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# African Cassava MOSAIC



Report of an Interdisciplinary Workshop held at Muguga, Kenya, 19-22 February 1976

Editor: Barry L. Nestel

Cosponsored by the East African Agriculture and Forestry Research Organization  
and the International Development Research Centre

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*Editor:* **Barry L. Nestel**  
*International Development Research Centre*  
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## Breeding for Resistance to African Cassava Mosaic Disease: Progress and Prospects\*

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### Introduction

GERM PLASM derived from the former East African breeding program at Amani, Tanzania, is still the main source of resistance to African cassava mosaic disease (CMD) being used in breeding, and so it is useful to begin by restating the essential features of this program. It began in 1935 when H. H. Storey made a world-wide search for cultivars of *M. esculenta* resistant to CMD. He found some with a degree of resistance (e.g. F279 from Java which is still favoured around Mombasa) and obtained higher resistance (e.g. 37244E) by intercrossing some of them. However, in general he concluded that even higher levels of resistance were needed and began to transfer resistance from other species of *Manihot* by interspecific crossing and repeated backcrossing to cassava. He used the following species: *Tree species: Manihot glaziovii* Muell.-Arg. (Ceara rubber), *Manihot dichotoma* Ule. (Jaquie Manicoba Rubber), *Manihot catingea* Ule., 'Tree' cassava – believed to be a natural hybrid of *M. glaziovii* and cassava; *Herbaceous species:* (taxonomy disputed by Rogers and Appan, 1970) *Manihot melanobasis* Muell.-Arg. and *Manihot saxicola* Lang.

All the tree species were graft susceptible to CMD, but they conferred to their progenies a form of field resistance in which plants tended to remain free of disease or produced only mild and frequently transient symptoms. They were also resistant to cassava brown streak (CBS). Of the herbaceous species, *M. melanobasis* contributed strong resistance to CBS but not to CMD, and *M.*

*saxicola* was susceptible to both diseases (Nichols 1947).

Considerable progress had been made by the time that I became responsible for the program in 1951. My general conclusions on the value of the germ plasm were as follows: (1) some of the 3rd backcross derivatives of *M. glaziovii* (e.g. 46106/27) provided the best combinations of yield, root quality, and CMD and CBS resistances, but though CMD resistance was satisfactory for inland areas it was frequently inadequate for coastal regions; (2) some of the "tree" cassava selections also showed promise, but the good resistance of the corresponding *M. dichotoma* series was not successfully combined with good yield potential. Work with *M. catingae* began late and little backcross material was assessed; (3) *M. melanobasis* was the best source of resistance to CBS, but its hybrids had a characteristic growth cycle which seemed to reduce the effectiveness of the mechanisms of resistance to both CMD and CBS, though it enhanced their yield potential (Jennings 1957, 1959).

The inheritance of resistance in the backcross progenies was assessed by the Gilbert (1967) method, which estimates the additive parental effect or "parental value" of each parent and then calculates the statistical significance of these values and that of any interaction between them by an analysis of variance. The additive and interaction mean squares denote generalized specific combining ability respectively (GCA & SCA), and the sum of the two parental values estimates the mean expected for their progeny in the absence of specific combining ability. The results (Table 1) show that resistance to both CMD and CBS was inherited in a predominantly additive

\* This paper was tabled at the meeting; the author was unable to attend.

way, though there was also a significant SCA effect for CMD resistance. A high parental value indicates a potent source of resistance: a *M. dichotoma* source had the highest, but it is interesting that only the *M. glaziovii* source is being exploited at present, resistance breeding being based almost entirely on one derivative of this species.

In view of the limited effectiveness of *M. glaziovii* derivatives in coastal regions, I attempted in 1953 to obtain higher resistance by intercrossing resistant hybrids, hoping to release recessive genes for resistance and to recombine genes which had been dispersed during the process of backcrossing. This proved successful and segregates (e.g. 5318/34) showing much higher resistance were obtained (Fig. 1). Moreover, their resistance was stable over a wide range of conditions. From this material I distributed pollinated seed to a large number of African countries in 1956. Further breeding based upon it has been reported from Ghana (Doku 1969), but the most important work occurred at Moor Plantation, Nigeria, where in 1958 M. J. Ekandem selected hybrid 58308 from seed derived from my selection No. 5318/34: this later became the main source of resistance used at IITA.

