International Journal of Agriculture and Plant Science
www.agriculturejournal.in
Online ISSN: 2664-7664, Print ISSN: 2664-7656
Received: 09-12-2022, Accepted: 25-12-2022, Published: 11-01-2023
Volume 5, Issue 1, 2023, Page No. 11-18

Combining ability in maize for fall armyworm (*Spodoptera frugiperda* J.E Smith) resistance

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Abstract
Maize plays significant roles in the economies of Sub-Saharan Africa, from which a larger percentage of the populace derive their source of livelihood. However, the emergence of the fall armyworm menace is posing serious threat to the cultivation and productivity of maize in Africa. As a polyphagous pest, the FAW is capable of being host to over 80 species of crops including maize the main staple food crop of the sub-region. Host plant resistance offers a safe, reliable and cost-effective control to the fall armyworm challenge. Combining ability analysis is required to identify superior genetic material and determine the gene action responsible for their inheritance. The diallel mating design was used to generate the progenies by employing the Griffing's method in RCBD. These progenies were then evaluated for their tolerance level against fall armyworm leave feeding damage. The analysis of variance for the combining ability revealed highly significant differences (P<0.001) among GCA and SCA effects indicating both additive and non-additive gene actions controlled the inheritance of the traits among the maize lines. Best general and specific combiners for fall armyworm resistance were identified as the lines with negative GCA and SCA values. Negative GCA values indicate the ability of inbred lines to transmit genes for resistance to the progenies. The positive GCA values for the trait imply that the inbred lines are susceptible and are therefore capable of transmitting genes for susceptibility to their progenies.

Keywords: maize, inbred lines, combining ability, GCA, SCA, resistance, additive, non-additive

Introduction

Maize (*Zea mays* L., 2n = 2x = 20) as a major staple food crop in Africa accounts for more than 50 % of the total caloric intake of local diets (Sinha, 2007). Its production in sub-saharan Africa is constrained by both abiotic and biotic stresses including the fall armyworm, which is of recent introduction into the continent. This voracious pest causes wide spread damage to maize resulting in extensive yield losses above 50 %, facilitated by plant growth stage, susceptibility level and the extent of infestation. Host plant resistance, a major component of an integrated pest management approach, offers a safe, reliable and cost-effective alternative to control FAW. Usually, maize varieties that are resistant to pests possess poor agronomic qualities limiting the use of HPR in integrated pest management (Prassana, 2018). According to FAO (2018) and Kasoma *et al.* (2020) the need has arisen to develop FAW resistant maize genotypes for the continent, which is to be preceded by rigorous screening to identify resistant genes. Combining ability analysis among potential maize lines is required to identify superior genetic material and determine the gene action responsible for their inheritance (Kasoma et al., 2020; Fasahat *et al*., 2016) [16, 10]. Combining ability of inbred lines is seen to be the ultimate factor to determine future usefulness and commercial utility of the lines for hybrids development. Traits with inheritance under the control of additive and non-additive gene actions are improved through recurrent selection and heterosis breeding, respectively (Bernado, 2020). GCA is linked to genes having largely additive effects while SCA is an indicative of genes having dominance and epistatic effects (Falconer, 1996; Griffing, 1956a) [9, 13].

GCA effects for parents and SCA effects for crosses have been estimated in wheat (khalid *et al*., 2013), rice (Qu *et al*., 2012), sorghum (Makanda *et al*, 2010), maize (Dehghanpour, 2013), cotton (Zeng, 2015), chickpea (Bicer and Sakar, 2008). Top crosses, poly cross, diallel cross design, line × tester analysis, partial diallel cross, North Carolina and triallel cross designs have been used to reveal the patterns of inheritance of diverse traits, including pest resistance, in numerous crops (Townsend *et al*., 2013) [34]. Widstrom *et al*. (1972) [36] studied the inheritance of resistance to FAW using eight inbred lines and found additive gene action to be of prime importance than non-additive in conditioning resistance to leaf-feeding by FAW. Williams *et al*. (1989) concluded that general combining ability was highly significant source of variation for FAW resistance among some hybrids; implying additive genetic variance should be effective for selection for FAW resistance. Widstrom *et al*. (1992) [37] utilized several cycles of selection to develop germplasm with resistance to FAW. The objective of this study was to estimate the combining ability effects and inheritance of selected maize genotypes and to select desirable parents and single cross hybrids with fall armyworm resistance for breeding programs in Ghana.

