

Determination of the inheritance of resistance to cassava mosaic disease

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IJASR 2020

VOLUME 3

ISSUE 5 SEPTEMBER – OCTOBER

ISSN: 2581-7876

Abstract – Understanding the mode of inheritance of resistance to the disease and general combining abilities of the available germplasm is crucial in the development of genotypes with resistance to that disease. Research study was conducted to determine the inheritance of resistance to cassava mosaic disease. Analysis of individual experiments was performed, and mean squares used to determine general combining ability. Most parents expressed varying general combining ability (GCA) effects across sites for most of the traits evaluated. Only Kaleso had negative GCA effects for cassava mosaic disease severity and its progression in both two locations. The magnitude and sign of the GCA effect of a parent did not necessarily correlate with their per se performance, indicating the presence of non-heritable gene and epigenetic action. A number of progenies outperformed their best parent expressing high heterosis percentages. The progenies from MM96/4271 and Kaleso had high positive heterosis for fresh storage root yield, harvest index and storage root number and negative heterosis for the progression of cassava mosaic disease, comparatively to the values of the best parents. The study has revealed the presence of potential cassava mosaic disease resistance among the five elites parents used. These parents could be selected for cassava crop improvement in cassava mosaic disease resistance breeding programme.

Keywords: Cassava mosaic disease; general combining ability; inheritance; resistance.

1. INTRODUCTION

Genetic based resistance for diseases and pests has been among the major objectives in cassava breeding since the 1930s. Through intra-specific and inter-specific crosses with *Manihot glaziovii* Muell.-Arg. progenies with high levels of disease and insect pest resistance were developed (Legg and Fauquet, 2004). Host plant resistance is the most common form of genetic resistance so far exploited in most of the research institutions in Africa such as the IITA and NARS. But the success rate of these breeding programs has been limited (Kawano et al., 1998). Many progenies have been evaluated over several generations before a few desired varieties could be identified making the process expensive (Ceballos et al., 2016). There is a need to determine the inheritance of important traits such as cassava mosaic disease resistance, and how it is related to parameters such yield, harvest index, dry matter and number of roots per plant in the improvement of cassava productivity.

Choice of parents in a hybridization programme may be selected on the basis of their *per se* performance or the performance of their progeny (Falconer, 1981; Ceballos et al., 2016). According to Dabholkar (1992), selection of parents based on additive genetic effects increases the probability of obtaining progenies with desirable traits (Kulembeka, 2010). In contrast, selection of parents based on non-additive genetic effects such as dominance, epistasis, maternal or cytoplasmic effects is likely to result in a very small proportion of the progeny expressing the desired traits (Van Heerwaarden et al., 2008). There is genotypic variability in cassava for flowering and seed setting ability, seed germination, potential to pass on favorable traits to their progeny, and in hybrid vigor (Ceballos et al., 2004; El-Sharkawy, 2003). Varieties with low genetic diversity when crossed express low level heterosis whereas those with high genetic variability when crossed express high heterosis depending on the extent of gene frequency divergence (Mungoma and Pollak, 1988).

Combining ability concept is of specific importance in breeding (Zhang et al., 2015). Combining ability is also used to evaluate the result of cross combinations in self-pollinating crops (Grausgruber, 2016). The objective of the study was to determine the inheritance for resistance to cassava diseases and pests.

2. MATERIALS AND METHODS

Two trials were conducted at KALRO- Kakamega and Alupe research farms from June 2016 to June 2017. KALRO-Kakamega is in Kakamega County in western Kenya in Upper midland. Alupe is located in Busia County in western Kenya and fall in Upper Midland or Low Midland. Five elite parents were selected based on their performance on diseases resistance and the farmer preference in particular agro-ecological zone. The five parental genotypes each with 12 progenies generated through poly-cross mating design were evaluated in two locations. In order to generate families, the five parents were planted in isolated crossing block at KALRO-Alupe and allowed to random mate. The seeds were harvested from each parent, dried and planted in a seedbed before being transplanted into the field. Cuttings from these seedlings were used in the evaluation trial where only the seedlings that produced at least twenty quality cuttings per seedling were included in the trial. Furthermore, the choice of parents was also made based on the yield and yield components as these are also factors that influence the cultivation of farmers.

