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AGRONOMIC PERFORMANCE AND BREEDING POTENTIAL OF SELECTED INBRED LINES FOR IMPROVEMENT OF PROTEIN QUALITY OF ADAPTED UGANDAN MAIZE GERMPLASM

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ABSTRACT

The use of exotic Quality Protein Maize (QPM) donors to broaden the germplasm base used by breeders is important. This study evaluated the potential QPM inbred donors from CIMMYT for improvement of the protein quality of adapted maize lines in Uganda. Experimental plots were planted at Namulonge Agricultural and Animal Research Institute (NAARI) which is a known hot spot for several foliar diseases. Six QPM and six non QPM inbreds were planted in a Randomised Complete Block Design (RCBD) design with 3 replicates in 5-m rows. The twelve parental materials were crossed in a 6 X 6 half diallel mating design with QPM donors as males. Incidence and severity of major diseases were scored 4 times during the season while key agronomic descriptors were recorded. The field evaluation revealed that CML159 and CML144 are very susceptible to Maize streak virus (MSVD) and Turcicum leaf blight (TLB), two of the major foliar diseases in Uganda. CML173, the earliest maturing donor with the best plant aspects had moderate resistances to the major foliar diseases. CML176 with the exception of high MSV severity had moderate resistances to other diseases, good plant aspects, high protein quality and quantity. CML181 is MSVD resistant, moderately resistance to other diseases but had the lowest tryptophan level. CML182 was very susceptible to MSVD, TLB and had a poor plant aspect. Significant genotype sum of squares were divided into general (GCA) and specific (SCA) combining ability. Results indicated the existence of genetic divergence for all the diseases analysed, where additive effects were predominant. QPM donors CML176 and CML173 were superior in terms of GCA for the major foliar diseases, plant aspects and protein quality and quantity. We, therefore, recommend these lines for inclusion in Ugandan QPM breeding programs.

Key Words: Combining ability, diallel cross, Gray leaf spot, Rust, Maize streak virus, Turcicum leaf blight, Uganda, Quality protein maize

RÉSUMÉ

L'utilisation de donneurs du maïs protéinique exotique de qualité (QPM) est importante en vue d'élargir la base du germoplasme utilisé par les cultivateurs. Cette étude a évalué les donneurs QPM inbred potentiels de CIMMYT pour l'amélioration de la qualité de protéine des lignées de maïs adaptées en Ouganda. Des parcelles expérimentales étaient plantées à l'Institut de Recherches Agricole et Animalière (NAARI) qui est connu comme foyer important pour plusieurs maladies foliaires. Six inbred QPM et six inbred non-QPM étaient plantés dans un arrangement de blocs complets au hasard (RCBD) avec répliqués en rangées de 5m. Les douze matériels parent étaient croisés selon un croisement demi allélique à 6X6 avec des donneurs QPM comme males. L'incidence et la sévérité des

maladies principales étaient mesurées 4 fois pendant la saison tandis que les descriptions agronomiques-clés étaient enregistrées. L'évaluation du terrain a révélé que CML159 et CML144 sont très susceptible au streak virus du maïs (MSVD) et brunissure de Turcicum (TLB), deux des maladies foliaires les plus importantes en Ouganda. CML 173, le donneur à la croissance la plus précoce avec le meilleur aspect de plante, avait une résistance modérée face aux maladies foliaires les plus importantes. CML 176 à l'exception d'une sévérité élevée de MSV, de bons aspects de plantes, une quantité et une qualité élevée de protéine. CML 181 est résistant au MSVD, modérément résistant aux autres maladies mais présentant le niveau de tryptophane le plus bas. CML 182 était très susceptible au MSDV, TLB et avait un aspect de plante médiocre. Des sommes de carrés significatives de génotypes étaient divisées entre capacité générale (GCA) et spécifique (SCA) de combinaison. Les résultats ont indiqué une divergence génétique pour toutes les maladies analysées où les effets additifs étaient prédominants. Les donneurs QPM, CML 176 et CML 176 étaient supérieurs en terme de GCA pour la plupart de maladies foliaires, aspect de plantes, quantité et qualité de protéine. Nous recommandons donc ces lignées pour inclusion au sein de programmes de culture QPM en Ouganda.