Materials and methods

Plant Material

The lines that were promising by exhibiting tolerance to FAW foliar feeding from a screening and with desirable mean performances from the initial analysis were selected for the improvement programme. These included MP 704, MP 702, MP 708, MP 713, MP 706, MP 701, MP 705, MP 707, CML 126, CML124, CML 122, CML 331, CML 123, CML 334, CML 346, CML 264 and CML 330. Two of the CIMMYT lines CML 124 and CML 343 though susceptible, were included due to their desirable agro-morphological characteristics being earliness and high yielding, respectively. The inbred line CML 124 takes 47 days to anthesis which can be considered as an extra early maturing line.

Location, land preparation, planting and experimental design

This research was carried out at the Animal Science maize breeding pipeline experimental station, Kwame Nkrumah University of Science and Technology, Kumasi Ghana. The research period spanned from May to December, 2020 in two seasons. This site is located at latitude 6°40'38.8"N and longitude 1°32'42.28"W at an elevation of 277 m.a.s.l. Mean annual rainfall in the station is 1500 mm and an average monthly temperature of not less than 20 ºC (20-25 ºC). Land preparation involved ploughing and harrowing, followed by pre-emergence weed control with Sunphosate (Glyphosate, 360 g/L) applied at 5.0 L/ha and Gramoxone (Paraquat) applied at 3.5 L/ha. Field screening was carried out using Randomized Complete Block Design (RCBD) with 3 replications. An experimental plot consisted of 5 m long single row with 0.75 m between rows planted to 13 hills per row. Blocks were separated by 2 m alleys with intra row planting distance of 0.40 m. Recommended crop management techniques were applied. The diallel crossing scheme was used. The crosses were partitioned into two sets namely: Set 1: where all possible combinations involving parents, F1's and reciprocal crosses were made among the inbred lines from USDA-ARS including MP 702, MP 704, MP 705, MP 706, MP 707, MP 708, and MP 713. Set 2 involved parental and F1 crosses among the USA lines (MPs) and the CIMMYT lines including CML 122, CML 123, CML 124, CML 330, CML 346, MP 702, MP 705, MP 708, MP 713. The progenies were then evaluated for their tolerance level against fall armyworm leave feeding damage.

Data collection and analysis

The data on the levels of FAW injury were recorded 30 days 37 days and 44 days after planting based on the rating scale described by Davis *et al.* (1992) and Smith *et al*. (1994) guided by a modified scale of 1 (highly resistant) – 9 (highly susceptible described by Ni *et al*. (2011).

Combining ability estimation

The data on the FAW feeding damage were analysed to test for their significance of variation of the Crosses, GCA, SCA and the Reciprocals using Analysis of Genetic Design with R – (AGD – R) Version 5.0 (Rodríguez *et al*., 2015). The analysis was performed for set 1 cross using Griffing's RCBD method 1 model (fixed) 1 (Griffing, 1956) [13] in single environment.

The model for the analysis of variance is

$$Y_{ijk} = \mu + Rep_k + GCA_i + SCA_{ij} + m_i + r_{ij} + e_{ijk}$$

Where, yijk is the observed value; µ is general mean; Repk = the replication effect (k = 1, 2,.,r); GCAi = the general combining ability effect (i = 1, 2,...,p); SCAij = the specific combining ability effect (i = 1, 2,...,p and i = 1,2,...,p); mi = the maternal effect (i = 1, 2,...,p); rij = the reciprocal effect (i = 1,2,...,p and i = 1,2,...,p); eijk = residual

Results

Combining Ability for fall armyworm ratings for set one

The analysis of variance for combining ability revealed that the mean squares due to GCA and SCA effects were highly significant for the 30, 37 and 44 days after planting ratings for fall armyworm resistance (Table 1). The GCA/SCA ratio was < 50 % for FDR 1 and FDR 2 but was > 50 % for FDR 3. The highest positive and significant general combining ability (GCA) effect was recorded for MP 704 while MP 705, MP702, MP 707 and MP 706 recorded positive but not significant GCA effects. The parental line MP 713 recorded a negative GCA effect while MP 708 recorded negative but significant GCA effect (Table 2) during the 30 days ratings. With the 37 days after planting ratings, the general combining ability estimates of the parents revealed positive and highly significant GCA effect for MP 706, positive and significant effect for MP 707 as well. Two parents including MP 702 and MP 705 recorded positive but non-significant GCA effects while MP 704 recorded a negative and non-significant GCA effect. This was in sharp contrast to the earlier situation. MP 708 and MP 713 however, recorded negative and significant GCA effects which corroborated the earlier result. These ideal genotypes can be selected in addition to the good combiners for cultivar development programmes. From the analysis, it was observed that two parental lines recorded positive and significant GCA effects which included MP 707 and MP 706 ratings for the 44 days. MP 713 exhibited negative but significant GCA effect while MP 702, MP708, MP 704 and MP 705 showed negative GCA accounts.

