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Combining ability for grain yield and resistance to maize streak virus in maize

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Abstract

Combining ability effects for grain yield, yield-related traits and resistance to maize streak virus (MSV) were determined using 10 parents, 45 single crosses and five standard hybrid checks. Genotypes were evaluated at three locations (Ngaramtoni, Inyala, and Igomelo) over two seasons (2012/13 and 2013/14) using a 6 x 10 simple lattice design with two replications. Data were collected for days-to-50% silking (DSL), days-to-50% anthesis (DA), reaction to MSV disease, plant height (PHT), ear height (EHT), number of ears per plant (EPT), husk cover of cobs (HSC) and grain yield (YLD). General combining ability (GCA) and specific combining ability (SCA) effects were significant ($P < 0.05$) for all traits except DA and DSL. Parental line TL2012-42 was the best general combiner for YLD, while the parents TL2012-41, TL2012-1 and TL2012-42 were the best combiners for maize streak virus resistance, with negative GCA effects of -10.9%, -10.8% and -10.7%, respectively. The highest SCA effect for grain yield (4.80) was detected in the hybrid TL2012-7/TL2012-38. Crosses such as TL2012-38/TL2012-55 and TL2012-25/TL2012-26 had negative SCA effects for their MSV reaction. The above parental lines and hybrids can be recommended for direct production, or breeding to enhance grain yield and MSV resistance in maize varieties for Tanzania.

Keywords: *combining ability, diallel analysis, heritability, hybrid, maize streak virus*

Introduction

Maize (*Zea mays* L., $2n = 2x = 20$) is an important staple food crop, supporting over 850 million people in sub-Saharan Africa. In Tanzania alone, maize production takes place in all seven agro-ecological zones, covering an area of over two million hectares (Cairns et al, 2013; Kage et al, 2013). However, its yield is low due to several foliar diseases, particularly by maize streak virus (MSV). This requires development of novel genotypes with high grain yield, combined with resistance to MSV, and other biotic and abiotic stresses (Mrutu et al, 2014).

Maize streak virus belongs to the genus *Mastrevirus* of the family Geminiviridae (Shepherd et al, 2010). It is naturally confined in African grasses and is transmitted exclusively by leafhoppers, particularly *Cicadulina mbila* Naude (Karavina, 2014). The disease spreads effectively under warm and wet conditions that favors oviposition of the vector (Shepherd et al, 2010). Once acquired by the leafhopper, the virus remains in the insect's gut and is subsequently transmitted to the host. Maize streak symptoms are manifested as chlorotic spots and streaks in longitudinal lines of maize leaves. Chlorosis result from failure of chloroplasts to develop in the tissue surrounding the vascular bundles, thereby reducing photosynthesis (Oluwafemi et al, 2007). In susceptible cultivars, severe chlorosis causes stunted growth, poor ear formation, reduced seed set, yield loss or premature

plant death (Shepherd et al, 2010; Karavina, 2014). Maize streak virus is among the most destructive viral diseases of maize, causing up to 100% yield losses in susceptible genotypes (Alegbejo et al, 2002). Globally, MSV is ranked the third most devastating foliar diseases of maize following northern leaf blight and gray leaf spot (Martin and Shepherd, 2009). High incidences of the disease have been reported in Kenya, Tanzania, Uganda, Zambia, Mozambique, South Africa, Nigeria, and Cameroon (Olaoye, 2009; Shepherd et al, 2010; Gichuru et al, 2011). This poses a serious threat to food security across the continent, particularly where MSV resistant varieties are unavailable.

Estimation of combining ability and heritability for disease resistance and key agronomic traits in maize inbred lines and their crosses has significantly contributed to commercial hybrid maize breeding (Sher et al, 2012). Parents with high general combining ability (GCA) effects, and crosses with good specific combining ability (SCA) effects are vital in the development of hybrids, and for direct production, respectively (Balestre et al, 2008). Variance due to GCA is associated with additive genetic effects, while SCA variance relates to non-additive genetic effects, largely arising from dominance, over-dominance and epistasis (Falconer, 1975).

