

Maize Mosaic Virus and Other Maize Virus Diseases in the Islands of the Western Indian Ocean

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ABSTRACT

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The cultivation of maize (*Zea mays*) has increased in recent years in the islands of the Western Indian Ocean region, especially in Mauritius where an important program of agricultural diversification is being implemented with the view of achieving self sufficiency in food requirements. The presence of six viruses, namely maize mosaic, maize streak, maize stripe, maize chlorotic stripe, maize dwarf mosaic, and sugarcane mosaic, have been observed. Three of the viruses, maize mosaic, maize stripe, and maize chlorotic stripe, are transmitted by the planthopper, *Peregrinus maidis*, while maize streak virus (MSV) is vectored by the leafhopper, *Cicadulina mbila*, and sugarcane mosaic and maize dwarf mosaic viruses are aphid-borne. MSV is considered to be the most important disease in Mauritius and Rodrigues, while in Reunion maize mosaic virus (MMV) is

the most prevalent. MMV has been the most extensively studied virus and three strains, designated MMV-Fine (MMV-F), MMV-Coarse (MMV-C), and MMV-Broken (MMV-B), have been identified, while numerous host-adapted strains of MSV have been sorted out. A maize breeding program has produced hybrids resistant to MMV and MSV in Mauritius, while in Reunion cultivar Revolution or hybrids issuing from it, which are resistant to MSV, are cultivated.

The causal agent of maize stripe has yet to be identified, and the pathogenicity of the 45 nm isometric particles associated with maize chlorotic stripe virus has to be proved. Studies have revealed that the disease referred to as maize line is in fact caused by MMV-B. No maize-infecting mycoplasma or spiroplasma has been identified in the region.

Maize (*Zea mays* L.) has been grown for more than 250 yr in the islands of Mauritius, Reunion, Rodrigues, and Madagascar, which are situated in the Western Indian Ocean region. However, except in Rodrigues, maize is not a staple of the diet in those islands. In Mauritius and Reunion, sugarcane (*Saccharum officinarum* L.) has been the backbone of the economy, while in Madagascar the economy is more diversified and in Rodrigues maize is the most widely grown crop.

In order to obviate the dangers associated with monoculture and with a view of achieving self sufficiency in food requirements, an important program of agricultural diversification was launched in Mauritius in the 1960's. Emphasis is placed on crops that could either be intercropped with sugarcane or grown in fallow lands between two cane rotations. Maize is one of the several crops that are suitable for development in this way. The local maize cultivar, which is resistant or tolerant to the main diseases and pests present, has proved unsuitable for cultivation in sugarcane fields

because of its erratic yield, marked tendency to lodge, excessive height, abundant foliage, and long growth cycle (140 days). When maize is intercropped with sugarcane, a significant reduction in sugar yield results.

Foreign dwarf hybrids with suitable agronomic characteristics proved susceptible to endemic diseases and pests. Their cultivation led to epidemics of virus diseases long known in the island and other virus diseases became apparent for the first time. A research program was therefore initiated at the Mauritius Sugar Industry Research Institute to identify and assess the economic importance of maize virus diseases (Anonymous, 1974, 1975, 1976, 1977, 1978, 1979, 1980, 1981; Autrey, 1980; Autrey and Ricaud, 1982; Ricaud and Felix, 1976, 1978a,b). This program was conducted in conjunction with a hybridization scheme aimed at blending the resistance of the local maize cultivar with the desirable agronomic characters of the imported hybrids. Since maize and sugarcane are graminaceous plants with several diseases in common and the vectors

of some of these disease pathogens feed on both crops, it was feared that intercropping could result in the increase of such diseases, especially in sugarcane.

MAIZE VIRUSES IDENTIFIED IN THE WESTERN INDIAN OCEAN REGION

The following viruses of maize have been identified in the four islands: maize streak virus (MSV), maize mosaic virus (MMV), maize stripe virus (MStpV), maize line virus (MLV), maize dwarf mosaic virus (MDMV), maize chlorotic stripe virus (MCSV), and sugarcane mosaic virus (SCMV). The vector of MSV is the leafhopper *Cicadulina mbila* Naude, while MMV, MStpV, the so-called MLV, and MCSV are transmitted by *Perezgrinus maidis* (Ashmead). SCMV and MDMV are aphid-borne.

MAIZE MOSAIC VIRUS

Distribution. This disease was first reported in Mauritius (as stripe) by Shepherd (1929) who, like Stahl (1927) and Priode (Briton-Jones, 1933) in the Caribbean Islands, observed three syndromes in the field. Shepherd found plants with three patterns of striping, namely very fine stripes, coarse stripes, and broad chlorotic bands. Ricaud and Felix (1976) confirmed Shepherd's observations. After Kulkarni (1973) showed the existence of two virus diseases (MLV and MStpV) caused by apparently isometric particles, Ricaud and Felix (1976) concluded, on the basis of transmission work and evidence from electron microscopic examinations of the association of rhabdovirus particles with the disease, that the fine striping corresponded to MMV. As a result of transmission studies and positive serological reactions with Kulkarni's antisera, they also showed that the coarse striping and the broad bands were due to MLV and MStpV, respectively.

Autrey (1980), on the basis of various criteria, identified three different strains of MMV which he designated as MMV-Fine (MMV-F), MMV-Coarse (MMV-C), and MMV-Broken (MMV-B), and he produced evidence that what had been called MLV by Kulkarni (1973) was in fact MMV-B. The first two strains corresponded to what had been described as MMV-*raya fina* and MMV-*raya gruesa* by Lastra (1977). In Reunion, Etienne and Rat (1972) identified maize stripe on the basis of transmission and symptoms and Guthrie (1977) suggested that the disease could be MLV. The disease described by Etienne and Rat (1972) was that caused by MMV-C. Autrey (1980) has identified the three strains in Reunion. In Madagascar, C. Ricaud (*personal communication*) observed MMV-F on the east coast and the disease was diagnosed by serological tests (Autrey, 1980). In Rodrigues, despite extensive surveys in 1980 and 1981, Autrey (*unpublished*) did not observe the presence of MMV.

Symptoms. The complete syndromes associated with the strains of MMV have been reported by Autrey (1980). In the field the three distinct striping patterns (Fig. 1) have been observed and described as follows. Symptoms of the first pattern (MMV-F) are fine yellow stripes very close to each other and running all along the leaf lamina on most leaves except the lower ones, where small chlorotic spots can be seen between the stripes. On the upper leaves, the stripes cover the whole surface of the lamina, giving the latter a yellow appearance. Symptoms of the second pattern (MMV-C) are coarse yellow stripes running parallel to the veins and separated by green areas on all the leaves except the two or three lower ones, on which the pattern of striping is identical to that on the lower leaves as described for MMV-F. Along these coarse stripes, brown necrotic localized spots can be observed. Finally, symptoms of the third pattern (MMV-B) are discontinuous yellow

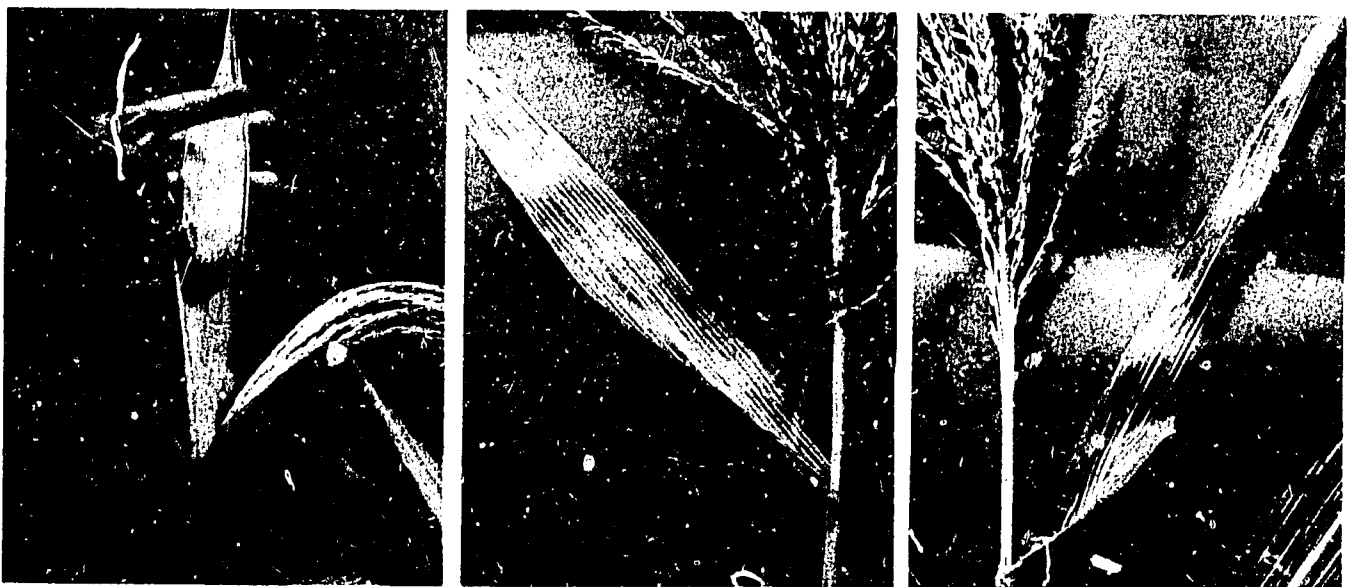


Fig. 1. Symptoms of maize mosaic virus (MMV) strains in field-collected maize plants. MMV-F (left), MMV-C (middle), and MMV-B (right).

stripes of variable length and separated by wide green areas, especially on the uppermost leaves. In plants showing these symptoms, the basal leaves again show the same fine striping as in the first and second patterns described above. This striping evolves into the coarse stripe pattern on the intermediate leaves and, eventually, into the discontinuous pattern.