Mots Clés: Capacité de combinaison, croisement bi-allélique, Cercosporiose, rouille, virus streak de maïs, Brunissure de Turcicum, Ouganda, Maïs protéinique de qualité

INTRODUCTION

CIMMYT QPM germplasm has been used worldwide in several ways including donor stocks, developing new QPM germplasm, direct releases of QPM varieties as such in national programmes and to extract lines for hybrid work. CIMMYT based QPM germplasm has been released in several countries (Antonio and Claudio, 2002; Garcia and Souza Jr., 2002) however, a major weakness of CIMMYT germplasm is that almost all of it has been found to be susceptible to major diseases especially MSVD and TLB (Pixley, 2001).

Simultaneous improvement of grain yield, disease resistances and protein concentration is feasible and a systematic breeding effort should lead to important new sources of productive and valuable QPM germplasm (Dudley *et al.*, 1996). However, the efficient use of heterosis requires populations with high combining ability abilities for important traits (like yield and disease resistances) (Griffing, 1956; Vasal *et al.*, 1992) and high protein concentration.

Genetic-statistical methodologies that assists in the selection of parents, based on their combining ability and potential to produce promising segregating populations have been developed, including diallel analysis. Frequently, this is based on the concepts of general (GCA) and specific (SCA) combining abilities established by Sprague and Tatum (1942), where one of the Griffings (1956) four techniques for estimation of general and specific combining abilities is employed. Diallel analysis also explains genetic control of traits, which further guides breeding and selection methods (Ramalho *et al.*, 1993; Cruz and Regazzi, 1994).

The evaluation of populations using these methods can support hybrid programmes and supply good open pollinated varieties, since populations with high frequency of favourable alleles are important sources for plant selection (Miranda and Viegas, 1987). In addition, this evaluation will allow breeders to concentrate efforts in those populations with higher potential of producing superior progenies.

Makerere University together with the Uganda National Cereal Program acquired many QPM donor lines from CIMMYT for her breeding programmes. The objectives of this study were to characterize QPM donors for adaptability and analyze their combining abilities with respect for resistance to the major maize foliar diseases in Uganda.

MATERIALS AND METHODS

Germplasm used. A total of 12 maize inbred lines (Table 1) were evaluated. Nine of these, namely, CML176, CML173, CML144, CML159, CML182, CML181, CML395, CML444 and CML387 were obtained from CIMMYT. The first six CIMMYT inbred lines were QPM inbred lines and the latter 3 were normal maize inbred lines known to have some good traits. For example, CML444 was previously found to have good combining abilities although it is also susceptible

to ear rot. Similarly, CML387 is reported to be resistant to MSVD, while CML395 has a semi-dent, big conical white grain that is popular with local farmers. Also included in the evaluations were three recycled lines developed by the National Cereals' Programme. These were PED49A, PED49B and 136R, and have been improved for tolerance to drought, MSVD, TLB and also found to have good combining abilities (Justus Imanywoha-Pers. comm.).

Experimental set-up. To evaluate for disease reactions and assess key agronomic characteristics, experimental plots were established at the Namulonge Agricultural and Animal Production Research Institute (NAARI) which is known as a hot spot for several foliar diseases (CIMMYT, 2003). Inbred lines were planted in a field previously grown with maize and in 3 replications of a randomised complete block design (RCBD). Plots were single rows 5m long, 0.75m between rows and had an inter-plant spacing of 0.3m with 17 plants of each inbred line. Standard agronomic practices were used to raise the plants. In addition, known susceptible checks DK for MSVD and CML206 for TLB and GLS were included in the experiments to ensure a high and sustained disease pressure during the experimental period.

The parental lines were subsequently crossed in a 6 X 6 half diallel mating design with QPM donors as males. Crosses were performed in the September – December 2003 season referred to henceforth as season 2003B. To avoid the xenia effect (Bulant *et al.*, 2000), pollen within each plot was controlled by hand pollination. At harvest only healthy ears were selected, hand shelled and packaged. The F_1 hybrids composed of the normal crosses were planted in a randomized block design the following season (i.e., 2004A) season at Namulonge. Plot sizes were as previously described. Some seeds were saved to represent F_1 populations. Towards maturity the F_1s were evaluated for the major foliar diseases namely MSVD, TLB GLS and leaf rust under natural infestation at Namulonge.

Field measurements. Incidence and severity of major foliar diseases i.e., MSVD, TLB GLS and leaf rust were monitored for two seasons. During each season disease was scored 4 times. The presence of the MSVD, TLB and GLS were assessed from about 30 days after flowering on a scale of 1 to 5 where, 1 = resistant and 5 = susceptible (CIMMYT, 2000). Ear rot was scored at harvest as the percentage of ears that were rotten.

