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REVIEW

Viruses and virus diseases of maize in tropical Africa

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INTRODUCTION

Maize (*Zea mays*) is a major staple food in Africa. Although production has increased over the last 10 years, this increase has not been sufficiently large in relation to human population growth. In the subsistence agriculture of the African tropics, average yields of maize remain low at about 1–1·5 tonnes/ha, to a great extent as a result of pests and diseases. Among numerous pathogens, several viruses are known to infect maize and their effect can be devastating. Host-plant resistance is currently the most effective method for the control of maize virus diseases in Africa (Rossel & Thottappilly, 1988). Adequate knowledge of all the virus diseases and their strains which occur in Africa's main maize-growing areas is a prerequisite for effective control through resistance breeding.

Of more than 32 viruses reported on maize worldwide (Damsteegt, 1981; Brunt *et al.*, 1990), seven are known to occur on maize in tropical Africa. Some of these are of local importance, others appear widespread, while some occur occasionally as natural infections of minor importance.

Information on virus diseases of maize in several African countries is still scanty (Shoyinka, 1988). Therefore it is hoped that this description will stimulate more research, which will lead to better understanding of maize viruses in Africa. This information will be useful to plant breeders in setting priorities in breeding for resistance to viruses. Information on symptomatology, transmission, geographical distribution and properties of viruses is summarized here based on a literature review, surveys in various countries, and detailed characterization of viruses occurring in Nigeria carried out at the International Institute of Tropical Agriculture (IITA), Ibadan, in recent years.

VIRUS DISEASES IN TROPICAL AFRICA

Maize streak geminivirus (MSV)

A condition of maize described by Fuller as 'mealie variegation', as early as 1901, was shown to be transmitted by *Balclutha* (=*Cicadulina*)

