EVALUATION OF MAIZE (*Zea mays* L.) GERMPLASM FOR RESISTANCE TO MAIZE STREAK VIRUS DISEASE

by

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INTRODUCTION

Maize streak virus disease (MSV) occurs throughout Africa south of the Sahara, and in the western Indian Ocean islands of Reunion, Mauritius and Malagasy. It has for a long time been recognized as one of the most serious foliar diseases of maize in the low elevation areas of East Africa. This disease, caused by a leafhopper-transmitted virus, causes severe losses in maize grain yields when infection takes place at the early stages of plant growth. It has been demonstrated experimentally that severity of yield loss caused by MSV is directly related to time of infection. Maize seedlings infected at the 2nd leaf stage suffer a grain weight loss of about 55 percent. Infection of plants at the 4th, 6th, 8th and 10th leaf stage results in a yield reduction of 45, 40, 33, and 25 percent respectively. Yield loss from this disease is a result of pronounced chlorosis which appears as narrow broken stripes along the veins of the maize leaves as the virus interferes with development of chloroplasts in tissues surrounding the vascular bundles, consequently leading to stunting and reduced photosynthesis.

The first description of maize streak virus was done by Fuller in 1901 (6) in South Africa, by which time the disease had already been troublesome for some time. A detailed study of its method of transmission was done and reported by Storey between 1925 and 1928. The disease was reported in East Africa in 1936.

In Tanzania, the disease has persisted since then, and severe outbreaks, though erratic over the years, have been experienced. A breeding program developed by the National Maize Research Program in which one of

the objectives was to breed for resistance to MSV in existing commercial and introduced varieties was initiated in 1974. Recurrent selection was used under natural field conditions, but little progress was made. A new open-pollinated variety, "Tuxpeno," on which considerable effort had been expended (by the above procedure) to raise the level of MSV resistance, was placed in commercial production in 1978 during which a severe MSV outbreak occurred. The new variety and several others grown in that season showed little resistance to that epidemic. The situation aroused national attention, and "Tuxpeno" was temporarily suspended from production. A different approach towards development of MSV-resistant commercial varieties was needed.

The following experiment was conducted to evaluate various sources of resistance to MSV and their potential use as sources of resistance in the National Maize Research Program. The best sources based on this evaluation will be used in a breeding program designed to incorporate MSV resistance into adapted commercial varieties.

LITERATURE REVIEW

Nature of the Virus

Among leafhopper-borne viruses, maize streak virus is unique. Through a series of studies on streak disease of maize, Storey (13, 14, 15, 16) showed that in many aspects the disease was a typical virus disease. However, the critical evidence, i.e. the filterability of the virus, which would have certainly placed it in the group of virus diseases was lacking until in 1932 (18). At that time he was able to demonstrate that it was filterable. Fluids containing the virus could pass thin membranes to feed leafhoppers, and by this process the vectors took in the virus from the fluid and subsequently transmitted it to healthy maize plants. This was the final piece of evidence Storey needed to prove that the streak disease of maize was indeed caused by a virus, hence the name Maize Streak Virus (MSV) disease.

Further work with this virus by Bock, et al. (1) and Storey (14) showed MSV to be different from known leafhopper-transmitted viruses in morphology and incubation period in the vector. Storey (14) found that the incubation period was between 6 and 12 hours at 30°C. It has been found that in all other leafhopper-transmitted viruses the incubation period is rarely less than 3 days (26).

Several attempts have been made to characterize the virus of maize streak disease. Whitcomb and Davis (26) thought that the virus must be small and relatively stable, and that it must contain RNA. In other attempts to characterize the virus, polyhedral virus-like particles were found in nuclei of cells from MSV diseased maize plants by electron

microscopy (10), while virus-like polyhedrals, 18-20 nm. in diameter were found in the nuclei of cells of streak diseased maize leaves (25).

Finally, Bock, et al. (1) reported the first detailed description of the virus after successfully purifying and studying the morphology and properties of MSV. They confirmed that there were several closely related strains of the virus, and in the plant, the organism is a small isometric virus, probably containing RNA with hexagonal particles 20 nm. in diameter. The particles usually occur in pairs measuring 30 x 20 nm. The four strains isolated from maize (Zea mays), sugar cane (Saccharum officinarum), guinea grass (Panicum maximum) and millet (Eleusine coracana), are identical morphologically but not serologically. They are serologically related however, and are probably host-adapted strains of one virus. Failure of one strain to protect against another was also observed (2). For example, maize is susceptible to cane streak, but infection by cane streak does not give protection against later infection by the maize isolate.

The nature of the virus within the vector is much less known, but was studied and reported in detail by Storey (21). He infected non-viruliferous Cicadulina mbila with tissues of viruliferous individuals, and concluded that the virus was most abundant in the intestine of the vector, and that only small amounts were present in the salivary glands. Multiplication and persistence of the virus within the vectors was also indicated, since C. mbila was found to remain infective for 9 weeks after as little as a 15-second acquisition feed, but experimental proof that the virus multiplies within the vector is lacking (2).

Transmission of MSV

Maize streak virus is one of a large class of viruses that cannot be transferred from plant to plant by mechanical innoculation. Furthermore, it cannot be transmitted through the seed nor by sap innoculation. An extensive investigation on MSV transmission was conducted by Storey (14, 15, 16, 20, 21, 22). He established that the principal and probably the only method by which MSV spreads from plant to plant is through the agency of some species of leafhoppers belonging to the genus Cicadulina. It is probable the most Cicadulina species are capable of transmitting maize streak virus disease. Cicadulina mbila, C. storeyi, C. bipunctata zeae, C. latens and C. parazeae all have been shown to be vectors of MSV (12). Storey (21) demonstrated that C. mbila, the most prominent of the known vectors could become viruliferous by feeding for a period as short as 15 seconds in the mesophyll of a chlorotic area of an infected leaf. Transfer of the disease to a healthy plant by the vector may be achieved by feeding for at least 5 minutes, but it may take longer. It appears that temperature is very important in MSV transmission as leafhoppers become viruliferous after a latent period of approximately 12 hours at temperatures ranging from 30-35°C, and increased to 85 hours at 16°C. Ability to transmit MSV persists in the infected leafhoppers throughout their lives and nymphs can pick up the virus as they feed on diseased plants. However, the virus cannot be passed to the next generation of leafhoppers through the egg (15).

The ability of the vector to transmit MSV has been found to be inherited as a simple dominant gene linked with sex, which affects the

permeability of the gut wall to the virus (2, 19). In Cicadulina mbila, infectivity seems to vary between sexes, being more frequently found in females than in males (15).

Host Resistance to MSV

The first source of resistance was reported by Fielding (5) in a variety called Peruvian Yellow, in South Africa. This was confirmed by Rose (13), who found that next to Peruvian Yellow, Arkells Hickory was the most resistant variety. Selections from the F_2 generation of the crosses between the above two varieties (referred to as "P x H" crosses) gave lines which were bulked to produce a highly resistant variety. This variety outyielded the parental varieties and the "P x H" crosses under conditions of severe MSV infection. Use was made of this "P x H" resistance to develop a commercial MSV tolerant three way cross hybrid called SA 31 in South Africa, where most of the breeding for improved resistance to MSV had been done.

The "P x H" source of resistance was introduced into East Africa by Storey (23), and from it, he derived inbred lines which bred true for resistance to MSV. However, initial attempts to incorporate this resistance into East African maize failed. Unfortunately, Storey's lines were not carefully maintained, and consequently, they have been lost (3). Other sources of resistance have been found in local varieties from the islands of Reunion and Mauritius, and several have been introduced in Kenya where research on MSV has been underway for some time. "Revolution" has shown high levels of resistance to MSV in Kenya since it was introduced in 1975.