In the glasshouse when plants are inoculated in the coleoptile stage, the symptoms of the three symptom types appear on the fourth leaf as fine stripes and remain similar until the sixth leaf. For MMV-F, the pattern of fine striping persists throughout the whole life of the plant, giving 22 stripes/cm across the lamina of a fully developed leaf of a mature plant. For MMV-C and MMV-B on the seventh leaf, the main veins show continuous chlorosis, while along the smaller veins in between the chlorosis is discontinuous and appears as yellow spots or streaks. Beginning with the eighth leaf, chlorosis starts to be restricted to the main veins, and on the ninth leaf the main veins are yellow, giving two to four stripes per cm across the lamina. This pattern is retained on all subsequent leaves for MMV-C. For MMV-B from the tenth leaf onwards, the stripes become discontinuous and there appears to be a gradual phasing out of the chlorosis. Eventually only a few short yellow stripes are seen while the rest of the lamina is completely green. When plants are infected late in the cycle, the distinctive striping is visible on the leaves surrounding the ears.

Virus-vector relationships. The planthopper, *P. maidis*, is the only insect known to transmit the three types of MMV. It is often abundant on maize, clustering in the leaf axils and under the leaf sheaths, but it is not an efficient vector, as determined with insects from field and greenhouse populations on both maize and *Sorghum verticilliflorum* (Steud.) Stapf. Nymphs appeared to be more efficient vectors than adults. Starving has no significant effect on transmission of MMV-F and MMV-B. There was an indication, however, that it lowered the efficiency of transmission of glasshouse cultures of MMV-C but not of field-collected cultures (Autrey, 1980). The virus was acquired in less than 15 min but effective acquisition took 24 hr. The latent period in the vector was 9 days for MMV-F and 12 days for MMV-B and MMV-C. The virus could be transmitted in feeding periods of 15 min but transmission was more effective after 24 hr. Studies have revealed that MMV-F and MMV-C were very similar in behavior and differed from MMV-B, which appears to have less affinity with its insect vector (Autrey, 1980).

Virus-host plant relationships. The latent period of the strains in maize hybrid LG 11 varied with ambient conditions and was shorter in warm than cool seasons. Efficiency of transmission increased in the warm season and this was related to the incidence of the disease in the field (Autrey, 1980). The length of the latent period, irrespective of the strain, was shorter in short-cycle genotypes than in cultivars with long growth cycles, as in the local Mauritian one. The latent period also varied with the stage of growth of the plant. In hybrid LG 11, it was in general shortest for MMV-F and

longest for MMV-B, irrespective of whether the plant was inoculated in the coleoptile stage or 10-20 days after emergence. In general, the virus-host plant relationships confirm the different behavior between the strains, MMV-F and MMV-C appearing more virulent than MMV-B (Autrey, 1980).

Mechanical, dodder, and seed transmission. Attempts at transmitting the virus mechanically either by rubbing or inoculation with a hypodermic needle by the method of Harpaz (1959) were unsuccessful for the three strains. Two dodder species, *Cuscuta campestris* Yuncker and *C. reflexa* Roxb., failed to establish themselves on maize plants, although the latter species can parasitize a graminaceous plant, *Bambusa multiplex* Raeusch. Seed transmission was attempted with the three strains by using ears collected in the field from plants infected early, midway and late in the growth cycle. From 12,683 seeds sown, no plant was found with symptoms of the disease (Autrey, 1980), confirming earlier results obtained by C. Ricaud and S. Felix (*personal communication*) with 1,000 seeds from plants infected with MMV-F.

Host range. MMV-F and what was believed to be MLV were observed in the field in *S. verticilliflorum* and were transmitted from maize to *S. verticilliflorum* and vice versa by Ricaud and Felix (1976). Subsequently, a large number of tropical and temperate cereal species, sugarcane hybrids, and grasses, some of these known to be the hosts of other plant rhabdoviruses, were inoculated with the three strains of MMV (Autrey, 1980). Among the tropical and temperate grasses, only *S. verticilliflorum* and *Rottboellia exaltata* L. became infected and showed symptoms typical of the three strains. The latent periods in *S. verticilliflorum* and *R. exaltata* were, respectively, 13 and 26, 15 and 37, and 15 and 42 days for MMV-F, MMV-C, and MMV-B. Of all the other species inoculated, only spring barley (*Hordeum vulgare* L.) became infected and symptoms were similar to those caused by the strains in maize. In the field the three syndromes were found in *S. verticilliflorum* in Mauritius and in *R. exaltata* in Reunion (Autrey, 1980). MMV was found to have a very limited host range and this was in agreement with the findings in other countries where the virus has been reported (Herold, 1972).

Epidemiology. In Mauritius the three strains of MMV are prevalent in many locations in the east, west, and southwest of the island where there is no break in the crop cycle during the year. In other sectors of the island, the disease is rarely present or is totally absent. The exact incidence was determined in 13 consecutive plantings of the local cultivar in the east of Mauritius, which revealed that MMV-F was far more important than MMV-C and MMV-B and that the disease was more severe in the warm season with a second peak in the cool season (Fig. 2). In imported hybrids, the incidence of MMV either in full stand or intercropped with sugarcane has been found to be low, reaching a maximum of 5.9% in 1976 in hybrid United 530 in the east of Mauritius (Anonymous, 1977; Autrey and Ricaud, 1982).

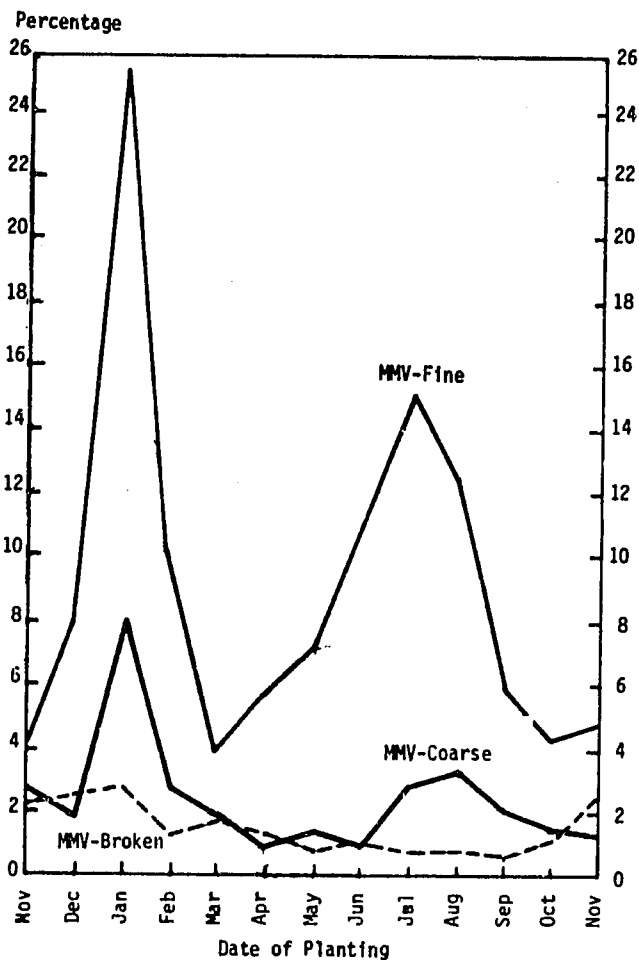


Fig. 2. Relative incidence of the three syndromes of maize mosaic virus in the east of Mauritius (November 1977 -November 1978).