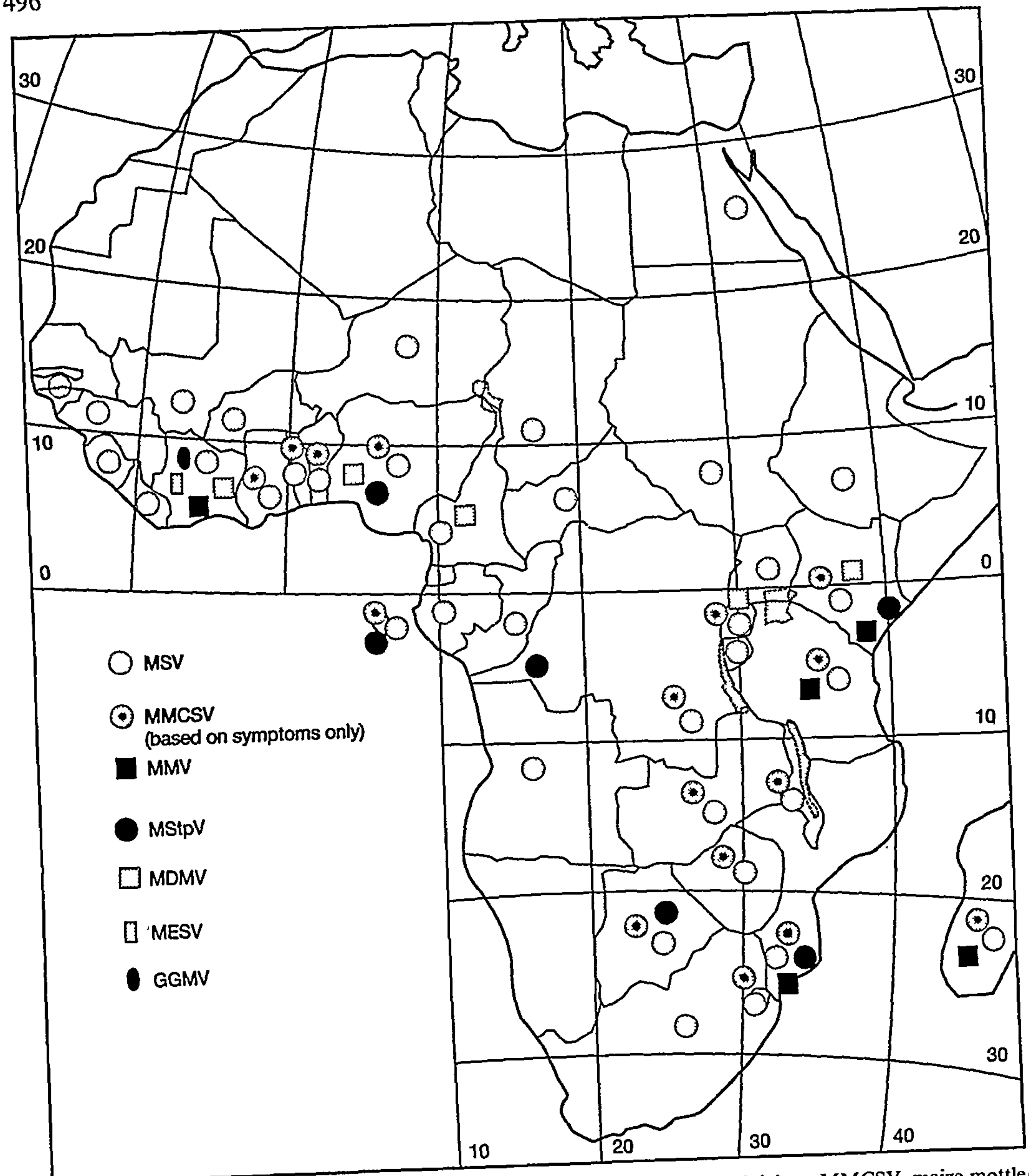

Fig. 1. Distribution of maize viruses in tropical Africa. MSV, maize streak geminivirus; MMCSV, maize mottle/chlorotic stunt virus; MMV, maize mosaic rhabdovirus; MStpV, maize stripe tenuivirus; MDMV, maize dwarf mosaic potyvirus; MESV, maize eyespot virus; GGMV, guinea grass mosaic potyvirus.

mbila Naudé. It was renamed 'maize streak' by Storey in 1925. Storey's studies on the relationship between this suspected virus and the insect vectors provided a series of classic papers of great interest and importance in plant virology (Storey, 1925; 1928; 1931; 1932; 1933; 1938; 1939); two of these papers have been reproduced in the American Phytopathological Society Phytopathological Classics (Campbell & Breuhl, 1986). Since the original work by Storey, MSV has been the subject of much additional research.

Geographical distribution

Maize streak geminivirus is widely distributed in sub-Saharan Africa from Sudan to South Africa and Kenya to Sierra Leone (Fig. 1, p. 496) and in adjacent islands, e.g. Mauritius, Réunion, Madagascar, Sao Tomé and Principe. Maize streak virus is also reported from Egypt (Ammar, 1983) and Yemen. A virus of pearl millet (*Pennisetum americanum*) and wheat (*Triticum aestivum*) in India has been reported as MSV (Seth *et al.*, 1972a, b), but the exact identity of this virus and its relationship to MSV is uncertain.

Symptoms

Symptoms in maize consist of prominent white, chlorotic streaking developing over and along the veins on most of the leaf laminae (Fig. 2a, p. 498). Streaks range from broken to almost continuous, and as the virus is systemic, symptoms appear only on the inoculated and subsequent leaves. Severity of symptoms depends on genotype and time of infection. In highly sensitive varieties, chlorotic striping may develop into uniform chlorosis of the entire lamina, which may result in progressive necrosis followed by dieback of the plant, particularly if infection has occurred at the early seedling stage.

Host range

MSV has a wide host range within the Gramineae (Damsteegt, 1983) and occurs naturally on various indigenous grasses (Rose, 1978). It causes a serious disease of maize in many regions of Africa (Fajemisin *et al.*, 1976; Fajemisin & Shoyinka, 1977). In addition to maize, other introduced crops such as wheat, oats (*Avena sativa*) and sugar cane (*Saccharum officinarum*) have been reported to be naturally infected with MSV (Gorter, 1953; Rose, 1973, 1978; van Rensburg & Kuhn, 1977). Indigenous African crops such as pearl millet, sorghum (*Sorghum vulgare*) and finger millet (*Eleusine coracana*) may also be infected with MSV (Rose, 1978). However, in Nigeria, no infected sorghum, millet or finger millet plants were found during an MSV epidemic in 1983, when the incidence of MSV in maize was nearly 100% (IITA, 1983).

Wild grasses including *Brachiaria deflexa*, *B. distichophylla* and *Axonopus compressus* were found to be naturally infected with MSV in Nigeria (Rossel & Thottappilly, 1985). These authors were unable to transmit MSV isolates from *Brachiaria mutica*, *B. deflexa*, *Eleusine indica*, *Oryza sativa*, *Rottboellia cochinchinensis* and *Panicum maximum* to selected IITA maize varieties. Streak isolates from *P. maximum* and *R. cochinchinensis* were readily transmitted by *Cicadulina storeyi* (reported as *C. triangula*) to their original hosts (IITA, 1984). In recent studies at IITA (Mesfin *et al.*, 1992), 24 isolates originating from cereal crops or wild grasses were transmitted to the maize cv. 'Golden Bantam'. However, several attempts to transmit some of the isolates to another MSV-susceptible variety ('Pool 16') proved unsuccessful.