Table1: Analysis of variance of GCA and SCA effects for fall armyworm traits

	Mean	**Squares**		
	Df	FDR 1	FDR 2	FDR 3
REP	2	0.44	1.88	0.15
Cross	48	2.44***	3.54***	2.51***
GCA	6	2.39***	10.09***	9.4***
SCA	21	4.57***	4.69***	2.4***
Reciprocal	21	0.33	0.51	0.64
Maternal	6	0.55	0.92	0.65
No Maternal	15	0.24	0.35	0.63
Residual	96	0.47	0.69	0.76

Table 2: GCA effects of FAW ratings using Griffing RCBD Method 1 Model 1

Parent	GCA1	GCA2	GCA3
MP706	0.02	0.77***	0.57***
MP707	0.04	0.29*	0.71**
MP702	0.05	0.19	-0.00
MP705	0.16	0.06	-0.16
MP704	0.33**	-0.14	-0.23
MP708	-0.41**	-0.54	-0.27
MP713	-0.19	-0.64	-0.60**

The specific combining ability (SCA) estimates revealed that the hybrid MP 707 * MP 702 produced the highest positive SCA effect which was highly significant with MP 707* MP 704 MP 713 * MP 702 MP 706 * MP 704 also having positive and a highly significant SCA effects. The hybrids MP 713 * MP 707, MP 708 * MP 707, MP 708 * MP 705 and MP 713 * MP 705 on the other hand recorded positive SCA effects. Negative SCA and non-significant effects were recorded for hybrids MP 713 * MP 704, MP 708 * MP 704, MP 708 * MP 706, MP 705 * MP 702, MP 706 * MP 705. These hybrids were found to be ideal specific combiners as they revealed negative but significant SCA effects in addition to the above progenies that had negative effects as well. They included MP 708 * MP 702, MP 707 * MP 705, MP 706 * MP 702, MP 713 * MP 708, MP 705 * MP 704 and MP 704 * MP 702 (Table 3). During the 37day rating the following crosses recorded negative as well as non-significant SCA effect for the fall armyworm foliar damage scores namely MP 708 * MP 702, MP 713 * MP 705, MP 707 * MP 705, MP 713 * MP 704, MP 707 * MP 706, MP 706 * MP 702, MP 713 * MP 706, MP 706 * MP 705 and MP 713 * MP 708. Four hybrids comprising MP 708 * MP 707, MP 708 * MP 704, MP 704 * MP 702, MP 706 * MP 704 and MP 705 * MP 704 recorded negative but significant SCA effects.

Table3: SCA effects of FAW ratings using Griffing RCBD Method 1 Model 1

HYBRID	SCA FDR1	SCA FDR2	SCA FDR3
MP705*MP702	-0.39	1.74***	0.76*
MP707*MP704	1.26***	1.32***	0.57
MP713*MP707	0.4	1.07***	0.32
MP713*MP702	1.24***	0.27	-0.58
MP708*MP706	-0.11	0.21	0.68*
MP708*MP705	0.04	0.15	0.32
MP707*MP702	2.05***	0.01	-0.54
MP708*MP702	-0.71**	-0.05	-0.49
MP713*MP705	0.02	-0.06	0.33
MP707*MP705	-0.67*	-0.12	0.74*
MP713*MP704	-0.16	-0.18	-0.51
MP707*MP706	1.03**	-0.21	-0.15***
MP706*MP702	-0.79**	-0.27	1.03**
MP713*MP706	-0.08	-0.35	0.05
MP706*MP705	-0.61*	-0.39	-0.73*
MP713*MP708	-0.79**	-0.42	0.31
MP708*MP707	0.05	0.70*	-0.44
MP708*MP704	-0.1	-0.99**	-0.17
MP704*MP702	-1.17***	-0.99**	-0.06
MP706*MP704	0.99***	-1.19***	-0.88**
MP705*MP704	-0.89***	-1.36***	-0.62*

For the 44 days ratings, the hybrids MP 713 * MP 702, MP 707 *MP 702, MP704 * MP 702, MP 708 * MP 702, MP 713 * MP 704, MP 708 * MP 707 and MP 708 * MP 704 produced negative SCA effects whereas MP 707 *MP 706, MP 706 * MP 705, MP 706 *MP 704 and MP 705 * MP 704 revealed negative but significant SCA effect for the quantitative trait under consideration. The GCA effect revealed MP 707 and MP 706 as poor general combiners for resistance against leave feeding damage by fall armyworm larvae having a positive and significant GCA effect. MP 713 was also an ideal general combiner since it recorded a negative but significant GCA effect. Similar to the 30 days after planting ratings, the reciprocal mean square was again not significant.