#### Techniques of field experimentation

In the Amani work, all susceptible genotypes planted in October–November rapidly became diseased, but plants of resistant genotypes remained symptom-free for longer, some 10–20% of them becoming diseased in April or May. For these genotypes, symptom intensity tended to be low before April–May, relatively high during these months, and then low again. Symptoms often disappeared by July, and if plants were retained after their dormant period they were normally symptom-free. It was found that a check to growth during April or May, for example by cutting the stem tips, increased the percentage of plants showing symptoms, and that this technique could be used to facilitate selection for high levels of resistance: genotypes (e.g. 5318/34) which withstood this treatment without producing symptoms also remained symptom-free when grown in the coastal environments associated with resistance breakdown. In a similar experiment done at IITA in 1975, growth checks were applied from June onwards to April-planted material of 58308. A more complicated situation was found because the younger plants had a greater capacity to recover from their symptoms. Nevertheless, the treatments considerably influence the disease intensity. In this experiment almost 100% of the

58308 plants showed symptoms at some stage, emphasizing that we are dealing with a tolerance situation and not resistance to infection. However, the conclusion is that we have a means of regulating the intensity of the disease in both the East African and IITA situations, providing an option for increasing the intensity of selection for resistance (Jennings 1957, 1960).

#### The present position in East Africa

The Amani program was terminated in 1957 and a collection of the germ plasm was established first at Serere, Uganda, then at Kakamega, Kenya, and finally at Mtwapa, near Mombasa. It includes the following:

Type of Material	No. of Genotypes
Cultivars of <i>M. esculenta</i>	12
Backcross hybrids of <i>M. glaziovii</i>	47
Backcross hybrids of <i>M. dichotoma</i>	7
Backcross hybrids of 'Tree' cassava	7
Backcross hybrids of <i>M. melanobasis</i>	3
3rd bc <i>M. glaz.</i> × 3rd bc <i>M. dich.</i>	4
3rd bc <i>M. glaz.</i> × 1st bc <i>M. melan.</i>	8
3rd bc <i>M. dich.</i> × 1st bc <i>M. melan.</i>	3

All this material has some resistance to CMD, but less than 20% of the clones belong to the highly resistant category obtained by inbreeding and typified by 5318/34 and 58308. Seed material collected from the plot would therefore be expected to segregate widely for resistance and may not include representatives of this resistance category.

Five genotypes have been chosen for distribution to farmers. The choice made emphasizes the point that high resistance to CMD is not an important criterion determining a farmer's choice: none of the highly resistant genotypes was chosen.

Their first choice is 46106/27, a 3rd backcross *M. glaziovii* derivative of moderate mosaic resistance. Its popularity is based upon its root quality, reliability on sandy soil, and good habit. As well as being first choice at Mombasa, about 500 ha are grown around Tanga, Tanzania, and a smaller area near Dar es Salaam. It is largely mosaic-free on a Mombasa estate where it is grown in a large block, but is 100% diseased in farmers' plots where it is surrounded by diseased plants of local varieties. Second choice is F279, one of H. H. Storey's original importations from Java. It owes its position as second favourite entirely to the quality of its roots; 54140/10 (from intercrossing *M. glaziovii* and *M. dichotoma* derivatives), 59284/33 (3rd backcross *M. glaziovii* hybrid) and 5543/106 (from intercrossing *M. melanobasis* and *M. glaziovii* derivatives) have also been released

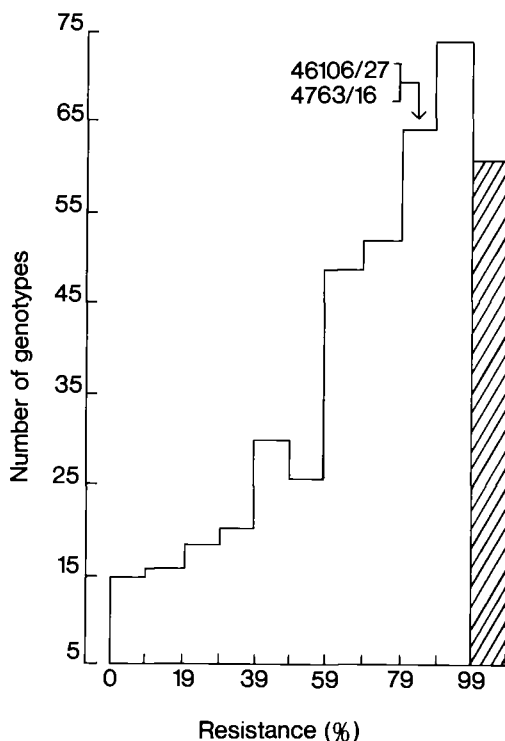


Fig. 1. Segregation for CMD resistance following intercrossing of 3rd bc *M. glaziovii* hybrids (resistance level of parents indicated by arrow).

because of their high yield potential, but they are recommended only for livestock feeding because of their high HCN content (above 50 mg/kg fresh root).