Vectors

Maize streak virus is transmitted by leafhoppers of the genus *Cicadulina* China. There are 22 species of *Cicadulina*, 18 of which occur in Africa (Webb, 1987). Of these, eight have been confirmed to be vectors of MSV: *C. arachidis* China, *C. bipunctata* (=*bipunctella*) (Melichar), *C. ghaurii* Dabrowski, *C. latens* Fennah, *C. mbila*, *C. parazeae* Ghauri, *C. similis* China and *C. storeyi* (=*triangula*) China (Storey, 1925; 1936; Fennah, 1959; Rose, 1962; Dabrowski, 1987a; Okoth & Dabrowski, 1987; Webb, 1987; Okoth *et al.*, 1988; Reynaud, 1988). *C. mbila* appears to be the most important vector of MSV in East Africa (Storey, 1928) and recent studies show it is the most abundant vector across major ecological zones (forest, southern guinea savanna and northern guinea savanna) and seasons in Nigeria (Asanzi, 1991). Leafhopper vectors may either move within the crop (Autrey & Ricaud, 1983), or migrate from maturing crops (van Rensburg & Kuhn, 1977; Rose, 1978) or from perennial alternative hosts (Rose, 1978; Autrey & Ricaud, 1983).

Maize streak virus is transmitted in a persistent manner and the latent period in *C. mbila* is 6–12 h (Storey, 1925; 1928). Okoth *et al.* (1988) found a minimum latent period in *C. storeyi* (reported as *C. triangula*) of 14–18 h and a median latent period (LP_{50}) of 16–20 h. Asanzi (1991) found LP_{50}s of 14–24 h and 12–14 h for *C. arachidis* and *C. ghaurii*, respectively. Storey (1925; 1938) demonstrated that *C. mbila* can acquire MSV from infected plants within 15 s and inoculate it in as little as 5 min. For *C. storeyi*, Zagre (1983) found a minimum acquisition access period of 30 s and transmission after 2 h inoculation access period. Asanzi (1991) found minimum aquisition access periods of 15 min and 1 h for *C. arachidis* and *C. ghaurii*, respectively, and a minimum inoculation access period of 1 h for both species. The transmission efficiency increases with increasing duration of acquisition and inoculation feedings. The nature of MSV within its insect

Fig. 2. (a) Symptoms of maize streak virus consisting of prominent white, chlorotic streaks developing over and along the veins on most of the leaf lamina. (b) Plant infected with maize mottle/chlorotic stunt virus, showing vague mottling and chlorosis in newly developing whorl leaves. (c) Symptoms of maize stripe virus consisting of yellow to light-green uninterrupted stripes or bands along the veins of the leaf. (d) Maize dwarf mosaic virus symptoms: irregular chlorosis, mottle, striping, and ring-like flecks. (e) Maize mosaic virus symptoms characterized by continuous yellow stripes along the main leaf veins.

vectors was studied in detail by Storey (1932; 1938; 1939). More recently MSV has been shown to be circulative in its vector (Nault & Ammar, 1989) but no replication could be demonstrated in *C. mbila* or *C. chinai* (Boulton & Markham, 1986).

Agrobacterium-mediated inoculation of maize plants with MSV has been reported (Grimsley *et al.*, 1987; Lazarowitz *et al.*, 1989). The use of agroinoculation procedures should assist in the characterization of virus strains, epidemiological studies and to evaluate performance of resistance sources.

Strains and serological relationships

Maize streak virus occurs in distinct strains (Storey & McClean, 1930; McClean, 1947) and some of the strains seem to be adapted to particular host species (Storey & McClean, 1930; Bock *et al.*, 1974; Ricaud & Felix, 1978). Isolates from maize, *P. maximum*, *E. indica* and sugar cane were reported by Bock (1974) to be morphologically indistinguishable and serologically related, but not identical. Maize, sugar cane and *Panicum* strains were reported by Bock *et al.* (1974). Ricaud & Felix (1978) identified maize, sugar cane and *Coix lachryma-jobi* strains and concluded that the maize and *C. lachryma-jobi* strains were closely related. Hughes *et al.* (1991) have recently concluded that the causal agent of streak disease in sugar cane is distinct from MSV and referred to it as sugar-cane streak virus (SSV). Briddon *et al.* (1992) reported that the *Panicum* strain is sufficiently distinct from MSV, at the sequence level, to be considered a separate virus and named it *Panicum* streak virus (PSV).

A virus infecting *Digitaria setigera* (previously reported as *D. sanguinalis*) has been described from Vanuatu, South Pacific (Dollet *et al.*, 1986; Donson *et al.*, 1987) and was earlier referred to as a strain of MSV (Pinner *et al.*, 1988). Recent studies have shown that the causal agent, *Digitaria* streak virus (DSV), is serologically related but not identical to MSV (Dollet *et al.*, 1986; Dekker *et al.*, 1988; Briddon *et al.*, 1992).

Pinner *et al.* (1988) compared 24 isolates of MSV derived from different host plants and identified 14 of these as belonging to the maize strain. However, these authors concluded that no adaptation to grass hosts has occurred as all the isolates which they tested were transmissible to maize cv. Golden Bantam using *C. mbila* as a vector. However, results of recent work (Mesfin *et al.*, 1992) tend to support the concept of host adaptation.