At the International Institute of Tropical Agriculture (IITA), research on MSV has resulted in the release of populations and inbred

lines with high levels of resistance to MSV. The technique used at IITA involves the use of large screen houses where thousands of maize plants are grown and then infested with large numbers of artificially reared viruliferous leafhoppers released into the screen houses after acquiring the virus in mass rearing cages. This approach essentially eliminates escapes, thus providing a more reliable technique of screening for resistance to MSV. However, some of the populations derived from this method (e.g., TZY-SR, TZW-SR and Tanzaniz-IITA streek resistant population (Tanz.-IITA)) have demonstrated low yield potential and other poor agronomic characteristics (9).

Inheritance of Resistance to MSV

Early attempts to breed for resistance to MSV were hampered by the limited number of sources of resistance. Another problem was the lack of sufficient information on the inheritance of resistance to MSV. This was further complicated because experiments to determine the mode of inheritance were done under field conditions with a low incidence of natural infection. The inheritance of resistance as found in one variety called "Peruvian Yellow" was of a complicated nature and apparently did not follow Mendelian ratios (7). When susceptible varieties were crossed with "P x H" maize, the F_1 plants did not show a great reduction in total percentage infection as compared to the susceptible parent, but the severity of the disease in the plant population was greatly reduced.

Storey, et al. (22) set up experiments in glasshouses to find out if genetic information that would assist in the breeding of streak resistant maize would emerge from this apporach. Maize plants selected from lines raised in South Africa, and resistant to an East African isolate of streak

virus, were used to develop lines that bred true for resistance after four generations of selfing. Crossing them to susceptible lines gave heterozygotes that gave an infection reaction intermediate between the parents. The F_2 generation from the cross segregated in a 1:2:1 ratio; backcrossing to either parent segregated in a 1:1 ratio. It was concluded that resistance in this case was controlled by a major gene, and that reactions were modified by minor genes.

Inheritance studies conducted at IITA using the maize population TZ-Yellow indicated that resistance to this disease is controlled by one or a few genes, modified slightly by the background genotype (8). More recent studies by Kim, et al. (9) using generation mean analysis, have shown that in the inbred line IB 32 (selected from the resistant population TZ-Yellow), additive gene action at a minimum of 3 loci conditions resistance to MSV.

MATERIALS AND METHODS

Eight genetically different sources of resistance and one susceptible variety were chosen as the parents for this experiment. The parents and their origins are as follows:

Resistant Parents

1. UK-H37: a top-cross between "Revolution" and a French hybrid INRA 508.

2. UK-198 MSV-resistant lines imported into Kenya
3. UK-330 under the Crop Virology Project, from
4. UK-329 the Reunion islands.

5. TZY-SR: A MSV-resistant population selected from the resistant source TZ-Yellow.

6. "Revolution": A MSV-resistant population from the Reunion islands.

7. Tanzania-IITA: A MSV-resistant population developed from IITA, CIMMYT and Tanzanian varieties, at IITA.

8. VH-Composite: A MSV-resistant composite developed from white and yellow inbreds of diverse origin, in South Africa.

Susceptible Parent

9. 7721: A composite of selected families from the open-pollinated variety Tuxpeno-1.

The susceptible parent, sources, and their F_1 progeny made by crossing each resistant source to the susceptible parent were received from CIMMYT, Mexico, and planted under irrigation at Ilonga Agricultural Research Institute, Tanzania, in June 1979. Each F_1 was advanced to the F_2 generation by making plant to plant crosses and simultaneously making backcrosses to each parent of a given F_1. Thus from each pair of resistant x susceptible parents, six genetic categories were obtained, i.e., P_1 (resistant), P_2 (susceptible), F_1, F_2, P_1F_1 and P_2F_1. Each resistant x susceptible cross and its related generations was designated as a population.

In March 1980, the field evaluation experiments were planted at two locations in Tanzania, i.e. Ilonga Agricultural Research Institute and Bwanga Experimental Station. A split-plot design with 4 replications was used at each location. The parental combinations were the main plots while the genetic categories served as sub-plots. Planting was done on a spacing of 75 cm. between rows and 30 cm. between plants. Plot sizes varied according to the kind of genetic category. The parents and F_1's consisted of single row plots of 18 plants each. The F_2's consisted of 6 row plots of 18 plants each, and the backcross generations consisted of 4 row plots of 18 plants each.

Weeding was delayed until flowering time at each location to enhance the intensity of natural infection. The weeds consisted largely of grasses known to be hosts of the vector of MSV, thus attracting and maintaining the vector population in the experimental area for a longer time. Release of viruliferous leafhoppers to further enhance the intensity of natural infection would have been desirable but was not possible due to technical limitations.

MSV ratings were taken at flowering time. Rating was done on an individual plant basis in each generation using a rating scale of 1 to 6 as follows:

1. No symptoms.
2. Chlorotic spots developing on one or several leaves. None on the later leaves.
3. Numerous spots appearing on all leaves and tending to be slightly elongated. May gradually decrease in younger leaves.
4. Moderate streaking in old and young leaves. Chlorotic spots larger than in 3 and mostly elongated.

5. Severe streaking in 60% of leaf area. Plants may be stunted.

6. Severe streaking in 75% of leaf area, and plants severely stunted. Some may be dead.

Plants with ratings of 5-6 generally had poor tassel development and many produced no ear shoots. The F_2 plants in most cases showed little vigor and many showed signs of leaf senescence as early as two weeks after flowering.

Weighted plot mean scores were calculated by multiplying the number of plants in each rating class by the rating class, adding the products and dividing the sum by the total number of plants in each plot. For example, if a particular plot had two plants in Class 1, nine plants in Class 2, four plants in Class 3 and two plants in Class 4, the mean MSV score for that plot would be 41/18 or 2.28.

Analysis of variance was performed on a plot mean basis. The data at Bwanga location was highly variable, apparently due to the low incidence of infection at that location as compared to Ilonga location (Appendix Table 1-8). Consequently, except for generation means of the two experiments, all results are based on data obtained at Ilonga.

A formula used by Burton (4) for the determination of heritability was applied to obtain broad sense heritability estimates for each population. The formula was $\frac{VF_2 - VF_1}{VF_2}$ where VF_1 and VF_2 are the variances of the F_1 and F_2 generations of each cross in question. The genetic variance, $VF_2 - VF_1$, is actually an estimate of the sum of the following variances:

1. Total genetic variance including:
   (a) Additive genetic variance (Vg)
   (b) Variance due to dominance deviations from the additive scheme
   (c) Variance due to interaction of non-allelic genes.
2. Variance due to interaction of the genotypes and the environment.

RESULTS AND DISCUSSION

The mean MSV ratings and the percentages of infected plants for each of the resistant parents at the two locations are presented in Table 1. Mean MSV ratings for the parental, F_1, F_2, and backcross generations of each population for both locations appear in Tables 3 and 4. The mean MSV ratings for the resistant parents ranged from 1.20 to 3.84 and from 1.08 to 3.04 at Ilonga and Bwanga respectively. UK-330 had the lowest rating at Ilonga while at Bwanga the lowest rating was shown by UK-198. UK-329 appeared to be the least resistant among the resistant parents at both locations with a mean rating of 3.84 and 3.04 at Ilonga and Bwanga respectively. The average MSV score for the 8 resistant parents combined was 1.96 at Ilonga and 1.61 at Bwanga.

Comparisons of mean MSV ratings at Ilonga (Table 2) indicated significant differences among the sources of resistance. UK-198, UK-330, "Revolution" and Tanz.-IITA, all showing high levels of resistance, did not differ significantly. UK-H37, TZY-SR and VH-Composite appeared to be less resistant (than the above sources) based on their MSV ratings, but the differences among them were not significant. The least resistant source, UK-329, differed significantly from all the other sources of resistance.