Development of high yielding and MSV resistant cultivars is the most economically and environmentally sustainable option (Shepherd et al, 2010; Gich-

uru et al, 2011). In Tanzania MSV resistance studies only commenced a decade ago, focusing on open pollinated varieties. However, these varieties are low yielding. Previous studies have identified genes conferring resistance to MSV among diverse maize germplasm (Pernet et al, 1999; Shepherd et al, 2010). Germplasm harboring such genes should be utilized in hybrid development programs, aiming to develop cultivars with enhanced resistance to MSV. The virus has previously been reported to be predominantly controlled by major dominant resistance genes, and several minor genes with additive gene effects (Roder et al, 1995). This suggests that there should be the potential to select good general and specific combiners, using genetic analysis. There is no information on the combining ability and gene action controlling grain yield and resistance to MSV among inbred lines available in Tanzania. However, such knowledge would guide selection of breeding lines. Therefore, the objective of this study was to determine the combining ability for grain yield, yield related traits and resistance to MSV among elite maize inbred lines and their hybrid progenies, by evaluating these across six environments. Good combiners will be used for hybrid breeding while superior hybrids will be recommended for direct production.

Materials and Methods

Plant material, mating design and trial management

Ten inbred lines were crossed using a half-diallel mating design to generate 45 F1 hybrids. Table 1 presents the details of the inbred lines that were used as parents for hybrid development. The reaction type of the parental lines were obtained from the passport data supplied by the International Maize and Wheat Improvement Centre (CIMMYT)/Zimbabwe, the International Institute of Tropical Agriculture (IITA)/Nigeria and the University of KwaZulu-Natal (UKZN). Also, Nyaligwa (2014) confirmed these reactions types based on assessments carried out at Ngaramtoni Research Farm of Selian Agricultural Research Institute in northern Tanzania. Sixty genotypes consisting 10 inbred parental lines, their 45 newly developed hybrid crosses and five three-way hybrid checks were eval-

uated at Ngaramtoni (30°18'S;36°34'E, 1,520 masl), Inyala (8.8570°S;33.6386°E, 1,613 masl) and Igomelo (8°46'S;34°23'E, 1,118 masl) sites in Tanzania during the 2012/13 and 2013/14 growing seasons. The three sites are hotspot areas for MSV, allowing for the evaluation of the genotypes under natural infection. The genotypes were evaluated using a 6 x 10 alpha lattice design with two replications in two row plots 5.0 m in length. The spacing between and within rows was 75 cm and 30 cm, respectively. A total of 150 kg ha⁻¹ of di-ammonium phosphate (P₂O₅) was applied at planting. Calcium ammonium nitrates was top dressed at six weeks after planting at 150 kg ha⁻¹. Trials were conducted during the main cropping season under rain-fed conditions. Sowing, flowering and harvesting dates, as well as growing conditions of the six testing sites are provided in Table 2.

Data collection

Maize streak virus incidence and severity was recorded as the percentage of diseased plants per plot and assessed at 8 day intervals from two weeks after germination until flowering time. A visual scale of 1 to 5 was used, where 1 indicated high resistance with no symptoms, 2 represented resistance with light symptoms, 3 identified resistance with moderate streaking, 4 stood for susceptibility with severe streaking, and 5 represented high susceptibility with severe streaking and stunting (Storey and Howland, 1967). The number of days-to-50% anthesis (DA) and number-of-days-to-50% silking (DSL) were recorded from the planting date until 50% of the plants in each experimental plot attained 50% anthesis or silking, respectively. Plant height (PHT) was measured in centimeters from ground level to the first tassel branch and ear height (EHT) was recorded as the distance from ground level to the upper most ears bearing node. The later variables were determined from 10 randomly selected and tagged plants at 50% anthesis. Additionally, the number of ears per plant (EPT) was counted. Husk cover (HSC) was assessed using a visual scale ranging from 1 designating very short husks to 5 indicating long husks providing the best cover of to the cob, respectively. Grain yield (YLD) per plot was measured at 12.5% moisture content using

Table 1 - List of parental inbred lines used in the study, their yield potential and MSV reaction.