At various points throughout the growth of the plants, key agronomic characteristics were recorded. These included days to 50% of the plants with pollen, days to 50% of the plants with silking, pollen shed duration (determined as the interval between the onset and end of pollen shed days) and plant aspects (measure of general appeal and appearance, scored on a scale of 1-5 where, 1 = good, 5 = poor) (CIMMYT, 2002). Anthesis to silking intervals (ASI) was also measured as described by Banziger *et al.* (2000).

TABLE 1. Germplasm source, pedigree and adaptation of parental maize lines used in the study

Parental line	Germplasm source	Pedigree	Adaptation
CML144	Pop62 CIMMYT	Pob62c5HC182-2-12-B-B-3-1-#-#	Tropical
CML159	Pop63 CIMMYT	Pob63c2HC5-1-3-1-B-2-1-1-B*	Tropical
CML173	Pop68 CIMMYT	Pop68C1HC180-13-1-1-B-2-B-B	Subtropical
CML176	Pop63/67 CIMMYT	[P63-12-2-1-/P67-5-1-1]-1-2-BB	Subtropical
CML181	S. Africa	UWO417-B-2-1-1-B-B	Subtropical
CML182	S. Africa	WOMTA1-B-1-1-1-B-B	Subtropical
CML387	CIMMYT, Zimbabwe	[EV7992#/EV8449-SR]C1F2-334-1(OSU8i)-1-1-B-B-3-B*4	Mid-altitude
CML395	IITA, Zimbabwe	90323(B)-1-B-1-B*4	Mid-altitude
CML444	Pop43C9 CIMMYT	P43C9-1-1-1-1-1-BBBB	Mid-altitude
PED49A	NAARI-Uganda	Recycled line	Mid-altitude
PED49B	NAARI-Uganda	Recycled line	Mid-altitude
136R	NAARI-Uganda	Recycled line	Mid-altitude

Sources: CIMMYT, 2002; Dr. Justus Imanywoha, personal communication

Analysis of grain protein content and quality for each inbred line were done at the Melkassa Agricultural Research Center QPM laboratory in Ethiopia, following procedures described by Villegas *et al.* (1984). Briefly, the pericarps and germs of 20 kernels of each sample (line) were carefully removed and the remaining endosperms air-dried overnight. Thereafter each sample was finely ground, the resulting flour was defatted. The concentrations of nitrogen and tryptophan were colorimetrically were determined for duplicate subsamples. The lysine content of kernels was not measured because the procedure was costlier than that for tryptophan and also because lysine and tryptophan concentrations in the protein of *o2* endosperm are highly correlated ($r = 0.85$) (Pixley, 2001). Tryptophan levels were analysed using Jaime (2004) colorimetric method that is based on Hopkins-Cole reaction in which 1 molecule glyoxylic acid and 2 molecules tryptophan form a coloured compound with a maximum absorption at 560nm.

Statistical analysis. For field disease assessments, disease (MSVD, GLS, TLB and RUST) scores for plants in each row were averaged to yield mean scores, which were subsequently subjected to analysis of variance (ANOVA). Where differences were significant, Fisher's Least Significance Difference (LSD) (Steel *et al.*, 1997) at 5 percent probability was used to separate means. All analyses were done using GenStat (Lane and Payne, 1996).

For combining ability estimates, the mean disease reactions of the parents and their single crosses per row were subjected to ANOVA using PROC VARCOMP METHOD 1 (SAS, 1990). Based on the significance of the F-tests, the significant mean squares of the treatments were partitioned further into GCA and SCA effects using Griffing's Method 2, Model 1 (Griffing, 1956), where cultivars are fixed effects and only experimental error is a random effect (Ramalho *et al.*, 1993).