The mean MSV rating for the susceptible parent averaged over all eight populations was 5.53 at Ilonga and 4.20 at Bwanga, reflecting the high susceptibility of this variety. The frequency distribution of the total number of plants rated in the susceptible parent at Bwanga (Appendix Tables 1-8) indicates more variability than was observed at Ilonga for the same parent. Among 548 plants of the susceptible parent rated for

Table 1. Mean MSV ratings and percentage of infected plants for the resistant parents at two locations.

Resistant Parent	Ilonga		Bwanga	
	Mean	% Infection	Mean	% Infection
UK-H37	2.02	42	1.43	32
UK-198	1.58	51	1.08	8
UK-330	1.20	17	1.12	13
UK-329	3.84	79	3.04	59
TZY-SR	2.10	63	1.87	64
Revolution	1.31	39	1.32	23
Tanz-IITA	1.33	33	1.25	19
VH-Composite	2.31	56	1.77	40
$\bar{x}$	1.96		1.61	

Table 2. Comparisons for mean MSV ratings of the resistant parents at Ilonga.

Resistant Parent	Mean
UK-H37	2.02 b
UK-198	1.58 a
UK-330	1.20 a
UK-329	3.84 c
TZY-SR	2.10 b
Revolution	1.31 a
Tanz-IITA	1.33 a
VH-Composite	2.31 b

Means with the same letter are not statistically different at the 5% level according to Duncan's Multiple Range Test.

MSV at Bwanga, 83 or 15.41 percent were scored as symptom-free, while only 3 out of 527 or 0.57 percent of the plants representing the susceptible parent at Ilonga were scored as symptom-free. This observation attests to the adequacy of field infection at Ilonga location compared to Bwanga location during the 1980 growing season. Differences in severity of natural infection are also indicated between the two locations by the MSV ratings (Tables 3 and 4) and the frequency distribution of the total

Table 3. Mean MSV ratings of the parental, F_1, F_2, and backcross generations at Ilonga location.

Population	Generations					
	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
UK-H37 x 7721	2.02	3.70	3.83	4.87	5.02	5.39
UK-198 x 7721	1.58	2.17	2.54	3.75	4.14	5.68
UK-330 x 7721	1.20	2.23	2.73	3.49	4.66	5.52
UK-329 x 7721	3.84	4.48	4.86	4.93	4.80	5.64
TZYSR x 7721	2.10	2.49	2.81	3.30	4.60	5.35
Revolution x 7721	1.31	2.16	3.04	3.43	4.64	5.55
Tanz-IITA x 7721	1.33	2.36	2.76	3.97	4.52	5.47
VH-Comp x 7721	2.31	2.91	4.07	4.20	4.59	5.61
$\bar{x}$	1.96	2.81	3.33	3.99	4.62	5.53

Table 4. Mean MSV ratings for the parental, F_1, F_2, and backcross generations at Bwanga location.

Population	Generations					
	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
UK-H37 x 7721	1.43	1.93	2.78	3.71	3.42	4.50
UK-198 x 7721	1.08	1.81	1.88	3.43	3.48	3.81
UK-330 x 7721	1.12	1.44	2.24	2.45	3.38	4.53
UK-329 x 7721	3.04	3.33	3.34	3.28	4.14	3.75
TZY-SR x 7721	1.87	2.46	2.82	2.87	3.60	4.20
Revolution x 7721	1.32	1.67	1.71	3.52	3.70	4.31
Tanz-IITA x 7721	1.25	1.69	2.55	2.80	3.16	4.38
VH-Comp. x 7721	1.77	1.81	2.66	2.79	3.39	4.15
$\bar{x}$	1.61	2.01	2.49	3.10	3.53	4.20

number of plants (Appendix Tables 1-8) for the parental, F_1, F_2, and backcross generations. The MSV ratings at Bwanga were considerably lower than those at Ilonga in all generations of each population except for the F_1 generation involving the line Tanz-IITA and the F_2 generations involving TZY-SR and "Revolution."

A comparison among the eight populations (Table 5) shows that the populations behaved differently depending on the source of resistance. The differences among populations 2, 3, 5, 6 and 7 were not significant, but each one of them differed significantly at the 5% level from populations 1, 4 and 8. The differences among populations 1, 4 and 8 were significant at the 5% level. Populations 1, 4 and 8 involved the lines UK-H37, UK-329 and VH-Composite respectively. These populations performed relatively poorly with respect to MSV reaction, and it is interesting to note that the resistant parents involved in these populations had plants appearing in the severely infected classes (5 and 6) in the frequency distribution of plants rated for MSV (Appendix Tables 1-8). A striking difference in performance between resistant parents TZY-SR and UK-H37 (with mean MSV ratings of 2.10 and 2.02 respectively) in crosses with the susceptible parent is evident (Table 3 and Table 5). Although their mean MSV ratings were not significantly different, the F_1, F_2, P_1F_1 and P_2F_1 generations involving TZY-SR had lower MSV ratings than did similar generations where UK-H37 was involved, and their overall means (parents included) were significantly different.

Differences in mean MSV ratings among generations for each population appear in Table 3 and were compared using Duncan's multiple range test in Table 6. A significant difference between the susceptible common

Table 5. Comparisons among population means. Each population mean is the overall mean of the parental, F_1, F_2, and backcross generations.

Pop. No.	Population	Mean
4	UK-329 x 7721	4.76 a
1	UK-H37 x 7721	4.14 b
8	VH-Comp. x 7721	3.95 c
5	TZY-SR x 7721	3.44 d
7	Tanz-IITA x 7721	3.40 d
6	Revolution x 7721	3.35 d
2	UK-198 x 7721	3.31 d
3	UK-330 x 7721	3.30 d

Means with the same letter are not significantly different at the 5% level according to Duncan's Multiple Range Test.

Table 6. Comparison of mean MSV ratings for each generation in all eight populations at Ilonga location.

UK-H37 x 7721		UK-198 x 7721		UK-330 x 7721		UK-329 x 7721	
Generation	Mean	Generation	Mean	Generation	Mean	Generation	Mean
P_2	5.39 a	P_2	5.68 a	P_2	5.52 a	P_2	5.64 a
P_2F_1	5.02 b	P_2F_1	4.14 b	P_2F_1	4.66 b	F_2	4.93 b
F_2	4.87 b	F_2	3.75 c	F_2	3.49 c	F_1	4.86 b
F_1	3.83 c	F_1	2.54 d	F_1	2.73 d	P_2F_1	4.80 b c
P_1F_1	3.70 c	P_1F_1	2.17 e	P_1F_1	2.23 e	P_1F_1	4.48 c
P_1	2.02 d	P_1	1.58 f	P_1	1.20 f	P_1	3.84 d

Means with the same letter are not significantly different at the 5% level.

Table 6 continued.

TZY-SR x 7721		Revolution x 7721		Tanz-IITA x 7721		VH-Comp. x 7721	
Generation	Mean	Generation	Mean	Generation	Mean	Generation	Mean
P_2	5.35 a	P_2	5.55 a	P_2	5.47 a	P_2	5.61 a
P_2F_1	4.60 b	P_2F_1	4.64 b	P_2F_1	4.52 b	P_2F_1	4.59 b
F_2	3.30 c	F_2	3.43 c	F_2	3.97 c	F_2	4.20 c
F_1	2.81 d	F_1	3.04 d	F_1	2.76 d	F_1	4.07 c
P_1F_1	2.49 e	P_1F_1	2.16 e	P_1F_1	2.36 e	P_1F_1	2.91 d
P_1	2.10 f	P_1	1.31 f	P_1	1.33 f	P_1	2.31 e

Means with the same letter are not significantly different at the 5% level.

parent and the resistant parents was observed in each population. The F_1 generation was more resistant than the susceptible parent but less resistant than the resistant parent in each case. With the exception of the F_1 generations involving UK-H37, UK-329 and VH-Comp., all F_1 MSV scores were biased slightly towards those of their resistant parents. In the field, these particular F_1's looked more vigorous than their parents and the F_2 generations. This response probably reflects, in large part, the influence of hybrid vigor on the MSV scores. The mean MSV score for the F_2 generation exceeded significantly that of the F_1 generation in each population with the exception of the two populations involving UK-329 and VH-Comp. as sources of resistance. Many F_2 plants were low in vigor and showed signs of senescence of the lower leaves at the time of rating for MSV symptoms.