Combining ability estimates for set two

The analysis of variance showed highly significant difference for the general and specific combining abilities in all the ratings of the lines as well as the crosses abilities to resist the FAW leaf feeding damage with the exception of FDR1 GCA which was not significant (Table 6).

General combining abilities (GCA) for CIMMYT and GRIN Inbred Lines

The estimates of the general combining ability revealed CML 122, CML 123, CML 330, CML 346, MP 702, MP 705, MP 708 and MP 713 producing negative GCA effects during the first foliar damage rating with only CML124 (1.22***) registering a highly significant positive effect. Similarly, CML 122, CML 123, MP 702, MP 708 and MP 713 during the second fall armyworm larvae leave damage rating had negative GCA effects while CML 124, CML330, CML 346 and MP 705 recorded positive GCA effects. During the third fall armyworm damage rating, four parents comprising CML 122, CML 346, MP 705 and MP 713 had negative GCA effects (table 5). However, five parents produced positive effect with one being significant including CML 123, CML 330, MP 702, MP 708 and CML 124 (Table 5).

Specific combining abilities estimated for crosses obtained from CIMMYT and GRIN maize lines

For FDR1 specific combining abilities, the crosses that were desirable included 1*3, 1*4, 1*6, 1*7, 1*8, 1*9, 2*3, 2*6, 2*7, 2*8, 2*9, 3*4, 4*6, 4*8, 5*6, 5*7, 5*8, 5*9, 6*9 and 7*9. These displayed negative to highly significant negative specific combining abilities. The other crosses had positive or significantly positive SCA effects (Table 5). The FDR 2 ratings revealed the following crosses to have desirable specific combining ability effects comprising 3*1, 1*4, 1*6, 1*7, 1*9, 2*5, 2*7, 2*8, 2*9, 3*4 and 7*9. All the other crosses had undesirable effects as they recorded positive to significantly positive specific combining abilities. The 44 days after planting and the third rating after natural infestation produced similar results in reference to the above scenarios. Here, the desirable crosses consisted of 1*2, 1*3, 1*4, 1*6, 1*7, 1*8, 2*7, 2*8, 2*9, 3*4, 3*6, 3*8, 4*5, 4*8, 5*6, 5*7, 6*8, 6*9, 7*8, 7*9 and 8*9.

Table4: Means, mean squares and probabilities of combining ability variables for fall armyworm traits estimated in maize inbred lines, hybrids and their reciprocals derived from USDA-ARS evaluated in Ghana.

GENOTYPE	TYPE	FDR1	FDR2	FDR3	GENOTYPE	TYPE	FDR1	FDR2	FDR3
MP702	PARENT	4.03	4.72	4.4	MP706*MP708	RECIPROCAL	4.33	4.27	5.40
MP704	PARENT	3.93	3.01	3.67	MP706*MP713	RECIPROCAL	4.60	3.90	3.80
MP705	PARENT	3.87	3.95	5.03	MP707*MP702	RECIPROCAL	4.33	4.13	4.90
MP706	PARENT	3.87	5.43	4.61	MP707*MP704	RECIPROCAL	2.40	4.67	4.11