Pedigree	Code	Origin	YP (t ha ⁻¹)	Reaction type
09MAK1-77	TL2012-55	UKZN/South Africa	1.97	Resistant
V457-1-VLO835	TL2012-17	SARI†/Tanzania	2.76	Susceptible
CML390	TL2012-41	CIMMYT/Kenya	2.46	Moderate resistance
CML505	TL2012-1	CIMMYT/Kenya	0.60	Resistant
WPopX1368 STR S7 Inb.6	TL2012-26	IITA/Nigeria	2.08	Moderate resistance
MAS[MSR/312]-119-5-1-1-3-B	TL2012-25	CIMMYT/Zimbabwe	2.19	Resistant
P43-1-1-1-BBB	TL2012-38	SARI/Tanzania	1.63	Moderate resistance
SML125	TL2012-42	SARI/Tanzania	3.52	Resistant
CML509	TL2012-68	CIMMYT/Kenya	1.89	Resistant
MAS[MSR/312]-119-5-1-4-1-BB	TL2012-7	CIMMYT/Zimbabwe	1.07	Moderate resistance

†SARI = Selian Agricultural Research Institute; CIMMYT = International Maize and Wheat Improvement Centre, IITA = International Institute of Tropical Agriculture; UKZN = University of KwaZulu-Natal; YP = yield per plot.

Table 2 - Sowing, flowering and harvesting dates, and growing conditions of the six testing sites during the 2012/13 and 2013/14 seasons.

Site	Season	Sowing dates*	Flowering dates	Harvesting dates	Region	Mean annual rainfall (mm)	Temperature (°C)		Soil type
							Min	Max	
Ngaramtoni	2012/13	07/12/2012	09/02/2013 to 22/02/2013	22/4/2013	Arusha	214	17	29	Clay silt loam
Ngaramtoni	2013/14	19/12/2013	21/02/2014 to 03/03/2014	22/4/2014		400	14	30	
Inyala	2012/13	23/12/2012	25/02/2013 to 10/03/2013	23/5/2013	Mbeya	650	23.5	33.7	red clay loam
Inyala	2013/14	09/01/2014	14/03/2014 to 27/03/2014	15/6/2014		450	24.8	37.6	
Igomelo	2012/13	25/12/2012	27/02/2013 to 12/03/2013	27/5/2013	Mbeya	450	25	31.8	Red sandy loam
Igomelo	2013/14	14/01/2014	19/03/2014 to 01/04/2014	06/06/2014		650	23.7	30	

*Day/Month/Year

a digital scale and later converted into t ha⁻¹.

Data analysis

Data were subjected to combined analysis of variance after testing for normality, independence and homogeneity of variance. Half-diallel analyses was then performed using Model I and Method II according to Griffing (1956). SAS program version 9.3 (SAS, 2011) was used to perform this analysis. The total sums of squares were partitioned into genotype, environment and genotype x environment interactions. The sum of squares of genotypes were further partitioned into general and specific combining ability using the model: $Y_{ij} = \mu + g_i + g_j + S_{ij} + (1/r) \sum_k \epsilon_{ijk}$, where μ = population mean, Y_{ij} = observed entry mean of the i^{th} and j^{th} genotypes, g_i = the general combining ability effects of i^{th} parent, S_{ij} = the specific combining ability of the cross between i^{th} and j^{th} parents, $\sum_k \epsilon_{ijk}$ = the environmental effects associated with the observation ijk^{th} and r = replication. GCA and SCA effects were estimated using a general linear model procedure of SAS and their relative importance was measured by the ratio of GCA to SCA, according to Baker (1978) as $[2MS_{GCA} / (2MS_{GCA} + MS_{SCA})]$, where MS_{GCA} and MS_{SCA} stands for the mean squares for GCA and SCA, respectively. The narrow sense heritability (h^2) was calculated according to the formula proposed by Hallauer et al (2010) as $h^2 = [GCA / (GCA + SCA + error)] * 100$. Further, Pearson's correlations coefficients were estimated to deduce the relationships among studied traits.

