory at a temperature of 28 ± 2 °C and relative humidity of 70 ± 5% to enhance oviposition. A heater fan and a humidifier were used for regulating the temperature and relative humidity, respectively. After two weeks the maize-weevil cultures were sieved using a mesh sieve (Endecotts Ltd, UK), to remove the weevils from the grain. The maize grain was later returned to the plastic jars and incubated under the same conditions, to allow the eggs to hatch and F_1 progenies to emerge. The test hybrids were infested using these newly emerged F_1 weevil progenies of age 0 to 7 days old.

Grain infestation with the weevils and data collection

Before the screening, the grain was first subjected to cold treatment at -20 °C for 14 days, to eliminate all growth stages for any pests that could have infested the grain in the field. Afterward, the grain was acclimatized by leaving it under weevil-free room temperature conditions, for seven days. Later on, 50 g of each genotype were weighed into 250 cm^3 glass jars with perforated lids fitted with < 1 mm gauze mesh for ventilation and blockage of weevil escape. Thirty-two unsexed adult weevils of age 0–7 days were used to infest the grain. The experiment was arranged in the laboratory in a randomized complete block design with each treatment (weevil-grain culture) replicated six times. The weevil-grain cultures were first incubated for 14 days to allow oviposition. Afterward, the weevils were sieved out of the cultures and the grain was maintained at a temperature of 28 ± 2 °C and relative humidity of 70 ± 5% until the end of the screening exercise. During the incubation period, the grain was monitored every two days to record and remove any F_1 weevil progeny that emerged. The recording interval was maintained at two days to avoid mating between the F_1 weevils that would result in mixed weevil generations that might occur after two days. Recording F_1 weevil emergence continued until no more weevils were emerging from each of the genotypes. Data were recorded for the number of parental weevils alive and dead. The F_1 weevil progenies emerging every two days (F_1 weevils alive and dead) were recorded until no more F_1 weevils were emerging and the total was determined. The median development period (MDP) was calculated as the period in days from the middle of the oviposition period to the emergence of 50% of the F_1 weevil progenies (Dobie 1977). Dobie's index of susceptibility (DIS) was calculated based on the total F_1 weevil emergence and the median development period (Dobie 1974). It was calculated using the formula:

$$\mathrm{DIS} = \frac{\ln\ F1\ weevil\ progeny\ emergence}{Median\ Development\ Period} \times 100$$

Data analysis

Data on the F_1 weevil emergence, median development period, Dobie's index of susceptibility and parental weevil mortality were analyzed using SAS version 9.1 based on the general linear model procedure (SAS-Institute 2003). The genetic information of the parameters was obtained by subjecting the data to Griffing's method 1 model 1 (Griffing 1956). Estimation of general combining ability (GCA), specific combining ability (SCA), and reciprocal effects (REC), and the partitioning of reciprocal effects into maternal (MAT) and non-maternal effects (NMAT) of the 10 parental lines, was done using DiallelSAS05 program (Zhang et al. 2005) in SAS. Genotypes were considered as fixed effects, while the environments and replications within environments were considered as random effects (Singh and Chaudhary 2004). The model used in the analysis was: $Y_{ijkl} = \mu + \alpha_l + \beta_k(\alpha_l) + g_i + g_j + r_{ij} + s_{ij} + g_i\alpha_l + g_j\alpha_l + r_{ij}\alpha_l + s_{ij}\alpha_l + e_{ijkl}$, where Y_{ijkl} = observed measurement for the ijth cross in the kth replication nested in the lth environment, μ = is the population mean; g_i and g_j = general combining ability (GCA) effects for the ith and jth parental lines, respectively; r = reciprocal effects, such that $r_{ij} = -r_{ji}$; s_{ij} = specific combining ability (SCA) effect for the ijth cross; $g_i\alpha_l$ and $g_j\alpha_l$ are the interactions of the GCA effects of the ith and jth parental lines with the lth environment, $r_{ij}\alpha_l$ is the interaction of the reciprocal effects with the lth environment, $s_{ij}\alpha_l$ is the interaction of the SCA effects with the lth environment, and e_{ijkl} = error term associated with the ijth cross evaluated in the kth replication nested in the lth environment where i = j = 10 parents, k = 3 replications, and l = 2 environments. The relative significance of the GCA, SCA and reciprocal effects was determined, based on the proportion of these factors to the total genetic effects (Singh and Chaudhary 2004).

Table 2 Mean square for F_1 weevil progeny emergence, median development period, Dobie index of susceptibility and parental weevil mortality in the F_1 hybrid seed

Source	DF	Mean Squares			
		F_1 weevils emerged	Median development period	Dobie's index of susceptibility	Parental weevil mortality
REP	2	413.17	10.33	70.73	99.02
GENOTYPE	99	254.27***	68.47***	14.01***	159.61***
GCA	9	613.85***	310.83***	65.29***	426.14***
SCA	45	173.55***	33.12*	17.66***	88.18***
REC	45	263.07***	55.34***	34.53***	177.73***
MAT	9	605.56***	154.42***	71.36***	414.62***
NMAT	36	177.45***	30.58*	25.32***	118.51***
ERROR	198	78.26	20.01	7.07	43.20
R^2		0.63	0.63	0.62	0.76
Hybrid mean		16.54	43.15	5.86	16.28
GCAss (%)		21.95	41.27	20.00	24.27
SCAss (%)		31.02	21.99	27.00	25.11
RECss (%)		47.03	36.74	53.00	50.61

*, *** indicate the value is significant at $P \leq 0.05$ and $P \leq 0.001$, respectively

