

GENETICS OF TOLERANCE TO MAIZE STREAK VIRUS IN QUALITY PROTEIN MAIZE INBREDS INTROGRESSED INTO RESISTANT CULTIVARS

Omolaran Bashir Bello*

Department of Biological Sciences, Fountain University, Osogbo, Nigeria

* E-mail: obbello2002@yahoo.com, obbello@fountainuniversity.edu.ng

Abstract

The use of maize streak virus (MSV) resistance cultivars as donors in broadening the quality protein maize (QPM) inbreds would not only reduce the virulence of the disease but also improve grain yield and quality protein in Africa. This experiment was conducted to evaluate the general (GCA) and specific (SCA) combining ability of MSV resistance and QPM inbred lines for MSV resistance disease, grain yield and quality protein. Five QPM lines and five MSV-resistant cultivars were introgressed in a partial diallel design excluding reciprocals. The obtained 45 F_1 crosses, 10 parents and 2 local varieties that served as checks were evaluated at the Lower Niger River Basin Authority, Oke-Oyi, Nigeria in 2014 and 2015 cropping seasons. The QPM lines derived from TZEQI 76, TZEQI 87 and TZEQI 79 that were introgressed with MSV resistant Acr. 91 Suwan-1-Sr C_1 featured as most promising for grain yield, MSV resistance and grain quality protein. SCA and GCA variances were highly significant for all studied characters, implying that both non-additive and additive genetic effects were the vital portion of the genetic variances governing these characters. The ratio of k_2GCA/k_2SCA that was more than one for grain yield and less than one for MSV resistance, lysine and tryptophan characters, indicating that except for grain yield, non-additive gene action played a major role in conditioning the inheritance of these characters. The evidence from this investigation would be worthwhile for developing MSV disease resistant, high grain yielding of quality protein maize varieties in Africa.

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1. INTRODUCTION

Conventional maize has poor nutritional quality with 10% protein, based on the paucity of two essential amino acid contents of lysine and tryptophan that are the prerequisite to dietary protein supplement of human and monogastric animals (Krivanek et al. 2007; Mbuya et al. 2010). The protein of conventional maize that contains tryptophan and lysine levels of 0.35 and 1.81% respectively, is less than 50% concentration recommended by the Food and Agriculture Organization for human nutrition (Prasanna et al. 2001). Therefore, infants that consumed conventional maize without protein supplement are prone to malnutrition and health problems including kwashiorkor, underweight, impaired intellectual development, and susceptibility to infections (Mbuya et al., 2010). The QPM has *opaque-2* (*o2*) genes that were incorporated with modifiers containing twice the tryptophan ($> 0.8\%$) and lysine ($> 4.0\%$) levels in the

whole kernel, compared to conventional maize (Krivanek et al. 2007). However, the *o2* gene has been liable to high lodging, ear and foliar diseases.

In tropical Africa, production of maize is inhibited by many biotic stress factors such as diseases and pests, which appreciably lower the quality and quantity of productivity (Akinbode et al. 2014; Muiru et al. 2015). Maize grain yield losses of about 70% due to disease infections are dependent on many factors, including genetic constitutions of the genotypes and the growth stage during infections (Bua and Chelimo 2010). Diseases of maize under commercial cultivation in the tropics include maize streak virus (MSV) which is transmitted by *Cicardulina spp* (Olakojo et al. 2005ab). The MSV constitutes one of the foremost production constraints of maize in the Southern and Northern savannas of Nigeria, occurring as mixed infections and favored by humid and warm weather conditions (Olakojo et al. 2005b). The

occurrence and severity of MSV disease dependent on many factors, including genetic constitutions of the genotypes and the growth stage during infections. MSV infecting susceptible cultivars at the third leaf stage become sternly stunted, producing abnormal and fewer kernels, and absolute crop failure (Magenya et al., 2008; Karavina et al., 2014a). In Nigeria, MSV decreases grain yield of maize especially at the late cropping seasons during prolong drought spell. In the 1970's, the disease reached an epiphytotic stage, causing major yield loss in the pandemic agro-ecological zones of Nigeria. The collaborative breeding exertions by the maize scientists at both national and international institutes with the introgression of genes for diseases and pests resistance paved the way in developing and releasing the promising maize varieties (hybrids and open pollinated varieties) with elevated grain yield potential and adaptation to various agro-ecological stresses in Nigeria. The symptoms of MSV disease comprised of broken narrow chlorotic streaks that run uniformly on the leaf veins across the leaf surface. The mass of streaking hinges on the susceptibility of the variety. The parallel chlorotic streaks might fuse completely or partially resulting to irregular green lines within the veinlets. The chlorotic streaks usually resulted in chloroplasts development failure in the tissues enveloping the vascular bundles thereby reducing photosynthesis, growth, and yield. Since MSV infection could be transmitted only by the vector, *Cicadulina* leafhopper, the form of streak epidemics are caused by leafhopper migration activity, fecundity, survival and climatic factors.