MP707	PARENT	6.83	4.53	4.33	MP707*MP705	RECIPROCAL	5.90	6.00	5.40
MP708	PARENT	4.77	4.53	4.27	MP707*MP706	RECIPROCAL	4.30	5.33	6.13
MP713	PARENT	5.37	4.60	4.33	MP707*MP708	RECIPROCAL	3.90	3.73	5.40
MP702*MP704	HYBRID	4.33	3.50	3.80	MP707*MP713	RECIPROCAL	4.40	3.33	4.37
MP702*MP705	RECIPROCAL	4.30	5.20	4.83	MP708*MP702	HYBRID	3.67	2.5	3.42
MP702*MP706	HYBRID	5.4	7.23	3.67	MP708*MP704	HYBRID	3.43	3.49	2.97
MP702*MP707	HYBRID	4.03	3.73	4.9	MP708*MP705	RECIPROCAL	4.40	3.30	3.40
MP702*MP708	RECIPROCAL	4.27	3.97	4.23	MP708*MP706	HYBRID	3.83	5.07	4.43
MP702*MP713	RECIPROCAL	4.27	3.87	3.33	MP708*MP707	HYBRID	4.00	4.77	5.43
MP704*MP702	RECIPROCAL	4.83	3.80	3.92	MP708*MP713	HYBRID	4.73	4.77	3.97
MP704*MP705	RECIPROCAL	4.47	6.13	4.40	MP713*MP702	HYBRID	4.00	3.17	4.00
MP704*MP706	HYBRID	4.30	4.47	5.10	MP713*MP704	HYBRID	5.37	3.87	2.93
MP704*MP707	HYBRID	6.87	4.37	3.93	MP713*MP705	RECIPROCAL	3.77	3.67	2.90
MP704*MP708	RECIPROCAL	3.87	3.63	3.63	MP713*MP706	HYBRID	3.97	4.83	5.20
MP704*MP713	RECIPROCAL	5.9	3.70	2.63	MP713*MP707	HYBRID	4.00	3.87	4.33
MP705*MP702	HYBRID	4.5	5.23	4.70	MP713*MP708	RECIPROCAL	3.73	3.60	3.53
MP705*MP704	HYBRID	4.6	5.77	4.50			Pr(>F)	Pr(>F)	Pr(>F)
MP705*MP706	HYBRID	5.5	3.67	3.20	CROSS		2.94E-12	4.52E-12	3.73E-07
MP705*MP707	HYBRID	5.87	5.93	5.00	GCA		0.00013	7.45E-12	3.14E-10
MP705*MP708	HYBRID	3.77	2.33	2.90	SCA		8.88E-16	1.68E-11	7.18E-05
MP705*MP713	HYBRID	3.8	3.40	2.73	RECIPROCAL		0.823879	0.771088	0.669991
MP706*MP702	RECIPROCAL	5.67	7.03	4.23					
MP706*MP704	RECIPROCAL	3.70	4.93	6.03	MEAN SQ		M. SQ.	M. SQ.	M. SQ.
MP706*MP705	RECIPROCAL	5.70	4.20	4.03	CROSS		2.441176	3.535572	2.505862
MP706*MP707	HYBRID	3.33	5.13	6.30	GCA		2.393549	10.08726	9.398068
					SCA		4.569856	4.685442	2.403932
					RECIPROCAL		0.326111	0.513792	0.63859
					RESIDUAL		0.466172	0.685435	0.763886

Table 5: General and Specific Combining Abilities estimates of USDA-ARS and CIMMYT inbred lines for fall armyworm resistance

No.	GCA	FDRI	FDR2	FDR3
1	CML122	-0.15	-0.49**	-0.08
2	CML123	-0.16	-0.38**	0.18
3	CML124	1.22***	0.78***	0.47**
4	CML330	-0.09	0.27*	0.17
5	CML346	-0.21*	0.02	-0.24
6	MP702	-0.16	-0.08	0.13
7	MP705	-0.19	0.05	-0.13
8	MP708	-0.12	-0.03	0.07
9	MP713	-0.13	-0.13	-0.56 **
MALE	FEMALE	SCA FDR1	SCA FDR2	SCA FDR3
2	1	0.19	0.52	-0.27
3	1	-0.84**	-0.45	-0.43
4	1	-0.08	-0.64*	-1.23***
5	1	0.67*	0.30	0.52
6	1	-0.08	-1.22***	-0.39
7	1	-0.51	-0.91**	-0.09
8	1	-0.36	0.46	-0.17
9	1	-0.76**	-1.09***	0.11
3	2	-0.42	0.1	0.33
4	2	0.59*	0.90**	0.49
5	2	0.13	-0.72	0.80*
6	2	-0.58*	0.3	0.18
7	2	-0.3	-0.37	-0.48
8	2	-0.11	-0.79*	-0.4
9	2	-0.57*	-1.31***	-1.3***
4	3	-0.16	-0.8*	-0.39
5	3	0.67*	0.71*	0.45
6	3	1.95***	0.09	-0.25
7	3	1.09***	0.46	0.31
8	3	0.73**	0.71*	-0.43
9	3	0.80**	0.54	0.33
5	4	0.42	0.18	-1.25***
6	4	-0.34	0.33	0.12
7	4	0.07	0.66*	0.83*
8	4	-0.31	0.25	-0.12
9	4	0.12	0.45	0.71

6	5	-0.52*	0.48	-0.35
7	5	-0.53	0.01	-0.92*
8	5	-0.44	0.54	1.36***
9	5	-0.64*	0.38	0.46
7	6	0.00	0.15	0.46
8	6	0.06	0.24	-0.77
9	6	-0.03	0.63*	-0.37
8	7	-0.47	0.61	-0.66
9	7	-0.6*	-0.14	-1.45***
9	8	0.65*	0.66*	-0.23

Table 6: Means, mean squares and probabilities of combining ability variables for fall armyworm traits estimated in maize inbred lines, hybrids and their reciprocals derived from USDA-ARS and CIMMYT evaluated in Ghana.