Results

Analysis of variance

Combined analysis of variance revealed significant differences ($P < 0.05$) due to genotypes, environments and their interaction effects among the studied traits. Further, highly significant effects of the GCA and SCA for grain yield and MSV reaction were observed. Based on the Baker's ratio, GCA effects contributed approximately 48.9% and 97.7% YLD and MSV expression, respectively (Table 3). Dominance gene action contributed 98.3% to the expression of ear height, while additive gene action accounted for only 1.7% of the variation. Plant height, EPT and HSC had Baker's ratios of 62.3%, 79.6%, and 70.8%, respectively. The number of days to anthesis and silking had Baker's ratios below 50%. Narrow sense heritability estimates were the highest (95%) for MSV reactions, followed by EPT (61.3%). Grain yield and

other agronomic traits demonstrated low heritability below 50% (Table 3).

Mean performance and correlation among traits

Table 4 shows the mean performances of the studied traits evaluated across six environments. Grain yield differed significantly among genotypes, varying from 1.92 to 7.75 t ha⁻¹ with a mean of 4.45 t ha⁻¹. Hybrid TL2012-68/TL2012-42 (7.73 t ha⁻¹) was the highest yielder, followed by TL2012-41/TL2012-17 (6.78 t ha⁻¹). The three study sites were characterized by heavy MSV infection during the two growing seasons due to warm and wet weather conditions experienced during the vegetative and anthesis growth stages, which favored leafhopper infestation and disease spread. The lowest reaction to MSV was observed on hybrid TL2012-25/TL2012-26, albeit with a low yield. Interestingly, the parents of this hybrid also had low MSV reactions. Hybrids TL2012-68/TL2012-1 and TL2012-68/TL2012-25 recorded the tallest and shortest plant height, respectively. Nine hybrids yielded better than the highest yielding check, PAN-NAR 4M-19 (5.6 t ha⁻¹), while the second highest yielding check, UH615 (5.3 t ha⁻¹), was on the 14th position. However, these checks were susceptible to MSV with severity scores of 61.23% and 82.53%, respectively. On the other hand, thirteen hybrids performed better than the resistant check SC627, which had a severity score of 39.23%. Maximum ear height was recorded on hybrid TL2012-1/TL2012-41, while the minimum was recorded on TL2012-7/TL2012-25. Ear prolificacy varied significantly among the hybrids, ranging from 1.67 to 3.5, which were displayed by the genotypes TL2012-26/1 and TL2012-1/TL2012-17, respectively. Husk cover ranged from a score of 1 to 4. Hybrid TL2012-38/TL2012-41, which took 65.75 days 50% flowering, was recorded as the earliest genotype, while the latest hybrid took 76.82 days to maturity.

Pearson's correlations showing the relationships among studied traits are presented in Table 5. The correlation of MSV reaction with grain yield and other traits were variable and non-significant owing to differential responses of test hybrids. On the other hand, grain yield was significantly and positively correlated with EHT ($r = 0.46$) and DA ($r = 0.36$), but negatively correlated with DSL ($r = -0.36$). Other significant positive relationships were observed on DA with PHT ($r = 0.46$), EPT ($r = 0.31$) and HSC ($r = 0.36$), as well as on DA with HSC ($r = 0.31$).

Table 3 - Combined analysis of variance for grain yield, yield components and MSV reaction of maize genotypes evaluated across six environments.