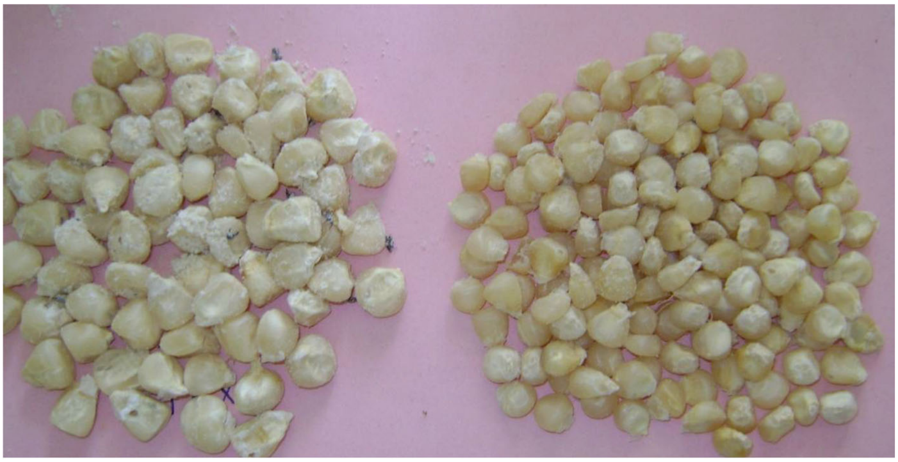
Results

F_1 hybrid seed assessment for genetic variation

The mean squares for the F_1 weevil emergence (FWE), median development period (MDP), Dobie's index of susceptibility (DIS), and parental weevil mortality in the F_1 hybrid seed are shown in Table 2. The mean squares for the F_1 weevil progenies that emerged from the F_1 seed indicated that all the main effects namely genotype and sub-components effects that include, general combining ability (GCA), specific combining ability (SCA), reciprocal effects (REC), maternal (MAT), and non-maternal effects (NMAT) were all highly significant ($P < 0.001$). The mean number of the F_1 weevil progenies that emerged was 17 weevils (Table 2). The reciprocal effects contributed 47.0%, SCA effects constituted 31.0%, whereas GCA effects constituted 22.0% of the genotype sum of squares for the number of F_1 weevil progeny emergence (Table 2). The mean squares for the median development period (MDP) indicated that all main effects were significant ($P < 0.05$–$P < 0.001$). The mean MDP was 43.2 days.

The GCA effects contributed 41.3%, the SCA effects contributed 22.0%, while the reciprocal effects contributed 36.7% of the genotype sum of squares for the MDP (Table 2). Means squares for Dobie index of susceptibility (DIS), revealed that all effects including genotype, GCA, SCA, MAT and NMAT were highly significant ($P < 0.001$). The reciprocal effects constituted the largest proportion of the genotype sum of squares amounting to 53%; this was followed by the SCA effects which constituted 27%, whereas the GCA effects constituted 20% of the genotype sum of squares. Similarly, for parental weevil mortality, the mean squares indicated that all main effects were highly significant ($P < 0.001$); the reciprocal effects constituted 50.6% of the genotype sum of squares, SCA effects constituted 25.1%, while GCA constituted 24.3%. The mean parental weevil mortality was 16 weevils.

Differences were observed between the crosses and reciprocal crosses. An example of the response of F_1 hybrid seed generated from crosses between resistant and susceptible parental lines is presented in Fig. 1a. when a susceptible line, MV102, was used as a female parent in the cross MV102 × MV142, the resulting



(a) Susceptible reaction of hybrids produced from MV102 (susceptible parent) x MV142 (resistant parent) on the left, while their reciprocal cross on the right shows a resistant phenotype.

(b) Susceptible reaction of hybrids produced from MV44 (susceptible parent) x MV102 (susceptible parent) on the left and their reciprocal cross on the right.

Fig. 1 Response of experimental hybrids to weevil attack. **a** shows a cross between susceptible and resistant parental lines and **b** their reciprocal cross

hybrid seed was susceptible to weevil attack. However, the hybrid seed that was generated by the reciprocal cross (MV142 × MV102) was resistant to weevil attack. On the other hand, the hybrid seed generated from both main and reciprocal crosses between susceptible parental lines (e.g. MV44 and MV102) was susceptible to weevil attack (Fig. 1b).

F_2 full-sib grain assessment for genetic variation

Mean squares for F_1 weevil progeny emergence, median development period (MDP), Dobie's index of susceptibility (DIS), and parental weevil mortality in the F_2 full-sib grain obtained from the 45 single cross hybrids and their reciprocals (45) generated from the 10-parent diallel mating scheme are shown in Table 3. The mean squares for F_1 weevil progenies that

Table 3 Mean squares for F_1 weevil progeny emergence, median development period, Dobie index of susceptibility, parental weevil mortality in F_2 full-sib grain and F_2-open pollinated grain