The backcross generations showed a dramatic shift from F_1 mean scores toward the recurrent parental types (Tables 3 and 6). Furthermore, differences in mean MSV scores of P_1F_1 vs. P_2F_1 were significant for each population except UK-329 x 7721 where the backcrosses did not differ significantly from each other. The F_1 generation differed significantly from either backcross generation in each population with the exception of populations UK-H37 x 7721 and UK-329 x 7721 where the F_1 vs. P_1F_1 generations and the F_1 vs. P_2F_1 generations respectively, did not differ significantly.

Histograms of MSV ratings of parents, F_1, F_2 and the backcross generations for each population are presented in Figures 1 to 4. Mean MSV ratings for each generation averaged over all eight populations are presented in Table 7, and their histogram in Figure 5. A characteristic

pattern is displayed by the relative position of parents in relation to the F_1, F_2 and backcross generations in each population. This pattern, however, is less conspicuous in populations UK-H37 x 7721 and UK-329 x 7721. Regression of backcross generations toward the parental MSV ratings is indicated, and the F_1 is intermediate in reaction to MSV symptoms (Figures 1-4). The same pattern was obtained when each generation was averaged over all eight populations (Figure 5). If we look at the position of the F_1 relative to the parents and the calculated midparent (MP), resistance to MSV appears to be transferred from resistant parent to the F_1 in an incompletely dominant manner. As pointed out earlier, however, hybrid vigor does seem to influence the degree of MSV symptom expression and may mask the expression of resistance and make determination of type of gene action more difficult. This situation is in general agreement with work done by Storey and Howland (24) who found that resistant by susceptible crosses produced intermediate hybrids showing moderately severe streak symptoms, but relatively little ill-effects from virus infection. They also demonstrated that a major gene was primarily involved in conditioning resistance. They also indicated the gene was not completely dominant and that there was considerable diversity in generation distribution attributable to modifying factors.

The F_2 and backcross data in this experiment, however, failed to indicate the number of genes conditioning resistance to MSV as they could not fit any known genetic ratios. Since the experiment was done under natural field infection conditions, it is realized that such conditions were inadequate for critical genetic analysis with respect to number of genes conditioning resistance. No further attempts were made to determine the number of genes by other methods. Generation mean analysis has been used on MSV data obtained under artificial infection conditions (using viruliferous

Figure 1

Histograms of mean MSV ratings for parents, F_1, F_2, and backcross generations of populations UK-H37 x 7721 and UK-198 x 7721 at Ilonga location.

Figure 1a

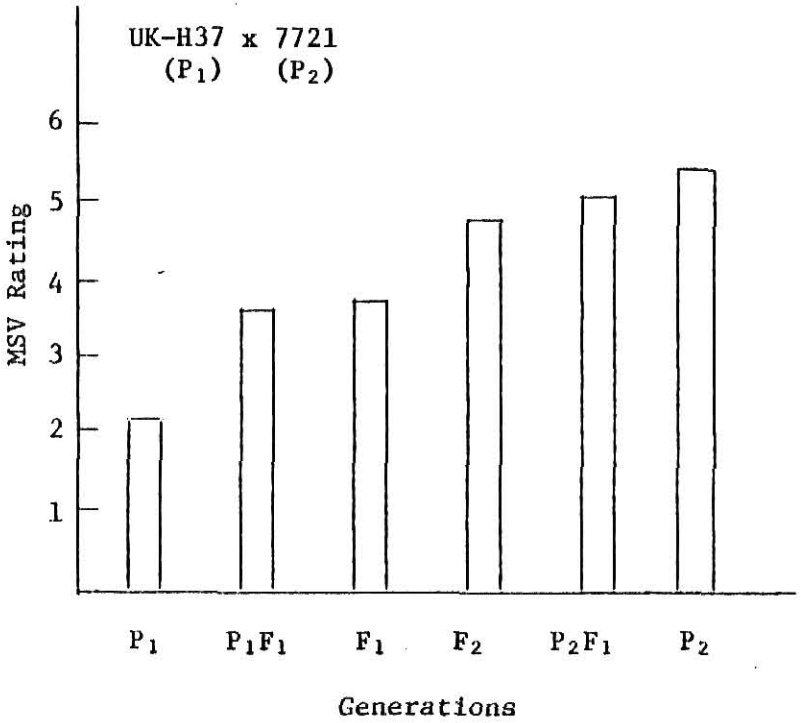


Figure 1b

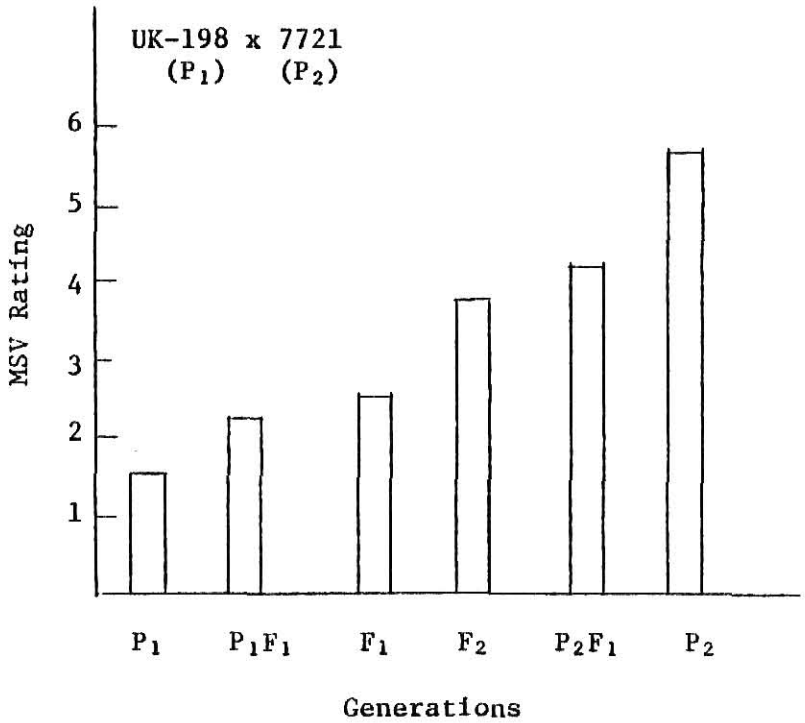


Figure 2

Histograms of mean MSV ratings for parents, F_1, F_2, and backcross generations of populations UK-330 x 7721 and UK-329 x 7721 at Ilonga location.