Genetic gains for stress tolerance and grain yield in maize can be achieved through breeding (Sharma et al. 2012; Aaron 2013). This is feasible by incorporation of desirable attributes from selected parents into another maize genotype through outcrossing, and subsequent selection (Bello et al. 2012a; Wilson et al. 2014). Complementary QPM inbreds are the most important germplasm in maize breeding because their desirable genes

upon crossing could produce hybrids of improved yield, stress resistance/ tolerance, and nutritional qualities. Breeding of host plant tolerance/ resistance strains with either separated or combined quantitative and qualitative genes had been accentuated to be the most efficient, reliable, economical, environmentally friendly and economically sustainable means of controlling diseases (Bua and Chelimo 2010; Shepherd et al., 2010; Karavina et al. 2014b; Muiru et al. 2015). Tolerance/ resistance to diseases of specific crosses may not always be predicted from information of pedigree or by assessing parental performance. Knowledge of various sources of tolerance/ resistance interactions among the crosses could hasten the development of higher grain yielding genotypes adapted to the agro-ecology through suitable breeding procedures. QPM genotypes, however, are vulnerable to diseases due to soft flourey endosperm that fosters the growth of fungi (Mbuya et al. 2011). Currently, improved QPM genotypes are routinely assessed for disease tolerance/ resistance, high yield potential, and adaptation in various agro-ecologies of Nigeria, in order to identify favorable genotypes that can replace the existing commercial ones (Bello and Olawuyi, 2015).

To initiate an efficient breeding program of QPM tolerant/ resistant to diseases and high yielding, good information on combining ability of the breeding materials and genetic factors governing the inheritance of these essential agronomic characters are necessary. Understanding the interaction of various sources of resistance among crosses could accelerate breeding of high yielding cultivars via specific breeding techniques. Significantly, however, MSV-resistant strains could be reliably predicted using diallel analyses. The diallel analyses are commonly used to estimate combining ability which useful guide in determining the best hybrid combinations. Further, it helps in the selection of appropriate parental inbreds for hybridization, evaluation of genetic diversity, classification and

estimation of heterotic pattern, and hybrid development (Zare et al. 2011; Bidhendi et al. 2012; Khan et al. 2014; Bello and Olawuyi, 2015). A suitable avenue to achieve this is by using a diallel mating system that is usually used in maize development programs to ascertain general (GCA) and specific combining abilities (SCA). Variances attributed to GCA and SCA show the nature of genetic effects involved in the expression of quantitative characters. GCA variance comprises additive gene portion, while SCA involves the non-additive portion of the total genetic variance resulting from the epistatic and dominance variations (Amiruzzaman et al. 2013, and Izhar and Chakraborty 2013).

With the understanding of genetic mechanisms, breeding of high yielding QPM varieties with disease tolerance/ resistance could enhance food security and reduce malnutrition in resource-poor setting that depend on maize as a staple in the developing countries. In this context, this study explored the value of different MSV-resistance sources for auspicious alleles in enhancing grain quality and yield of quality protein maize, with the aim of identifying the best segregants from the crosses either suitable for further breeding programmes or for direct cultivation in the Savanna of Nigeria.

2. MATERIALS AND METHODS

Germplasm used

Five QPM lines and five MSV-resistant cultivars were introgressed in a partial diallel design excluding reciprocals [$n(n-1)/2$] (number of parental lines). The obtained 45 F₁ crosses, 10 parents and 2 local varieties that served as checks were evaluated at the Lower Niger River Basin Authority, Oke-Oyi, Nigeria (8° 30'N and 8° 36' E) in 2014 and 2015 cropping seasons. The pedigree of QPM inbreds and MSV resistant cultivars and two checks is presented in Table 1.