RESULTS

Significant differences were observed among the inbred lines for all the traits assessed (Table 2). The results showed that CML173 was the earliest

TABLE 2. Agronomic properties, protein quality and quantities and major diseases of twelve parental maize lines evaluated Namulonge Agricultural and Animal Production Research Institute (NAARI) in Central Uganda

Parents	SD	PND	ASI	PSD	Aspects	% Try	% Prot	QI	% ER	MSVD	Rust	GLS	TLB
CML144	72	75	-3	3	2.5	0.95	9.94	0.68	77	2.87	1.13	1.63	3.5
CML159	68	69	-1	3	2.5	1.1	7.74	0.78	0	3.50	1.13	1.25	2.88
CML173	60	58	2	5	1	0.99	8.92	0.71	0	2.37	2.38	2.38	2.13
CML176	67	68	-1	2	2	0.95	9.53	0.68	0	2.48	2.38	1.00	2.13
CML181	69	70	-1	1	1.5	0.84	8.7	0.60	0	1.00	1.25	1.13	2.13
CML182	67	70	-3	1	1.5	0.95	7.99	0.68	64	2.87	1.13	1.38	1.88
CML387	74	75	-1	2	2	0.57	10.56	0.41	0	1.00	2.00	1.38	2.50
CML395	76	77	-1	5	1.5	0.47	10.52	0.33	0	1.12	1.25	1.13	2.25
CML444	77	78	-1	3	2	0.51	10.15	0.37	0	1.00	2.88	1.00	2.13
PED49A	67	68	-1	6	1.5	0.81	7.92	0.58	33	3.50	1.23	2.13	3.50
PED49B	70	68	2	6	1.5	0.92	9.77	0.66	0	1.75	1.13	1.50	2.00
136R	70	68	2	7	1.5	0.74	9.13	0.53	28	1.00	2.63	1.38	1.88
Mean	69.5	70.3				0.82	9.24	0.58		2.07	1.69	1.44	2.41
LSD (5%)	1.69***	1.69***				0.04***	0.04***	NS		2.24NS	0.39***	0.57***	0.89**
CV (%)	1.4	1.4				2.1	0.2	1.7		75.3	16.1	27.8	26.0

SD is Days to 50% Silking; PND is days to 50% pollen; ASI=Anthesis silking interval; PSD=Pollen shed duration; Aspects scored on a scale of 1 to 5 where 1 is good and 5 is poor; Try=tryptophan level; Prot=Protein level; QI=Quality index; Ear rot (ER) scores in percentages; MSVD=Maize streak virus disease; GLS=gray leaf spot; TLB=Turcicum leaf blight

maturing line (SD 60 days) while CML144 had a long maturity period (SD 72 days). Similarly, CML173 had the longest pollen shed duration (5 days) whereas CML181 and CML182 took the shortest time to shed their pollen (1 day). In general pollen shed duration varied between 1 to 5 days. There was a high variability among inbred lines for anthesis-to-silking interval (ASI) (Table 2). The ASI varied from 1 to 3 days, but in general good flower synchrony was observed with an ASI of 1 day being the most common. However, for CML159 and CML173, the silks emerged before the tassel started shedding pollen. Fortunately, the silks of these lines have long reception duration that enabled good nicking to take place and subsequent fertilization. There was a wide variation in plant aspects among the inbreds, with CML173 having the best overall score. Laboratory analyses revealed high variability in tryptophan level and quality index (QI) among the QPM donors. CML159 had the highest tryptophan level (1.10) whereas CML181 had the lowest (0.84). CML159 also had the highest QI (0.78) followed by CML173 (0.71). CML181 had the lowest QI signifying poor percentage lysine in protein. CML181 is therefore a very poor QPM donor. With the exception of PED 49A &B, all the non-QPM recurrent parents had low tryptophan level. With the exception of MSVD, all other diseases had significant ($P<0.05$) variations (Table 2) indicating genetic variability among the 12 cultivars. Average disease scores were 2.07 for MSVD, 1.69 for rust, 1.44 for GLS and 2.41 for TLB (Table 2). For MSVD CML159 registered the highest severity (3.5) and was significantly different from the other QPM donors whereas for the recurrent non-QPM parents PED49A had the highest severity (3.5) and was significantly different from the rest. CML181, CML387, CML444 and 136R were the only MSVD resistant parents. Moderate to low severities of MSVD were cited on the other remaining lines (Table 2). Significant variation ($P<0.001$) to the rust disease was also observed among the lines. CML173 and CML176 had the highest severities (2.38) among the QPM donors. Whereas among the non-QPM, CML444 had the highest severity (2.88) followed by 136R (2.63). GLS had a significant ($P \leq 0.01$) variability. Among the QPM, CML 173 had the highest severity (2.38) with only CML176 being resistant. PED49A had the highest severity (2.13) with CML444 being the only resistant non-QPM. Others had moderate to low severities. There was a significant ($P \leq 0.01$) variation in reaction of the inbreds to TLB. All the parental materials were susceptible to TLB with CML144 and PED49A having the highest severities (3.5) followed by CML159. Others had moderate to low severities.