Maize streak virus from Nigeria was found by Guthrie (1977) to react with antiserum to MSV from East Africa and this has been confirmed at IITA. Great diversity in the serological reaction of MSV isolates has been detected using polyclonal and monoclonal antibodies (Dekker *et al.*, 1988; Pinner *et al.*, 1988; Pinner & Markham, 1990). Ngwira (1988) demonstrated a serological relationship amongst MSV isolates from Nigeria, Malawi, Uganda, South Africa and Egypt. Peterschmitt *et al.* (1991) have recently characterized MSV isolates from 11 African countries and reported that all isolates belong to the same serotype. In recent work at IITA with 24 isolates originating from grasses and cereal crops, 19 of the isolates reacted with a polyclonal antiserum to a severe MSV isolate from maize (Mesfin *et al.*, 1992).

Differences in virulence have been observed amongst MSV isolates tested; some of them cause mild symptoms similar to the original symptoms in grasses and are transmissible to maize at low rates (Rossel & Thottappilly, 1985; Mesfin *et al.*, 1992). The latter authors found isolates from *Dactyloctenium aegyptium*, *Digitaria horizontalis*, *Setaria barbata*, *A. compressus* and *B. lata* to be the most severe on maize.

Particle structure

Bock *et al.* (1974) were the first to report successful virus purification and preparation of an antiserum to MSV. The virus had an unusual particle and appeared to be an association of two particles occurring in doublets, referred to as geminate and leading to the term 'geminiviruses'. MSV has quasi-icosahedral particles 18×30 nm.

In purified preparations, a small number of 20×20-nm single particles have also been detected (Bock *et al.*, 1974). The bisegmented particles have a sedimentation coefficient of about 76S and the single particles have a sedimentation coefficient of 54S (Bock *et al.*, 1974). Virus-like particles of *c.* 18–20 nm diameter have been seen in the nuclei of MSV-infected hosts but not in those from healthy plants (Sylvester *et al.*, 1973). The nucleic acid of MSV is single-stranded DNA existing predominantly as closed circular molecules of molecular mass $7{\cdot}1 \times 10^5$ Da (Harrison *et al.*, 1977; Harrison, 1985).

The coat protein of MSV particles typically consists of a single species of molecular mass 28 000 Da (Bock *et al.*, 1977). Each particle encapsulates a DNA molecule of *c.* 2700 nucleotides. A Nigerian MSV isolate has been sequenced by Mullineaux *et al.* (1984), a Kenyan isolate by Howell (1984), and a South African isolate by Lazarowitz (1988). Although there is evidence for a bipartite genome in the case of whitefly transmitted geminiviruses, only one DNA species has been detected in MSV (Mullineaux *et al.*, 1984).

In 1978, the viruses having geminate particles were recognized as a distinct group by the International Committee on the Taxonomy of Viruses (ICTV) as distinguished by the size and predominantly geminate appearance of the virus particles in the electron microscope and the evidence that these viruses contain single-stranded DNA (Mathews, 1979). Maize streak virus was adopted as the type member of the group.

Control

Various cultural practices have been suggested for the control of MSV. These include 'barriers' of bare ground between early- and late-planted maize fields to reduce leafhopper movement and subsequent spread of the virus (Gorter, 1953), the avoidance of maize plantings downwind from cereal crops planted earlier, and the use of crop rotations that will minimize invasion by viruliferous leafhoppers (Rose, 1978). Insecticides have also been used to control the vectors (Rose, 1978; Rothwell, 1979; Barrow, 1992); however, resistance breeding is perceived as the most practical solution for the control of MSV. Resistance to streak was first identified in East Africa (Storey & Howland, 1967). At IITA, resistance was found within IITA's maize population TZ-Yellow; the local variety Revolution collected by the Institut Recherche Agronomique Tropicale (IRAT) in Réunion was also confirmed to be resistant (Soto *et al.*, 1982). Improved challenge methods using artificial infestations with infective leafhopper vectors both in screenhouses and in the field were developed and further improved at IITA (Leuschner *et al.*, 1980; Soto *et al.*, 1982; Alam, 1983; Dabrowski, 1987b; Bosque-Pérez & Alam, 1992).

Resistance to MSV in the majority of IITA open pollinated varieties and hybrids manifests itself as reduced disease severity combined with low field disease incidence (Soto *et al.*, 1982). Highly resistant IITA varieties have been shown to have low virus titre (Asanzi, 1991). Resistance to MSV in IITA maize germplasm is controlled by two or three major gene pairs with possible involvement of minor genes (Kim *et al.*, 1989). Immunity to MSV has been detected in inbred lines and an experimental hybrid in South Africa (Barrow, 1992).