Procedures of cross pollination

As described by Bello and Olawuyi (2015), prior to flowering initiation, maize stands were examined daily for pollen shedding and ear shoot emergence. Before silks protrusion, ear shoots were cut and cover up with a semi-transparent shoot-bag, cramped safely against the maize stalk. This is done to achieve uniform silk emergence and avert dislodging by rainfall and/or the wind. To enable proper development of silks, there is need to create adequate space between the shoot-bag and shoot tip. Thereafter, the tassel bag is buttoned with a paper clip against the tassel. When the silks extruded and receptive, the plants were pollinated using the pollens of the desired genotype.

Table 1. Pedigree of QPM inbreds, MSV resistant cultivars and two checks

S/N	Genotype	Pedigree
1	TZEQI 76	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 11-39-2-2-2-8
2	TZEQI 79	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 11-39-2-2-8-8
3	TZEQI 74	TZE COMP5-Y C6S6 Inb 10 × Pool 18 SR QPM BC1S6 2-2-1-1
4	TZEQI 87	TZE COMP5-Y C6S6 Inb 31B × Pool 18 SR QPM BC1S6 7-45-2-3-4-7
5	TZEQI 91	TZE-Y Pop STR C0 S6 Inb 142 × Pool 18 SR QPM BC1S6 4-35-5-8-4-8
6	Acr. 91 Suwan-1-Sr C ₁	Suwan-1
7	TZB-SR SGY	TZB-SR
8	AK-9528-DMRSR	Pop 28 SR
9	Ikenne 88 TZSR-Y-1	TZSR-Y-1
10	IK.91 TZL Comp 3-Y C ₁	TZL Comp 3
11	Afo	Open pollinated variety check
12	Oba Super 5	Commercial hybrid check

To pollinate, there is need to lightly shacked the covered tassel bag to dislodge the pollen, unstapled the pins and then dispense pollen onto exposed silks. Lastly, the tassel bag is stapled on the pollinated shoot till harvesting period to preclude undesirable apparent pollen. The maize grains of the hybrids are stored separately in bags for further assessment.

Experimental design and cultural practices

Based on the agronomic standard of cultivating maize in the savanna zone of Nigeria, the experimental field was ploughed, harrowed and ridged with 0.75 m spacing between ridges. Each plot comprised four 5 m long rows with 50 cm intra-row gave a plant density of 53,333 plants ha⁻¹. Pre-emergence (a.i. 3kg/l Metolachlor and 170g/l Atrazine ha⁻¹) and post-emergence (a.i. 3kg/l Paraquat ha⁻¹) herbicides were applied after land preparation for weed control. The 45 F₁ hybrids, their respective parents and the two checks were evaluated on 24th and 10th July, 2014 and 2015, respectively, under artificial infection, laid out in randomized complete block designs (RCBD) with four replications. Three maize seeds were sown per hole and later thinned to two at 2 weeks after planting (WAP) Supplemental hand weeding was carried out at four WAP before fertilizer was applied. Fertilizers were applied at the rate of 40 kg P₂O₅ ha⁻¹ (single superphosphate), 40 kg K₂O ha⁻¹ (muriate of potash) and 80 kg N ha⁻¹ (urea).

MSV inoculation and disease infection

Acquisition Access Period (AAP) of a two-day was given to the reared *Cicadulina mbila* leafhoppers on MSV-infected maize seedlings. Carbon dioxide immobilization/anaesthetization of leafhoppers was done before invading the leaf whorl of the plants to inhibit take off (Leuschner et al., 1980). The viruliferous leafhoppers were subjected to two days inoculation access period (IAP) at 2 to 3 leaf stage in order to obtain a severe expression of the virus. Inoculation was carried out by dispensing a small plastic vial containing three leafhoppers encircled onto the distal part of the youngest leaf of every plant

stand. A two-day inoculation access was given to the leafhoppers before being killed by spraying Dimethoate 40 EC. The Furanan (carbosulfuran 5% m/v) was used to spray the trapped plants in the each plot in order to restrain leafhoppers in transmitting the virus. Dimethoate 40EC was sprayed at 3 weeks intervals prior to physiological maturity.