Source of variation	DF	Mean squares							
		F_2 full-sib grain				F2-open pollinated grain			
		F_1 weevils emerged	Median development period	Dobie's index of susceptibility	Parental weevil mortality	F_1 weevils emerged	Median development period	Dobie's index of susceptibility	Parental weevil mortality
ENV	1	82,052.33***	1022.00***	463.77***	8.07	6428.80***	2.41	38.52***	7.26
REP(ENV)	4	7572.90	313.30	63.51	499.01	645.49**	2.45	4.70***	15.78
GENOTYPE	99	1792.57***	32.53***	13.74***	53.73***	1442.04***	107.44***	16.03***	32.13*
GCA	9	13,812.74***	215.69***	106.50***	95.63*	4350.95*	280.10***	50.32**	34.14
SCA	45	884.48***	21.33***	7.66***	45.48**	1281.29***	130.09***	17.53***	42.50*
REC	45	432.66	10.04	2.66	53.51***	1021.01***	50.09***	7.68***	21.37
MAT	9	404.42	10.73	2.32	129.67**	2701.34**	211.28***	28.08***	16.52
NMAT	36	439.72	9.87	2.74	34.47**	600.93**	9.80	2.58**	22.58
ENV*GENOTYPE	99	359.40***	6.69**	2.04***	18.71	433.19***	5.90	1.58***	34.62*
GCA*ENV	9	572.67***	5.81	2.51**	40.36*	1810.63***	3.94	5.55***	28.01
SCA*ENV	45	295.75**	6.04	1.70**	16.83	305.46***	4.98	1.11*	31.38
REC*ENV	45	380.73***	8.34**	2.38**	15.37	285.43***	7.32*	1.26*	39.19*
MAT*ENV	9	713.05***	11.39**	5.17***	19.51	273.25*	12.96**	1.55*	23.28
NMAT*ENV	36	297.65*	7.57*	1.68*	14.34	288.47***	5.91	1.19*	43.17**
ERROR	396	171.23	4.44	0.89	16.5	135.0	5.17	0.77	24.09
R^2		0.82	0.78	0.86	0.55	0.77	0.85	0.86	0.41
Hybrid mean		44.33	46.64	7.77	9.22	36.14	44.48	7.87	9.30
GCAss (%)		67.60	57.90	67.37	16.19	27.43	23.78	28.53	9.66
SCAss (%)		21.60	29.81	24.23	38.51	40.39	55.03	49.69	60.12
RECss (%)		10.80	14.03	8.40	45.30	32.18	21.19	21.78	30.22

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively

emerged from the F_2 full-sib grain indicated that all the main effects namely genotype, general combining ability (GCA) and specific combining ability (SCA) effects, were significant ($P < 0.05$–$P < 0.001$); while reciprocal effects (REC), maternal (MAT), and non-maternal effects (NMAT) were not significant. All the interactions between the main effects and the environment were also significant ($P < 0.05$–$P < 0.001$). The mean number of F_1 weevil progenies that emerged was 44.3 weevils. GCA effects constituted the highest proportion of 67.6%, followed by SCA with 21.6%, while the reciprocals effects contributed the least 10.8% of the genotype sum of squares for the number of F_1 weevil progeny emergence.

The mean squares for the median development period (MDP) indicated that all main effects were highly significant ($P < 0.001$), except for reciprocal, maternal and non-maternal effects that were not significant. The interactions between GCA and environment, and SCA and environment were not significant ($P > 0.05$); while the remaining interactions between genotype and environment, reciprocal effects and environment, maternal effects and environment, and non-maternal effects and environment were significant ($P < 0.05$–0.01). For the Dobie's index of susceptibility (DIS), all the main effects were significant ($P < 0.001$) except the reciprocal, maternal and non-maternal effects. Furthermore, all interactions that are, GCA × environment, genotype × environment, reciprocal effects × environment, maternal effects × environment, SCA × environment, and non-maternal effects × environment were significant ($P < 0.05$–$P < 0.001$). The GCA effects contributed 57.9% and 67.4%, SCA effects contributed 29.8% and 24.2%, while reciprocal effects contributed 14.0% and 8.4% of the genotype sum of squares for MDP and DIS, respectively. For parental weevil mortality, all the main effects namely genotype, GCA, SCA, reciprocal effects, maternal and non-maternal effects were highly significant ($P < 0.05$). For the interactions, the GCA × environment interactions was significant ($P < 0.05$), while the rest of the interactions were not significant. The mean parental mortality was 9.2 weevils. The reciprocal effects accounted for 45%, SCA effects 38.5%, while GCA effects contributed 16.2% of the genotype sum of squares.

F_2 open-pollinated grain assessment for genetic variation

Means squares for the F_1 weevil emergence, median development period, the Dobie's index of susceptibility, and parental weevil mortality in the ten parental lines and F_2 open-pollinated grain of the 45 experimental hybrids and their reciprocal crosses are shown in Table 3. Mean squares for the F_1 weevil progenies that emerged from the F_2 open-pollinated seed indicated that all main effects namely environment (ENV), genotype, general combining ability (GCA), specific combining ability (SCA), reciprocal effects (REC), maternal (MAT) and non-maternal effects (NMAT) were significant ($P < 0.05$–0.001). Furthermore, all the interactions between the main effects and the environment were also significant ($P < 0.05$–0.001). SCA effects constituted the highest proportion of 40.4% to the genotype sum of squares, followed by reciprocal effects with 32.2%, while GCA effects contributed 27.4%.

The mean squares for median development period (MDP) indicated that genotypes, GCA, SCA, effects were highly significant ($P < 0.001$) except for reciprocals, maternal and non-maternal effects. For the interactions, only reciprocal × environment and maternal effects × environment were significant ($P < 0.05$–$P < 0.01$). The interactions between genotype × environment, GCA × environment, SCA × environment, and non-maternal effects × environment were not significant. GCA effects constituted 23.8% of the genotype sum of squares, SCA contributed 55.0%, while reciprocal effects contributed 21.2%. The mean median development period was 44.5 days. Regarding the Dobie's index of susceptibility (DIS), all the main effects and interactions were significant ($P < 0.05$–0.001). GCA effects contributed 28.5%; SCA effects contributed 49.7%, while reciprocal effects contributed 21.8%. The mean DIS value was 7.9. For parental weevil mortality, only genotype and SCA mean squares were significant ($P < 0.05$); the remaining main effects (including the GCA effects) were not significant. For the interactions, only genotype × environment, reciprocal effects × environment and non-maternal effects × environment was significant ($P < 0.05$); while the rest of interactions were not significant. GCA effects contributed 9.7% of the genotype sum of squares; SCA effects contributed