GENOTYPE	TYPE	FDR1	FDR2	FDR33	GENOTYPE	TYPE	FDR1	FDR2	FDR3
CML122	PARENT	5.17	5.43	5.40	CML330*CML346	H	3.67	3.63	3.33
CML123	PARENT	4.80	4.83	5.27	MP702*CML330	H	3.90	4.47	4.47
CML124	PARENT	5.13	5.77	5.56	MP705*CML330	H	3.87	4.43	5.37
CML330	PARENT	4.23	4.77	5.36	MP08*CML330	H	4.20	4.70	5.03
CML346	PARENT	4.30	4.00	3.57	MP713*CML330	H	4.07	4.17	4.83
MP702	PARENT	4.03	4.23	5.53	MP702*CML346	H	3.53	3.97	4.00
MP705	PARENT	4.83	4.77	5.33	CML330*CML123	H	4.60	5.93	5.43
MP708	PARENT	4.47	3.50	5.43	MP705*CML346	H	3.57	3.63	3.13
MP713	PARENT	4.83	4.57	4.34	MP708*CML346	H	3.83	4.60	5.57
					MP713*CML346	H	3.63	4.53	4.10
CML122*CML123	HYBRID	4.23	4.50	4.47	MP705*MP702	H	4.30	5.20	4.83
CML122*ML124	HYBRID	4.87	4.57	4.93	MP708*MP702	H	4.27	3.97	4.23
CML122*CML330	HYBRID	3.90	4.00	3.33	MP713*MP702	H	4.27	3.87	3.60
CML122*CML346	HYBRID	4.63	4.70	4.53	MP708*MP705	H	3.97	2.70	3.60
MP702*CML122	HYBRID	3.93	3.00	4.27	MP713*MP705	H	3.80	3.40	2.73
MP705*CML122	HYBRID	3.20	4.17	4.2	MP713*MP708	H	4.73	4.77	3.97
MP708*CML122	HYBRID	3.83	5.07	4.43					
MP713*CML122	HYBRID	3.43	2.90	3.90					
CML123*CML124	HYBRID	5.23	5.40	5.57	Pr(>F)				
CML123*CML346	HYBRID	3.93	3.97	5.47	REP		0.412779	0.012066	0.007567
MP702*CML123	HYBRID	3.63	4.77	5.13	CROSS		3.48E-28	1.66E-24	3.68E-28
MP705*CML123	HYBRID	4.17	4.07	4.27	GCA		0	2E-14	4.01E-07
MP708*CML123	HYBRID	4.13	3.97	4.30	SCA		2.66E-15	8.46E-13	1.22E-08
MP713*CML123	HYBRID	3.40	3.47	3.03					
CML330*CML124	HYBRID	5.07	5.00	5.20	MEAN SQUARE				
CML346*CML124	HYBRID	5.57	5.50	5.17	REP		0.231872	1.547968	2.289803
MP702*CML124	HYBRID	3.87	5.10	4.93	CROSS		2.034024	2.276154	1.828713
MP705*CML124	HYBRID	6.00	6.00	5.40	GCA		7.037004	4.457131	2.87891
MP708*CML124	HYBRID	5.23	5.27	5.00	SCA		1.513581	1.687666	1.646094
MP713*CML124	**HYBRID**	**4.43**	**3.50**	**4.73**	RESIDUAL		0.260602	0.340844	0.45468

Table 7: Components of genetic parameters for fall armyworm traits in set I and II genotypes

Parameter	FDR 1	FDR 2	FDR 3
σ^2gca	0.16***	0.08**	0.06*
σ^2sca	0.20***	0.33***	0.41***
σ^2e	0.26	0.34	0.45
σ^2p	0.89	1.03	0.99
σ^2A	0.31	0.16	0.12
σ^2D	0.2	0.34	0.41
h^2b	0.58	0.48	0.54
h^2n	0.35	0.16	0.12
GCA /SCA	0.76	0.25	0.14
Baker Ratio	0.6	0.33	0.23