MSV Symptom rating

All plots were rated for the MSV infection from seedlings to physiological maturity. It was carried out firstly at a week interval till the disease was identified and then weekly. MSV severity infection was rated using 10 plants in the central part of the plot and averaged using a modification of an ordinal scoring scale of 1-5 described by Badu-Apraku et al. (2012), as follows: 1 = slight infection, with less than 10% of the leaves light green streaks, 2 = light infection, with 10-25% of the leaves having broken light green and a few yellow streaks, 3 = moderate infection, with 26-50% of the leaves covered by mixed green and yellow streaks, 4 = heavy infection, with 51-75% of the leaves covered with yellow streaks, leading to premature death of the plant and light cobs, 5 = very heavy infection, with 76-100% of the leaves covered by severe yellow streaks and necrosis, leading to premature death of the plant and light cobs.

Grain yield measurements

Grain yield was determined according to the procedure described by Bello et al. (2012b). At crop maturity, ears were harvested and weighed for each plot separately and grain yield ha⁻¹ at 15% grain moisture content was determined by the following formula:

$$\text{Grain yield (kg ha}^{-1}\text{)} = \frac{\text{Fresh wt.} \times (100 - \text{MC}) \times 0.8 \times 10,000 \text{ m}^2}{(100 - 15) \times 7.5 \text{ m}^2}$$

Where Fresh weight = weight of ears plot⁻¹ at the time of harvest,

0.8 = Shelling percentage,

10,000 m² = Area per hectare,

15% = Standard grain moisture for grain storage,

7.5 m² = Area of plot harvested (5m × 0.75m × 2).

Grain yield was measured from ear weight per plot (assuming 80% shelling percentage) and converted to tonnes per hectare after adjusting to 12.5% moisture content.

Proximate analysis of tryptophan and lysine

A single step papain hydrolysis method described by Hornandez et al. (1969) was applied for protein solubilization. Iron ions oxidized acetic acid to glyoxylic acid with the application of sulphuric acid. The indole ring of free tryptophan which bound in soluble proteins reacted with glyoxylic acid and a violet-purple compound was generated. The intensity of the violet-purple color was measured at 545 nm with a spectrophotometer. The drawing of optical density standard curve against tryptophan concentration, the percentage of tryptophan in the sample was noted as follows:

$$\% \text{ tryptophan in protein} = \frac{\% \text{ tryptophan in sample}}{\% \text{ protein in sample}}$$

The relationship between tryptophan and lysine in the maize endosperm protein was reported by Hornandez et al. (1969), therefore, the tryptophan was utilized as the factor for protein quality assessment, then, the obtained value was multiplied by 4 to attain lysine value (Sentayehu, 2008).

Statistical analyses

The diallel analysis was carried out applying Model I (Fixed model) Method 2 (Parents and hybrids with no reciprocal crosses) according to Griffing (1956) The mean squares for GCA and SCA were tested against their respective error variances inferred from ANOVA using the SAS software program version 9.2 (SAS, 2012). Percentage coefficient of variation ($P < 0.05$) was used to calculate the degree of variation. Standard errors (SE) for all the effects were computed utilizing error mean squares from hybrids for the untransformed data. Differences in character means were also

measured using the least significant difference (LSD) test.

3. RESULTS AND DISCUSSION

Grain Yield

A significant difference ($P < 0.05$) were recorded in the parents for grain yield across the two years of experimentation (Table 2). Three QPM inbred lines TZEQI 76, TZEQI 87 and TZEQI 79 expressed the greatest grain yielding with 5.65, 5.63 and 5.58 t ha⁻¹ respectively, while Afo, the OPV check, exhibited the lowest grain yield of 2.16 t ha⁻¹; 62% below the highest yielding TZEQI 76. The Suwan-1-SR C1 was highly productive among MSV resistant varieties having the greatest yield advantage of 59 % over Afo but 5 % yield decrease compared to Oba Super 5. All the hybrids differed significantly with an elevated grain yield potential than their respective parents (Table 2). The QPM x QPM crosses were superior yield performance followed by QPM x MSV resistant and MSV resistant x MSV resistant varieties. QPM TZEQI 76 was a common parent with better performance for yield in all the selected hybrids. The highest yielding hybrid was QPM TZEQI 76 x TZEQI 74 (7.22 t ha⁻¹) with a productivity increase of 21 % over Oba Super 5 check. Acr. 91 Suwan-1-Sr C₁ also produced crosses of high grain yield with some QPM inbreds. Acr. 91 Suwan-1-Sr C₁ x QPM TZEQI 76 with 6.94 t ha⁻¹, representing 17 % yield increase over Oba Super 5.