CML144 had the highest (76.92 %) ear rot incidence followed by CML182 (63.64 %). Generally very low incidences of ear rots were observed on non-QPM lines. In fact the incidence ear rots recorded on these lines ranged from 0% to 33.33%. Clearly, augmentations of disease using susceptible booster lines (DK for MSV, CML206 for TLB and rust) were successful since a high disease pressures prevailed in both seasons. This provided a good disease environment to evaluate the maize lines for resistance to the major foliar diseases.

Combining abilities. Based on the significance of the F-test, the sum of squares for treatments was partitioned into sum of squares for general combining ability (GCA) and specific combining ability (SCA). Both GCA and SCA effects were important for resistance to all diseases with the exception of GLS where the SCA effects were not significant ($P>0.05$). The GCA effects for the diseases accounted for 89.7% of the total variation, indicating the predominantly additive nature of the inheritance of resistance to the diseases in question. There were also dominance effects, as indicated by the significant SCA effects (Table 3). GCA was significant for all the diseases with the highest being for TLB followed by MSVD and GLS. SCA was only significant ($P<0.01$) for MSVD and TLB.

The GCA effects for MSVD accounted for 91% of the total variation (Table 3), indicating the predominantly additive nature of the inheritance of resistance to MSVD. There were also dominance effects, as suggested by the significant SCA effects. Based on the GCA values for the parents (Table 4), CML181 ranked best general combiner for MSVD followed by CML176, CML144 and CML173. CML159 was the worst general combiner followed by CML182. Greater reductions in the MSVD scores were obtained in CML181, CML176 and CML144; thus, these

QPM donor lines are good sources of resistance MSVD. For the non-QPM, all the CIMMYT normal maize lines (CML) were generally good combiners for the MSVD resistance with the greatest GCA reductions being obtained in CML395 followed by CML444 and CML387. All the Ugandan lines had positive GCA with PED49B having the highest value (i.e., were more susceptible). The greatest SCA effects were obtained from single crosses CML444/CML159 (-0.71), CML395/CML181 (-0.66), PED49A/CML144 (-0.44) and 136R/CML159 (-0.39) (Table 5). These single crosses therefore produced superior hybrids resistant to MSVD.

The GCA effects for TLB accounted for 97% of the total variation and hence additive gene action largely determine resistance to TLB (Table 3). Estimates of GCA effects varied both among resistant and susceptible lines, indicating variability in resistance to TLB (Table 4). The greatest GCA reductions in the TLB severity scores were obtained from inbreds CML173 (-0.4), CML181 (-0.31), CML182 (-0.17) and CML176 (-0.16). The most susceptible QPM donors were CML144 (0.63) and CML159 (0.52). Among the non-QPM greater GCA reductions were obtained in PED 49B (-0.15), 136R (-0.12), CML 387 (-0.05), CML444 (-0.03), CML395 (-0.01). The only non-QPM parent with a positive GCA value was PED49A (0.45); it was the third most susceptible line among the 12 parents evaluated after CML144 (0.63) and CML159 (0.52). The most promising QPM donors were CML173, CML181, CML182 and CML176. The

TABLE 3. Mean squares for the analysis of variance of severity score for maize steak virus disease (MSVD), Turcicum leaf blight (TLB) and Gray leaf spot (GLS) in 12 parental maize lines and their single-cross hybrids (F_1s)

Sources of variation	df	Mean squares		
		MSVD	TLB	GLS
Replication	2	0.083333	1.350476	2.949405
GCA	5	7.5887319**	11.657548**	0.455358*
SCA	22	0.752462**	0.340826**	0.107008NS
Error	54	0.055556	0.074550	0.066689
GCA/SCA		0.91	0.97	0.81

SCA=Specific combining ability, GCA= General combining ability
MSVD=Maize streak virus disease, GLS=Gray leaf spot, and TLB= Turcicum leaf blight
** = P<0.01; * = P<0.05

TABLE 4. Estimates of General Combining Ability (GCA) effects of twelve inbred lines for severity scores of Maize Streak Virus Disease (MSVD), Turcicum leaf blight (TLB) and Grey leaf spot (GLS) at NAARI, in Uganda