The population of *P. maidis* was found to be higher in the eastern and northern sectors of the island than elsewhere. The planthopper population was higher in the warm than in the cool season, especially in November when a large number of nymphs of various instars were encountered (Autrey, 1980). It is not believed that *S. verticilliflorum* plays an important role in the carryover and severity of the disease, particularly since transmission from it to maize is inefficient. Continu-

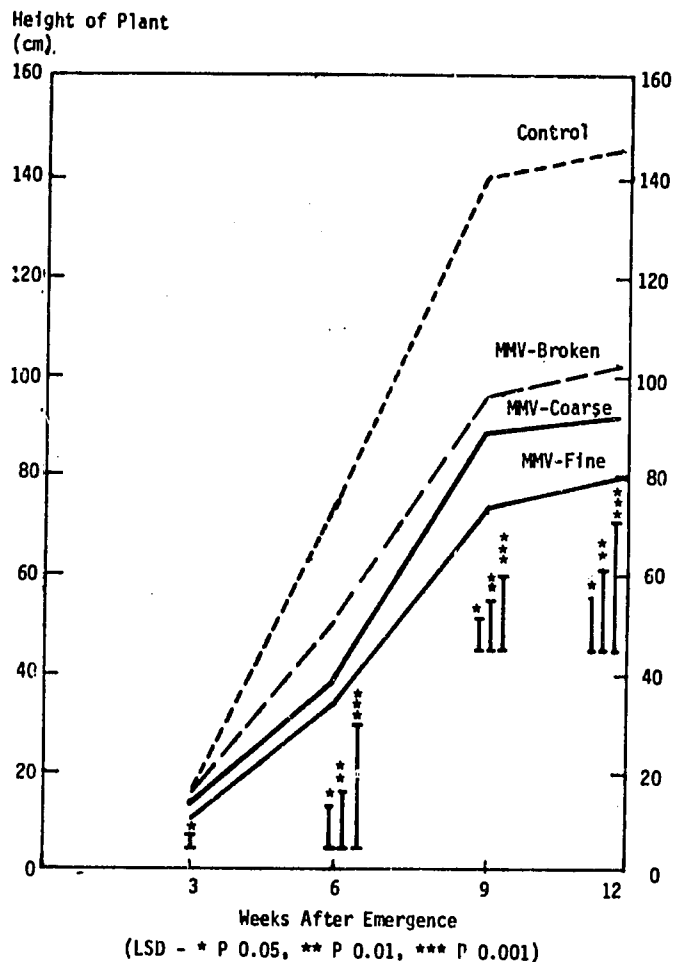


Fig. 3. Effects of three isolates of maize mosaic virus on growth of maize hybrid LG 11 under glasshouse conditions. (LSD - * P 0.05, ** P 0.01, *** P 0.001)

ous cropping is the main factor responsible for the high incidence of the disease in maize.

In Reunion the exact incidence of MMV in the field has not been determined, but it appears that the three strains are more prevalent on local cultivars than in Mauritius (Autrey, unpublished).

In the field, both in the local cultivar and in the imported hybrids, Autrey (1980) observed that MSV masked symptoms of initial MMV infection. On very

TABLE 1. Effects of the three isolates of maize mosaic virus (MMV) on growth and yield of maize hybrid LG 11 inoculated at the coleoptile stage under glasshouse conditions.

Infecting virus strain/ statistical parameter	Plant parameters ^a					Cob parameters ^a				Dry weight of seeds ^a (g)
	Height (cm)	Stalk diameter (mm)	Leaf area (mm ²)	Fresh weight (g)	Dry weight (g)	Length (cm)	Diameter (mm)	Fresh weight (g)	Dry weight (g)	
MMV-Fine	78.3 a ^b	14.0 a	280.0 a	83.2 a	28.5 a	10.7 a	34.6 a	54.9 a	41.1 a	34.1 a
MMV-Coarse	88.6 a	15.4 ab	418.5 b	87.0 a	24.5 a	13.3 b	39.7 b	87.0 b	60.2 b	43.9 b
MMV-Broken	101.5 b	16.4 b	451.8 b	130.7 b	50.3 b	15.1 b	41.9 b	91.1 b	60.5 b	50.4 b
Healthy control	143.6 c	22.8 c	617.1 c	310.6 c	110.0 c	17.9 c	46.1 c	156.9 c	102.7 c	80.2 c
SE	4.5	0.6	19.5	11.9	2.0	0.8	0.9	8.9	4.0	5.5
CV %	5.3	4.5	5.4	9.6	4.6	6.8	2.8	11.2	9.4	13.0

^a Data expressed per plant per plot. Mean of three replicates.

^b Duncan Multiple Range test. Means followed by the same letter do not differ significantly from each other at P = 0.05 level.

TABLE 2. Effects of maize mosaic virus-fine isolate inoculated at two stages in the growth cycle of maize hybrid LG 11.

Infecting virus/ statistical parameter	Plant parameters ^a			Cob parameters ^a				Dry weight of seeds ^a (g)
	Height (cm)	Fresh weight (g)	Dry weight (g)	Length (cm)	Diameter (mm)	Fresh weight (g)	Dry weight (g)	
MMV-Fine Stage I	97.1 a ^b	307.9 a	165.9 a	11.5 a	36.1 a	119.4 a	65.1 a	41.9 a
MMV-Fine Stage II	117.8 b	356.0 ab	181.2 a	14.0 b	35.1 a	144.8 a	82.2 a	43.8 a
Healthy control	133.9 b	453.6 b	250.0 b	15.8 c	43.0 b	212.3 b	140.8 b	88.0 b
SE	7.3	50.9	11.1	0.5	0.8	16.6	11.6	7.4
CV %	7.7	16.8	6.8	4.8	2.7	12.8	14.7	15.7

^a Data expressed per plant per plot. Mean of three replicates.

^b Duncan Multiple Range test. Means followed by the same letter do not differ significantly from each other at P = 0.05 level.

TABLE 3. Effects of maize mosaic virus-fine strain on growth and yield of the local maize (*Zea mays* L.) variety under field conditions.

Infecting virus/ statistical parameter	Plant parameters ^a			Cob parameters ^a				Dry weight of seeds ^a (g)
	Height (cm)	Stalk diameter (mm)	Fresh weight (g)	Length (cm)	Diameter (mm)	Fresh weight (g)	Dry weight (g)	
MMV-Fine	148.0 a ^b	21.8 a	364.0 a	17.0 a	39.0 a	134.0 a	88.3 a	62.5 a
Healthy control	174.8 b	23.8 a	510.0 b	23.0 b	53.0 b	304.0 b	202.3 b	157.3 b
SE	6.9	1.3	32.9	0.7	1.9	12.1	10.2	11.8
CV %	7.1	9.4	14.7	6.3	6.9	10.9	13.5	20.3

^a Data expressed per plant per plot. Mean of three replicates.

^b Duncan Multiple Range test. Means followed by the same letter do not differ significantly from each other at P = 0.05 level.

rare occasions in local cultivars only, symptoms of MMV masked those of MSV, in instances where sequential infection occurred in plants with mild symptoms of MSV. Co-infections of MMV-F and MMV-C were also observed in the local variety but not with MMV-B. In glasshouse and field trials with imported hybrids, it was found that MSV protected against the three strains of MMV but not vice versa and that inoculation of MSV to MMV-infected plants proved lethal (Autrey, 1980). Cross-protection tests between the three syndromes of MMV in the glasshouse revealed that MMV-B could protect against the two other strains and MMV-C could do so against MMV-F, whereas the latter could not protect against the two other strains (Autrey, 1980). These results would be expected if it is assumed that MMV-B is the mildest of the three strains. That no additive damaging effect was observed in these tests indicated that the three strains are closely related.

Yield loss assessment. In glasshouse trials the three strains adversely affected growth (Fig. 3) and yield (Table 1) when plants of hybrid LG 11 were inoculated in the coleoptile stage (Autrey, 1980). The effects of MMV-F were more severe, owing probably to the adverse effects of the striping on the photosynthetic area. When the fine strain was inoculated in the same hybrid at two stages in the crop cycle, namely coleoptile and 30 days after emergence, height and fresh weight of plants were affected significantly only when the virus

was introduced in the coleoptile stage; fresh weight and dry weight of cobs and dry weight of seeds were affected at both stages of inoculation (Table 2). In the field the results obtained in the glasshouse were confirmed in hybrid LG 11.