Component	FDR 1	FDR 2	FDR 3
σ^2gca	0.00	0.13	0.17
σ^2sca	0.78	0.76	0.31
σ^2m	0.008	0.013	0.00
σ^2e	0.47	0.68	0.75
σ^2p	1.26	1.73	1.40
σ^2A	0	0.26	0.33
σ^2D	0.77	0.76	0.31
h^2b	0.62	0.59	0.46

h^2n	0.00	0.15	0.23
GCA – SCA Ratio	0.00	0.17	0.53
Baker Ratio	0.00	0.26	0.52

Discussion

The desirable inbred lines selected for improvement for fall armyworm resistance and other agronomic utilities were partitioned into sets one (USDA-ARS germplasm) and two (USDA-ARS and CIMMYT germplasm) for combining ability studies to reveal the inheritance and gene action of the trait. In set one, the GCA and SCA analysis revealed significant variation among the parents and the hybrids derived from the crosses among the parents for the fall armyworm resistant trait. In general, the parental lines MP 704, MP 708, MP 713, MP 705 and MP 702 were the best general combiners and could therefore be considered for selection and progeny development. Also, the hybrids MP 713 * MP 704, MP 708 * MP 704, MP 705 * MP 702, MP 708 * MP 702, MP 713 * MP 708, MP 705 * MP 704, MP 713 * MP 702, and MP 704 * MP 702 were found to be ideal specific combiners as they could be exploited. The **set two** analyses similarly revealed highly significant differences among the GCA and SCA parameters in all the ratings, but for FDR1 where the GCA was not significant. Across all the ratings, CML122 and MP 713 turned out to be the most promising parents while CML 123, CML 346, MP 702, MP 705 and MP 708 offered some level of hope. The parental line CML 124, an extra early maturing genotype, generally emerged as a poor combiner across board. CML 124 during the preliminary screening stage came out as a highly susceptible inbred line. On the other hand the hybrids 1*3, 1*4, 1*6, 1*7, 2*7, 2*8, 2*9, 3*4, and 7*9 emerged as the ideal specific combiners recording negative to highly significant negative estimates. This is a demonstration of the presence of genes transmitted for the protection against fall armyworm larvae attack. However, the crosses 1*5, 2*3, 2*4, 2*6, 3*5, 3*7, 3*9, 4*6, 4*7, 4*9, 5*8, 5*9, 6*7 produced undesirable effects. In a similar study, Kasoma *et al*. (2021) [16] found both the general and specific combining ability effects to be significant for the traits of interest. Mahdiyeh and Bahram (2014) also reported GCA and SCA to be significant. Negative GCA values indicate the ability of inbred lines to transmit genes for resistance to the progenies. The positive GCA values indicate the potential of the inbred lines to transmit genes for susceptibility to their progenies. GCA estimates proved the possibility of selecting inbred lines that can be combined effectively to generate hybrids that are resistant to fall armyworm. Gichuru and Njoroge (2011) and Yazachew *et al*. (2017) in their studies recorded similar findings. Significant variations detected confirmed both additive and non-additive gene actions contributed significantly toward controlling the inheritance of the trait. Progeny selection and heterosis breeding will be effective for future breeding programme. This corroborated the findings by Kamara *et al*, (2014); Yazachew *et al*. (2017) who detected significant differences and concluded both additive and non-additive gene action involved the inheritance of the traits of interest. The selection of parents on basis of their combining ability and understanding of the genetic control of desirable traits ensure the efficiency of breeding activities (Nadarajan and Gunasekaran, 2005; Sleper and Poehlman, 2006). Ojulong et al. (1995) and Karayaa *et al*. (2009) observed and attributed largest negative GCA effects to resistant maize inbred lines while assigning largest positive GCA effects to insect damage. Significant negative general combining ability (GCA) effects of parental materials for biotic stresses were also reported by earlier authors (Kumar, 2006; Sharma, 2010 and Brar *et al*., 2011) for fruit fly and severity of powdery mildew. Widstrom *et al*. (1972) [36] concluded that additive gene action was more significant than non-additive in conferring resistance to leaf-feeding by FAW. Williams *et al*. (1989; 1995) indicated general combining ability to be highly significant source of variability for FAW resistance among hybrids. Widstrom *et al*. (1992) [37] adopted several cycles of selection to develop germplasm with resistance to FAW. The significance of both additive and dominance gene effects on FAW parameters corroborated previous findings (Alvarez *et al*., 2002). The lines with negative GCA were found to be the best general combiners for fall armyworm. The selection of parents on basis of their combining ability and understanding of the genetic control of desirable traits ensure the efficiency of breeding activities (Nadarajan and Gunasekaran, 2005 [21]; Sleper and Poehlman, 2006) [21, 31]. The estimated GCA/SCA ratio was < 50 % for FDR 1 and FDR 2 but was however, > 50 % for FDR 3. This ratio of the combining ability variance parameters, also known as predictability ratio, throws more light on the type of gene action operating in the expression of a character. It thereby allows inferences to be drawn regarding the optimum allocation of resources in hybrid breeding. This result proved that FDR 1 and FDR 2 were not under the effects of additive gene action but non-additive gene action influencing the expression of the said trait. Additive gene effect was on the other hand, found to be responsible for the expression of the trait in FDR 3 as GCA/SCA of 0.53 was recorded. According the accounts of Singh *et al*. (1986) [29] and Kulembeka *et al.* (2012), the closer the GCA/SCA ratio is to one, the higher the influence of GCA, whereas a ratio with a value less than 1 means SCA operating. Fehr (1993) [11] was of the view that if both the GCA and SCA values are not significant, epistatic gene effects may play a significant role in determining the characters under consideration. The above argument therefore suggests that the gene action conferring the resistance of the maize lines to fall armyworm leave feeding damage is under the influence of non-additive gene expression, specifically dominance while additive gene action contributed less to the variation. The Baker ratio from the analysis also indicated that FDR 1 and FDR 2 again recorded a ratio of ≤ 0.26 while FDR 3 recorded a ratio of 0.52, similar to the result obtained from the GCA/SCA ratio above. Mahdiyeh, and Bahram (2014) recorded a Baker ratio > 0.80 implying a greater contribution of the additive gene effects in the genetic control of traits. Baker (1978) found out that high ratios of GCA/SCA meant the additive gene action makes a large contribution to the expression of specific traits than non-additive gene action. Therefore, in the current study dominance gene action controlled the expression of the trait in FDR 1 and FDR 2 while FDR 3 was slightly due to additive gene action. This corroborated the analysis of variance for the combining ability indicating that dominance made major contribution with additive gene action making a minute contribution. A high GCA estimate represents higher heritability but less environmental effects. It may also result in less gene interactions and higher achievement in selection. (Topal *et al*., 2001; Chigeza *et al*., 2014) [5]. It is worthy to note that elite parent with high GCA effect has large adaptability. A more direct comparison of GCA and SCA effects of each rating was made by calculating the estimates of GCA and SCA variances (Griffing, 1956) [13]. The estimates of SCA variances were higher than the GCA variances in all situations for FDR1, FDR2 and FDR3 (table 7). Kasoma (2020) [16] reported comparatively larger SCA variances for all FAW related traits than GCA variances. The additive variances ranged from 0.00 in FDR 1 to 0.33 in FDR 3 while the dominance variance spanned from 0.31 in FDR to 0.77 in FDR 1. Similarly, Kasoma *et al*. (2020) [16] had smaller σ^2A than σ^2D during the first fall leave damage rating. These culminated in higher broad sense heritabilities compared to the narrow sense heritability estimates. The broad-sense and narrow-sense heritability estimates for FAW-related traits ranging from 0.15 to 0.90 and 0.37 to 0.39, respectively, were reported by Kasoma (2020) [16] for FAW-related traits.