MSV disease rating

The highly significant difference ($p < 0.05$) among the parents were also obtained for MSV disease expression (Table 2). It is obvious that MSV resistant x MSV resistant varietal crosses were most resistant to MSV disease, followed by QPM x MSV resistant while QPM x QPM crosses were most susceptible. Acr. 91 Suwan-1-Sr C₁ was most resistant to MSV resistance with a score of 1.01 and combined favourably with some QPM inbreds to produce resistant hybrids with improved yield. Acr. 91 Suwan-1-Sr C₁ x TZEQI 76 that had the highest yield

among QPM x MSV genotypes was outstanding with 6 and 45% highly resistance compared to Afo and Oba Super 5, respectively. For the two susceptible checks, their grain yield and quality protein potentials were however, undesirably lowered by the MSV resistance. The ratings of the MSV susceptible checks signify the virulence of the pathogen, and those inoculations of the virus were very effective.

Grain quality protein

Acr. 91 Suwan-1-Sr C₁ combined favorable for high Lysine and Tryptophan among some MSV resistant parents. This implies that Acr. 91 Suwan-1-Sr C₁ was mostly immune to MSV with high frequencies of favouring alleles compared with other parents. Cross Acr. 91 Suwan-1-Sr C₁ x TZEQI 76 expressed the greatest Lysine (3.99) and Tryptophan (1.01) among the QPM x MSV resistant crosses with 33 and 37% advantage, respectively over Oba Super 5. The QPM lines derived from TZEQI 76, TZEQI 87 and TZEQI 79 that were introgressed with MSV resistant Acr. 91 Suwan-1-Sr C₁ featured as most promising for grain yield, MSV resistance and grain quality protein in this study. This shows that promissory QPM inbreds of diverse origins converted to MSV resistant attributes with high grain yield and sustainable quality protein attributes could be adapted to the tropical environments. Therefore, these four putative materials identified to meet these criteria could either be utilized as parental germplasm in the development of new synthetics maize and hybrids or be used in widen genetic base in the future breeding programmes. It appears that Acr. 91 Suwan-1-Sr C₁ not only has MSV resistant gene that can be transgressed to other maize cultivars but could be an excellent source for both grain yield and quality protein genes. The parental means of Acr. 91 Suwan-1-Sr C₁ depicted that breeding potential for MSV resistant could be utilized to discriminate QPM lines in imminent breeding impetus. These four crosses are recommended to be cultivated directly on commercial production, though, after further assessment at different locations

and years to confirm their promising performance. The error of variance of the means that were small for all the four traits could be the optimal number of replications (four) and data utilized in estimating the components of variance for the traits in the two cropping seasons.

Combined analysis of variance

Combined analysis of variance of QPM inbreds and MSV resistant genotypes for MSV rating, grain yield and quality protein evaluated across two years are presented in Table 3. Crosses mean squares were decidedly significant for all the four investigated attributes, signifying that the parental materials utilized in this studied were broadly diverse and that the genotypes contributed in a different way among crosses that were involved in obtaining hybrids. It also signifies that the heritable variability could be developed for all the selection processes in the breeding programs. Non-significant interaction mean squares between crosses and years were observed for all the studied characters, denoting that the performance of the crosses was identical across the two years. Mean squares due to SCA and GCA were vastly significant for all studied characters, implying that both non-additive and additive genetic effects were the vital portion of the genetic variances governing these characters. These results also indicate that the genotypes differed in genic frequencies dispersion. These results not only underscore the potential of developing diverse parents for improving the hybrids, but served as novel alleles' sources in the diversification and broadening the genetic base of acclimatized genotypes, to maintain genetic gain in the hybrid productivity. Several researchers reported additive genetic effects that were very imperative for grain yield (Derera et al., 2008; Bello and Olaoye, 2009; Vivek et al., 2010; Sibiyi et al., 2011, Ibrahim, 2012; Bello and Olawuyi, 2015).

Mean squares due to the interaction between both SCA and GCA and years were non-significant for characters, showing that both genetic effects (non-additive and additive) were similar in across years.