For the local cultivar under field conditions it was only possible to assess reliably the effects of MMV-F since the numbers of plants infected with MMV-C and MMV-B were too small in the experimental plots. MMV-F reduced significantly height and fresh weight as well as yield (Table 3). Significant linear relationships between stages of infection and both height of plant and yield were obtained for MMV-F (Fig. 4), and the data showed a tendency for an increasing effect of

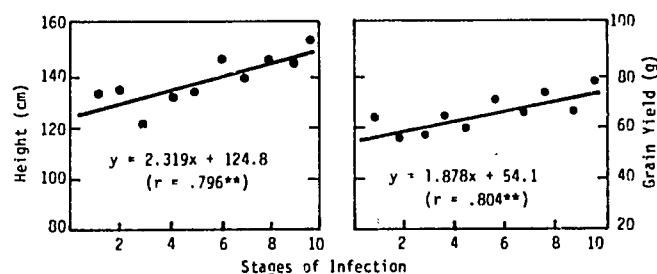


Fig. 4. Relationship between growth (left) and yield (right) to the stage of infection in the local maize variety infected with maize mosaic virus-Fine. Data are expressed on a per plant per plot basis.

TABLE 4. Susceptibility of maize hybrids to maize mosaic virus strains fine, coarse, and broken under glasshouse conditions.

Hybrids	Disease index ^a			
	MMV-Fine (x)	MMV-Coarse (y)	MMV-Broken (z)	
			Observed	Estimated
M 5 x R 14	90.00	45.00	56.79	74.73
M 15 x R 14	90.00	45.00	90.00	74.73
R 18 x DeKalb XL 24	90.00	90.00	63.43	49.90
R 22 x DeKalb XL 24	90.00	90.00	63.43	49.90
R 22 x United 530	56.79	71.57	26.57	25.91
M 14 x R 14	50.77	50.77	26.57	31.20
M 24 x R 14	63.43	50.77	26.57	44.22
Topcross 1	33.21	45.00	0	16.32
Local x R 14	26.57	39.23	0	12.68
M 23 x R 14	0	0	33.21	6.99
Mean	59.08	52.73	38.66	

^a Expressed as arcsine $\sqrt{\%}$ infected plants. 10 plants of each hybrid inoculated with each MMV isolate.

Multiple correlation analysis

$$z = a + bx + cy$$

$$a = 6.993$$

$$b = 1.028 [R = 0.831 (R \text{ is significant at } P = 0.01 \text{ level})]$$

$$c = -0.552$$

the disease in relation to the stages at which infection occurs (Autrey, 1980). It was also found that the effect on yield was more severe than that on height.

Control. In Mauritius control of MMV is carried out by successful destruction of the weed *S. verticilliflorum*

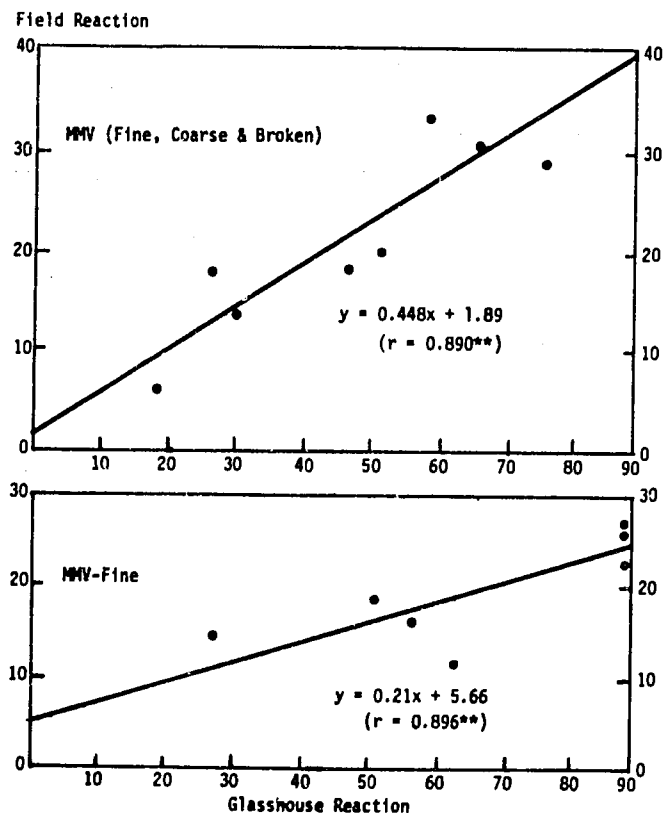


Fig. 5. Correlation between glasshouse and field reaction to maize mosaic virus in nine maize genotypes. Plotted values are expressed as Disease index = Arcsine $\sqrt{\%}$ infected plants.

with the herbicide Glyphosate; the use of systemic insecticides Carbofuran and Omethoate does not result in reduction in infection levels. Emphasis was placed on research for resistant genotypes. Screening of a large number of hybrids from Europe and Africa, of pure lines from local cultivars in Mauritius and Rodrigues, and of progeny from back crosses of these pure lines as well as crosses between the latter and foreign hybrids was carried out by Autrey (1980). All foreign hybrids (250) proved susceptible to the three strains while pure lines of the local variety and hybrids issuing from them failed to become infected even after a second or third exposure to insects.

A group of 10 selected hybrids used in four tests showed an array of reactions to the three strains. Disease susceptibility was generally highest with MMV-F and least with MMV-B (Table 4). A correlation between reaction in the glasshouse and in the field was obtained for MMV-F as well as for MMV as a whole (Fig. 5), showing the validity of the glasshouse test (Autrey, 1980). In these tests it was possible to obtain a hybrid highly resistant to MMV and four moderately resistant, two slightly susceptible, and three highly susceptible hybrids (Autrey, 1980). The highly resistant hybrid, M 23 x R 14, will be bulked for use on a large scale if it has other desirable agronomic characteristics.

Purification. The purification procedure used by Autrey (1980) is detailed in Fig. 6. The virus was purified by homogenizing one part of infected maize leaves in four parts of 0.2M phosphate buffer, pH 9.2, containing 0.05% thioglycolic acid. After straining through cheesecloth and centrifuging at low speed, the supernatant was treated with 0.5% decolorizing charcoal for 30 sec and filtered through a Celite pad (Standard Super Cel). The virus particles were pelleted by centrifugation in a Beckman Type 30 rotor at 60,000 g for 15 min.