Figure 2a

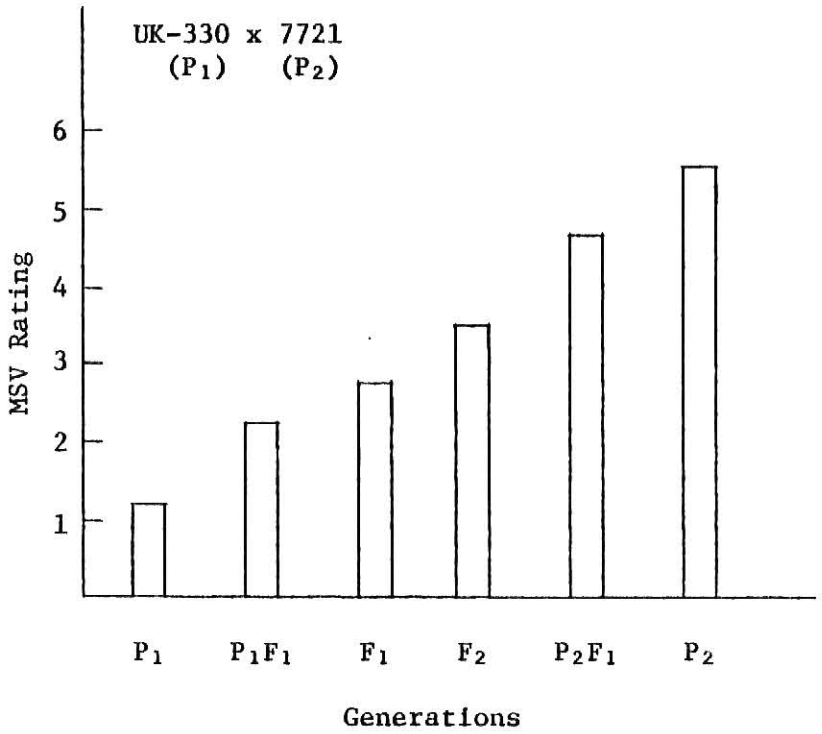


Figure 2b

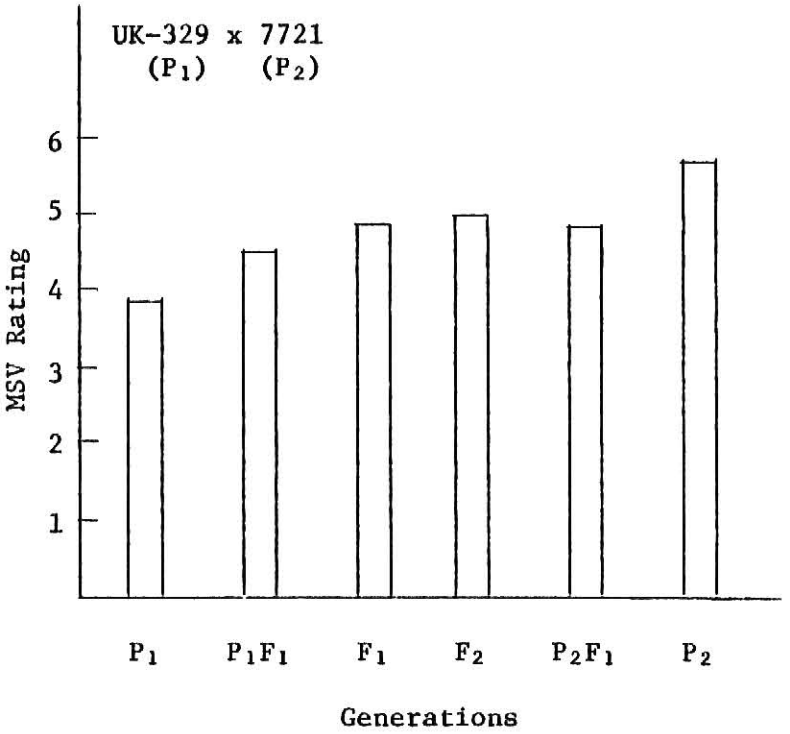


Figure 3

Histograms of mean MSV ratings for parents, F_1, F_2, and backcross generations of populations TZY-SR x 7721 and Revolution x 7721 at Ilonga location.

Figure 3a

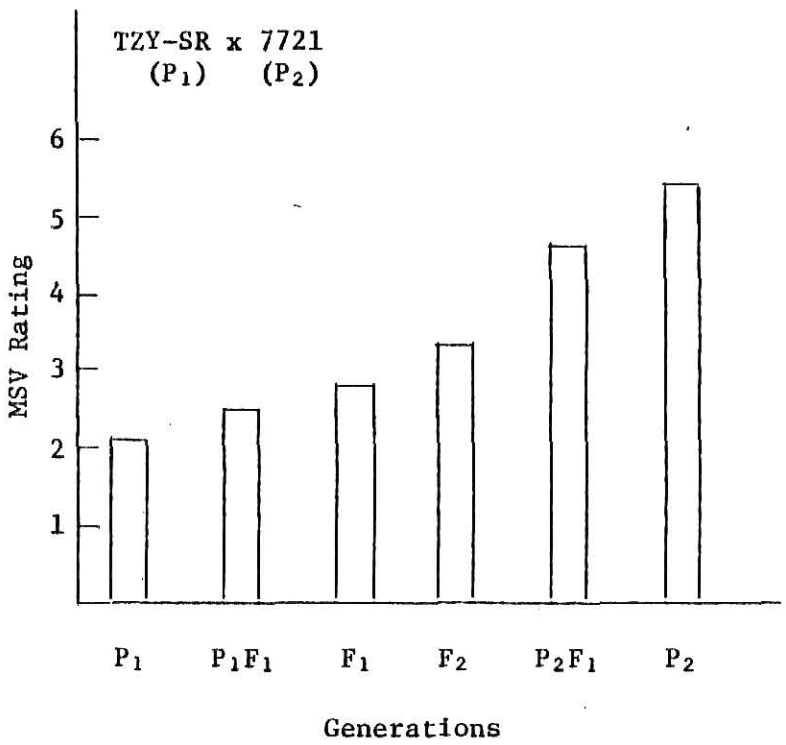


Figure 3b

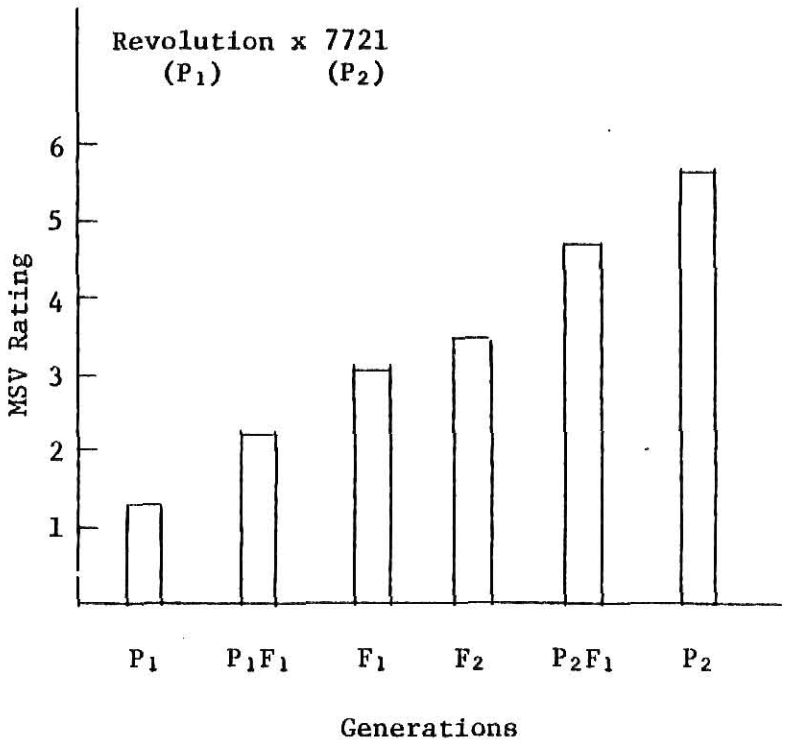


Figure 4

Histograms of mean MSV ratings for parents, F_1, F_2, and backcross generations of populations Tanz.-IITA x 7721 and VH-Comp. x 7721 at Ilonga location.