Maize populations that combine resistance to MSV with other desirable characters have been developed at IITA. Some high-yielding, introduced varieties, as well as varieties traditionally grown in various countries in Africa, have been converted into MSV-resistant ones at IITA in a co-operative effort with the International Maize and Wheat Improvement Centre (CIMMYT) in Mexico and national programmes in Africa (Efron *et al.*, 1989). Numerous breeding programmes in Africa are using resistance sources developed at IITA to incorporate resistance into their varieties (Efron *et al.*, 1989).

While it is difficult to obtain accurate information on the adoption and spread of MSV-resistant varieties in Africa, it is known that such varieties have been multiplied and are grown by farmers in several countries including Benin, Burkina Faso, Cameroun, Ghana, Nigeria, and Togo (Fajemisin, 1992). Additionally, MSV-resistant maize germplasm is recommended for use in several other African countries (Fajemisin, 1992).

Maize mottle/chlorotic stunt virus (MMCSV)

While working with MSV in East Africa in the mid-1930s, Storey observed a virus-like condition which was transmissible by the same leafhopper vectors used in transmission studies with MSV (i.e. *C. mbila*, *C. parazeae* and *C. storeyi*). The disease was transient and the symptoms resembled those of nutrient deficiency. The agent responsible was named 'maize mottle virus' (MMV), since transmission by *Cicadulina* spp. was demonstrated (Storey, 1937).

A prominent 'chlorotic stunt' disease of maize which has been known in Nigeria for a number of years, causes characteristic mottle symptoms in its early stages like those described by Storey and was thus thought to be a manifestation of MMV (Rossel *et al.*, 1980). This condition was found to be transmitted by *C. storeyi* (=*C. triangula*). Because of its vector and the fact that in Nigeria mottle symptoms are normally followed by prominent chlorotic stunt symptoms, Rossel & Thottappilly (1983) suggested the name maize mottle/chlorotic stunt.

Geographical distribution

Maize mottle/chlorotic stunt may occur through-out tropical Africa (Rossel, 1984). Disease symptoms have been observed on maize in all ecological zones of Nigeria. Similar or identical diseases have been observed in Benin, Togo, Ghana, Burkina Faso, Sao Tomé, Zaire, Kenya, Rwanda, Tanzania, Zambia, Zimbabwe, and Botswana during surveys conducted by IITA researchers (Fig. 1, p. 496).

Symptoms

Newly-developing whorl leaves show vague mottling and chlorosis (Fig. 2b, p. 498) followed in sensitive genotypes by progressive shortening of the internodes and more or less conspicuous chlorosis, resulting in stunted growth.

Host range

While only maize is known to become infected with MMCSV, the disease is restricted to Africa and it seems probable that it originated from African grasses. However, the original host(s) of MMCSV have not been found. Grasses that are hosts of *Cicadulina* vectors of MMCSV would be the most likely candidates. Difficulties in purifying sufficient virus and the resulting lack of detection techniques makes the search for original hosts difficult.

Vectors

Maize mottle/chlorotic stunt is transmitted in a persistent manner by both *C. storeyi* and *C. mbila*. After an acquisition access period of 24 h on infected plants, leafhoppers transmitted MMCSV readily to a series of maize seedlings using daily transfers for up to 2 weeks (Rossel & Thottappilly, 1983). Maize mottle/chlorotic stunt can be acquired by *C. storeyi* in a minimum acquisition access period of 3 h; an equal duration inoculation access period is sufficient for transmission to occur (Rossel & Thottappilly, 1983).

Particle structure

Isometric particles 40 nm in diameter have been observed in purified extracts of MMCSV (Rossel & Thottappilly, 1983).

Control

Most MSV-resistant varieties and inbred lines developed at IITA show a moderate-to-high level of resistance to MMCSV. It is possible that during resistance screening both MSV and MMCSV were inoculated to plants in the field, as *C. storeyi* leafhoppers used for MSV field screening are known to transmit MMCSV (Rossel & Thottappilly, 1983). Sources of resistance to MMCSV obtained from IITA are being used by a seed company (Seed Co-op Company of Zimbabwe Ltd, Southerton, Harare) in Zimbabwe to develop maize hybrids for that region, where MMCSV is considered to be of major importance.

Maize stripe tenuivirus (MStpV)

Geographical distribution

Maize stripe disease was first reported by Storey (1936) from Tanzania. The same or similar diseases have since been reported from Kenya (Kulkarni, 1973a), Venezuela (Trujillo *et al.*, 1974; Lastra, 1977), USA (Tsai, 1975; Gingery *et al.*, 1979; 1981), Nigeria (Fajemisin & Shoyinka, 1977), India (Raychaudhuri *et al.*, 1977), the Philippines (Exconde, 1977), Perú (Nault *et al.*, 1979), Guadeloupe (Migliori & Lastra, 1980), Zaire, Sao Tomé (IITA, 1980), Australia (Greber, 1981), Mozambique (Bauwen, 1981), Mauritius and Réunion (Autrey, 1983) and Botswana (Gingery, 1983). It seems the disease has a worldwide distribution and occurs where the planthopper vector, *Peregrinus maidis* (Ashmead) overlaps with maize (Gingery, 1985).