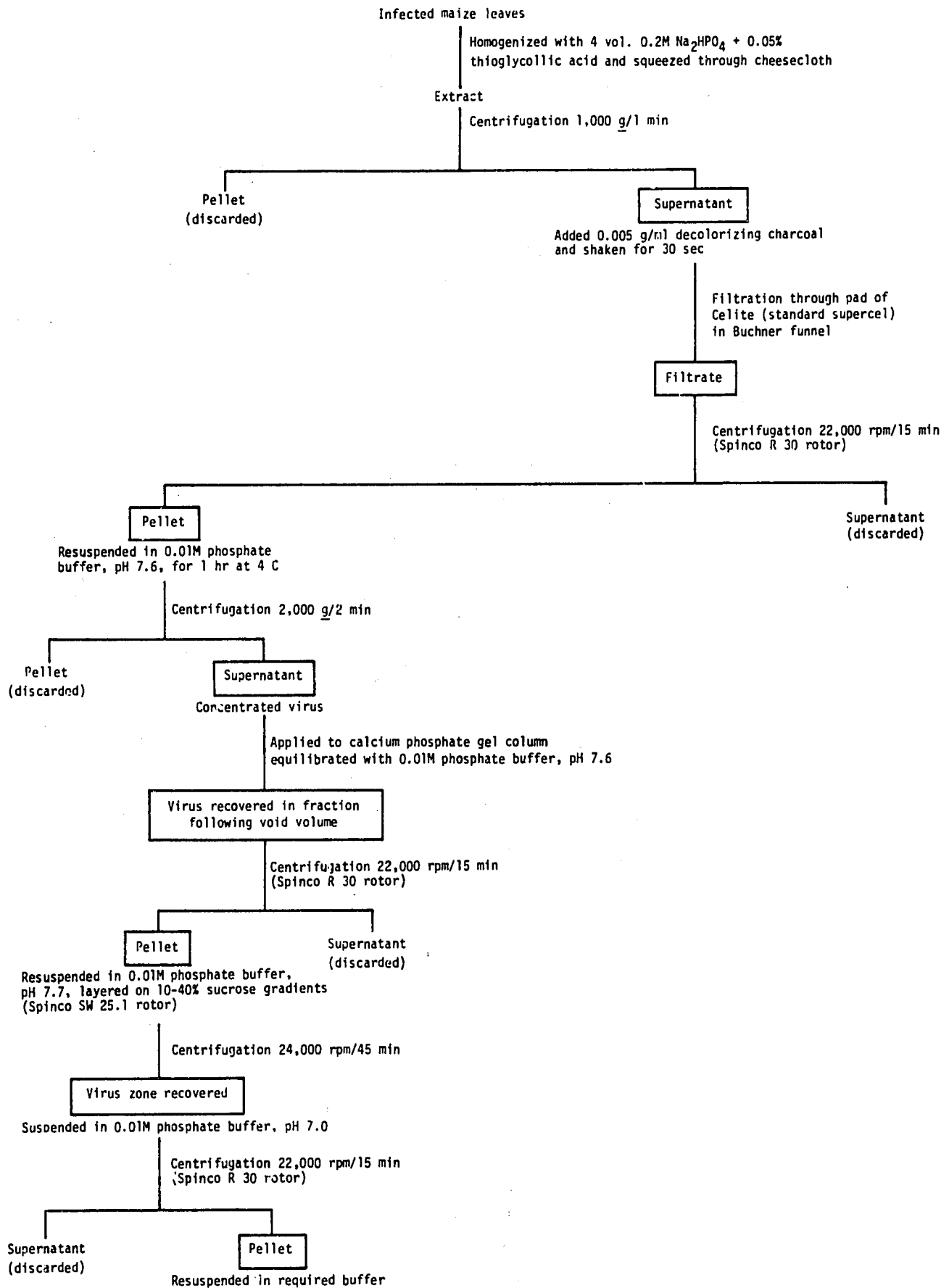


Fig. 6. Procedure to purify maize mosaic virus by differential centrifugation, column chromatography, and sucrose density gradient centrifugation.

After resuspending in 0.01M phosphate buffer, pH 7.6, the virus was applied to a column of calcium phosphate gel equilibrated with the same buffer. After recovery from the column, the particles were again pel-

leted and resuspended in 0.01M buffer before being centrifuged on 10-40% sucrose gradient at 90,000 g for 45 min.

Pure virus preparations were obtained by removing the light scattering zones (Fig. 7) and centrifuging at 60,000 g for 15 min. The yield was found to be highest with MMV-F and least with MMV-B, and yield from *S. verticilliflorum* was higher than from maize. The virus particles from the three strains did not differ in size. They were found to contain RNA, to be sensitive to lipophilic solvents, and to be highly unstable at room temperature. Planthoppers injected with purified preparations transmitted the virus but the insects failed to acquire virus particles from such preparations when fed through a Parafilm membrane. The sedimentation coefficient of MMV-F and MMV-C was found to be 820S and that of MMV-B, was 835S (Autrey, 1980).

Serology. Antisera prepared by injection of purified preparation in rabbits were found to be highly specific and did not react with antigen from healthy plants and those infected with MSV, MDMV, MStpV (Fig. 8) (Autrey, 1980), and MCSV (Autrey, unpublished). The titers for MMV-F, MMV-C, and MMV-B were 1/32, 1/32, and 1/64, respectively, with crude sap from infected maize plants. The method used is demonstrated for MMV-B antiserum in Fig. 9. The rhabdovirus proved to be poorly immunogenic and a second series of antisera prepared with particles fixed with formaldehyde gave identical results.

The three strains proved serologically identical in a large number of immunodiffusion tests (Fig. 10). Precipitation lines with antigens from maize, *S. verticilliflorum*, and barley fused completely. The three strains from Reunion (Fig. 11) and the fine strain from Madagascar proved serologically identical to the three strains existing in Mauritius. The MMV antigen in Mauritius reacted positively with an antiserum to MMV-*raya fina* prepared by Lastra (1977) in Venezuela and tests showed that this antiserum was not as highly specific as the ones prepared in Mauritius (Autrey, 1980).

With the ELISA technique, the virus could be diagnosed in crude sap up to a dilution of 1:20,000 (Autrey, 1980).

MAIZE STREAK VIRUS

Distribution. MSV occurs throughout the four islands and in East Africa. It is considered to be the most important virus disease in Mauritius (Ricaud and Felix, 1976) and Rodrigues (Autrey, unpublished; C. Ricaud, *personal communication*). In Mauritius as with MMV, MSV is most prevalent in the east, west, and southwest, but elsewhere plantations are rarely free from it. In Rodrigues it is more prevalent in the central part of the island where 100% infection is not uncommon, while in the coastal part infection may range from 100% to a negligible level. The disease is quite common in Reunion but exact data on its incidence are lacking.

Symptoms. In plants inoculated in the coleoptile stage, MSV induces white to yellow spots 4-5 days after



Fig. 7. Light-scattering zone observed with maize mosaic virus-Fine (top) and virus particles observed in purified preparations (bottom).

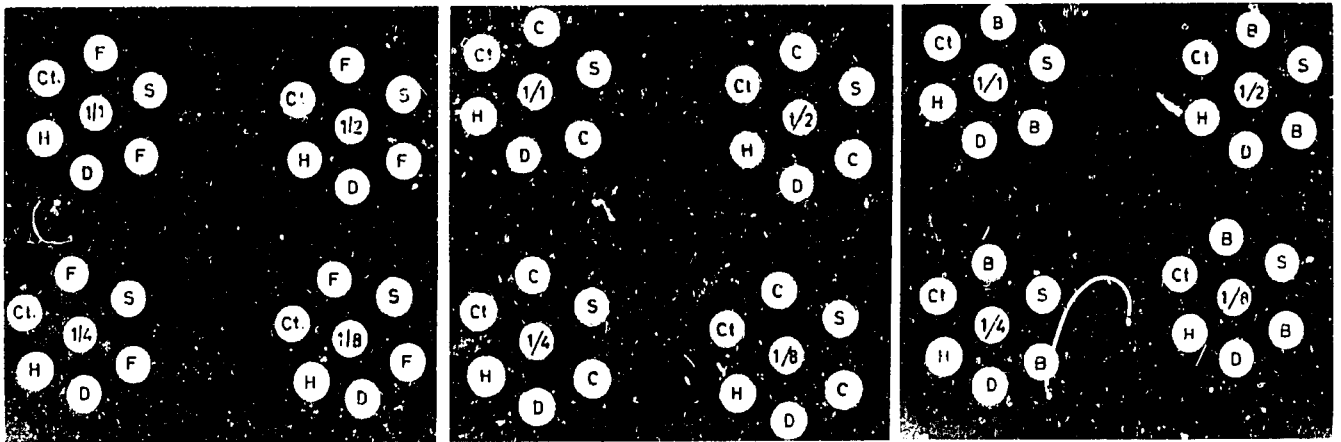


Fig. 8. Serological test to demonstrate specificity of the antisera to three strains of maize mosaic virus (MMV). F, C, B-antigen to MMV-Fine, -Coarse, -Broken, respectively. H = healthy antigen; S = maize streak virus; D = maize dwarf mosaic virus; Ct = control (saline water).

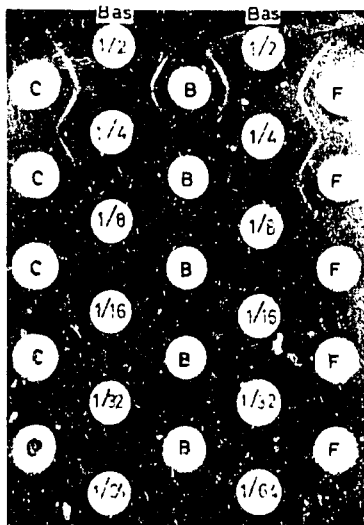


Fig. 9. Determination of titer of antiserum (Bas) to maize mosaic virus (MMV)-Broken against its homologous antigen and antigens of MMV-Coarse (C) and MMV-Fine (F).

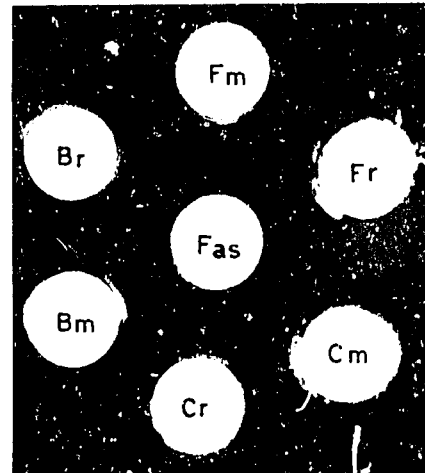


Fig. 11. Serological test with maize mosaic virus (MMV) antigens from Reunion and Mauritius with antiserum to maize mosaic virus-Fine (Fas). Fm, Fr = MMV-Fine from Mauritius and Reunion; C-m, Cr = MMV-Coarse from Mauritius and Reunion; Bm, Br = MMV-Broken from Mauritius and Reunion.

