Plant Pathology Bulletin 2: 203-217, 1993

Viruses and Mycoplasmal Agents Affecting Maize in the Tropics

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Accepted for publication: August 10, 1993

ABSTRACT

Tsai, J. H., and Falk, B. W. 1993. Viruses and mycoplasmal agents affecting maize in the tropics. Plant Pathol. Bull. 2:203-217.

It is known that at least five viral and two mollicate plant pathogens affected maize (*Zea mays*) in the tropics todays. The pathogen dicussed here includes maize stripe virus (MStV), maize mosaic virus (MMV), maize rayado fino virus (MRFV), Corn stunt spiroplasma (CSS), and maize busby stunt mycoplasma (MBSM).

Key words: maize viruses, maize mycoplasmal diseases.

INTRODUCTION

Maize (*Zea mays* L.) is one of the major cereal crops, it ranks third in production following wheat and rice with an average of 380 million tons produced annually on 120 million ha by 53 countries. It is the world's most widely grown crop in almost all tropical areas of the world including tropical highlands over 3000 m in altitude, to temperate areas as far north as the 65th latitude. Because the ecological conditions differ between the temperate areas and the tropics, the disease agents and their insect vectors also are different under these different conditions. To date at least five viral and two mollicute plant pathogens affecting maize are known in the hot and humid tropics and subsequently identified and characterized. They include maize dwarf mosaic virus (A and B), maize stripe virus, maize rayado fino virus, maize mosaic virus, corn stunt spiroplasma and maize bushy stunt mycoplasma. This chapter deals only with the last five pathogens which are considered economically important in the tropics.

MAIZE STRIPE VIRUS (MStV)

Maize stripe disease was first described in 1936 in E. Africa (120). Storey recognized two types of symptoms, one with narrow yellow stripes on the leaves, the other with broad stripes (120). Kulkarni (85) demonstrated that two symptoms of maize stripe were associated with two distinct pathogens and were transmitted persistently by *Peregrinus maidis* (Ashmead). Later Bock *et al.* (13) proved that the narrow yellow stripe was caused by a rhabdovirus (71). To date maize stripe has been reported from Venezuela (58,125), Florida (125), the Philippines (41), Mauritius (117), Australia (67,68), Peru (110) and Taiwan (29,134).

Symptomatology and host range

Initial symptoms on the inoculated plants are fine chlorotic stipplings between the veins which later develop into continuous chlorotic stripes of varying width and intensity (126), often with a 'brushed out' appearance (67) towards the tips of stripes (Fig. 1A, B). Young plants at the 4 to 5-leaf stage inoculated with MStV often exhibit complete chlorosis on the emerging whorl leaf, and the center leaf usually remains folded and bent (126).

The host range of MStV includes *Zea* spp., and several *Sorghum* spp. as well as *Rottboellia exaltata*. This virus can infect barley, rye, oats, wheat and triticale under experimental conditions (43,67,134).

Biochemical and serological properties of MStV nucleoproteins

MStV is a member of newly recognized tenuivirus group which includes rice stripe virus (RSV), rice hoja blanca virus (RHBV), rice grassy stunt virus (RGSV) and European wheat striate mosaic virus (EWSMV). This group exhibits several unique properties different from other characterized RNA plant viruses (55). Thin, filamentous, sometime circular infectious nucleoprotein particles have been associated with tenuivirus infected plants (29,57,74,79,104,123). The nucleoprotein particles are composed of a ca. 35,000 Mr nucleocapsid protein

and 4–5 species of RNA (45,79,123). The purified MStV nucleoprotein can be resolved into 4 components by rate-zonal sucrose density gradient centrifugation. When analyzed by denaturing gel electrophoresis, the 5 RNAs have molecular weights of 0.52, 0.78, 0.81, 1.18 and 3.01×10^6. When analyzed by nondenaturing gel electrophoresis, a mixture of 10 RNAs can be seen, five ss-RNAs of the sizes given above and five ds-RNAs with molecular weights two times the ss-RNAs. The additive size of the 5 RNAs suggests a ca. 18-kb (8.8 kb, 3.4 kb, 2.3 kb, 2.2 kb and 1.3 kb) RNA genome for MStV (45). It has been shown that five ss-RNA segments of opposite and complementary polarities are encapsidated separately (42).