Each of the sixty five genotypes was planted in a plot size of eight meter square as dimensions. Two rows plot with four plants per row per genotype were planted at a spacing of 1 meter between rows and 1 meter between plants. Eight cuttings, each with 20cm of length from each genotype were used for planting in each plot. Cassava mosaic disease spreader rows were planted using infected planting materials from highly susceptible clones called Matuja. The spreader rows were planted after every 10 genotypes to ensure high disease pressure in the trial plots. The spreader rows were planted at the same spacing as plots and maintained in a similar manner in order to strengthen the inoculation of the cassava mosaic disease. The experiment was laid out in a randomized completely block design. Weeding was done as required but no fertilizer and supplementary irrigation was applied.

Data was collected on cassava mosaic disease, harvest index, number of storage root, fresh storage root yield and dry mater content.

Analysis of individual experiments was performed, and mean squares used to determine general combining ability (Beil and Atkins, 1967; Hausmann et al., 1999). General combining ability was calculated as the positive or negative deviation of the mean offspring performance of a genotype from the grand mean of all the offspring included in the particular mating design (Grausgruber, 2016). The parental varieties were considered as a fixed reference population; consequently the results only pertain to this set of heterozygous genotypes. The data was then arranged according to family means for analysis of variance (ANOVA) per site for all traits for general combining ability effects in SAS version 9.3 (SAS, Inc. 2002).

Heterosis was calculated as follows:

$$\text{Better parent heterosis (BPH) (\%)} = \frac{(F_1 - BP)}{BP} \times 100$$

Where, F_1 is the mean value of the F_1 cross and BP is the mean value of better parents, respectively.

3. RESULTS

3.1. Determination of general combining ability (GCA)

There were significant differences ($P < 0.05$) between entries in almost all the traits measured. Progenies significantly differed in Kakamega and not in Alupe for number of root per plant. Across sites progenies differed significantly for cassava mosaic disease incidence and severity, harvest index and fresh storage root yield. General combining ability (GCA) mean squares were highly significant for all the evaluated traits in both two sites, except for fresh storage root yield at Alupe.

Among the five parental lines, MM96/4271, MM96/0686, MM97/0293 and Kaleso were the parents which negatively contributed toward disease expression in their progenies with negative GCA effect for cassava mosaic disease resistance in the two sites (Tables 1 and 2). Clones, MM96/4271 and MM96/0686 had negative GCA effect in Kakamega (Tables 1) but not at Alupe, while clone MM97/0293 had negative GCA effect only in Alupe (Tables 2). Kaleso showed negative GCA effect in both two sites. Clone MM97/0293 showed the highest FSRY of 24.9tha^{-1} with a positive GCA effect when grown at Kakamega (Table 1), while it showed a negative GCA effect with the lowest FSRY at Alupe (Table 2). At the second position was clone MM96/4271 with 20.06tha^{-1} and 10.99tha^{-1} when grown at Kakamega and Alupe, respectively and with a positive GCA effect.

Parental clone MM96/4271 had negative GCA effects for dry matter content and the progression of cassava mosaic disease for both two sites, but had positive effect at Kakamega and negative ones at Alupe for harvest index and the number of storage roots (Table 2).

The parental clone, MM97/0293 had positive GCA effect for all the evaluated traits in both sites. The GCA effect for the progression of cassava mosaic disease was negative at Kakamega (Table 1) and positive at Alupe for parental clones MM97/0293 and MM96/0686 (Table 2). Negative GCA effect was also observed at Alupe for harvest index, number of storage roots and dry matter content (Table 2).

The parental clone, Kaleso had negative GCA effect for progression on cassava mosaic disease in both sites, but showed positive effect at Kakamega and negative at Alupe for dry matter content. Clone, Kaleso had also a positive GCA effect for the progression of cassava mosaic disease at Alupe, but a negative effect at Kakamega and positive at Alupe for harvest index and number of storage roots.

The parental clone, MM96/0686 had positive GCA for harvest index and a negative GCA effect for number of storage roots and dry matter content for both sites (Tables 1 and 2). Clonal genotype, MM96/0686 had positive effect at Alupe and negative effect at Kakamega for the progression of cassava mosaic disease.