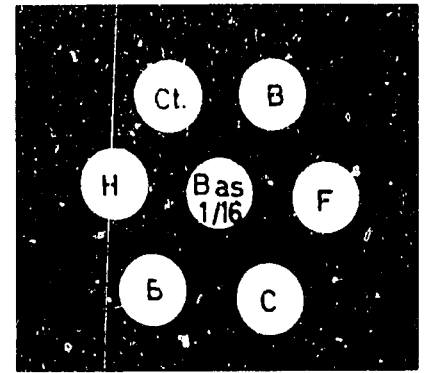
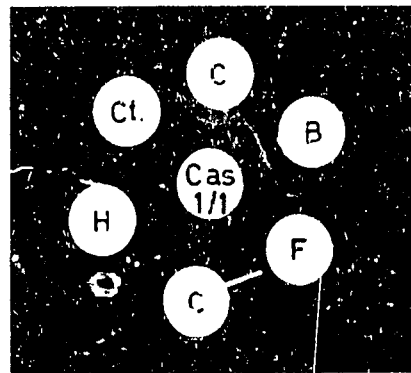
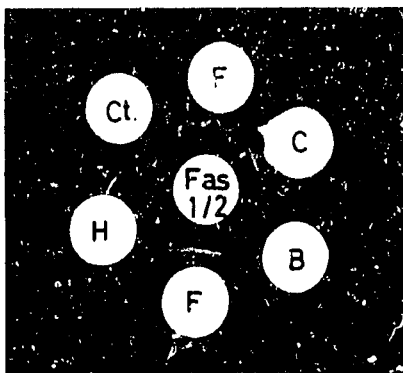


Fig. 10. Determination of serological relationships between the three strains of maize mosaic virus (MMV) by double diffusion in agar gel. F, C, B-antigen to MMV-Fine, -Coarse, and -Broken, respectively; H = healthy antigen; Ct = control (saline water); Fas, Cas, and Bas = antisera to MMV-Fine, -Coarse, and -Broken, respectively.

inoculation. The spots elongate and fuse to give 2 mm wide streaks of varying length. The disease does not form stripes like MMV. In highly susceptible varieties the whole leaf lamina may become nearly chlorotic while in resistant ones the number of spots may be greatly reduced to a few on a fully developed leaf (Fig. 12). Infected plants of susceptible cultivars are dwarfed and very often enations are visible on the midrib (Fig. 12). The local Mauritian maize cultivar shows high resistance to the disease and in the field it is common to observe plants which have recovered from infection (Autrey, *unpublished*; Ricaud and Felix, 1976).

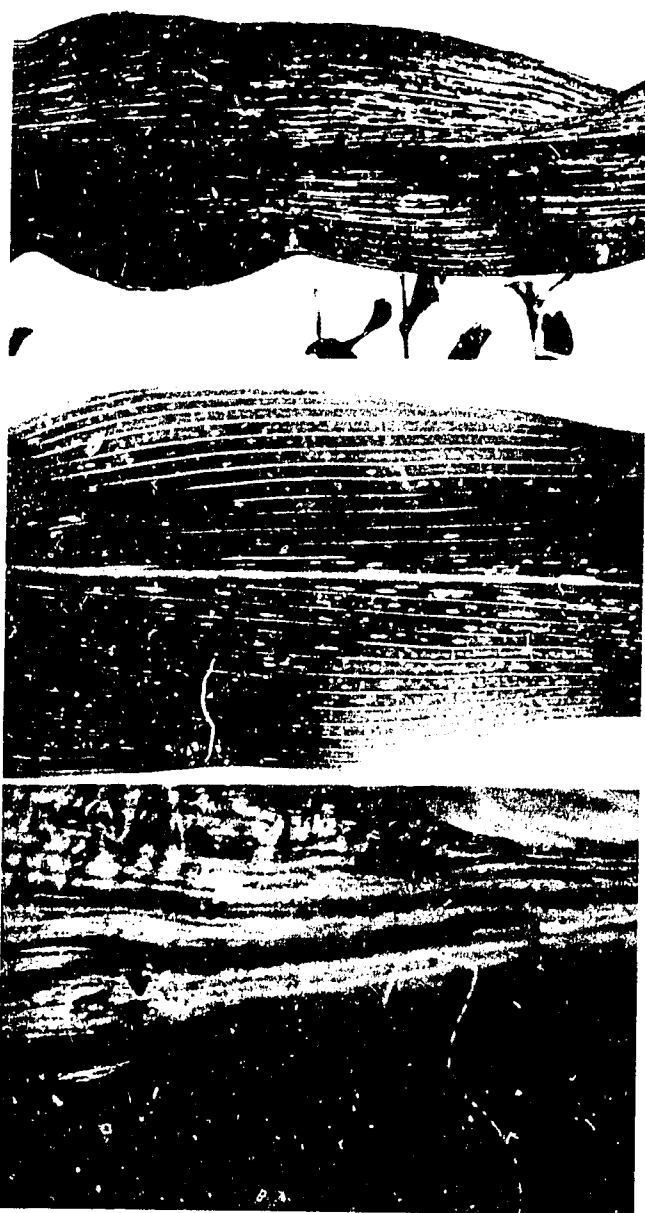


Fig. 12. Responses to maize streak virus in a susceptible (top) and a resistant maize cultivar (middle) and enations (arrows) on midrib of infected leaf (bottom).

Virus-vector-host plant relationships. The leafhopper, *C. mbila*, was first discovered in Mauritius in 1972 (J. R. Williams and H. Dove, *personal communication*). The virus is transmitted very efficiently by the leafhopper, *C. mbila*, (*C. Ricaud and S. Felix, personal communication*), but detailed studies on the interrelationships between virus-vector and host plant have not been carried out. Another leafhopper, *C. triangula* Ruppel, failed to transmit MSV in glasshouse tests (J. R. Williams and H. Dove, *personal communication*).

Host range. MSV has the widest host range among the viruses of maize reported in the area. The following species have been found with streak symptoms in the field by Ricaud and Felix (1976, 1978a,b): *Brachiaria eruciformis* (J. E. Smith) Griseb., *B. reptans* Gard and C. E. Hubb., *Cenchrus echinatus* L., *Coix lachrymajobi* L., *Digitaria didactyla* Willd., *D. horizontalis* Willd., *D. timorensis* (Kunth) Balansa, *Panicum maximum* Jacq., *Paspalum conjugatum* Berguis, and *Saccharum* hybrids. Several host-adapted strains of MSV have been found in these species and only *B. eruciformis*, *B. reptans*, *C. echinatus*, and *C. lachrymajobi* play a role in the epidemiology of MSV in maize (Ricaud and Felix, 1976). Isolates from these four graminaceous hosts induced symptoms similar to the maize strain when inoculated in various hosts and MSV can be readily acquired from and transmitted to them (Ricaud and Felix, 1978a).

Epidemiology. Although MSV was first recorded in Mauritius years ago (Shepherd, 1924), its exact incidence in the local variety was apparently never determined. In 1974 100% infection was found in plantings made in the west of Mauritius in the warm season while in the dry cool season infection was less than 5% (Anonymous, 1975; Ricaud and Felix, 1976). In imported hybrids intercropped with sugarcane in the western and eastern sectors, 40-50% infection was found in Anjou 360 and United 530 (Anonymous, 1977; Ricaud and Felix, 1979). In plantings made close to scrub land, high infection levels have been found. In other plantings far from scrub land, infection is limited and does not exceed 2-5% (Autrey, *unpublished*; Ricaud and Felix, 1976). However, with continuous cropping up to 100% MSV infection was found in a planting of hybrid United 530 made alongside a 6 wk earlier planting of the same hybrid in which infection was low (Autrey and Ricaud, 1982).

The incidence of MSV and MMV was determined in 13 successive monthly plantings of the local cultivar in the east of Mauritius (Autrey, 1980). Infection by MSV was at a peak in March and October plantings at the beginning of the cool-dry and warm-wet seasons, respectively, while for MMV peak infection occurred in the January planting (Fig. 13). The incidence of MMV was higher than MSV, except in March, April, and October. In general, spread of MSV was rapid early in the vegetative cycle, while for MMV maximum spread was in the middle of the vegetative cycle (Autrey, 1980; Autrey and Ricaud, 1982).