Source of Variation	DF	YLD	MSV	PHT	Mean squares				
					EHT	EPT	HSC	DA	DSL
Genotype (G)	54	30.51***	4416.22***	17010.05***	4661.01***	1.79***	4.23***	71.58***	112.69***
Environments (E)	5	360.79***	545.70***	19321.83**	1361.13***	11.01***	9.37***	567.57***	539.90***
GXE interaction	270	3.41***	157907.67***	5986.716*	1269.41***	0.71***	2.20***	36.40***	37.22***
GCA	9	16.14***	20802.20***	14835.02**	32.85***	2.87***	4.56***	30.60ns	40.51ns
SCA	45	33.75***	1001.23***	17921.590***	3896.76***	1.47***	3.77***	79.80***	118.30***
Replication (within E)	6	0.16	31.02	4396.86	35.17	0.46	0.45	1.32	3.29
Error	324	0.71	88.65	4942.79	1219.92	0.34	0.8667	3.09367	5.68906
Total	982	450.86	39814.06	4259407	19075.19	10.99	30.29	790.36	857.6
h ² (%)	-	31.9	95.0	39.4	0.6	61.3	49.6	27.0	24.6
GCA/SCA (Baker ratio) %	-	48.9	97.7	62.3	1.7	79.6	70.8	43.4	40.6

*, **, and *** denote significance differences at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively; DF = degree of freedom; YLD = grain yield (t ha⁻¹); MSV = MSV disease reaction in %; PHT = plant height in cm; EHT = ear height in cm; EPT = number of ears per plant; HSC = husk cover of cob; DA = days to 50% anthesis; DSL = days to 50% silking; h² = narrow sense heritability

Estimates of GCA and SCA effects

GCA effects for grain yield were generally not significant among inbred lines. However, some parents like TL2012-42 showed significant positive GCA effects of 0.7 for yield (Table 6). Highly significant GCA effects were observed for the reaction to MSV, with 60% of the lines demonstrating significant negative GCA effects. The best general combiners for reaction to MSV included the inbred parents TL2012-41 (-10.926%), TL2012-1 (-10.792%) and TL2012-42 (-10.748%). Further, inbred line ITL2012-17 exhibited significant GCA effects of 0.346 and -0.225 for the number of ears per plant. Inbred lines TL2012-55 and TL2012-7 were among the best combiners for husk cover of cobs. The parent TL2012-17 was the best general combiner for EPT. About 45% of the crosses had significant SCA effects on grain YLD. Among these, crosses between inbred line TL2012-7 with several inbred lines including TL2012-55 and TL2012-17 had significant positive SCA effects (Supplementary Table 1). On the other hand, crosses TL2012-38/TL2012-55 and TL2012-25/TL2012-26 had significant negative SCA effects for their MSV reactions of -10.892 and -19.451, respectively. Furthermore, several hybrids sharing the common male parent TL2012-55, such as hybrids TL2012-38/TL2012-55 (18.576) and TL2012-68/ (21.392), were high specific combiners for ear height. Hybrid TL2012-1/TL2012-17 (0.962) was among the genotypes with the highest SCA effects on the number of ears per plant. High and positive SCA effects for husk cover were observed on hybrid TL2012-1/TL2012-55 (1.075) among others. Eight hybrids had significantly high SCA effects for the number of days to 50% anthesis. Of these, only TL2012-42/TL2012-55 (-4.406) and TL2012-38/TL2012-41 (-3.666) revealed negative SCA effects (Supplementary Table 1). Seven hybrids, including TL2012-42/TL2012-55 (-4.277) and TL2012-38/TL2012-17 (-3.219), were considered as best combiners for DSL because they had negative SCA effects on the number of days to 50% silking.

Discussion

Variability among genotypes and trait correlations Assessment of general and specific combining ability in maize is important for yield enhancement and stress tolerance (Ali et al, 2014). Parental inbred lines and their hybrid progenies are recommended for breeding or direct production, based on their GCA and SCA effects, respectively (Lou et al, 2011). Significant differences due to GCA and SCA effects observed among the studied traits of test genotypes reflect the influence of both additive and non-additive forms of gene action. Observed variability for GCA and SCA may facilitate selection of the best combiners for genetic improvement in maize (Bello et al, 2012). In the present study, the Baker's ratio ranged from 1.7% for ear height to 97.7% for MSV resistance, implying high predictability for the GCA effects (Baker, 1978). The MSV reaction which had a high Baker's ratio (97.7%), is possibly controlled by a few major and numerous minor genes with additive effects. Hence, selection strategies that accumulate additive genes would be appropriate in improving the trait. Recurrent selection can therefore be used to develop maize varieties with enhanced resistance to MSV. Narrow sense heritability (h²) is directly related to the proportion of additive gene effects (Kearsey and Pooni, 1997), hence traits showing high h² can effectively be advanced through selection.