Lines	MSVD	TLB	GLS
CML144	-0.12[4]	0.63[12]	-0.1[3]
CML159	0.77[11]	0.52[11]	0.2[10]
CML173	0.05[8]	-0.4[1]	0.07[9]
CML176	-0.12[4]	-0.11[6]	-0.08[4]
CML181	-0.4[1]	-0.31[2]	0.04[7]
CML182	1.47[12]	-0.17[3]	0[6]
CML387	-0.05[6]	-0.05[7]	-0.05[5]
CML395	-0.2[2]	-0.01[9]	-0.2[1]
CML444	-0.14[3]	-0.03[8]	-0.14[2]
49A	0.04[7]	0.45[10]	0.04[7]
49B	0.23[10]	-0.15[4]	0.23[12]
136R	0.2[9]	-0.12[5]	0.2[10]

Rank numbers (as superscripts) 1-12 represent the best general combiner to the worst general combiner respectively for each trait

following crosses CML136R/CML159, CML444/CML182, PED49A/CML181, PED49A/CML144, CML136R/CML176 produced superior hybrids resistant to TLB (Table 5). Considering the magnitude of general combining effects, resistance to TLB is mainly due to additive effects.

Analysis of variance for GLS indicated a highly significant difference among genotypes. Only values for GCA were significant ($P<0.05$) indicating that differences among parents were due to GCA (Table 3). The SCA effects were non-significant in the analysis of variance for GLS, although a negative effect was indicated in some single crosses (Table 5). CML176 (1.0) and CML181 (1.13) were the most resistant QPM donors whereas CML173 (2.38) and CML 144 (1.63) were very susceptible. CML159 (1.25) and CML182 (1.38) were moderately resistant (Table 2). Based on the GCA values (Table 4), CML144 and CML176 were the best line and produced several GLS resistant progenies. Both had negative GCA effects. CML182, CML181, CML173 and CML159 had positive effect with CML159, having the highest positive effect. Among the non-QPM parents, CML395 was the best line followed by CML444 and CML387. All had negative GCA effects. The lines PED49A, 136R and PED49B had positive effect, with PED49B having the highest positive effect.

DISCUSSIONS

Field evaluation generated wide variations in response of these parental materials to agronomic factors and diseases. With such low ASI, complete

TABLE 5. Estimates of specific combining ability of twenty eight single cross hybrids for severity scores of Maize streak virus diseases (MSVD), Turcicum leaf blight (TLB) and Grey leaf spot (GLS) during the season 2004A at NAARI, in Uganda

SC	AMSVD	TLB	GLS
CML387/CML144	0.07^{14}	-0.05^{9}	0.05^{23}
CML395/CML144	-0.08^{10}	0.03^{14}	-0.1^{5}
CML444/CML144	0.38^{27}	0.05^{15}	0.04^{21}
PED49A/CML144	-0.44^{4}	-0.43^{3}	-0.04^{11}
136R/CML144	0.0^{12}	0.34^{25}	0.2^{28}
PED49A/CML159	0.47^{26}	0.58^{28}	0.16^{26}
CML444/CML159	-0.71^{1}	-0.34^{5}	-0.16^{1}
136R/CML159	-0.39^{5}	-0.55^{1}	-0.10^{5}
CML395/CML173	0.25^{21}	0.06^{17}	-0.07^{9}
CML444/CML173	0.01^{13}	0.08^{19}	-0.03^{13}
136R/CML173	0.13^{17}	0.07^{18}	0.03^{18}
PED49B/CML173	0.15^{18}	0.10^{21}	0.0^{5}
CML387/CML176	0.27^{23}	-0.11^{8}	0.03^{18}
CML395/CML176	-0.08^{10}	-0.03^{11}	0.18^{27}
CML444/CML176	0.26^{22}	0.19^{22}	0.02^{16}
PED49A/CML176	-0.24^{6}	0.01^{13}	-0.06^{10}
136R/CML176	-0.20^{7}	-0.12^{7}	-0.02^{14}
CML387/CML181	0.35^{25}	0.09^{20}	-0.09^{8}
136R/CML181	0.20^{19}	-0.02^{10}	-0.14^{2}
CML395/CML181	-0.66^{2}	-0.03^{11}	-0.04^{11}
PED49A/CML181	0.3^{24}	-0.29^{6}	0.02^{16}
PED49B/CML181	0.08^{15}	0.31^{23}	0.03^{18}
CML387/CML182	-0.12^{9}	0.05^{15}	0.15^{25}
CML395/CML182	0.23^{20}	0.33^{24}	0.10^{24}
CML444/CML182	-0.51^{3}	-0.45^{2}	0.04^{21}
PED49A/CML182	1.27^{28}	-0.43^{3}	-0.14^{2}
PED49B/CML182	-0.17^{8}	0.47^{27}	-0.13^{4}
136R/CML182	0.11^{16}	0.34^{16}	-0.10^{5}