Table 4 General combining ability effects for F_1 weevil emergence and median development period exhibited in the ten parental lines under F_1 hybrid seed, F_2 full-sib grain and F_2 open pollinated grain

Parent	F_1 hybrid seed		F_2 grain		Open pollinated grain	
	F_1 weevils emerged	Median development period	F_1 weevils emerged	Median development period	F_1 weevils emerged	Median development period
MV13	0.46	− 0.70	1.25	0.17	0.77	− 0.24
MV21	0.53	1.17*	− 5.75**	0.07	− 3.00*	1.92***
MV31	0.91	2.15***	− 2.42	0.63*	− 2.09	0.68***
MV44	6.93***	− 3.62***	14.14***	− 2.02***	9.52***	− 0.09
MV63	− 1.11	− 1.73**	2.34	− 0.02	0.15	− 0.62**
MV75	− 1.56	− 1.47**	4.28*	0.03	1.73	− 1.97***
MV102	2.96**	− 2.42***	18.40***	− 2.45***	8.38***	− 2.95***
MV142	− 3.07**	2.05***	− 9.38***	0.90***	− 6.88***	1.56***
MV154	− 1.87	1.43**	− 4.96**	0.57*	1.38	0.94***
MV170	− 4.17**	3.13***	− 17.91***	2.13***	− 9.96***	0.76***
Standard Errors	± 1.10	± 0.55	± 1.78	± 0.26	± 1.28	± 0.19

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively

60.1%, while reciprocal effects contributed 30.2%. Mean parental weevil mortality was 9.3 weevils.

General combining ability estimates under F_1 hybrid seed

Results for the general combining ability effects regarding the response of the ten parental lines to weevil infestation, as exhibited by the F_1 weevil progeny emergence and the median development period in F_1 hybrid seed, F_2 full-sib and open-pollinated grain are presented in Table 4. For parameter of the F_1 weevil progeny emergence under F_1 hybrid seed, parents MV44 and MV102 displayed positive and highly significant ($P < 0.01$–$P < 0.001$) GCA effects; while parents MV170 and MV142 displayed negative and highly significant ($P < 0.01$) GCA effects. Under F_2 full-sib grain, parents MV44 and MV102 displayed positive and highly significant ($P < 0.001$) GCA effects. On the other hand, parents MV21, MV154, MV170, and MV142 displayed negative and highly significant ($P < 0.01$–$P < 0.001$) GCA effects. For F_2 open-pollinated grain, the results showed that parents MV21, MV170 and MV142 displayed negative and significant ($P < 0.05$) GCA effects, while parents MV44 and MV102 manifested positive and highly significant ($P < 0.001$) GCA effects. The rest of the parents did not display significant ($P > 0.05$) GCA effects as regards to the response to the F_1 weevil progeny emergence.

In F_1 hybrid seed, parents MV21, MV154, MV31, MV170 and MV142 displayed positive significant GCA effects; whilst parents MV44, MV63, MV75 and MV102 exhibited negative and highly significant ($P < 0.01$) GCA effects for the MDP. For F_2 full-sib grain, parents MV154, MV31, MV170, and MV142 exhibited positive significant ($P < 0.05$) GCA effects, while parents MV44, and MV102 exhibited negative and highly significant ($P < 0.001$) GCA effects for the MDP. For F_2 open-pollinated grain, parents MV21, MV154, MV31, MV170 and MV142 exhibited positive and highly significant ($P < 0.001$) GCA effects, while parents MV63, MV75, and MV102 exhibited negative highly significant ($P < 0.01$–$P < 0.001$) GCA effects for MDP (Table 4).

Results for the general combining ability effects regarding the response of the ten parental lines to weevil infestation, as exhibited by the Dobie's index of susceptibility and parental weevil mortality in F_1 hybrid seed, F_2 full-sib and open-pollinated grain are presented in Table 5. The results for Dobie's index of susceptibility as manifested in theF_1 hybrid seed, F_2 full-sib grain and F_2 open-pollinated grain revealed

Table 5 General combining ability effects for Dobie index of susceptibility and parental weevil mortality exhibited in the ten parental lines under F_1 hybrid seed, F_2 full-sib grain and F_2 open pollinated grain

Parent	F_1 hybrid seed		F_2 grain		Open pollinated grain	
	Dobie's index of susceptibility	Parental weevil mortality	Dobie's index of susceptibility	Parental weevil mortality	Dobie's index of susceptibility	Parental weevil mortality
MV13	− 0.03	− 1.16	0.15	0.76	0.14	0.08
MV21	− 0.77*	− 0.68	− 0.33*	1.31**	− 0.45***	− 0.11*
MV31	− 0.43	− 1.49*	− 0.38**	− 1.11**	− 0.23**	0.00
MV44	1.27***	− 5.69***	1.27***	− 1.11**	0.54**	− 0.03
MV63	0.46	1.37*	0.25	− 0.01	0.20*	0.12*
MV75	0.18	0.99	0.34*	0.53	0.53***	− 0.02
MV102	0.52	− 0.23	1.51***	− 1.23**	1.09***	− 0.07
MV142	− 0.35	2.11***	− 0.84***	0.33	− 0.81***	0.04
MV154	− 0.63	0.09	− 0.28*	− 0.18	− 0.00	− 0.02
MV170	− 0.23	4.5***	− 1.69***	0.71	− 1.02***	0.01
Standard Errors	± 0.36	± 0.62	± 0.13	± 0.41	± 0.09	± 0.05

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively

the following: in the F_1 hybrid seed, parent MV44 exhibited positive highly significant GCA effects, while parent MV21 exhibited negative significant ($P < 0.05$) GCA effects. Under F_2 full-sib grain, parents MV44, MV75, and MV102 exhibited positive significant ($P < 0.05$–$P < 0.001$) GCA effects, while parents MV21, MV154, MV31, MV170, and MV142 exhibited negative significant ($P < 0.01$–$P < 0.001$) GCA effects. For F_2 open-pollinated grain, parents MV44, MV63, MV75, and MV102 exhibited positive significant ($P < 0.05$–$P < 0.001$) GCA effects, while parents MV21, MV31, MV170 and MV142 exhibited negative and highly significant ($P < 0.01$–$P < 0.001$) GCA effects.