The factors affecting disease incidence, spread, and carryover are the alternate hosts, vector populations,

Percentage

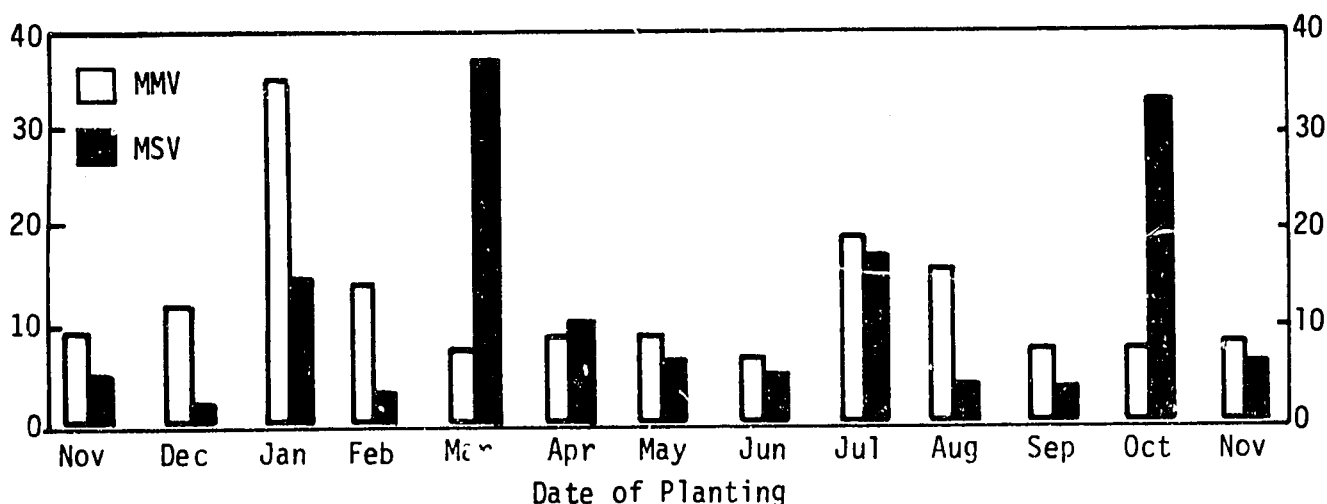


Fig. 13. Comparative incidence of maize mosaic virus (MMV) and maize streak virus (MSV) in the east of Mauritius (November 1977 - November 1978).

and maize cropping. Because a large number of perennial and annual weeds harbor MSV, epidemics occur frequently in imported hybrids which are highly susceptible. The annual alternate hosts, which grow throughout the year, help to bridge the gap between two successive maize crops. The severity of epidemics of MSV depends also on the proximity to scrub land, since in plantings established in these areas there is extensive and rapid spread of MSV by leafhoppers which have acquired the virus from perennial reservoirs. In this case disease buildup is linear with time. With the same conditions in the local cultivar, disease development shows a marked lag phase due to greater resistance to infection (Autrey and Ricaud, 1982). When planting is made away from hill slopes and scrub land, disease buildup is usually slow but when a second crop follows in the immediate vicinity, disease buildup is exponential and in such conditions 100% infection has been observed (Autrey and Ricaud, 1982).

In Rodrigues the high incidence of MSV in the central part of the island is due to continuous cropping and abundant vector populations which exceed those usually encountered in Mauritius (Autrey, unpublished).

Yield loss. Losses from attacks of MSV can be quite severe in imported hybrids. Ricaud and Felix (1979) assessed yield reductions in the order of 28 and 24% in hybrids Anjou 360 and United 530 for infection levels of 50 and 40%, respectively. In one field of United 530 a severe attack resulted in a total loss (Autrey and Ricaud, 1982). In the local cultivar which is tolerant to MSV, no precise yield-loss assessment has been carried out, but it is not thought that economic losses are sustained by growers. A correlation between stage of infection and reduction in yield was obtained in hybrids Anjou 360 and United 530 (Anonymous, 1976; C. Ricaud and S. Felix, personal communication). In Rodrigues, losses due to MSV are severe in the central part of the island, especially when drought conditions prevail and accentuate the dwarfing effect of the disease (Autrey, unpublished).

lished). In Reunion, cultivation of cultivar Revolution and its progenies has helped to reduce losses due to MSV.

Control. In Mauritius, C. Ricaud and S. Felix (personal communication) screened a large number of foreign hybrids in the glasshouse and in the field for resistance to MSV and they all proved susceptible. These two workers found genes for resistance in pure lines issuing from the local cultivar and in hybrids between these pure lines and imported genotypes. Autrey (1980) found genes for resistance in M 5 x R 14 hybrids issuing from pure lines of Mauritius and Rodrigues. No correlation was found between resistance to MMV and MSV (Table 5). Hybrid M 23 x R 14 was highly resistant to MMV but susceptible to MSV.

Among 113 lines and hybrids produced in Mauritius and screened in the glasshouse, the following results (the number of lines and hybrids for each category are in parentheses) were obtained: highly resistant (29),

TABLE 5. Infection level of maize mosaic virus (MMV) and maize streak virus (MSV) in 10 maize (*Zea mays* L.) hybrids under field conditions.

Hybrids	Disease index ^a	
	MMV	MSV
M 5 x R 14	36.16 a	32.31 e
M 15 x R 14	32.99 a	48.38 bcd
R 18 X Dekalb XL 24	30.40 ab	59.17 ab
M 14 x R 14	23.19 bc	42.39 de
R 22 x United 530	22.35 cd	62.30 a
M 24 x R 14	19.29 cd	40.72 de
Local x R 14	18.03 cd	44.48 cd
R 22 x DeKalb XL 24	17.91 cd	53.99 abc
Topcross 1	14.63 d	16.39 f
M 23 XR 14	6.58 e	53.55 abc

^a Expressed as arcsine $\sqrt{\%}$ infected plants. Means of three replications. Disease indices followed by the same letter are not significantly different from each other at P = 0.05.



Fig. 14. Symptoms of maize stripe virus in young (top) and adult (bottom) maize plants.

resistant (17), moderately resistant (15), slightly susceptible (11), susceptible (21), and highly susceptible (20) (Anonymous, 1981; Autrey, *unpublished*). In Rodrigues in four trials carried out in 1980, two hybrids issuing from crosses between pure lines of Mauritius and those of Rodrigues proved highly susceptible (Anonymous, 1981; Autrey, *unpublished*). As mentioned earlier, in Reunion the resistant cultivar Revolution is being used to control MSV carryover.

Purification, serology and histopathology. Despite extensive attempts by C. Ricaud (*personal communication*) and Autrey (*unpublished*), it has not been possible to obtain purified preparations of MSV by using the method of Bock *et al.* (1974). It is believed that the leaf material used is not sufficiently rich in virus particles, despite the severity of symptoms, to allow a reasonable yield to be obtained.

Antigens in crude sap and in partially purified preparations from maize and various hosts reacted positively with an antiserum to MSV supplied by K. R. Bock and the presence of the disease was diagnosed by immunodiffusion tests (Ricaud and Felix, 1976).

In ultra-thin sections of maize leaves, the crystalline nuclear inclusions described by Bock *et al.* (1974) and made of virus particles have been observed by Autrey (*unpublished*).

MAIZE STRIPE VIRUS

The condition described as maize stripe by Kulkarni (1973) was probably first observed by Shepherd (1929) in Mauritius. Later, Ricaud and Felix (1976) and Autrey (*unpublished*) found plants with the syndrome of the disease, *i.e.*, fine striping on lower leaves evolving quickly into broad chlorotic bands and goose-neck bending of the tassel (Fig. 14) in a few plants in the field. The pathogen was transmitted by *P. maidis* from maize to maize in the glasshouse (Autrey, *unpublished*; Ricaud and Felix, 1976) and from maize to barley (Autrey, *unpublished*).

Extensive attempts by C. Ricaud (*personal communication*) to purify the virus particles, claimed by Kulkarni (1973) to be the causal agent of the disease, have been unsuccessful. The recent report of Gingery *et al.* (1981) on a new type of virus particle, a filamentous nucleoprotein of 3 nm diam, as the causal agent of the disease explains Ricaud's failure to isolate isometric particles. Recently, however, Autrey and R. D. Woods (*unpublished*) found 28 and 40 nm diam particles in young plants showing typical symptoms of MStpV by immune serum electron microscopy (ISEM) with Kulkarni's MStpV antiserum. Whether these particles are the causal agent of maize stripe is not known at present. The MStpV antiserum is quite unspecific (Autrey, 1980; C. Ricaud and S. Felix, *personal communication*) and it apparently has antibodies to at least three viruses of maize (R. D. Woods, *personal communication*).

The disease has no economic importance in Mauritius and it has not been reported in the other islands. It is believed that MStpV is of such rare occurrence that it must have some alternate hosts which allow it to survive in the absence of maize. It is suspected that one of

the hosts could be *Setaria barbata* (Lam.) Kunth, because symptoms are found on this weed in the field (Autrey, unpublished).