SCA=Specific combining ability, MSVD=Maize streak virus disease, TLB= Turcicum leaf blight and GLS=Gray leaf spot. Rank numbers (as superscripts) 1-28 represents the best specific combiner to the worst specific combiner respectively for each trait

fertilization was possible without staggering the planting dates. Short ASI can also contribute to high ratio of ear setting to grain under drought conditions (Ribaut *et al.*, 1997). Anthesis-to-silking intervals greater than five (5) days may result in incomplete pollination (Edme and Gallaher, 1993). All these lines therefore, could be used in water limited environments (Banziger *et al.*, 2000). Ugandan lines had longer pollen shed duration than their CIMMYT's normal lines. The long pollen duration would provide pollen assurance over a longer duration and reduce on staggering of planting dates. For the development of early maturing lines, hybrids, synthetics or open pollinating varieties, CML 173 is the best candidate.

Protein quality analysis revealed a high variation among the QPM donors for tryptophan levels and quality index. CML159 had the highest tryptophan level (1.10) and quality index (0.78) whereas CML181 had the lowest tryptophan level (0.84) and quality index (0.6). Quality index correlates well with the percentage of tryptophan/lysine in protein. High QI shows high protein quality (AOAC, 1995). CML181with the lowest QI is therefore, a very poor *o2* donor. Other than PED49B, all the normal maize lines had low QI as expected.

Field disease assessment revealed great variability in response of the parental lines to the diseases. Only CML181 and 136R were MSVD resistant but others had moderate to low susceptibility. All the parents were susceptible to rust with CML444, 136R, CML173 and CML176 being the most susceptible. All the parents were susceptible to TLB with CML144, PED49A being the most susceptible. This variation in response suggests that some parents have resistances which could be exploited. For instance CML181 is a potential donor for MSVD resistance, CML176 for GLS resistance. The variation in response to ear rot suggests that some QPM donors have ear rot resistance and this may be related to both genetic and agronomic factors (like shoot bagging). To reduce the ear rot problem, only QPM varieties with tight husk cover that cover the entire ear were selected. This provides additional protection against the fungus (NRC, 1988).

The relative importance of additive versus nonadditive effects for diseases in diallel crosses is an indication of the type of gene action (Baker, 1978). The GCA effects for the diseases accounted for 89.7% of the total variation, indicating the predominantly additive nature of the inheritance of resistance to the diseases. There were also dominance effects, as suggested by the significant SCA effects (Table 3). Resistance figure (Table 4 and 5) is of negative (-) direction because resistant reactions in entries were indicated by lower ratings or extremely resistant, whereas the higher ratings or positive (+) direction indicated severe infections. Parents with the greatest negative GCA are potentially superior (resistant) and may be included in breeding programmes to select new inbred lines in advanced generations.

Generally maize streak is considered the most important viral pathogen in maize in Sub-Saharan Africa (Thottappilly *et al.*, 1993). Pixley (2001) reported those majorities QPM currently available and tested in East and Southern Africa almost have no resistance to maize streak. Field evaluation showed that among the QPM donors only CML181 was resistant to MSVD. Analysis of GCA revealed greater reductions in the MSVD scores in CML181, CML176 and CML144 (Table 4). The low ratings of these QPM donors could be due to their wide genetic base which possibly contained alleles for resistance to MSVD. These QPM donor lines are thus, good sources of resistance MSV with CML181 as the most important donor for MSVD resistance. The following single cross hybrids CML444/CML159, CML444/CML182, PED49A/CML181, PED49A/CML144, PED49A/ CML176 produced superior hybrids resistant to MSVD. These single crosses included parents with large negative GCA and large positive GCA indicating involvement of additive x dominant gene interaction. These suggest possible exploitation of heterosis at F_1 generation, as MSVD resistance would not be fixed in the following generations. As a consequence, these populations should be considered as priorities for inclusion in the MSVD resistance breeding programmes. On the other hand, some populations that did not present high GCA, such as 136R/CML159 demonstrated potentials to contribute with specific resistances. Considering the magnitude of general combining effects (91%), resistance to MSVD is mainly due to additive effects, but dominance is also important (significant SCA).