### Breeding in West Africa

Hybrid 58308, derived from Amani germ plasm,

is the main source of resistance being used by S. K. Hahn (1972, 1973, 1974), at IITA. It has contributed improved resistance to the IITA populations, but resistance tends to be recessive, and selections from the first generation of crossing are rarely as resistant as this parent. Nevertheless the symptoms are usually only moderately severe and transient, and yield reduction due to CMD infection is consequently minimal. Big advances in agronomic merit are being obtained by using breeding material from Latin America. This is contributing genetic factors which affect yield directly, and it is considered inadvisable to select too vigorously for CMD resistance amongst types with such good yield potential. The breeding method allows for intercrossing among large populations of improved plants, and so recessive CMD resistant forms like 53808 segregate in each generation (Fig. 2). Nevertheless, in a situation where big advances are possible by selecting directly for yield, and where the level of resistance is such that CMD has minimal effect, it seems unlikely that the resistance level of 58308 will be achieved by a high proportion of the selections, at least in the early stages of breeding.

It is undoubtedly correct to exploit this germ plasm even at the expense of high CMD resistance, which can be restored by further breeding. At this stage it is difficult to envisage situations where higher levels of resistance may be needed, but various possibilities could be discussed. For example, although the consequences for yield of low-severity CMD have been found negligible in the germ plasm studied so far, it is possible that selection for higher yields could produce genotypes for which high resistance is a greater asset than at present; it is possible too that 58308 derivatives may be found wanting in certain environments or when attacked by certain strains of the agent, or again the introduction of new germ plasm may

TABLE 1. Additive parental values for resistances to CMD and CBS.

Parent	Origin of parent	CMD	CBS
37244E	Java × Madagascar	21.7	7.5
Msitu	Local Kenya	10.9	3.4
Aipin Valenea	Brazil, via Congo	3.1	29.1
Macaxeira aipin	Brazil	6.0	25.7
Mbarika	Local, Tanzania	0.2	8.8
4070	1st bc <i>M. dichotoma</i>	28.3	32.4
43101/32	2nd bc <i>M. dichotoma</i>	46.2	4.7
4032	1st bc <i>M. glaziovii</i>	32.4	62.0
4318/22	2nd bc <i>M. glaziovii</i>	30.0	49.2
<i>M. melanobasis</i>	Surinam	11.6	82.6
<i>Percentage of between-family variation</i>			
Parental values (G.C.A.)		69.6	88.7
Interactions between parents (S.C.A.)		30.4	11.3