Maize stripe tenuivirus has not been reported to reach significant incidences in continental tropical Africa. However, the disease was seen on an epidemic scale in Sao Tomé during a survey conducted in 1978 (IITA, 1980).

Symptoms

At an early stage of disease development, infected plants show yellow to light-green uninterrupted stripes or bands along the veins of the laminae (Fig. 2c, p. 498). At this stage, the bands are narrow (0·5–1·0 cm wide), but they become wider on later leaves. Chlorotic bands may eventually cover the entire leaf lamina, a condition often followed by necrosis, dieback and extremely stunted growth.

Host range

In addition to maize, various grass species have been reported to be naturally infected with MStpV. In West Africa these include *Rottboelia* *cochinchinensis* (IITA, 1979; 1985), *Brachiaria deflexa*, *Hyparrhenia dissoluta* and *Setaria* spp. (Fajemisin & Shoyinka, 1977). Sorghum can also be infected with MStpV as reported from the USA (Gingery *et al.*, 1981), Australia (Greber, 1981) and Nigeria (IITA, 1985).

Vector

Maize stripe tenuivirus is transmitted by *P. maidis* in a persistent manner and it is not mechanically transmissible. After acquisition, the virus undergoes a latent period of at least 10 days in the vector (Tsai & Zitter, 1982). Transovarial passage from females to their progeny and replication in the vector have been demonstrated (Gingery, 1983).

Serological relationships and particle structure

In agar-gel diffusion tests, extracts from infected maize, and *R. cochinchinensis* from Nigeria reacted specifically with antisera to isolates of MStpV from East Africa and Florida (USA).

Kulkarni (1973a) observed isometric virus-like particles, *c.* 40 nm in diameter, in plants infected with MStpV in Kenya; Lastra (1977) reported a similar finding in Venezuela. However, repeated attempts by several other laboratories did not reveal such particles (Gingery, 1983). The particles found by Kulkarni (1973a) were thus considered by Gingery (1983) not to be the causal agent of MStpV. Later research carried out in the USA demonstrated the presence of an unusual, filamentous nucleoprotein particle *c.* 3 nm in width in plants infected with MStpV, and this nucleoprotein was found to be associated with infectivity (Gingery *et al.*, 1981). The virus has been placed in a separate virus group (Gingery *et al.*, 1981), named Tenuiviruses.

Control

IRAT has an ongoing project in Réunion to develop varieties resistant to MStpV and other maize viruses (Marchand & Hainzelin, 1986). The variety Revolution has been used as a source of resistance to MStpV. As virus pressure in Réunion island is severe, local maize cultivars have undergone intense natural selection for virus resistance or tolerance and are considered useful sources of resistance in the breeding programme (Marchand & Hainzelin, 1986). Some of IITA's MSV-resistant varieties, though bred in the absence of MStpV, also show resistance to the disease (IITA, 1979). The resistance seems to originate in part from the maize population TZ-Yellow from which one of the sources of MSV resistance (IB-32) was originally extracted. Among plants in the TZ-Yellow population, very few were susceptible to MStpV, and the MSV resistance donor, IB-32, was highly resistant to MStpV (Rossel & Thottappilly, 1985).

Maize dwarf mosaic potyvirus (MDMV)

Maize dwarf mosaic potyvirus, sugar cane mosaic virus (SCMV) and their variants, belong to a complex of potyviruses which infect tropical grasses. Recent work with SCMV strains demonstrated that they could be divided into four distinct potyviruses, namely MDMV, SCMV, Johnson grass mosaic virus and sorghum mosaic virus (Shukla *et al.*, 1989; McKern *et al.*, 1991). Based on this new classification system, all the reports of potyviruses from maize should be reassessed and regrouping needs to be considered.

Geographical distribution

Maize dwarf mosaic potyvirus and SCMV occur worldwide in temperate regions. Maize dwarf mosaic potyvirus has been a serious problem in most maize-growing areas of the USA since the early 1960s (Findley *et al.*, 1977; Gordon, 1981). Symptoms of MDMV were observed in maize grown at mid to high altitudes in Rwanda during a survey in 1983 (IITA, 1984). The virus has not been reported to be common in the lowland humid and sub-humid tropics of Africa. In several locations in Côte d'Ivoire, MDMV has been detected in maize (Fauquet & Thounevel, 1987) and its presence in Nigeria has also been confirmed (IITA, 1977). Sugar cane mosaic virus is considered an important disease of maize in the mid-altitude regions of East Africa (Kulkarni, 1973b). Sugar cane mosaic virus has been reported from maize in South Africa (von Wechmar, 1983), Madagascar and Réunion (Autrey, 1983). A potyvirus is reported from maize in Mozambique (Bauwen, 1981) but it is not clear if this is MDMV or SCMV.