For the parental weevil mortality results, under F_1 hybrid seed, parents MV63, MV170, and MV142 displayed positive significant ($P < 0.05$–$P < 0.001$) GCA effects whereas parents MV31 and MV44 displayed negative significant ($P < 0.05$ and $P < 0.001$) GCA effects. For F_2 full-sib grain, parent MV21 displayed positive significant ($P < 0.01$) GCA effects, whereas parents MV31, MV44 and MV102 displayed negative highly significant ($P < 0.01$) GCA effects. Under F_2 open-pollinated grain, only parent MV63 exhibited positive significant ($P < 0.05$) GCA estimates, while parent MV21 exhibited negative significant ($P < 0.05$) GCA effects.

The three seed/grain generations exhibited some differences in categorizing the ten parents based on their responses to weevil infestation as demonstrated by the differences between F_1 weevil emergence, median development period, the Dobie's index of susceptibility and parental weevil mortality in identifying weevil resistant parents. For instance, under F_1 hybrid generation, only two parents MV170 and MV142 were identified as resistant using F_1 weevil emergence; under F_2 full-sib generation, four parents MV21, MV154, MV170 and MV142 were identified as resistant by the same parameter; whereas under F_2 open-pollinated generation parents three parents MV21, MV170 and MV142 were identified as resistant. A similar trend was observed under Dobie's index of susceptibility. However, for the median development period, there were no major differences among the three generations towards identifying weevil resistant parental lines.

Rank of hybrids for maize weevil resistance

The list of the top 20 genotypes (hybrids/reciprocal crosses) that exhibited the highest level of resistance to weevil infestation and the five most weevil susceptible genotypes are presented in Table 6. There were significant ($P < 0.05$) variations among hybrids/

Table 6 List of top 20 and bottom five hybrids/reciprocal crosses, as regards to response to weevil infestation based on F_1 weevil progeny emergence parameter

F_1 hybrid seed		F_2 grain		Open pollinated grain	
Hybrid/check	F_1 weevils emerged	Hybrid/check	F_1 weevils emerged	Hybrid/check	F_1 weevils emerged
Top 20					
MV170 × MV13	6.00	MV142 × MV21	7.50	Check 2	8.17
MV75 × MV21	6.33	Check 2	10.50	Check 3	10.33
MV154 × MV142	6.70	MV170 × MV154	12.83	MV170 × MV44	12.50
MV154 × MV31	7.00	Check 3	13.13	MV170 × MV142	13.50
MV142 × MV170	7.00	MV170 × MV75	13.67	MV170 × MV31	14.00
MV75 × MV154	7.33	MV170 × MV21	20.33	MV31 × MV170	15.00
MV75 × MV102	7.33	MV21 × MV31	21.83	MV142 × MV13	15.83
MV13 × MV142	7.33	MV142 × MV170	23.67	MV170 × MV21	17.33
MV154 × MV102	7.60	MV170 × MV44	24.50	MV13 × MV75	18.00
MV142 × MV154	7.67	MV21 × MV170	25.33	MV170 × MV13	18.83
Check 3	7.70	MV63 × MV31	25.83	MV170 × MV63	19.33
MV63 × MV142	7.70	MV154 × MV170	26.50	MV142 × MV44	20.17
MV75 × MV31	8.00	MV13 × MV21	27.00	MV21 × MV154	21.16
MV63 × MV170	8.60	MV142 × MV154	27.83	MV154 × MV13	21.33
MV21 × MV102	8.70	MV75 × MV154	28.00	MV170 × MV102	21.83
Check 2	9.30	MV142 × MV13	28.83	MV63 × MV31	21.83
MV154 × MV13	9.60	MV63 × MV31	29.33	MV142 × MV170	22.67
MV63 × MV31	9.70	MV154 × MV31	29.67	MV142 × MV21	25.33
MV142 × MV13	9.70	MV63 × MV170	29.67	MV154 × MV142	25.67
MV154 × MV21	9.80	MV170 × MV13	30.33	MV75 × MV154	26.20
Bottom 5					
MV102 × MV44	32.00	MV102 × MV44	76.00	MV102 × MV63	64.00
MV44 × MV13	34.30	MV102 × MV63	77.33	MV102 × MV170	82.83
MV31 × MV170	45.00	MV44 × MV31	78.67	Check 7	102.00
Check 5	117.00	MV44 × MV75	79.18	MV102 × MV44	98.67
Check 7	122.00	Check 5	110.3	MV44 × MV21	
R^2	0.89		0.72		0.84
LSD (0.05)	14.77		20.73		13.74
Mean	17.84		46.47		38.85

reciprocal crosses towards their response to weevil infestations, as manifested by F_1 weevil progeny emergence from F_1 hybrid seed, F_2 full-sib grain and F_2 open-pollinated grain. However, crosses MV75 × MV154, MV154 × MV142, MV142 × MV170, MV154 × MV31 and MV170 × MV13 were consistently ranked among the top 20 hybrids under the three seed/grain generations. Most of the weevil resistant hybrids were generated from parental lines MV142, MV154 and MV170. On the other hand, cross MV102 × MV63 was consistently ranked among the bottom five hybrids under the three seed/grain generations. All in all, the ranking of the genotypes under the three seed categories exhibited some differences. For instance, under the F_1 hybrid seed, ten hybrids were superior to local checks 2 and 3, while under F_2full-sib grain only one hybrid was superior to local check 2 and two hybrids were superior to local check 3. On the other hand, under F_2 open-pollinated grain, the two local checks 2 and 3 were superior to all hybrids.