MAIZE LINE VIRUS

After the description by Kulkarni (1973) of a virus disease inducing coarse distinct striping in maize, Ricaud and Felix (1976), on the basis of symptomatology, transmission studies with *P. maidis*, and positive serological reactions with the MLV antiserum, concluded that MLV existed in Mauritius and induced the coarse striping observed on maize. Attempts at purifying the 28 and 34 nm isometric particles described by Kulkarni were, however, unsuccessful (Autrey, unpublished; C. Ricaud, personal communication). Crude sap of plants infected with MMV-F, MMV-C, and MMV-B were found to give strong positive reactions with Kulkarni's MLV antiserum, while purified preparations did not react (Fig. 15). Attempts to separate MMV and MLV by various methods over 2 yr were unsuccessful (Autrey, unpublished).

K. R. Bock (personal communication) reported the presence of 28 nm diam isometric particles in symptomless plants and his discovery of MMV in Kulkarni's MLV cultures allowed Autrey (1980) to prove that Kulkarni had in fact prepared an antiserum to subviral fragments of MMV. This explained the positive reaction observed with crude sap but not with purified preparations unless the latter are treated with butanol (Fig. 16). Autrey (1980) while working with Kulkarni's so-called MLV cultures in 1977 found that the syndrome corresponded to MMV-B. Consequently, MLV is considered a misnomer and it is proposed that it be referred to as MMV-B in the literature.

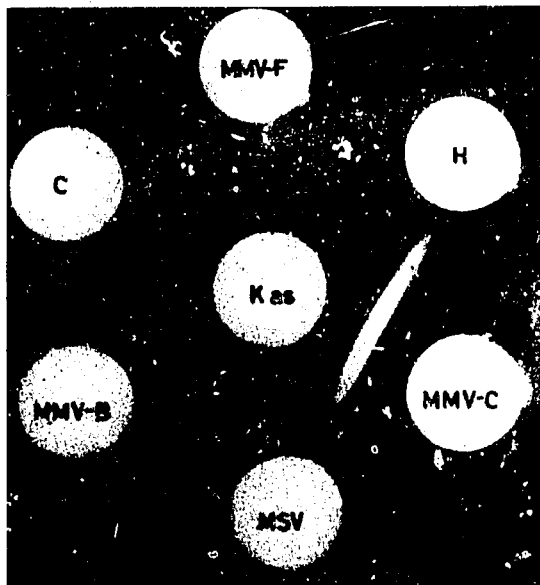


Fig. 15. Immunodiffusion test with Kulkarni's antiserum to maize line virus (Kas) and antigens to maize mosaic virus (MMV). MMV-F = MMV-Fine; MMV-C = MMV-Coarse; MMV-B = MMV-Broken; MSV = maize streak virus; H = healthy sap; C = control (saline water).

MAIZE CHLOROTIC STRIPE VIRUS

During a visit to Rodrigues in 1980, Autrey (unpublished) observed a hitherto undescribed striping syndrome consisting of fairly broad yellow bands in the interveinal tissue of the lamina (Fig. 17) of a few plants in two localities on the island. Electron microscopic examinations revealed the presence of isometric particles of 45 nm diam (Autrey and R. D. Woods, unpublished). Later the syndrome was discovered in the south of Mauritius and a pathogen associated with the disease was readily transmitted in the glasshouse by *P. maidis* (Autrey, unpublished). In an experimental plot in the

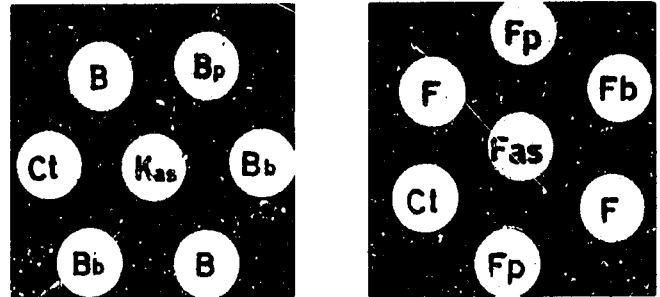


Fig. 16. Serological test with crude sap, butanol-treated, and untreated purified preparations of maize mosaic virus-Fine (MMV-F) and maize mosaic virus-Broken (MMV-B) against antisera to MMV-F (Fas) and Kulkarni's maize line virus (Kas). B, Bb, and Bp = crude sap, butanol-treated, and untreated purified preparations of MMV-B. F, Fb, and Fp = crude sap, butanol-treated, and untreated purified preparations of MMV-F.

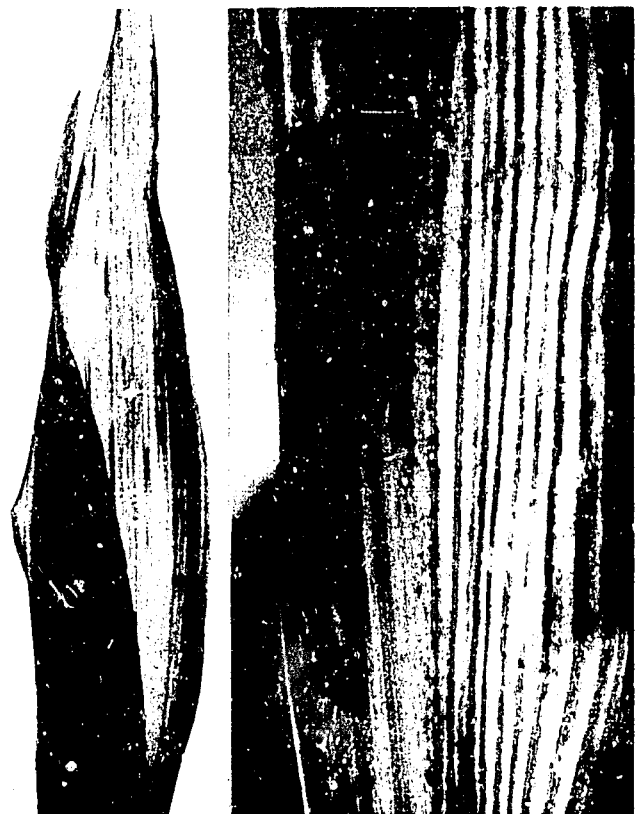


Fig. 17. Symptoms of maize chlorotic stripe virus on maize leaf.



Fig. 18. Symptoms of maize dwarf mosaic virus in maize (left) and *Stenotaphrum dimidiatum* (right).

south of Reunion, large numbers of plants (about 70%) were found with the same syndrome in 1981 (Autrey, unpublished). The syndrome is different from MMV, and the disease, called maize chlorotic stripe, is at present under study. It is not believed to be of economic importance in Mauritius and Rodrigues but could cause losses in Reunion. No report has been found in the literature of a similar virus in maize transmitted by *P. maidis*.

MAIZE DWARF MOSAIC VIRUS

A mechanically transmissible virus disease causing very mild mosaic symptoms in maize and *Stenotaphrum dimidiatum* (L.) Brongn. (Fig. 18) has been designated as MDMV by Ricaud and Felix (1976). The virus has been transmitted from maize to maize and to *S. dimidiatum* and *vice versa*. The symptoms are transient and in the glasshouse are visible at temperatures

below 20 C. The disease is rarely seen in the field. Virus particles 750 nm long, typical of the potyvirus group, have been found associated with the disease. The virus was serologically related to SCMV from Madagascar (Ricaud and Felix, 1976). Very often such particles can be seen in the electron microscope in field-collected plants infected with MMV (Autrey, 1980; C. Ricaud, personal communication). The disease is of no economic importance and has not been reported on the other islands.

SUGARCANE MOSAIC VIRUS

Mauritius is one of the three sugarcane growing countries where SCMV has not been reported. The virus is present on sugarcane in Reunion but infection in maize in the field is not common. In Madagascar, Baudin (1963) observed SCMV, which was believed to have been eliminated from the country, in maize and sugarcane. Later, Baudin (1969) reported that three out of 362 seedlings issuing from seeds of maize plants inoculated with SCMV showed symptoms of the disease, a factor which could be important in the epidemiology of the disease. The present status of SCMV in maize in Madagascar is not known to the author.

MYCOPLASMA AND SPIROPLASMA

No mycoplasma or spiroplasma have been reported in the four islands.

CONCLUSIONS

Studies carried out at the Mauritius Sugar Industry Research Institute during the 1970's have led to the identification of five viruses in maize, two of which have shown strain variations. The relative importance of the viruses in Mauritius has been determined and it is evident that MSV economically is the most important pathogen, especially if foreign cultivars are grown. Lately MMV has been found to be more prevalent than was previously believed and the cultivation of maize genotypes resistant to MSV could lead to a buildup of MMV in Mauritius. Such a situation exists in Reunion where it has been observed that MMV was the most important pathogen. The exact situation of the maize viruses in Madagascar at present is not known. It is thought that research should be orientated towards finding hybrids resistant to both MMV and MSV. Further work should determine the etiology of MStpV and the pathogenicity of the 45 nm diam isometric particles associated with MCSV.

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