Symptoms

Diseased plants show irregular chlorosis, mottle, striping, and a tendency to develop ring-like flecks (Fig. 2d, p. 498). Sensitive varieties may show extreme distortion and stunted growth. The severity of disease symptoms may vary widely among plants in open-pollinated maize populations (Louie & Darrah, 1980).

Host range

Maize and Johnson grass (*Sorghum halepense*) (for certain strains) are natural hosts of MDMV. Sugar cane, sorghum, maize, *Eleusine* spp., *Panicum* spp. and *Setaria* spp. are hosts of SCMV (Brunt *et al.*, 1990).

Vectors

Maize dwarf mosaic virus is transmitted in a non-persistent manner by several species of aphids including *Rhopalosiphum maidis*, *R. padi*, *Myzus persicae*, *Schizaphis graminum* and *Aphis craccivora* (Knoke *et al.*, 1983). While up to 25 aphid species have been identified as vectors in the USA, it is not known how many vector species occur in Africa. The virus is easily sap-transmissible and seed transmission, although at a low percentage, has also been reported (Ford *et al.*, 1989).

Strains and serological relationships

Within the MDMV group, several strains have been designated: A, B, C, D, E, F and O (Louie & Knoke, 1975; McDaniel & Gordon, 1985; Persley *et al.*, 1985). However, studies with virus-specific antibodies against seventeen SCMV strains from Australia and the USA demonstrated that the strains could be divided into four different potyviruses, and a new classification of strains has been proposed (Shukla *et al.*, 1989; McKern *et al.*, 1991).

Particle structure

Maize dwarf mosaic virus particles are flexous filaments 770 nm long and the virus belongs to the potyvirus group.

Control

Hybrids and open-pollinated maize populations with high levels of resistance to MDMV (or SCMV) have been, or are being developed by breeding programmes in various parts of the world including the USA (Findley *et al.*, 1981), Australia (Persley *et al.*, 1981) and Kenya (Louie & Darrah, 1980). This work has been facilitated by the development of techniques for large-scale artificial inoculation in the field (Eberhart, 1983).

Some East African maize populations and hybrids have shown moderate levels of resistance to SCMV when tested with isolates obtained from maize in Kenya (Louie & Darrah, 1980). Improved, open-pollinated maize varieties developed at IITA (TZPB, TZB, and TZSR-W) when tested with an MDMV isolate obtained at IITA, also showed moderate to high levels of resistance, although it manifested itself in segregating patterns (IITA, 1981; 1984).

Maize mosaic rhabdovirus (MMV)

Geographical distribution

MMV was originally reported from Hawaii (Kunkel, 1921). The virus has since been reported from several countries in South America, USA, Fiji, India, Spain, Tanzania, Mauritius, Réunion, Madagascar, Mozambique, Kenya and Côte d'Ivoire. A disease of maize, referred to as maize line virus, reported from Kenya (Kulkarni, 1973a) and Mozambique (Bauwen, 1981) is stated by Autrey (1983) to be caused by MMV.

Symptoms

Symptoms of MMV vary according to the strain and have been described in detail by Autrey (1983). Maize mosaic rhabdovirus fine (MMV-F) causes fine yellow stripes along most of the leaves (Fig. 2e, p. 498) except the lower ones where chlorotic spots appear. Maize mosaic rhabdovirus coarse (MMV-C) results in coarse yellow stripes parallel to the veins and a pattern of striping in the lower two or three leaves identical to that caused by MMV-F in these leaves. Brown necrotic spots may occur along the coarse stripes. Symptoms of MMV-broken (MMV-B) appear as discontinuous yellow stripes separated by wide green areas (Autrey, 1983). Internode shortening results in stunting of maize (Fauquet & Thouvenel, 1987).

Host range

The natural hosts of MMV are *Sorghum verticilliflorum*, *R. cochinchinensis*, *Setaria vulpiseta*, maize and sorghum (Herold, 1972; Autrey, 1983; Brunt *et al.*, 1990).

Vector

Maize mosaic rhabdovirus is transmitted by *P. maidis* in a persistent manner (Falk & Tsai, 1983). While the virus can be acquired in less than 15 min, optimum acquisition requires 24 h (Autrey, 1983). The latent period in the vector varies between 9 and 12 days. Transmission can occur in as short a period as 15 min but transmission efficiency increases with length of inoculation access period (Autrey, 1983). The virus is known to multiply in its vector. It is not seed-borne or sap-transmissible.

Particle structure

Maize mosaic rhabdovirus has bacilliform particles measuring 230 × 90 nm which is typical of rhabdoviruses.

Control

Destruction of alternative hosts such as *S. verticilliflorum*, is effective for the control of MMV in Mauritius (Autrey, 1983). Resistant maize hybrids have been identified (Autrey, 1983).