Comparison between generations based on the sum of squares proportions

The results indicated that different genetic effects (combining ability effects) were manifested in each seed/grain generation. For example, in F_1 hybrid seed generation, reciprocal effects generally constituted the largest proportion of the total genotype sum of squares which were 47.0, 36.7, 53.0 and 50.6% for FWE, MDP, DIS and PWM, respectively. On the other hand, the GCA effects constituted 22.0, 41.3, 20.0 and 24.3%, whereas the SCA constituted 31.0, 22.0, 27.0 and 25.1% for FWE, MDP, DIS and PWM, respectively. For F_2 full-sib grain generation, generally, GCA effects constituted the largest proportion of the total genotype sum of squares. The GCA percentages were 67.6, 57.9, 67.4, and 16.2% for FWE, MDP, DIS and PWM, respectively; while SCA were 21.6, 29.8, 24.2 and 38.5%, and reciprocal effects were 10.8, 14.0, 8.4 and 45.3% for FWE, MDP, DIS and PWM, respectively. For F_2 open-pollinated grain generation, on the other hand, the SCA effects constituted the largest proportion of the total genotype sum of squares. The proportions of SCA effects were 40.4, 55.0, 49.7, and 60.1% for FWE, MDP, DIS and PWM, respectively; while GCA effects were 27.4, 23.8, 28.5 and 9.7%, and reciprocal effects were 32.2, 21.2, 21.8 and 30.2 for FWE, MDP, DIS and PWM, respectively.

Discussion

Gene effects controlling the weevil resistance

All the three categories of seed exhibited significant genotype mean squares for weevil resistance parameters indicating genetic variation among hybrids for this important trait. The significant GCA effects indicated that additive gene effects were responsible for conditioning the weevil resistance parameters. This is consistent with previous findings (Tipping et al. 1989). Significant reciprocal effects and its components, such as maternal and non-maternal effects indicated that part of the genetic variation could be attributed to the direction of the crosses made. In general resistance of hybrids was high when the resistant parent was used as female for the cross which was consistent with previous findings (Tipping et al. 1989). The significance of GCA, SCA, and reciprocal effects indicated that all three elements of the genetic model contributed to variation among hybrids. This was in agreement with results reported by Kang et al. (1995) who observed additive, and non-additive gene effects, and maternal effects in the governance of weevil non-preference in F_1 hybrids of a 10-parent diallel. However, in the current study the level of their contribution depended on the seed generation used to evaluate the hybrids. In the F_1 hybrid seed, the reciprocal effects were more important than GCA and SCA effects, especially for the number of F_1 weevil progeny emergence. This underlined the importance of considering maternal and non-maternal effects for conditioning maize weevil resistance in the F_1 generation seed. This could be attributed to contribution of the seed's maternal tissues in conferring the first line of defence to the maize weevil attack. The influence of maternal effects is further enhanced through double fertilization (Faure et al. 2003). The maternal tissues, such as the testa (diploid, 2n), and the triploid endosperm (3n), which has double gene dosage from the maternal genotypes, were playing a big role in conferring resistance against the emerging F_1 weevil progenies. These results are consistent with Tipping et al. (1989) who reported significant maternal effects in F_1 hybrid seed, as opposed to seed in the subsequent generations. Consistent with this observation, the GCA effects were more important than SCA and reciprocal effects for the number of F_1 weevil progeny emergence in the F_2 full-sib grain. These results suggested the preponderance of additive gene effects in the governance of the number of F_1 weevil progeny emergence, while contribution of reciprocal effects was significantly reduced when the F_2 full-sib grain was evaluated. Different genetic information was also obtained when the hybrids were subjected to random pollination in a field trial of the 10 parent diallel cross and the grain was used for maize weevil resistance screening. SCA effects were more important than GCA and reciprocal effects when the F_2 open-pollinated grain was tested. These results suggested the predominance of the non-additive gene effects in conditioning hybrid resistance against weevil development and the subsequent emergence of F_1 progenies from the F_2 open-pollinated grain, which is in sharp contrast to findings obtained from evaluating F_1 seed and F_2 full sib grain.

There are different expectations for the role of reciprocal differences among the three seed categories of F_1 seed, F_2 full sib and F_2 half sib grain. The reciprocal effects declined in the F_2 The F_2 full-sib grain is relatively large from the single cross hybrid seed, whose endosperm compromises of two doses (2n) of genes from the single cross parent and one dose from the male parent of the same genetic composition (identity) as the female parent, implying that F_2 full-sib grain contains three doses (3n) of weevil resistance or susceptibility. Thus, through double fertilization genes responsible for weevil resistance are expected to accumulate in the F_2 full-sib grain by additive gene effects. For the F_2 half sib open-pollinated grain, it is only the female parent, which is known, the pollen parent is random thus manifesting varying doses of resistance, depending on the characteristics of the pollen source. Results also have implications for recycling seed of maize weevil resistant hybrids on-farm, because maternal genotypes and maternal tissues play significant roles for grain weevil resistance. The variations in response to maize weevil infestations exhibited by the different seed generations demonstrated the need to sensitize farmers on appropriate seed management. Smallholder farmers usually have a tendency of recycling hybrid seeds. Therefore, the risk of decline in weevil resistance that may arise with advancements in seed generations needs to be put into consideration when recycling maize seed, especially when single cross hybrids are deployed.