Figure 4a

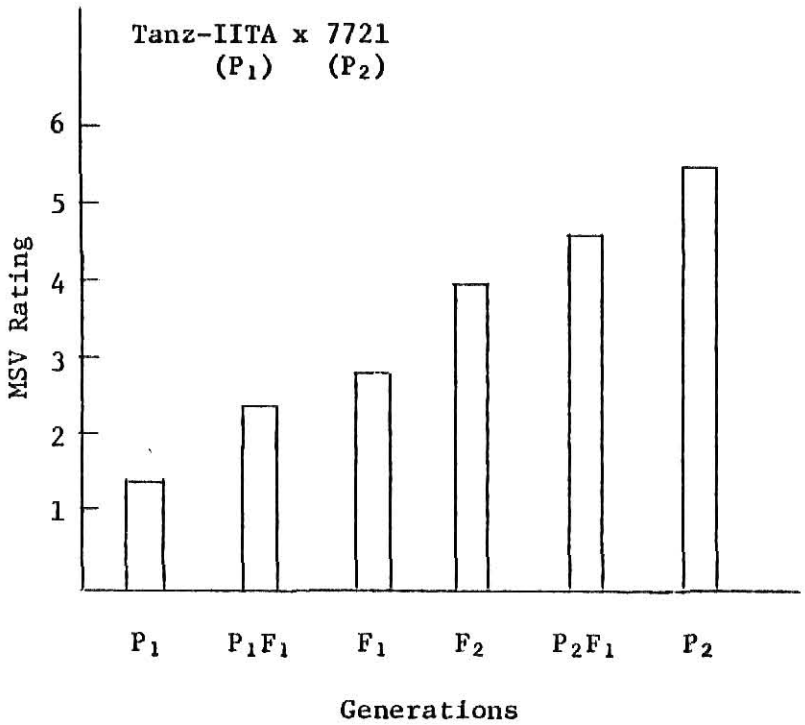


Figure 4b

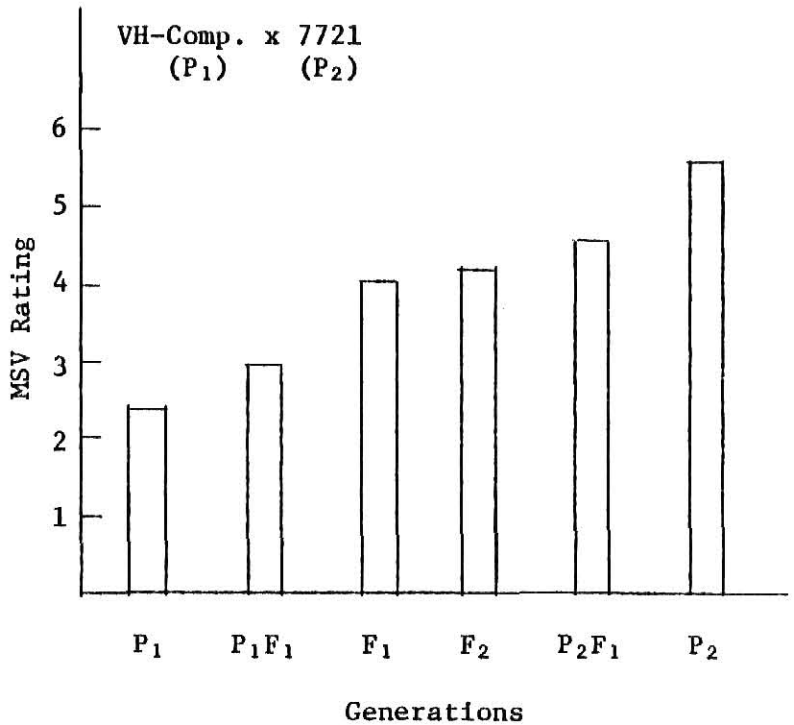
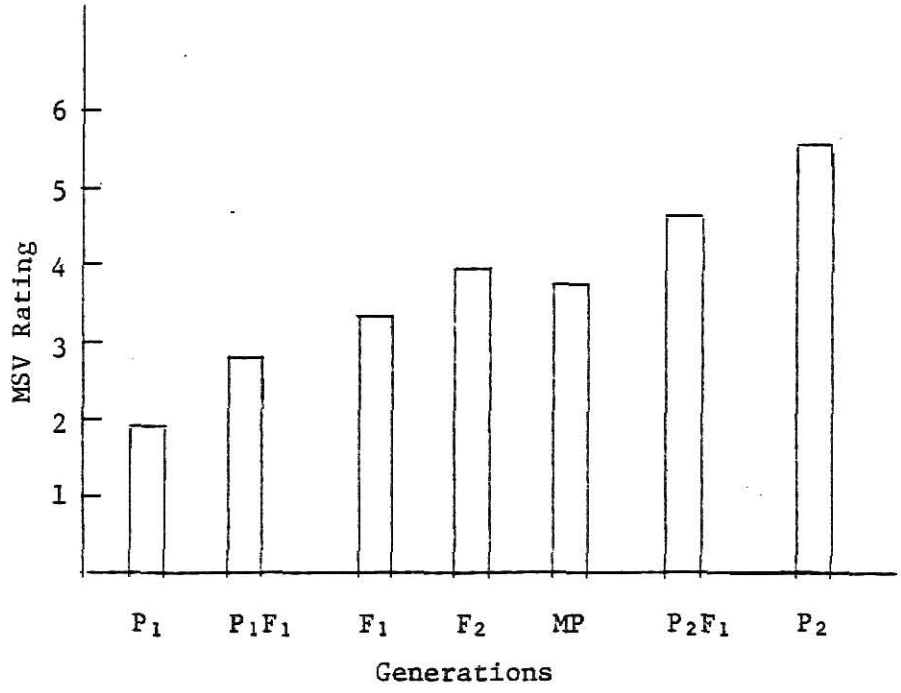


Table 7. Comparison of mean MSV scores in parental, F_1, F_2, and backcross generations averaged over eight populations

Generation	Mean MSV Score
P_2	5.53 a
P_2F_1	4.62 b
F_2	3.99 c
F_1	3.33 d
P_1F_1	2.81 e
P_1	1.96 f

Means with the same letter are not significantly different at the 5% level.

Figure 5. Histogram of MSV ratings for parents, F_1, F_2, and backcross generations averaged over eight populations.



MP = Calculated Mid-Parent.

leafhoppers) by Kim, et al. (9), and they found that in inbred line IB 32, resistance to MSV is conditioned by a minimum of 3 loci expressing additive gene action.

Heritability estimates, made on five of the eight populations using the F_1 and F_2 variances in each case, ranged from 0.34 to 0.52. Populations UK-198 x 7721, UK-330 x 7721, TZY-SR x 7721, "Revolution" x 7721 and Tanz-IITA x 7721 gave estimates of 0.39, 0.49, 0.34, 0.52 and 0.39 respectively. The rest of the populations gave negative estimates of heritability as their F_1 variances were higher than the F_2 variances. Considering the assumptions made in the use of the formula for calculating these heritabilities, the values obtained above should be interpreted with caution. However, when working under field conditions with infection rates approaching 100%, the problem of escapes should be minimized to the extent that progress reflective of heritability values similar to those reported above, or higher, could be achieved. Based on the means and frequency distributions of plants rated for MSV symptoms, the resistant parents involved in the populations showing negative estimates of heritability were less resistant and highly variable (Appendix Tables 1, 4 and 8), with plants falling in the highly susceptible classes (5 and 6) of the rating scale. It appears that little resistance was transferred from those sources into their F_1's and subsequent generations, as shown by the high mean MSV ratings of the F_1, F_2 and backcross generations of the three populations. The negative heritability values indicate zero heritability and probably came about because of very small differences between the three sources and the susceptible parent in response to MSV.