The non-significant correlation among studied traits with MSV severity confirms the presence of high variability among the experimental hybrids. This allowed selection of some promising MSV tolerant genotypes showing high grain yield response irrespective of their level of MSV severity. For instance, hybrids TL2012-41/TL2012-17 and TL2012-42/TL2012-17, yielded 6.78 t ha⁻¹ and 6.06 t ha⁻¹, but had high MSV severity of 64.48% and 71.80%, respectively (Table 4). Positive correlations were detected between grain yield with plant and ear heights suggesting that taller plants accumulate more biomass contributing to increased source to sink mobilization during photosynthesis.

Estimates of GCA effects among inbred lines

GCA effects are good measures of additive gene

Table 4 - Mean performance of grain yield, yield components and MSV reaction of the 10 best performing maize hybrids when evaluated across six environments.

Hybrid	YLD (t ha ⁻¹)	MSV (%)	PHT (cm)	EHT (cm)	EPT	HSC	DA(days)	DSL(days)
Traits of best ten yielding hybrids								
TL2012-68/TL2012-42	7.73	32.31	158.41	114.14	2.50	2.04	70.62	68.33
TL2012-41/TL2012-17	6.78	64.48	210.08	94.83	2.54	2.38	72.88	73.08
TL2012-42/TL2012-1	6.16	41.06	191.92	156.5	1.75	2.42	74.32	74.08
TL2012-42/TL2012-17	6.06	71.80	210.00	100.03	2.42	2.30	72.41	72.00
TL2012-26/TL2012-1	5.99	38.10	184.00	101.85	1.67	2.41	71.75	72.5
TL2012-38/TL2012-17	5.95	89.66	193.67	101.18	2.75	2.54	72.30	68.58
TL2012-42/TL2012-41	5.94	27.51	190.25	99.32	2.17	1.88	72.88	70.33
TL2012-17/TL2012-55	5.78	73.24	179.67	117.08	2.38	1.00	71.56	77.58
TL2012-26/TL2012-17	5.74	55.66	228.83	104.33	2.54	2.58	76.82	74.25
TL2012-7/TL2012-38	5.65	76.57	202.58	123.89	2.50	1.63	73.24	70.33
Traits of top ten resistant hybrids								
TL2012-25/TL2012-26	1.92	21.53	136.59	109.53	1.96	1.88	73.20	71.58
TL2012-68/TL2012-41	4.92	24.33	190.58	113.28	2.38	2.68	72.75	73.50
TL2012-1/TL2012-41	5.08	25.33	230.5	157.17	2.21	2.75	72.31	69.58
TL2012-42/TL2012-41	5.94	27.51	190.25	99.32	2.17	1.88	72.88	70.33
TL2012-26/TL2012-41	5.28	28.66	188.33	104.38	2.17	2.88	74.96	73.25
TL2012-68/TL2012-42	7.73	32.31	158.41	114.14	2.50	2.04	70.62	68.33
TL2012-42/TL2012-26	4.85	32.54	244.50	116.58	1.92	3.29	71.54	72.42
TL2012-25/TL2012-1	4.93	33.41	162.33	113.38	2.00	2.08	70.52	68.67
TL2012-68/TL2012-26	2.03	33.46	159.58	84.41	2.58	1.88	72.08	70.75
TL2012-42/TL2012-25	5.03	34.50	147.81	109.19	2.28	2.38	75.77	72.58
Standard checks								
PANNAR 4M-19	5.60	61.23	188.50	134.92	2.38	2.04	73.53	75.08
H308	5.06	76.33	180.00	120.25	2.13	4.00	76.71	71.92
H208	4.98	67.91	128.08	106.62	2.21	2.78	72.74	72.83
SC627	4.50	39.23	180.00	102.94	2.29	2.13	68.07	68.83
UH615	5.30	82.53	186.75	93.58	2.25	2.08	68.97	69.50
Grand mean	4.45	52.43	188.44	188.3	104.63	2.310	72.00	72.83
Minimum	1.06	20.21	104.53	56.58	1.29	1.00	64.39	68.33
Maximum	7.73	89.66	345.08	157.17	3.50	4.00	76.82	84.17
SE	0.843	9.415	70.305	0.581	5.732	0.931	1.759	2.385
CV (%)	19.14	17.96	37.34	25.83	5.48	40.39	2.44	3.28