General combining ability effects

The ten parents exhibited differences in their general combining ability effects for responses to weevil infestations. For F_1 weevil progeny emergence, genotypes exhibiting negative GCA effects were desirable. In this regard, parents MV170 and MV142 were significantly contributing to a reduction in the number of F_1 weevil progenies emerging from the F_1 hybrid seed. This suggested that parents MV170 and MV142 would be suitable parents for enhancing weevil resistance in hybrids. These lines were also among the superior parents for the median development period. For the median development period, genotypes that took longer periods for the weevils to develop and emerge were desirable because weevils would also take longer to multiply and thus cause less damage to the grain in the same time period than if they had multiplied quickly. Therefore, positive GCA effects were desirable for this trait. The parents MV21, MV154, MV31, MV170 and MV142 which exhibited positive significant GCA effects were desirable because once they were infested the weevils would take longer to develop and multiply. The same parents also exhibited positive and significant GCA effects in the F_2 open-pollinated grain. Except for the MV21, the same set of parents also displayed positive significant GCA effects when the F_2 full-sib grain was evaluated for the median development period. There was less consistency of the findings for GCA superiority when the parent weevil mortality was measured, because different a set of lines could be selected for maize weevil resistance according to this trait when different seed categories were evaluated. The study showed that inbred lines with significant and positive parent weevil mortality, which is desired, were observed for this trait, such as MV142, MV170, MV31 and MV44 in the F_1 hybrid seed; parents MV31, MV44, and MV102 in the F_2 full-sib seed and the MV21 from F_2 open-pollinated grain. However, two inbred lines MV31 and MV44 were consistently performing regardless of the seed generation which was evaluated as they were selected in both F_1 seed and F_2 full sib grain. This implies that more than one trait should be measured for grain weevil resistance and that the F_2 full sib grain which represents what farmers would store and get exposed to the maize weevils must be targeted for screening. This is also more practical because abundant F_2 grain can be produced by full sib mating of the F_1 plants for each hybrid. Furthermore, discrimination capacity was higher when the F_2 full sib grain was used to measure maize weevil resistance. A larger number of parental lines (four) were identified as resistant by measuring the number of F_1 weevil progeny emergence and Dobie's index of susceptibility under the F_2 full-sib generation. This illustrated the higher potential exhibited by targeting the F_2 full-sib generation grain to identify maize weevil resistant parental lines, as opposed to the F_1 hybrid generation seed and F_2 half sib open-pollinated grain.

Specific combining ability effects

Various crosses displayed negative significant SCA effects for the number of F_1 weevil progeny emergence in the three seed categories. However, some of the crosses exhibited differences in the manifestation of the SCA effects, resulting from the direction of the cross. For example, cross MV142 × MV102 in the F_1 hybrid seed category exhibited negative significant SCA effects, while its reciprocal cross (MV102 × MV142) exhibited positive significant SCA effects. The same occurrence was manifested in F_2 open-pollinated grain but was not observed in in the F_2 full-sib grain. These results suggest the presence of reciprocal differences as a result of non-maternal interaction effects for maize weevil resistance. However, this was not observed in F_2 full sib grain indicating that there could be less complications caused by non-fixable reciprocal effects when the F_2 full sib grain is evaluated for maize weevil resistance. The study also indicated that both reciprocal differences and the nuclear non-additive effects must be considered when designing hybrids. Another type of response exhibited was the manifestation of weevil resistance in a hybrid generated from a cross between a susceptible female parent (2n endosperm) and a resistant male parent (n pollen). This phenomenon would imply that two doses of susceptibility genes were combined with one dose of resistance genes in the endosperm but resulted in a resistant hybrid. For example, the susceptible × resistant crosses, such as MV44 × MV142, MV44 × MV21, MV44 × MV75, MV44 × MV170, MV102 × MV142, and MV102 × MV21, were resistant underlining the influence of non-additive gene effects. Due to the complications of accounting for SCA effects in a random pollinating maize field trial with many different hybrids, such as 45 crosses for the 10 parent diallel (resulting in F_2 half sib (HS) grain), it is prudent to use the F_2 full sib grain for maize weevil resistance screening. Therefore, selection of the lines was conducted based on the GCA effects in F_2 because GCA is fixable. The F_2 full sib (FS) grain represents the farmers' harvest that would be challenged by weevils. Farmers are most likely to grow one hybrid in a single field or a large plot and the grain would predominantly result from full sib mating of F1 plants. Due to the superiority of the GCA which is fixable superior lines were consistently identified in all the three seed categories (F1, F_2FS and F_2HS) but the F_2 generation was most discriminating.

Rank of hybrids for maize weevil resistance

High levels of consistency were exhibited when ranking the top 20 hybrids/reciprocal crosses that were resistant to weevils. Consequently, hybrids/reciprocal crosses MV75 × MV154, MV154 × MV142, MV142 × MV170, MV154 × MV31, and MV170 × MV13 were ranked among the top 20 hybrids under the three seed generations on the basis of the number of F_1 weevil progeny emergence. Similarly, hybrid MV102 × MV44 was consistently ranked among the worst five hybrids/reciprocal crosses. Based on the number of F_1 weevil progeny emergence, any grain generation could be used for the purposes of discriminating maize genotypes for maize weevil resistance. Hybrids MV170 × MV13 and MV75 × MV154 were ranked among the top 20 weevil-resistant as well as among the top 20 stable high yielding hybrids/reciprocals. Therefore, the two genotypes are good candidates for further evaluations regarding the two traits.