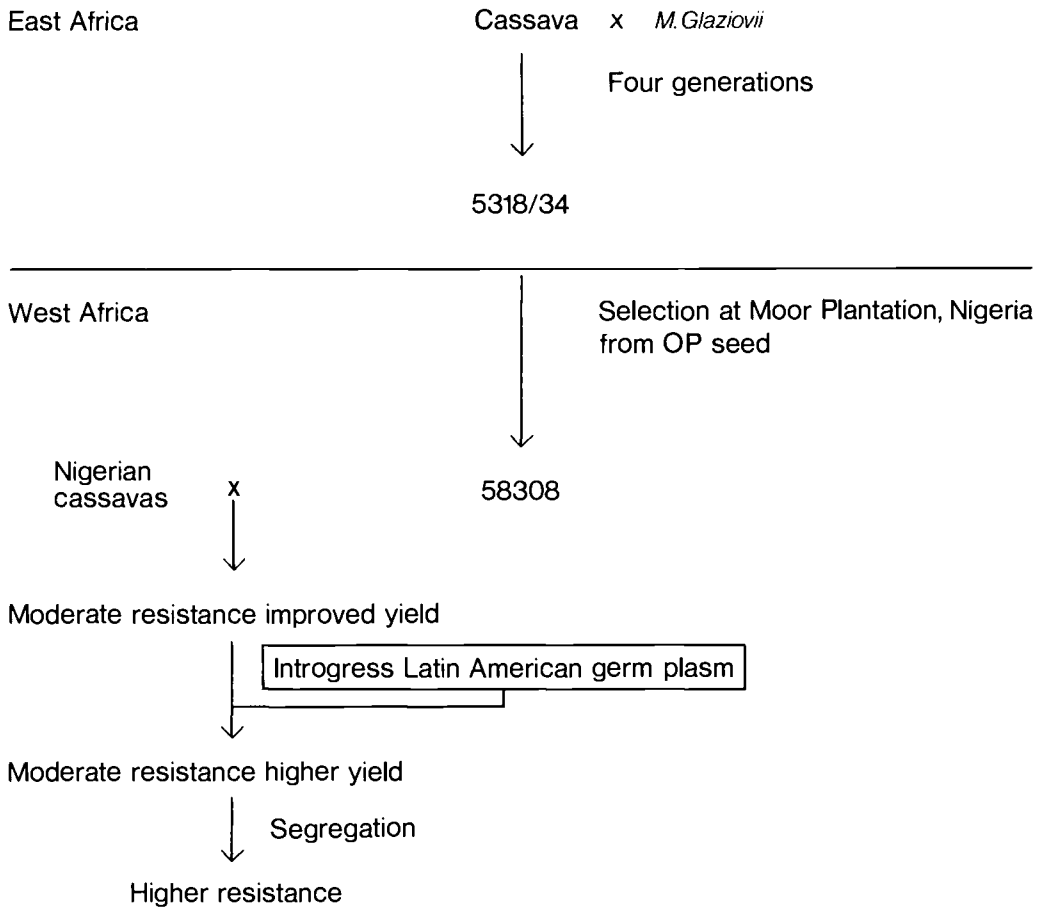


Fig. 2. Breeding for resistance to CMD at EAAFR0 in East Africa and at IITA in West Africa.

disrupt the resistance mechanism of the plants, as happened when I attempted to utilize germ plasm derived from *M. melanobasis* to improve yield (Jennings 1959, 1960). Thus, while we should maintain all our sources of resistant germ plasm so as to be able to respond to any such unforeseen circumstance, there seems no reason to question the considerable potential of the resistant material emerging from the present IITA breeding program. The parents of 58308 had adequate resistance for East Africa, the resistance of 58308 itself has been shown adequate for Nigeria and so has that of its progeny in Zaïre, Sierra Leone, and Liberia. It is likely that farmers will insist on planting mixtures of cultivars and that new cultivars will generally be grown adjacent to diseased plants and subject to continuous attack by infective vectors: a good resistance level will be required even if it is not the highest attainable.

#### Genetic studies in West Africa

Hahn has also used Gilbert's method to analyze his data, and for crosses among six parents he obtained the parental values given in Table 2 (Hahn 1973). He found that 58308 also contributed resistance to cassava bacterial blight (CBB), and concluded that resistance to CMD was controlled by quantitative genes with additive effects; it appeared to be a recessive character with a heritability of about 60%. The conclusions regarding CMD resistance are similar to those from the East African work.

During a recent stay at IITA I studied the inheritance of resistances to CMD and CBB in a  $6 \times 6$  diallel. The results (Table 3) accord with earlier ones and further analyses by  $W_r/V_r$  regression (Jinks 1954) emphasize the strongly recessive nature of genes for resistance to each disease (Fig. 3) (the positions on the graphs of