YLD = grain yield; MSV = disease reaction; PHT = plant height; EHT = ear height; EPT = number of ears per plant; HSC = husk cover of cob; DA = days to 50% anthesis; DSL = days to 50% silking; SE = standard error; CV = coefficient of variation

action (Griffing, 1956). Hybrid combinations involving the parental line TL2012-42 produced significantly high mean yield performance, suggesting that it transmits favorable genes to its progenies (Badu-Apraku and Oyekunle, 2012). Deployment of this inbred line into breeding programs should result in increased grain yields. Similarly, progenies derived from lines TL2012-41 and TL2012-1, which had significant negative GCA effects for MSV resistance, and which had reduced infection levels, could be used in MSV resistance breeding programs. Selection methods such as recurrent selection for general combining ability will maximize accumulation of additive resistance genes (Horner et al, 1976). In the same manner, TL2012-42 and TL2012-55 could be exploited to improve PHT and EHT due to their high positive GCA effects. Tall genotypes with high ear positioning or placement supports more ears, ultimately resulting to an increase in the final yield (Ali et al, 2012; Estakhr and Heidari, 2012). However, these traits may result to an increased susceptibility to lodging and to drought stress (Amiruzzaman et al, 2010; Estakhr and Heidari, 2012). The number of ears per plant is an indicator of increased grain yield potential, while long tipped-off husk covers provide maximum protection of the ear against bird damage, fungal infection, germination and insects that feed on maize cobs before harvesting. Therefore, lines TL2012-17 and TL2012-

55, which are good general combiners for these traits, are the best candidates for hybrid development. Early maturing genotypes promotes early harvesting and drought escape. On this basis, inbred lines, TL2012-1 and TL2012-68, with negative significant GCA effects for reduced number of days to anthesis and silking, respectively, are potential parents for hybridization.

Estimates of SCA effects and F1 hybrid performance

The superiority of parental inbred lines can be predicted based on the SCA effects of their progenies (Griffing, 1956). Hybrids TL2012-68/TL2012-42 and TL2012-7/TL2012-42, with positive SCA effects for grain yield, can be directly released as single cross hybrids for production in Tanzania or similar agro-ecologies in sub-Saharan Africa. Tall maize genotypes are important not only for increased grain yield but also for silage. Hence, hybrids TL2012-42/TL2012-17 (119.981 cm) and TL2012-7/TL2012-17 (126.52 cm), which showed good specific combining ability for plant height, can be released under intensive livestock production agro-systems, such as is practiced in the Arusha and Manyara areas. Hybrids TL2012-1/TL2012-17 (0.962) and TL2012-1/TL2012-55 (1.075) had high positive SCA effects for the number of ears per plant and husk covers, respectively. Early flowering hybrids TL2012-42/TL2012-55 (-4.406 days) and TL2012-42/TL2012-41 (-2.636 days) will be deployed

Table 5 - Pearson's correlations coefficients showing the relationships among studied traits.

YLD	1							
MSV	0.196 ^{ns}	1						
PHT	0.110 ^{ns}	-0.016 ^{ns}	1					
EHT	0.462 ^{**}	-0.007 ^{ns}	-0.004 ^{ns}	1				
EPT	0.196 ^{ns}	0.229 ^{ns}	0.007 ^{ns}	0.252 ^{ns}	1			
HSC	0.135 ^{ns}	0.120 ^{ns}	0.031 ^{ns}	0.357 ^{**}	-0.098 ^{ns}	1		
DA	0.384 ^{**}	0.017 ^{ns}	-0.121 ^{ns}	0.455 ^{**}	0.308 [*]	0.362 ^{**}	1	
DSL	-0.356 ^{**}	-0.140 ^{ns}	-0.107 ^{ns}	-0.073 ^{ns}	-0.079 ^{ns}	-0.124 ^{ns}	0.075 ^{ns}	1