Table 2. Genotypic means of parents and selected crosses for MSV rating, grain yield and quality protein evaluated across two years

Parent	Grain Yield	MSV	Lysine	Tryptophan
TZEQI 76	5.65	3.56	3.98	0.99
TZEQI 79	5.58	3.67	3.97	0.87
TZEQI 74	5.51	3.77	3.91	0.91
TZEQI 87	5.63	3.74	3.96	0.87
TZEQI 91	5.47	3.47	3.95	0.85
Acr. 91 Suwan-1-Sr C ₁	5.32	1.01	2.73	0.59
TZB-SR SGY	4.72	1.34	2.88	0.61
AK-9528-DMRSR	5.11	1.45	2.91	0.58
Ikenne 88 TZSR-Y-1	5.22	1.29	2.97	0.65
IK.91 TZL Comp 3-Y C ₁	5.13	1.57	2.99	0.59
Selected crosses				
TZEQI 76 x TZEQI 74	7.22	3.54	4.04	1.03
TZEQI 76 x TZEQI 79	7.19	3.60	4.02	1.04
TZEQI 76 x TZEQI 91	7.16	3.49	4.01	1.02
TZEQI 91 x TZEQI 87	7.04	3.54	3.96	0.89
TZEQI 79 x TZEQI 74	7.01	3.56	3.93	0.88
TZEQI 76 x TZEQI 87	7.02	3.59	3.97	0.86
Acr. 91 Suwan-1-Sr C ₁ x TZEQI 76	6.94	2.18	3.99	1.01
Acr. 91 Suwan-1-Sr C ₁ x TZEQI 87	6.91	2.25	3.98	0.88
Acr. 91 Suwan-1-Sr C ₁ x TZEQI 79	6.87	2.33	3.97	0.93
Acr. 91 Suwan-1-Sr C ₁ x TZB-SR SGY	6.83	2.41	3.98	0.91
Acr. 91 Suwan-1-Sr C ₁ x Ikenne 88 TZSR-Y-1	6.81	2.47	3.96	0.90
TZB-SR SGY x IK.91 TZL Comp 3-Y C ₁	6.74	2.91	3.94	0.90
TZB-SR SGY x TZEQI 76	6.43	2.84	3.92	0.93
Ikenne 88 TZSR-Y-1 x TZEQI 87	6.47	2.77	3.96	0.92
Ikenne 88 TZSR-Y-1 x TZEQI 74	6.52	2.92	3.95	0.91
Ikenne 88 TZSR-Y-1 x TZEQI 76	6.51	2.77	3.93	0.90
IK.91 TZL Comp 3-Y C ₁ x TZEQI 76	6.47	2.68	3.97	0.89
IK.91 TZL Comp 3-Y C ₁ x TZEQI 74	6.51	2.67	3.94	0.88
TZB-SR SGY x TZEQI 87	6.66	2.67	3.97	0.90
TZB-SR SGY x TZEQI 74	6.73	2.88	3.91	0.92
TZB-SR SGY x TZEQI 76	6.65	2.93	3.97	0.91
Varietal Checks				
Afo	2.16	2.31	2.01	0.55
Oba Super 5	5.74	3.95	2.67	0.65
SE	0.012	0.012	0.012	0.012
LSD (0.05)	0.97	0.55	0.68	0.11
CV (%)	10.45	8.11	7.37	3.68

Table 3. Combined analysis of variance of QPM inbreds and MSV resistant genotypes for MSV rating, grain yield and quality protein evaluated across two years

Source	Grain Yield	MSV	Lysine	Tryptophan
Year	6.34	4.73	3.62	6.92
Rep (Year)	7.82	9.38	12.72	13.53
Crosses	74.52**	78.66**	82.12**	75.94**
Crosses * Year	10.67	11.63	14.11	12.76
GCA	86.34**	91.13**	97.56**	89.23**
SCA	32.43*	45.81*	17.23	17.99
Year * GCA	20.11	31.09	11.73	14.22
Year * SCA	12.38	15.11	23.53	34.03
Pool Error	1.67	3.72	5.28	10.72
k ² GCA/ k ² SCA	1.87	0.06	0.78	0.81
CV%	10.5	6.9	5.4	6.8

* and ** significant at 0.05 and 0.01 levels of probability, respectively.