A positive GCA effect was recorded for the parental clone MM96/9308 for harvest index, progression of cassava mosaic disease at Kakamega. A positive GCA was recorded for the parental clone MM96/9308 for dry matter content and the progression of cassava mosaic disease at Alupe. Parental clones MM96/0686 and MM96/9308 had negative GCA for number of the storage roots in both two sites.

The GCA effects of the parental clones were not consistent in all locations. Some parental clones recorded positive GCA effects in one location but negative GCA effects in another location for the same trait (Tables 1 and 2).

3.2. Determination of heterosis

Determinations in this section are based on values of individual half-sib progenies in each of the 5 different families. The best parental clone for cassava mosaic disease severity ranged from -33.3% to 300% with an overall mean of 76.5%. Only four half sib families among sixty had negative better parent heterosis (BPH). Three half sib families, P4G1, P4G5 and P4G6 among the four had the highest negative heterosis (Table 3). For cassava mosaic disease incidence, the high negative heterosis was recorded for five half-sib families which are P3G5, P3G11, P4G1, P4G5 and P4G6 from parental clones, Kaleso and MM96/0686.

The best four families with desirable positive better parent heterosis (BPH) for fresh storage root yield were P4G1, P1G4, P3G11 and P3G7 (Table 3). Better parent heterosis for fresh storage root yield ranged from -86.1% to

82.4%, for P5G4 and P4G1. The best six families with positive heterosis for harvest index were P3G5, P3G1, P3G2, P1G2, P5G11 and P1G12 (Table 3). Better parent heterosis for harvest index ranged from -56.5% with P2G8 to 33.6% with P3G5. For the storage root number, the best four families with positive heterosis were P3G7, P3G5, P1G6 and P3G11. For the dry matter content, only two families, P4G12 and P3G2 had positive better parent heterosis. Better parent heterosis for dry matter content ranged from -28.6% to 8.1% (Table 3).

Table 1: Cassava mosaic disease, number of storage root, harvest index, storage root yield and dry matter content means performance and general combining ability effects of five parental genotypes evaluated at Kakamega during 2016-2017, season.

Parental genotypes	Cassava mosaic disease				Yield and yield components							
	Severity score		AUDPC		Storage root number		Harvest index		Dry matter (%)		Storage root yield	
	GC A	Mean	GCA	Mean	GC A	Mean	GC A	Mean	GC A	Mean	GC A	Mean
MM96/42	-		-	202.6	-		-		-	37.0	-	20.0
71	0.20	1.86	66.12	0	0.25	5.14	0.02	0.47	0.80	9	1.07	6
MM97/02			-	224.7						38.4		24.9
93	0.04	2.09	44.02	0	1.63	7.02	0.01	0.50	0.58	7	5.93	2
			-									
Kaleso	-		163.7	105.0	-		-			39.7	-	16.5
	0.51	1.54	2	0	0.40	4.99	0.02	0.47	1.83	2	2.49	0
MM96/06	-		-	239.7	-		-		-	37.2	-	18.9
86	0.01	2.05	29.02	0	0.65	4.75	0.00	0.48	0.60	9	0.07	2
MM96/93			302.8	571.6						36.8		14.5
08	0.68	2.74	8	0	0.34	5.05	0.03	0.52	1.00	9	4.43	6
Mean	-			268.7						37.8		18.9
		2.05	-	2	-	5.39	-	0.49	-	9	-	9

CMD Severity were assessed based IITA scale (1-5) where 1= resistant plants and 5=Severe damage; AUDPC=Area under the disease progress curve calculated from the monthly CMD incidence scores; GCA=general combining ability

Table 2: Cassava mosaic disease, number of storage root, harvest index, storage root yield and dry matter content means performance and general combining ability effects of five parental genotypes evaluated at Alupe during 2016-2017, season