The resistant parents included in this study were chosen specifically for their potential use as sources of resistance. Several of them appear

to possess high levels of resistance which appears to be heritable as was expected, based on previous work with resistant by susceptible crosses under controlled greenhouse conditions (24). None of the resistant parents demonstrated other desirable agronomic qualities that would enable them to be used as resistant commercial varieties per se.

The findings by Storey and Howland (24) that resistance to MSV is controlled primarily by a major gene with modifying factors, and the more recent demonstration by Kim, et al. (9) that resistance to MSV is conditioned by a minimum of three additive genes, and the data presented in this experiment indicate that MSV resistance is inherited as a comparatively simple character conditioned by one or very few genes. Therefore, a modified recurrent selection breeding program involving a backcross progeny test should be adequate for transferring resistance into susceptible but adapted commercial varieties. In this approach, the MSV resistant segregates would be recombined before proceeding to the next cycle.

Kim, et al. (9) has suggested the top cross seed production method for use in areas where MSV is known to cause heavy losses in yield. Under this approach, the adapted (or local) variety would be used as the female (seed parent) while the resistant line serves as the pollen parent. This suggestion is strongly supported by their data which showed a 25.6 percent yield increase under field conditions, of crosses between 20 susceptible open-pollinated varieties with resistant sources, as compared to the same 20 varieties grown alone. The high vigor exhibited by the F_1 generations in the evaluation experiment carried out at Ilonga indicates that advantage could be taken of this method to provide an immediate solution to the MSV problem, meanwhile the task of breeding for MSV resistance by the modified recurrent selection backcross program continues. However, the erratic

nature of MSV in Tanzania could make this approach impractical, because it is unlikely that a significant yield advantage over the present commercial varieties could be realized when top cross varieties, such as suggested above, are grown during a season with little MSV incidence. Therefore, any decision to adopt this approach must be supported by several years of experimental data.

As part of the effort to breed for resistance to MSV in Tanzania, the method used to determine the level of resistance or susceptibility both in breeding nurseries and in progeny trials needs to be re-examined and, perhaps, changed. The use of percent infection data as a criteria in selecting for MSV resistance has been used both in breeding nurseries and in progeny trials for a long time. One very serious shortcoming of this method is that it does not necessarily provide a picture of the severity of infection. Two different lines or families may show the same percent infection and yet differ greatly in the level of resistance they exhibit. Thus, with this procedure, materials possessing intermediate levels of resistance stand a good chance of being lost if selection is based on percent infection data alone. It is not entirely wrong to say that over the years, a lot of valuable material with respect to MSV resistance has been lost due to the apparent inadequacy of this technique. Looking at Table 1, if one were to discard some of the sources of resistance based on percent infection data alone, then TZY-SR with 63 percent infection would most probably be discarded together with UK-329 which shows 79 percent infection. If it was deemed desirable to eliminate any source showing more than 50 percent infection, then two more sources, UK-198 with 51 percent infection and VH-Comp. with 56 percent infection, would be eliminated, all of them at Ilonga location. However, looking at, and comparing their frequency

distributions in Appendix Tables 2, 4, 5, and 8, TZY-SR and UK-198 appear to be highly resistant sources. At Bwanga location, TZY-SR with a 64 percent infection, and the highest, would no doubt fall victim to this technique, although it appears to be quite resistant, as evidenced from Appendix Table 5.

The use of a rating scale such as the one used in this study, or some modification of it seems appropriate. The use of a rating scale instead of merely making counts of infected plants irrespective of infection severity will lead to a more accurate evaluation and handling of resistance genes for the MSV problem. Mean MSV ratings plus frequency distributions of rated plants, in combination, can serve as a reliable guide in the evaluation and selection for MSV resistance in the National Maize Research Program of Tanzania.

SUMMARY AND CONCLUSIONS

1. Eight sources of resistance to maize streak virus disease (MSV) were crossed to one susceptible variety. The sources classified as resistant were: 1) UK-H37; 2) UK-198; 3) UK-330; 4) UK-329; 5) TZY-SR; 6) "Revolution"; 7) Tanzania-IITA; and 8) VH-Composite. The susceptible parent was 7721, an open-pollinated variety. The parents, F_1, F_2, and backcross (i.e., P_1F_1 and P_2F_1) generations were evaluated under field conditions with natural infection at two locations at Ilonga and Bwanga in Tanzania. A split-plot design with four replications was used. MSV rating was done at flowering time on a scale of 1 to 6 (where 1=no symptoms and 6=extreme susceptibility). Analyses of variance were performed on a plot mean basis.

2. Mean MSV ratings for the resistant parents ranged from 1.20 to 3.84 at Ilonga and from 1.08 to 3.04 at Bwanga. UK-329 appeared to be the least resistant source at both locations. The MSV rating for the susceptible parent was 5.53 at Ilonga and 4.20 at Bwanga.

3. High levels of resistance were shown by UK-198, UK-330, TZY-SR, "Revolution" and Tanz-IITA. However, none of the sources possessed other desirable agronomic qualities that would enable them to be used as MSV-resistant commercial varieties per se.

4. Resistance to MSV appeared to be inherited as an incompletely dominant trait as expected, based on previous inheritance studies.

5. A modified recurrent selection breeding program involving a backcross progeny test is suggested as a means for transferring resistance to MSV into susceptible but adapted commercial varieties, using the genetic sources which showed the highest levels of resistance.

6. The use of percent infection data as the sole criteria for evaluating resistance to MSV in breeding nurseries and in progeny trials appeared to be inadequate for effectively measuring resistance, especially in materials with intermediate or low levels of resistance. The use of rating scales from which the frequency distribution of rated plants and mean MSV scores can be obtained is therefore suggested to facilitate more precise evaluation and handling of genes resistant to MSV in the maize breeding program in Tanzania.

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APPENDIX

Table 1

Frequency distribution of plants rated, means, and variances of all generations in UK-H37 (P_1) x 7721 (P_2) at two locations.

	Distribution per Population											
	Ilonga						Bwanga					
	UK-H37 x 7721						UK-H37 x 7721					
MSV Rating	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
1	35	19	8	6	6	1	41	124	19	66	68	8
2	9	24	8	7	12	0	15	40	8	27	23	5
3	4	45	9	22	16	2	1	8	6	14	27	0
4	6	54	9	21	22	4	3	8	6	32	23	9
5	4	39	12	23	37	17	0	17	7	77	80	25
6	2	25	14	89	118	38	1	9	5	56	27	23
n	60	206	60	168	211	62	60	206	51	272	248	70
$\bar{x}$	2.02	3.70	3.83	4.87	5.02	5.39	1.43	1.93	2.78	3.71	3.42	4.50
s^2	2.22	0.90	3.04	2.12	2.79	0.90	.58	2.24	3.21	3.67	3.37	2.74

Table 2

Frequency distribution of plants rated, means, and variances of all generations in UK-198 (P_1) x 7721 (P_2) at two locations.

	Distribution per Population											
	Ilonga						Bwanga					
	UK-198 x 7721						UK-198 x 7721					
MSV Rating	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
1	23	121	9	29	26	0	48	131	31	86	79	16
2	22	48	14	35	20	0	4	42	12	32	21	5
3	0	40	16	56	44	0	0	9	4	14	14	5
4	2	25	7	51	31	5	0	10	2	29	32	10
5	0	16	7	48	51	15	0	6	3	36	58	9
6	0	7	0	46	66	58	0	11	2	74	52	21
n	47	257	53	254	227	78	52	209	54	271	256	66
$\bar{x}$	1.58	2.17	2.54	3.75	4.14	5.68	1.08	1.81	1.88	3.43	3.48	3.81
s^2	0.34	1.98	1.59	2.62	2.91	0.35	0.07	1.93	1.91	4.75	3.95	3.99

Table 3

Frequency distribution of plants rated, means, and variances of all generations in UK-330 (P_1) x 7721 (P_2) at two locations.