Baker (1978) and Cisar et al. (1982) opined that the progeny performances might be predicted using the ratio of the component of combining ability variances. The closer the ratio to unity, the higher the predictability on GCA effects only. The ratio of k_2GCA/k_2SCA that was more than one for grain yield, suggested that additive genetic effect was predominant in the control of inheritance of grain yield, whereas less than one observed for MSV resistance, lysine and tryptophan implying that non-additive gene action were essential in the experience for these characters. This indicates that except for grain yield, non-additive gene action played a major role in conditioning the inheritance of these characters: MSV resistance, lysine and tryptophan. Meanwhile, additive gene effects are the key cause of resemblance between relatives, the predominance of additive variance over dominance among these genotypes implying that recurrent selection could be effective in enhancing MSV resistance. The preponderance of additive gene action governing MSV resistance has equally been noted for other foremost foliar diseases: northern leaf blight (Vieira et al., 2009), and grey leaf spot (Derera et al., 2008; Vieira et al., 2009; Vivek et al., 2010). Thus, it was inferred that breeding and selection programmes using additive gene action possibly are the most suitable in improving maize foliar disease resistance (Gichuru et al., 2011). However, the coefficients of experimental variation (CV %) estimates of the combined analyses of variance showed a better experimental precision, particularly for grain yield.

General combining ability effects

GCA estimates of the parents for the four studied characters are presented in Table 4. Significant GCA positive effects are desired for all the characters except MSV resistance, as the goal are higher MSV resistance, greater grain yield and quality protein. Regarding grain yield, all the genotypes studied had significant positive GCA, highlighting that they are good combiners for the development of high grain yielding hybrids. The significance GCA effects

also suggested the greater magnitude of additive gene action in controlling grain yield, and the variability of GCA effects that facilitate selection in the hybrid combinations for the best GCA (Kostetzer et al, 2009; Aly 2013). The QPM inbreds that expressed non-significantly positive effects depict that they could produce the same level of MSV resistance in their various hybrid combinations. For leaf diseases, negative GCA effects show the genetic impact to the observed resistance. With respect to MSV resistance, all the five MSV resistance cultivars produced negative GCA effects, indicated that they are most suitable sources for valuable resistance (Vivek et al., 2010) Characteristically, genetic studies on MSV tolerance in diverse sources have assigned tolerance to one single gene of additive effects with quantitative inheritance. It was reported that TZ-Y was a MSV tolerance, where inbred Ibadan 32 (IB32) was developed, TZ-Y had not only simply inherited, but also quantitatively inherited via additive genetic effects of a few genes (Olaoye (2009). A single key gene (labelled MSV 1) conditioning tolerance to MSV resistance in inbred Tzi4 obtained from IITA, Nigeria has been reported by Olaoye (2009). This has been proven by the resistance hybrids performance. It is obvious that all the QPM inbreds exhibited GCA effects for both Lysine and Tryptophan indicating *per se* performance, which enables the promising populations to be selected for use in breeding for crop improvement. The MSV resistance cultivars that possessed positive but non-significant effects denote that same level of performance could be recorded in their different combinations of hybrids.

Typically, the GCA effect is an essential tool for plant breeder in selecting parents (Bello and Olawuyi 2015). A low effect, either negative or positive depicts that the parent GCA value attained on the hybrid combinations does not be at variance considerably from the means of other populations evaluated. High negative or positive GCA values imply that the parent is significantly better or worse compared with the other parents of the diallelic cross, regarding

the mean progeny performance (Bello and Olawuyi 2015). Therefore, effective breeding strategies by exploiting promising genes in homozygous condition and broken the linkage blocks could appreciably reduce grain yield losses connected with MSV resistance. Furthermore, with the significant additive gene effects, these genotypes can be sustained in the heterozygous state (Oluwafemi et al., 2011).

Specific combining ability effects

SCA variances are usually estimated on occasion where significant SCA effects occur. SCA effects of the selected crosses for the four studied characters are shown in Table 5. With respect to grain yield, the best estimates for

SCA were observed in all the selected 21 crosses, signifying effect of dominant loci in the genetic control of the grain yield. These results are in line with other authors who evaluated SCA in maize (Mohammed, 2009; Vivek et al, 2009; Meseka and Ishaq, 2012; Rovaris et al., 2014).

Regarding MSV resistance, all the MSV x MSV and MSV x QPM crosses expressed significant negative SCA effects, implying the presence of dominance effects, while the QPM x QPM crosses that possessed non-significant positive value depicts no effect of dominance in the manifestation of MSV resistance investigated.