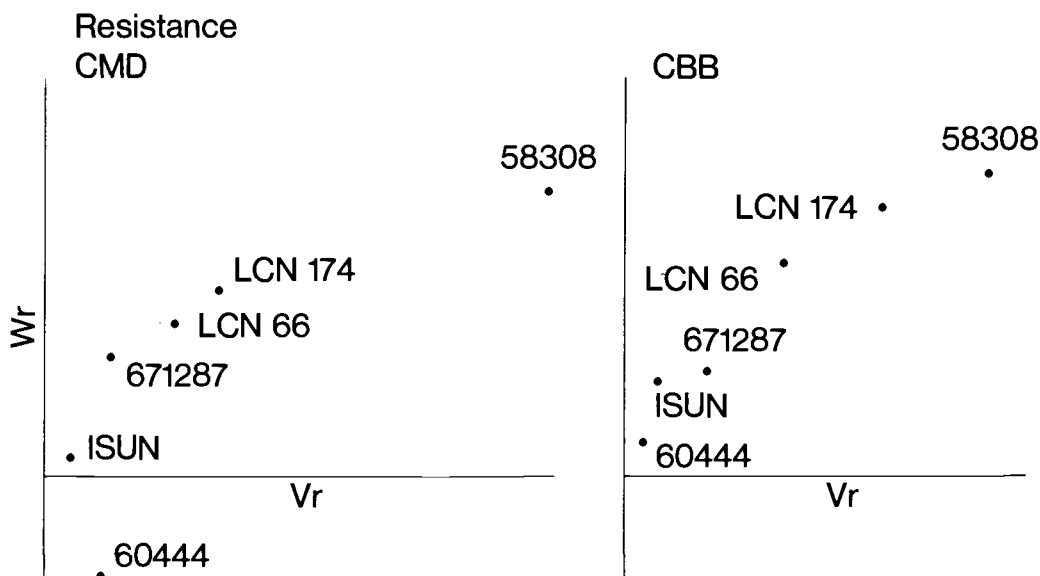


Fig. 3.  $W_r/V_r$  analyses for resistance to CMD and CBB in a  $6 \times 6$  diallel recorded at IITA.

TABLE 2. Parental values for resistance scores to CMD and CBB.

Parent	CMD <sup>a</sup>	CBB <sup>a</sup>
58308	1.505	1.105
58198	0.789	1.568
I sunikakiyan	1.667	1.846
Oyanrugba Funfun	1.636	1.758
Oyanrugba Dudu	1.641	1.681
Ogunjobi	1.485	1.672

*Analysis of variance*

General combining ability	9.558**	8.698**
Special combining ability	0.755	1.093

<sup>a</sup> Low scores denote high resistance.

58308 indicate that this parent carries mostly recessive genes for each resistance and those of LCN 66 and LCN 174 indicate that these parents are heterozygous).

My main objective was to determine whether the resistances to CMD and CBB were genetically linked. The evidence will be presented, though further work is necessary before definite conclusions can be drawn. Two particular results are relevant here. First, in an experiment where genotypes were propagated clonally for trial, a significant within-genotype (i.e. nongenetic) correlation was obtained between the intensities of CMD and CBB ( $r = 0.385$ ,  $df = 403$ ). Since CMD was present before the attack by CBB, a reasonable conclusion is that the presence of CMD weakened resistance to CBB. Hence it is particularly important to have CMD resistance where CBB is a

problem. Second, linkage between the two resistances, if confirmed, would suggest a very interesting genetic situation: the two resistances must derive from *M. glaziovii* seven generations of strong selection for non *M. glaziovii* characteristics have occurred since the first interspecies cross. Linkage persisting to this stage therefore suggests that blocks of resistance genes may be held together in a chromosomal situation which restricts their recombination with genes from *M. esculenta* — a situation which calls for cytogenetic study.

**Recommendations**

I would like to convey two ideas in this paper: the need to exploit the progress that has been made, and the need to conserve germ plasm so as to be able to respond to any new situation that might

TABLE 3. Parental values for percent resistance to CMD and CBB.

Parent	CMD	CBB
58308	24.5	32.4
*LCN 66	16.4	20.9
*LCN 174	16.4	26.2
671287	13.2	18.4
I sunikakiyan	6.6	8.5
60444	0.7	9.1

*Analysis of variance*

	MS	MS
G.C.A.	5611**	7914**
S.C.A.	722*	335*

\* LCN 66 and LCN 174 are both from the cross 58308  $\times$  I sunikakiyan.

arise. I need hardly say that control of CMD is unlikely to be achieved by any means other than by the use of resistant cultivars, and therefore suggest that the highest priority should be given to these two needs. My recommendations are: (1) Exploit IITA germ plasm by selecting for local adaptation at as many centres as possible in Africa and make appropriate arrangements to propagate rapidly and disseminate the selections. Some of the Mtwapa clones may also qualify for this. (2) Maintain seeds representing all sources of CMD resistance so that they are available for any contingency which might arise in the future. The facilities of the new germ plasm conservation unit at IITA should be used. (3) Arrange for seed from the Mtwapa collection to be moved to IITA for introgression into the breeding populations there. (Note that item 2 is suggested in addition to item 3, since new sources of resistance may be lost in a situation where selection is for *adequate* resistance combined with high yield potential). Available *M. dichotoma* derivatives for example are poor yielders. The alternative of creating a mosaic-resistance composite where first priority in selection is for CMD resistance can be postponed until a need is shown to exist. (4) Pursue genetic studies of CMD resistance, including resistance from sources not yet studied genetically,

and also cytogenetic studies of 58308 and the association between resistances to CBB and CMD.

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