Our study has shown that predominantly, additive genetic effects influenced resistance to GLS. This is in agreement with studies by Ulrich, *et al.*, 1990; Donahue, *et al.*, 1991; Gevers *et al.*, 1994; and Menkir & Ayodele, 2005 who have also concluded that GCA effects were more important than SCA effects for the trait. There were great variations in the genotypes to GLS susceptibility. This agrees with Bigirwa *et al.* (2001) who concluded that variation in response to *Cercospora zeae-maydis* is normally attributed to the background of the host material under test, those with susceptible background succumb. In general, the most susceptible parents had the highest positive GCA effects and produced the most susceptible hybrids which were as or more susceptible than both the parents indicating dominance of susceptibility. This corroborates findings by Menkir & Ayodele (2005), who observed that most of the crosses with one or more resistant parents produced resistant hybrids, whereas most crosses between susceptible lines generated susceptible hybrids. Although lines with negative GCA effects did tend to produce resistant hybrids, the relationship was weak since some lines with moderate resistance and moderate GCA produced resistant hybrids examples being 136R/CML181 and PED49B/CML182. The findings of Verma (2001) that GCA effects alone were not sufficient to predict the performance of hybrids suggested the presence of non-additive gene actions as well. The suggestion of Pratt *et al.* (1997) that different resistant gene products may be operational for GLS and that a diallel or generational mean analysis may not be adequate to reveal individual contribution of genes or that genetic background effects on expression of resistance are substantial appear to be true. Behaviour of different QTLs on different chromosomes reported by Saghai Maroof *et al.* (1996) also points in the same direction.

Considering the magnitude of general combining ability effects for TLB (97%), our result shows that the TLB resistance is additively inherited, a further testimony to Hughes and Hooker (1971) who also reported the polygenic nature of the resistance. SCA effects were also significant but were less important than the GCA effects indicating that dominance effects played part in inheritance of this disease although to a less extent (Barren *et al.*, 1993; Gevers *et al.*, 1994). Hakiza (1994) reported studies on interactive effects of both genes. This is consistent with published literatures, where several sources, including commercial hybrids possess single gene resistance (Smith and Kinsey, 1980; Turner and Johnson, 1980) while others possess minor or rate reducing resistance (Pratt *et al.* 1993; Pataky, 1994). Generally, the most susceptible parents with the highest positive GCA effects produced the most susceptible hybrids, more susceptible than the parents indicating dominance of susceptibility. Although lines with negative GCA effects did tend to produce resistant hybrids, the relationship was not as strong as it was in the case of those parents with positive effects. Some lines with high susceptibility and highly positive GCA produced exceptionally resistant single cross hybrids a case in point being PED49A/ CML144. This suggests involvment of additive x dominates gene interaction. Among the QPM donors, CML144 and CML159 contributed with large positive GCA values indicating greater susceptibility to TLB. However, CML173, CML176, CML181 and CML182 with large negative GCA values are potentially superior and may be included in breeding programmes to select new inbred lines in advanced generations (Ramalho *et al.*, 1993). With the exception of PED49A, all the other Ugandan elite non-QPM lines possessed great reduction in GCA scores signifying the polygenic form of resistance to TLB. These materials are recycled lines with TLB resistant Longe 1 (Okori *et al.*, 1999) ancestry. The findings are in close agreement with Adipala *et al.* (1993) who reported that most Ugandan varieties possessed this form of resistance (Polygenic). The finding of additive gene effects for the trait suggests the possibility of obtaining new cultivars from segregating population from crosses among the tested parents. Dual infection of TLB and MSVD were present exacerbating the already heavy TLB severity.

From a breeding perspective, each parental line with negative GCA effect would be conducive to increasing resistance to disease directly. It may be possible to find recombinants of these genotypes with resistance to most diseases in a large population. Once such a composite population is established, it can then be improved for disease

resistance by any suitable recurrent selection method.

Based on the GCA, SCA and tryptophan values, CML176 and CML173 are the most promising QPM donor parents for QPM breeding programmes in Uganda.

Clearly, augmentations of disease using susceptible booster lines (DK for MSVD, CML206 for TLB and rust) were successful since a high disease pressures prevailed in both seasons. This provided a good disease environment to evaluate the maize lines for resistance to the major foliar diseases. More research is needed to elucidate transgressive expression of tryptophan level in PED49B.

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