Conclusion and implications

The study illustrated that the F_2 full-sib grain was superior to F_1 hybrid seed and F_2 half sib grain derived by open-pollination in providing quality genetic information for parental line selection for good GCA effects. The GCA is fixable and would persist across generations. The maize inbred lines MV170 and MV142 significantly contributed to small number of F_1 weevil emergence in the F_1 hybrid seed, F_2 full-sib and F_2 half sib grain hence they were good general combiners. These lines were involved in the top 20 superior hybrids which were consistently ranked in the three seed categories. The decision of the seed generation to target for weevil screening would depend on other factors such as practicality of implementation and genetic expectations. In general, all seed generations showed that additive gene effects, non-additive gene effects and reciprocal effects were important for maize weevil resistance giving credence to previous findings. However, the three seed categories exhibited different levels of influence by the different types of gene effects governing the number of F_1 weevil progeny emergence from the seed, the insects' median development period, Dobie's index of susceptibility and parent weevil mortality. This provided opportunity for selecting the seed generation for use in evaluating hybrids for maize weevil resistance. Reciprocal effects were more important for governing the resistance parameters in the F_1 hybrid seed, GCA effects were predominant in the F_2 full-sib grain, while SCA effects were preponderant in the F_2 half sib grain. The information generated would be crucial for devising the strategy for breeding maize weevil resistant hybrids. Both the reciprocal differences of the non-maternal effects and SCA effects which were predominant in the F_1 and F_2 half-sib grain, respectively, are not fixable and therefore not useful for programmes targeting population improvement. Given the foregoing the F_2 full sib grain, which showed less complications caused by reciprocal cross differences in selecting superior inbred lines according to GCA effects, and revealed preponderance of the additive gene effects, which are fixable, would be recommended for improving maize hybrids for maize weevil resistance.

Acknowledgements We are thankful to the Alliance for Agriculture Revolution in Africa (AGRA) for funding this study through the African Centre for Crop Improvement (ACCI). We are also grateful to the National Crops Resources Research Institute (NaCRRI) of Uganda, the International Maize and Wheat Improvement Center (CIMMYT-Kenya) and the University of KwaZulu Natal, South Africa for providing maize germplasm used in this study.

Funding The Alliance for Agriculture Revolution in Africa funded this work.

Availability of data and material Data and germplasm can be made available for research purposes.

Code availability The diallel SAS code used is available in the public domain.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

References

Akmal M, Freed S, Bilal M, Malik MN (2020) A laboratory evaluation for the potential of entomopathogenic fungi against Tribolium castaneum (Herbst.) (Coleoptera: Tenebrionidae). TURJAF 8(6):1232–1235

Corrêa AS, Pereira EJG, Cordeiro EMG, Braga LS, Guedes RNC (2011) Insecticide resistance, mixture potentiation and fitness in populations of the maize weevil (Sitophilus zeamais). Crop pro 30:1655–1666

Crispim-Filho AJ, dos Santos FP, Pinto JF, Melo PG, dos Reis EF, Mendes-Resende MP (2020) Dealing with multiple traits in maize: a new approach for selecting progenies. Crop Sci 6:3151–3165

Dari S, Pixley KV, Setimela P (2010) The resistance of early generation maize inbred lines and their hybrids to maize weevil Sitophilus zeamais (Motschulsky). Crop Sci 50:1310–1317

Dhliwayo T, Pixley K (2003) Divergent selection for resistance to maize weevil in six maize populations. Crop Sci 43:2043–2049

Dobie P (1974) The laboratory assessment of the inherent susceptibility of maize varieties to postharvest infestation by Sitophilus zeamais. J Stored Prod Res 10:183–197

Dobie P (1977) The contribution of the tropical stored products center to the study of insect resistance in stored maize. Tropical Stored Prod Info 34:7–22

Faure JE, Rusche ML, Thomas A, Keim P, Dumas C, Mogensen L (2003) Double fertilization in maize: the two male gametes from a pollen grain have the ability to fuse with egg cells. The Plant J 33:1051–1062

Forbanka DN (2021) Post-harvest storage practices and insect pests of maize and beans in the North West Region of Cameroon. Afr Entomol 1:133–141

Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing systems. Aust J Biol Sci 9:463–493

Kang M, Zhang Y, Magari R (1995) Combining ability for maize weevil preference of maize grain. Crop Sci 35:1556–1559

Mutambuki K, Likhayo P (2021) Efficacy of different hermetic bag storage technologies against insect pests and aflatoxin incidence in stored maize grain. Entomol Res 1–2

Mwololo JK, Mugo S, Okori P, Tefera T, Otim M, Munyiri SW (2012) Sources of resistance to the maize weevil Sitophilus zeamais in tropical maize. J Agric Sci 4:206–215

Ngatia CM, Kimondo M (2011) Comparison of three methods of weight loss determination on maize stored in two farmer environments under natural infestation. J Stored Prod Postharvest Res 2:254–260

Singh RK, Chaudhary BD (2004) Biometrical genetics. Kalyani Publisher, New Delhi

SAS-Institute Inc. (2003) SAS system for windows, version 9.1. SAS Inst., Cary

Sserumaga JP, Makumbi D, Oikeh SO, Otim M, Machida L, Anani BY, Nhamucho E, Beyene Y, Mugo S (2021) Evaluation of early-generation tropical maize testcrosses for grain-yield potential and weevil (Sitophilus zeamais Motschulsky) resistance. Crop pro 139:105384

Tipping PW, Cornelius PL, Legg DE, Poneleit CG, Rodriguez JG (1989) Inheritance of resistance in whole kernel maize to oviposition by the maize weevil (Coleoptera: Curculionidae). ESA 82:1466–1469

Zaman S, Ahmad F, Javed N (2020) Pathogenicity of entomopathogenic fungi against Sitophilus granarius (L.) (Coleoptera: Curculionidae) under abiotic factors. Pak J Agric Sci 57(1)

Zhang Y, Kang MS, Lamkey KR (2005) Diallel-SAS05: a comprehensive program for Griffing's and Gardner-Eberhart analyses. Agron J 97:1097–1106