** = correlation is significant at the 0.01 level (2-tailed);
 * = correlation is significant at the 0.05 level (2-tailed);
 ns = non-significant; YLD = grain yield; MSV = disease reaction; PHT = plant height; EHT = ear height; EPT = number of ears per plant; HSC = husk cover of cob; DA = days to 50% anthesis; DSL = days to 50% silking

for production in Monduli, Simanjiro and Hai Districts, which frequently experience short rainy seasons.

Conclusions

Inbred line TL2012-42 had significant positive GCA effects for yield, while lines TL2012-41, TL2012-1, and TL2012-42 were good general combiners expressing reduced MSV reactions. These lines can be exploited in hybrid breeding programs to improve the traits. Crosses TL2012-7/TL2012-42, and TL2012-7/TL2012-68 had significant positive SCA effects for grain yield, suggesting that they could be selected for use as single cross hybrids. On top of these, crosses TL2012-38/TL2012-55 and TL2012-25/TL2012-26 had negative SCA effects for their MSV reactions; hence, they could be selected for production in hotspot areas of the disease. Overall, there is great potential for hybrid breeding for increased grain yield and resistance to MSV using the studied inbred lines. Traits evaluated in the study except for the number of days-to-50% anthesis and silking were significantly influenced by additive gene action, suggesting that genetic gains can be realized through recurrent selection. In addition, hybrid breeding and population development through bi-parental crosses can enable favorable genetic recombination for all the studied traits governed by non-additive genes. However, significant influence of the environment on the assessed traits has been observed. Therefore, a comprehensive genotype by environment interaction analysis should be carried out to investigate the role of the en-

vironment and to ascertain the stability or adaptation of the newly developed superior hybrids before they can be recommended for production. Since the number of MSV resistance genes involved in the parents are not yet known, further genome-wide association analysis is required to guide future gene pyramiding.

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Table 6 - Estimates of GCA effects of ten parental inbred lines used in the study.

Lines	yield	MSV	PHT	EHT	EPT	HSC	DA	DSL
TL2012-55	0.010ns	2.822*	1.299ns	7.143***	-0.104ns	0.266**	-0.179ns	0.561ns
TL2012-17	0.260ns	17.356***	16.448**	-4.653*	0.346***	-0.292**	0.143ns	-0.306ns
TL2012-41	0.326ns	-10.926***	-9.694ns	-1.373ns	-0.066ns	-0.006ns	-0.281ns	0.611ns
TL2012-1	-0.104ns	-10.792***	5.265ns	6.0627**	-0.083ns	-0.015ns	-0.955*	-0.597ns
TL2012-26	-0.463**	-7.182***	-9.716ns	-6.572***	-0.225***	0.064ns	0.414ns	0.561ns
TL2012-25	-0.378*	-4.047**	-13.076*	-5.466**	-0.054ns	-0.241*	0.359ns	0.534ns
TL2012-38	0.008ns	16.161***	-4.115ns	2.408ns	0.039ns	-0.031ns	-0.554ns	-0.406ns
TL2012-42	0.695***	-10.748***	15.128*	7.188***	0.069ns	0.035ns	0.40ns	0.036ns
TL2012-68	-0.147ns	-9.533***	3.439ns	-4.599*	0.013ns	-0.070ns	0.183ns	-0.906*
TL2012-7	-0.206ns	17.757***	-4.978ns	-0.138ns	0.063ns	0.290**	0.470ns	-0.089ns

*, **, and *** denote significance differences at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively; DF = degree of freedom; YLD = grain yield (t ha⁻¹); MSV = MSV disease reaction in %; PHT = plant height in cm; EHT = ear height in cm; EPT = number of ears per plant; HSC = husk cover of cob; DA = days to 50% anthesis; DSL = days to 50% silking

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