Parental genotypes	Cassava mosaic disease				Yield and yield components							
	Severity score		AUDPC		Storage root number		Harvest index		Dry matter (%)		Storage root yield	
	GC A	Mean	GCA	Mean	GC A	Mean	GC A	Mean	GC A	Mean	GC A	Mean
MM96/42			-	329.2								
71	0.14	2.13	18.60	0	0.19	3.99	0.01	0.49	3.54	2	0.28	9
MM97/02				409.0								
93	0.03	1.95	61.20	0	0.44	3.35	0.05	0.43	4.48	8	0.79	9.92
			-	146.0								
Kaleso	0.58	1.40	0	0	0.47	4.27	0.02	0.50	3.22	4	0.04	5
MM96/06				364.5								
86	0.29	2.28	16.70	0	0.07	3.73	0.04	0.52	4.18	8	1.05	6
MM96/93				434.5					15.4	52.4		10.1
08	0.18	2.17	86.70	0	0.17	3.63	0.01	0.47	3	9	0.60	1
Mean	-			347.8								
		1.98	-	0	-	3.79	-	0.48	-	6	-	1

CMD and CGM Severity were assessed based IITA scale (1-5) where 1= resistant plants and 5=Severe damage; AUDPC=Area under the disease progress curve calculated from the monthly CMD and CGM incidence scores; GCA=general combining ability

Table 3: Percentage of better parent heterosis for number of storage roots, harvest index, dry matter content, storage root yield and cassava mosaic disease at Kakamega and Alupe during 2016-2017, season

Materials	Cassava mosaic disease	Yield and yield components			
		Number of Storage root	Harvest index	Storage root yield	Dry matter (%)
P1G1	0.0	13.8	-4.3	27.2	-11.0
P1G2	175.0	7.1	25.0	20.5	-8.1
P1G3	250.0	-21.9	-13.0	-26.2	-5.6
P1G4	0.0	8.6	-12.1	53.6	0.6
P1G5	25.0	14.3	6.9	16.7	-5.0
P1G6	0.0	45.7	19.9	43.8	-10.9
P1G7	0.0	-26.7	12.8	-40.3	-22.6
P1G8	250.0	6.7	19.2	-32.9	-21.2
P1G9	275.0	31.4	-14.7	-5.5	-1.0
P1G11	0.0	-31.4	-37.8	-10.8	-28.6
P1G12	0.0	11.4	23.6	0.0	-2.1
P2G2	175.0	-4.4	-9.8	-29.6	-10.6
P2G3	75.0	-0.7	-38.6	16.1	-4.4
P2G4	0.0	-10.8	1.0	-27.2	-13.6
P2G5	300.0	-47.3	-44.8	-81.4	-19.8
P2G6	175.0	-50.0	-28.8	-41.0	0.9

P2G7	150.0	-35.1	-0.7	-56.4	-16.0
P2G8	50.0	13.5	-56.5	-35.9	-1.2
P2G9	0.0	-5.4	-44.9	-26.6	-12.8
P2G10	0.0	-23.7	-12.5	-36.6	-11.2
P2G11	50.0	-3.7	-13.9	-8.6	-1.2
P3G1	0.0	6.2	28.1	38.4	-7.7
P3G2	-0.3	-16.8	25.1	-16.7	6.7
P3G3	0.0	-23.5	12.4	5.5	-4.7
P3G4	0.0	7.1	-0.5	9.5	0.4
P3G5	0.0	49.3	33.6	-6.6	3.8
P3G6	0.0	-1.4	-25.5	-36.5	-18.4
P3G7	200.0	52.6	-5.8	47.0	-5.2
P3G8	0.0	3.3	4.5	16.1	-7.3
P3G9	125.0	-27.5	10.8	-10.8	-6.7
P3G11	0.0	40.7	3.3	49.5	0.7
P4G1	-33.3	19.3	0.3	82.4	0.9
P4G3	100.0	-35.6	-3.5	-29.6	0.5
P4G4	50.0	-40.0	-14.2	-46.6	-10.7
P4G5	-33.3	-67.8	-3.1	-56.7	-18.0
P4G6	-33.3	-13.3	8.8	-11.1	1.5
P4G7	0.0	-20.0	-1.4	13.9	3.3
P4G8	100.0	-17.0	10.7	15.1	0.3
P4G9	100.0	-28.9	5.6	-30.9	5.0
P4G12	50.0	15.2	3.1	13.2	8.1
P5G2	150.0	-38.8	-55.9	-65.3	0.3
P5G3	0.0	-36.6	11.9	-48.0	-8.6
P5G4	250.0	-66.3	-34.4	-86.1	-8.4

Table 3: Contd'