	Distribution per Population											
	Ilonga						Bwanga					
	UK-330 x 7721						UK-330 x 7721					
MSV Rating	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
1	45	102	7	30	12	1	49	157	31	161	63	8
2	9	55	25	49	12	0	7	31	9	33	27	3
3	0	35	18	71	16	3	0	5	0	17	12	5
4	0	22	11	57	35	3	0	10	6	22	19	5
5	0	16	5	52	54	11	0	3	11	56	72	24
6	0	8	0	46	80	46	0	2	0	18	25	24
n	54	238	66	305	209	64	56	208	57	307	218	69
$\bar{x}$	1.20	2.23	2.73	3.49	4.66	5.52	1.12	1.44	2.24	2.45	3.38	4.53
s^2	0.14	2.04	1.21	2.40	2.18	0.95	0.11	0.95	2.68	3.24	3.58	2.78

Table 4

Frequency distribution of plants rated, means, and variances of all generations in UK-329 (P_1) x 7721 (P_2) at two locations.

	Distribution per Population											
	Ilonga						Bwanga					
	UK-329 x 7721						UK-329 x 7721					
MSV Rating	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
1	11	15	3	8	9	0	18	73	16	105	41	17
2	3	19	1	6	13	0	5	19	7	30	16	6
3	3	25	3	18	23	0	1	20	7	23	7	4
4	13	47	7	46	26	6	5	26	7	39	37	7
5	14	48	20	67	54	12	7	55	11	65	75	13
6	9	88	24	117	104	49	8	35	10	53	61	19
n	53	242	58	262	232	67	44	228	58	315	237	66
$\bar{x}$	3.84	4.48	4.86	4.93	4.80	5.64	3.04	3.33	3.34	3.28	4.14	3.75
S^2	3.11	2.41	1.75	1.59	2.08	0.41	4.23	3.73	3.59	3.82	3.19	4.09

Table 5

Frequency distribution of plants rated, means, and variances of all generations in TZY-SR (P_1) x 7721 (P_2) at two locations.

	Distribution per Population											
	Ilonga						Bwanga					
	TZY-SR x 7721						TZY-SR x 7721					
MSV Rating	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
1	23	72	9	83	5	1	20	130	21	106	45	8
2	10	64	18	90	16	0	25	21	12	80	32	6
3	29	53	14	31	33	4	7	34	3	33	28	3
4	0	30	8	39	40	5	3	38	6	38	30	4
5	0	16	6	42	49	9	0	39	10	59	58	28
6	0	9	2	28	84	40	0	7	6	31	39	14
n	62	245	57	313	227	59	55	269	58	347	269	63
$\bar{x}$	2.10	2.49	2.81	3.30	4.60	5.35	1.87	2.46	2.82	2.87	3.60	4.20
S^2	0.84	1.93	1.83	2.80	1.96	1.17	0.71	2.69	3.41	3.04	2.69	2.87

Table 6

Frequency distribution of plants rated, means, and variances of all generations in Revolution (P_1) x 7721 (P_2) at two locations.

	Distribution per Population											
	Ilonga						Bwanga					
	Revolution x 7721						Revolution x 7721					
MSV Rating	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
1	42	101	6	49	14	0	36	160	39	51	55	10
2	20	60	21	52	18	0	7	33	9	18	20	5
3	7	38	20	63	23	0	4	11	4	8	10	6
4	0	21	17	43	30	6	0	11	2	17	23	4
5	0	20	10	36	45	18	0	7	2	49	81	19
6	0	1	0	55	104	44	0	8	2	32	34	27
n	69	241	74	298	234	68	47	230	58	175	223	72
$\bar{x}$	1.31	2.16	3.04	3.43	4.64	5.55	1.32	1.67	1.71	3.52	3.70	4.31
s^2	0.45	1.71	1.39	2.94	2.50	0.43	0.39	1.67	1.68	3.88	3.52	3.54

Table 7

Frequency distribution of plants rated, means, and variances of all generations in Tanz-IITA (P_1) x 7721 (P_2) at two locations.

	Distribution per Population											
	Ilonga						Bwanga					
	Tanz-IITA x 7721						Tanz-IITA x 7721					
MSV Rating	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
1	39	78	9	16	10	0	44	142	27	132	89	8
2	19	73	20	46	14	0	8	44	9	31	18	8
3	0	47	20	48	24	3	0	12	9	36	30	4
4	0	29	10	56	47	4	2	9	6	36	33	9
5	0	13	7	70	61	11	0	11	7	61	50	14
6	0	7	0	57	70	47	0	3	7	25	35	29
n	58	247	66	293	226	65	54	221	65	321	255	72
$\bar{x}$	1.33	2.36	2.76	3.97	4.52	5.47	1.25	1.69	2.55	2.80	3.16	4.38
S^2	0.22	1.76	1.40	2.31	1.99	0.65	0.42	1.44	3.79	3.28	3.74	3.19

Table 8

Frequency distribution of plants rated, means, and variances of all generations in VH-Comp. (P_1) x 7721 (P_2) at two locations.

	Distribution per Population											
	Ilonga						Bwanga					
	VH-Comp. x 7721						VH-Comp. x 7721					
MSV Rating	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2	P_1	P_1F_1	F_1	F_2	P_2F_1	P_2
1	19	69	5	24	9	0	31	151	27	140	70	8
2	7	43	10	28	14	0	9	32	5	21	14	14
3	6	37	6	30	32	2	5	15	8	20	19	4
4	6	34	11	54	41	4	7	11	6	19	27	6
5	5	29	20	88	54	10	0	12	9	57	61	9
6	0	23	14	64	87	48	0	9	5	36	31	29
n	43	235	66	288	237	64	52	230	60	293	222	70
$\bar{x}$	2.31	2.91	4.07	4.20	4.59	5.61	1.77	1.81	2.66	2.79	3.39	4.15
s^2	2.12	2.88	2.55	2.40	2.06	0.56	1.20	1.98	3.27	3.90	3.66	3.69

EVALUATION OF MAIZE (*Zea mays* L.) GERMPLASM FOR RESISTANCE TO MAIZE STREAK VIRUS DISEASE

by

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ABSTRACT

Eight sources of resistance to maize streak virus disease (MSV) were crossed with one susceptible variety. The sources classified as resistant were: 1) UK-H37; 2) UK-198; 3) UK-330; 4) UK-329; 5) TZY-SR; 6) "Revolution"; 7) Tanzania-IITA; and 8) VH-Composite. The susceptible parent was 7721, an open-pollinated variety. The parents, F_1, F_2, and backcross (i.e., P_1F_1 and P_2F_1) generations were evaluated under natural field conditions at two locations at Ilonga and Bwanga in Tanzania, in a split-plot design with four replications. MSV rating was done at flowering time on a scale of 1 to 6 (where 1=no symptoms and 6=extreme susceptibility). Analysis was performed on a plot mean basis.

High levels of resistance were shown by UK-198, UK-330, TZY-SR, "Revolution" and Tanz-IITA. However, none of the sources reflected other desirable agronomic qualities that would enable them to be used as MSV-rsistant commercial varieties per se. As expected, based on previous studies, resistance to MSV appeared to be inherited as an incompletely dominant trait.

A modified recurrent selection breeding program involving a back-cross progeny test is suggested as a means for transferring resistance to MSV into susceptible but adapted commercial varieties, using the genetic sources which showed high levels of resistance.

The use of percent infection data as the sole criteria for evaluating resistance to MSV in breeding nurseries and in progeny trials appeared to be inadequate for effectively measuring resistance, especially in materials with intermediate or low levels of resistance. The use of rating scales

from which the frequency distribution of rated plants and mean MSV scores can be obtained is therefore recommended to facilitate more precise evaluation and handling of genes resistant to MSV in the maize breeding program in Tanzania.