Conclusion

This study was carried out to reveal the gene action governing the inheritance of the fall armyworm trait conditioning the resistance to leave feeding by the FAW larvae to facilitate selection for breeding in the maize crop. The highly significant GCA and SCA effects of the measured traits generally revealed by the study indicated both additive and non-additive gene actions controlling the inheritance of the traits among the maize lines. Traits with inheritance under the control of additive and non-additive gene actions are improved through recurrent selection and heterosis breeding, respectively. In set 1, parental lines MP 702, MP 704, MP 705, MP 708 and MP 713 exhibited good general combining ability (GCA) effects and are highly recommended to be used in maize breeding for improvement programs. The best hybrid included MP 713 * MP 704, MP 708 * MP 704, MP 705 * MP 702, MP 708 * MP 702, MP 713 * MP 708, MP 705 * MP 704, MP 713 * MP 702, and MP 704 * MP 702. Across all the ratings, CML122 and MP 713 turned out to be the most promising parents while CML 123, CML 346, MP 702, MP 705 and MP 708 offered some level of hope in **set two.** On the other hand, the hybrids 1*3, 1*4, 1*6, 1*7, 2*7, 2*8, 2*9, 3*4, and 7*9 emerged as the ideal specific combiners recording negative to highly significant negative estimates for **set two** experiment. The negative GCA and SCA effects for FDR1, FDR 2 and FDR 3 would be desirable for FAW resistance breeding and should therefore be exploited for breeding programmes. The parental lines with significant and negative (GCA) effects have the genetic potential to transfer desirable traits to their progenies. The above desirable and potential hybrids are highly recommended for further evaluation and breeding.

Acknowledgement

Special appreciation goes to CIMMYT and USDA-ARS for supplying the maize seeds.

Conflict of interest

The authors declare no conflict of interestohal GS, Huber DM. Glyphosate effects on diseases of plants. International Journal of Agriculture and Plant Science Volume 31, Issue 1, 1997, Pages 144-152

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