Maize eyespot virus (MESV)

Geographical distribution

A virus serologically related to panicum mosaic sobemovirus (PMV) but named maize eyespot virus has been reported from Côte d'Ivoire (Fauquet & Thouvenel, 1987).

Symptoms

Maize eyespot virus causes yellow eye-spots on young leaves, which generally spread and cover the whole leaf as the plant ages. Infected plants are reduced in size (Fauquet & Thouvenel, 1987).

Host range

Maize is the only natural host reported so far; other graminaceous plants such as wheat and oats can be experimentally infected but are symptomless (Fauquet & Thouvenel, 1987).

Transmission

The virus is readily sap-transmissible, but no insect vectors have been identified.

Strains and serological relationships

Fauquet & Thouvenel (1987) reported a serological relationship with PMV but not with Saint Augustine decline virus, to which PMV is closely related.

Particle structure

Particles are isometric and 26 mm in diameter (Fauquet & Thouvenel, 1987).

Guinea grass mosaic potyvirus (GGMV)

Geographical distribution

Guinea grass mosaic potyvirus has been reported from maize in the central and southern parts of Côte d'Ivoire, where infection is probably widespread (Fauquet & Thouvenel, 1987).

Symptoms

Symptoms in maize consist of a green, slight mosaic on young leaves which later disappears on old leaves (Thouvenel *et al.*, 1978; Lamy *et al.*, 1979). The lack of prominent symptoms may explain why the disease has not been reported outside Côte d'Ivoire.

Host range and vector

Natural hosts are *P. maximum*, millet and maize. The aphid *R. maidis* transmits the maize strain (GGMV-B) in a non-persistent manner; GGMV is readily sap-transmissible but not seed-borne (Fauquet & Thouvenel, 1987).

Strains and serological relationships

Several serologically related strains have been distinguished: the Guinea grass strain (GGMV-A), the maize strain (GGMV-B), and the pearl millet strain (GGMV-D) (Fauquet & Thouvenel, 1987).

Particle structure

Guinea grass mosaic potyvirus has filamentous particles 825 ± 15 nm long and 13 ± 1 nm wide (Lamy *et al.*, 1979) and belongs to the potyvirus group.

VIRUS DISEASES IN NON-TROPICAL AFRICA

Several other virus diseases of maize occur in African countries outside the tropics. These include **cucumber mosaic cucumovirus** (CMV) which occasionally infects maize in southern Morocco (Lockhart & Elyamani, 1983) and **Cynodon chlorotic streak rhabdovirus** (CCSV), which was first observed on maize in southern Morocco in 1974 and subsequently found to be endemic in Bermuda grass, *Cynodon dactylon* (Lockhart & Elyamani, 1983; Lockhart *et al.*, 1985). Cynodon chlorotic streak rhabdovirus occurs in bermuda grass in France, Spain, Jordan and Tanzania. The virus causes stunting and chlorotic streaking in both bermuda grass and maize. It is transmitted by the delphacid planthopper *Toya propinque*. The virus particles are bullet-shaped and measure *c.* 72 × 240 nm. Cynodon chlorotic streak rhabdovirus appears to be primarily a virus of *C. dactylon* and only secondarily a virus of maize.

Maize yellow stripe tenuivirus (MYSV) (synonym: maize fine stripe, maize chlorotic stunt) has been reported from Egypt (Ammar *et al.*, 1984; 1990) and naturally infects maize, sorghum, wheat and barley. It is transmitted by *Cicadulina chinai* in a persistent manner (Ammar *et al.*, 1989; 1990). The particles are usually flexuous, 5–7 nm wide (Brunt *et al.*, 1990). This virus is tentatively considered to be a member of the tenuivirus group (Ammar *et al.*, 1990). The virus may infect maize elsewhere in Africa as both hosts and vectors occur outside Egypt.

Brome mosaic bromovirus (BMV) occurs in maize in South Africa, where it causes a mild mosaic or a lethal necrosis of seedlings (von Wechmar & van Regenmortel, 1966). Brome mosaic virus also occurs in grasses and wheat and it is transmitted by *Diuraphis noxia* and other grain aphids (von Wechmar & Rybicki, 1981).

Another virus reported from maize in South Africa is **barley stripe mosaic hordeivirus** (von Wechmar, 1983). Maize plants infected with this virus exhibit abnormal growth and yellowing (von Wechmar, 1983).

Barley yellow dwarf luteovirus (BYDV) has been found infecting maize in Morocco (Lockhart & Elyamani, 1983). Barley yellow dwarf luteovirus is known to infect wheat and barley in various African countries including Tunisia (Mamluck & van Leur, 1984), Egypt (Abdel-Hak, 1984), Ethiopia, Kenya (Torres, 1984) and South Africa (von Wechmar & Rybicki, 1984), but it is not known if the virus also infects maize in these countries. Further studies to ascertain if maize acts as a host for BYDV in tropical mid-altitude African regions appear justified.

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