Table 4. Estimates of GCA for QPM inbreds and MSV resistant genotypes for MSV rating, grain yield and quality protein evaluated across two years

Genotype	Grain Yield	MSV	Lysine	Tryptophan
TZEQI 76	0.98**	0.22	0.44*	0.65*
TZEQI 79	0.81**	0.16	0.37*	0.45*
TZEQI 74	0.75**	0.19	0.23*	0.53*
TZEQI 87	0.70**	0.11	0.39*	0.44*
TZEQI 91	0.94**	0.09	0.31*	0.39*
Acr. 91 Suwan-1-Sr C ₁	0.46*	-0.95**	0.28	0.27
TZB-SR SGY	0.68**	-0.89**	0.09	0.16
AK-9528-DMRSR	0.74**	-0.66**	0.15	0.20
Ikenne 88 TZSR-Y-1	0.34*	-0.81**	0.17	0.11
IK.91 TZL Comp 3-Y C ₁	0.39*	-0.78**	0.07	0.15

* and ** significant at 0.05 and 0.01 levels of probability, respectively.

Table 5. SCA effects of selected crosses for QPM inbreds and MSV resistant genotypes for MSV rating, grain yield and quality protein evaluated across two years

Crosses	Grain Yield	MSV	Lysine	Tryptophan
TZEQI 76 x TZEQI 74	0.73**	0.32	0.57*	0.78**
TZEQI 76 x TZEQI 79	0.97**	0.24	0.48*	0.62**
TZEQI 76 x TZEQI 91	0.81**	0.22	0.33*	0.75**
TZEQI 91 x TZEQI 87	0.88**	0.19	0.56*	0.64**
TZEQI 79 x TZEQI 74	0.99**	0.21	0.47*	0.57**
TZEQI 76 x TZEQI 87	0.75**	0.12	0.38*	0.71**
Acr. 91 Suwan-1-Sr C ₁ x TZEQI 76	0.85**	-0.78**	0.44*	0.57**
Acr. 91 Suwan-1-Sr C ₁ x TZEQI 87	0.94**	-0.72**	0.39*	0.69**
Acr. 91 Suwan-1-Sr C ₁ x TZEQI 79	0.72**	-0.93**	0.53*	0.73**
Acr. 91 Suwan-1-Sr C ₁ x TZB-SR SGY	0.85**	-0.45*	0.41*	0.66**
Acr. 91 Suwan-1-Sr C ₁ x Ikenne 88 TZSR-Y-1	0.87**	-0.89**	0.50*	0.20
TZB-SR SGY x IK.91 TZL Comp 3-Y C ₁	0.80**	-0.62**	0.44*	0.12
TZB-SR SGY x TZEQI 76	0.81**	-0.84**	0.36*	0.51**
Ikenne 88 TZSR-Y-1 x TZEQI 87	0.84**	-0.75**	0.41*	0.33*
Ikenne 88 TZSR-Y-1 x TZEQI 74	0.79**	-0.66*	0.45*	0.39*
Ikenne 88 TZSR-Y-1 x TZEQI 76	0.46*	-0.74**	0.47*	0.72**
IK.91 TZL Comp 3-Y C ₁ x TZEQI 76	0.68**	-0.83**	0.39*	0.63**
IK.91 TZL Comp 3-Y C ₁ x TZEQI 74	0.74**	-0.79**	0.43*	0.55**
TZB-SR SGY x TZEQI 87	0.34*	-0.67**	0.52*	0.71**
TZB-SR SGY x TZEQI 74	0.39*	-0.55*	0.48*	0.58**
TZB-SR SGY x TZEQI 76	0.98**	-0.47*	0.51*	0.69**

* and ** significant at 0.05 and 0.01 levels of probability, respectively.

With regard to quality protein, significant positive SCA effects were recorded for QPM X QPM and MSV x QPM crosses, whereas MSV x MSV showed non-significant positive effects. This also suggests that applying inbred-cultivar breeding for improving composite and synthetic cultivars is a feasible strategy for developing higher levels of MSV resistance, grain yield and quality protein.

4. CONCLUSION

The QPM lines derived from TZEQI 76, TZEQI 87 and TZEQI 79 that were introgressed with MSV-resistant Acr. 91 Suwan-1-Sr C₁ featured as most promising for grain yield, MSV resistance and grain quality protein. SCA and GCA variances were highly significant for all studied characters, implying that both non-additive and additive genetic effects were the vital portion of the genetic variances governing these characters. The ratio of k₂GCA/ k₂SCA that was more than one for grain yield and less than one for MSV resistance, lysine and tryptophan characters, indicating that except for grain yield, non-additive gene action played a major role in conditioning the inheritance of these characters. The evidence from this investigation would be worthwhile for developing MSV disease resistant, high grain yielding of quality protein maize varieties in Africa.

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