Materials	Cassava mosaic disease	Yield and yield components			
		Number of storage root	Harvest index	Storage root yield	Dry matter (%)
P5G5	200.0	-21.0	-25.0	-51.6	0.3
P5G8	225.0	-43.0	19.9	-49.6	-17.5
P5G9	225.0	-34.0	-48.7	-67.9	-1.8
P5G10	0.0	-7.8	10.5	-36.6	2.6
P5G11	125.0	-12.9	24.9	-39.8	-1.0
P5G12	0.0	-28.1	-16.6	-36.6	-14.6

4. DISCUSSION

4.1. General combining ability effects

When breeding for disease resistance, where the breeding objective is to progressively select progenies low numerical values, the best parents to be selected are those with negative general combining ability (GCA) effects. Relative to GCA effects and associated transmission of desirable additive gene action from parents to progeny, parental genotypes MM97/0293 and MM96/4271 had the highest positive and significant GCA effects for fresh storage roots yield, and negative GCA effects for cassava mosaic disease severity. This indicates that they were the best general combiners and desirable parents to utilize for the improvement of those traits. MM97/0293 and MM96/4271 were the best parents to be used in the improvement of storage root yield since it has high positive and significant GCA effects for this trait. This implies that this parental genotype made an above average

contribution to increase the fresh root yield in all its progenies. Parental clones with positive, GCA effects are deemed desirable because they contribute to an increase in fresh storage roots yield in their progeny while parents with negative effects contribute to a reduction. MM96/4271 was the best parent for developing progenies with high harvest index. There were inconsistent differences for GCA mean square for some traits across the environments. Most parental lines expressed varying GCA effects across sites for most of the traits evaluated, indicating the effect of the environment on the evaluated materials.

The results support the finding of were (2011), when he observed the presence of significant differences between genotypes in one environment and not in the other, indicating the presence of G x E interaction. Strong G x E effects has been reported for many important morphological and agronomic traits of cassava (Cach et al., 2006; Calle et al., 2005; Jaramillo et al., 2005).

The GCA effect is considered the intrinsic genetic value of a parent for a trait, which is attributable to additive gene action and it is fixable (Simmonds, 1979). Lower disease scores of a 1 to 5 severity scale specify higher disease resistance, so that negative GCA effects are required for disease resistance breeding (Kulembeka et al., 2012; Parkes et al., 2013). As reported by Kimani and Derera (2008), the presence of G x E and GCA x environment interaction pose considerable challenges to the development of widely adapted genotypes. The implication of this is that parents and crosses should be evaluated in more than two or more distinct environments before conclusions are made on their genetic potential (Owolade et al., 2008).

4.2. Determination of heterosis

A number of progenies outperformed their best parent values expressing high heterosis percentages. The high positive better parent heterosis being for fresh storage root yield, Harvest index, and storage root number was observed for progenies from MM96/4271 and Kaleso, and most negative better parent heterosis for the progression of cassava mosaic disease. When breeding for cassava mosaic disease resistance, the best crosses might be those that had the most negative heterosis. The expression of heterosis indicates the presence of genetic divergence between the parents (Mungoma, 1988; Tang et al., 1993; Tang et al., 2004) and confirms the significance of gene interaction in the progenies. The study supports that of Chikoti (2016), when most of the crosses recorded positive heterosis for fresh root yield, total biomass, plant height and root size and negative heterosis for cassava mosaic disease. The study agrees also with were (2011), when the crosses developed from Mercury x SS4 dominated the list of the top 20 crosses with high positive best parent heterosis for root yield and most negative best parent heterosis for cassava mosaic disease resistance.

5. CONCLUSION

High yielding cassava progeny with high dry matter content, high harvest index and resistant to cassava mosaic disease attack have been developed by evaluating cultivars from KALRO/Kakamega as parents. Parents and families with good combining ability for fresh storage roots yield and resistant to cassava mosaic disease damages were identified, implying that there is a potential of deploying these parental varieties in development of superior crosses and general progress in cassava breeding.

Acknowledgement

This publication was made possible through support provided by Alliance for Green Revolution in Africa (AGRA) Grant No. 2015 PASS 011. The opinions expressed herein are those of the author (s) and do not necessarily reflect the views of AGRA

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