The complete nucleotide sequences of MStV RNA 3 and RNA 4 have been determined as 2357 nt and 2227 nt in size, respectively (77,78). Two open reading frames (ORFs) are found in both RNAs. A 591-nt ORF is located near the 5' end of RNA 3 and another ORF of 948 nt is located near the 3' end in the viral complementary RNA (77). A 534-nt ORF is located at the 5' end of the RNA 4 encoding the 19,815 Mr major non-capsid protein (NCP); the other ORF of 858 nt is located at the 3' end RNA 4 encoding the 31,903 Mr nonstructural protein (78). Both RNAs have an ambisense coding strategy.

The 16,000 Mr (16K) protein which has been referred to as the NCP is found abundatntly in MStV-infected plants (49) and it can readily be found in sap from infected plants as crystals by phase-contrast light microscopy and the crystals react with antiserum to MStV NCP in immunofluorescence microscopy (19). The NCP is found as large aggregates forming filamentous electron opaque inclusion bodies (6) Recently study showed that fibrous intracellar inclusions can be readily found in paradermal sections of the leaf sheath of MStV infected maize (113).

The nucleotide sequence of MStV NCP gene has been determined. A 12-amino-acid sequence of the NCP was compared with nucleotide sequence data for MStV RNA 3 and RNA 4 and was found in perfect alignment with a 528-nt ORF of RNA 4. The deduced NCP molecular weight was 19,815, similar to that determined by SDS-PAGE analysis of the purified NCP. The NCP ORF is located 61 nt from the 5' end of RNA 4 (76).

Antisera to the 32,000 Mr (32 K) capsid and 16,500 Mr (16 K) NCP have been used for immunological analyses of extracts from MStV-infected maize plants and from inoculative *Peregrinus maidis*. The antiserum against the noncapsid protein was found to be very useful for detecting MStV infections in plants by indirect ELISA (29,41,49). Sap dilutions of 10^{-7} and purified 16.3-Kd protein as low concentration as 150 ng/ml were detectable. Other MStV-infected hosts such as rye (*Secale cereale*), itchgrass (*Rottboellia exaltata*) and oats (*Avena sativa*) were detected satisfactorily by indirect ELISA (43).

The 32 K protein was easily detected in extracts of both MStV-infected plants and inoculative *P. maidis* by ELISA and by immunological analysis of Western blots (49). The 32 K protein was detected only in individual *P. maidis* that also transmitted MStV to plants. The 16 K protein was only detected in MStV-infected plant hosts but not from extracts of groups or of individual MStV inoculative *P. maidis*. *In vitro* translation of MStV virion RNAs in rabbit reticulocyte lysates showed that both the 32 K and 16 K proteins were present in the translation products and thus virus-coded (49). We have begun to investigate why the 16 K protein is not detected in MStV-carrying *P. maidis*.

It was found that adding bentonite (200 μg/ml) to the purified preparations before injecting it into *P. maidis* greatly increased the transmission rate (45,57), and 2-mercaptoethanol (0.5%) was also essential for transmission (57). Additional evidence showed that the nucleoprotein infectivity was neutralized if the extracts were treated with antiserum prepared against purified nucleoprotein (57).

There are several other planthopper-borne viruses of gramineae which are related to MStV. One of these, rice stripe virus (RSV) from Japan, was reported to be composed of a 3–8 nm nucleoprotein (83,123). RSV also has been shown to be serologically related to MStV based on tests using antisera to their capsid proteins, however, MStV noncapsid protein antiserum did not react with RSV infected rice (59). In neutralization of infectivity tests, MStV and RSV antisera both neutralized MStV infectivity (59). Indirect ELISA and one dimensional peptide-mapping analysis on two other planthopper-borne viruses of gramineae, rice hoja blanca virus (RHBV) and *Echinochloa* hoja blanca virus (EHBV) in comparison with MStV showed that the MStV noncapsid and capsid proteins were different from those corresponding proteins of RHBV and EHBV (49). The MStV antisera to the capsid and noncapsid proteins reacted only with MStV infected plants, whereas the equivalent antisera of RHBV and EHBV reacted with plants infected with either of these viruses but not MStV. Western blot analysis also demonstrated that the antisera were specific, none of the noncapsid protein antisera reacted with any of the capsid proteins and *vice versa* (29,49).

Transmission characteristics of MStV

MStV is transmitted by *P. maidis* in a persistent-propagative manner. Nymphs of *P. maidis* transmitted MStV with ca twice the efficiency after a 24, 48, 68, 96, and 192 hr acquisition access period (AAP) as did adults. Macropterous adults (Fig. 1C) were slightly more efficient transmitters than brachypterous adults (Fig. 1D). The minimum AAP of MStV by nymphs was

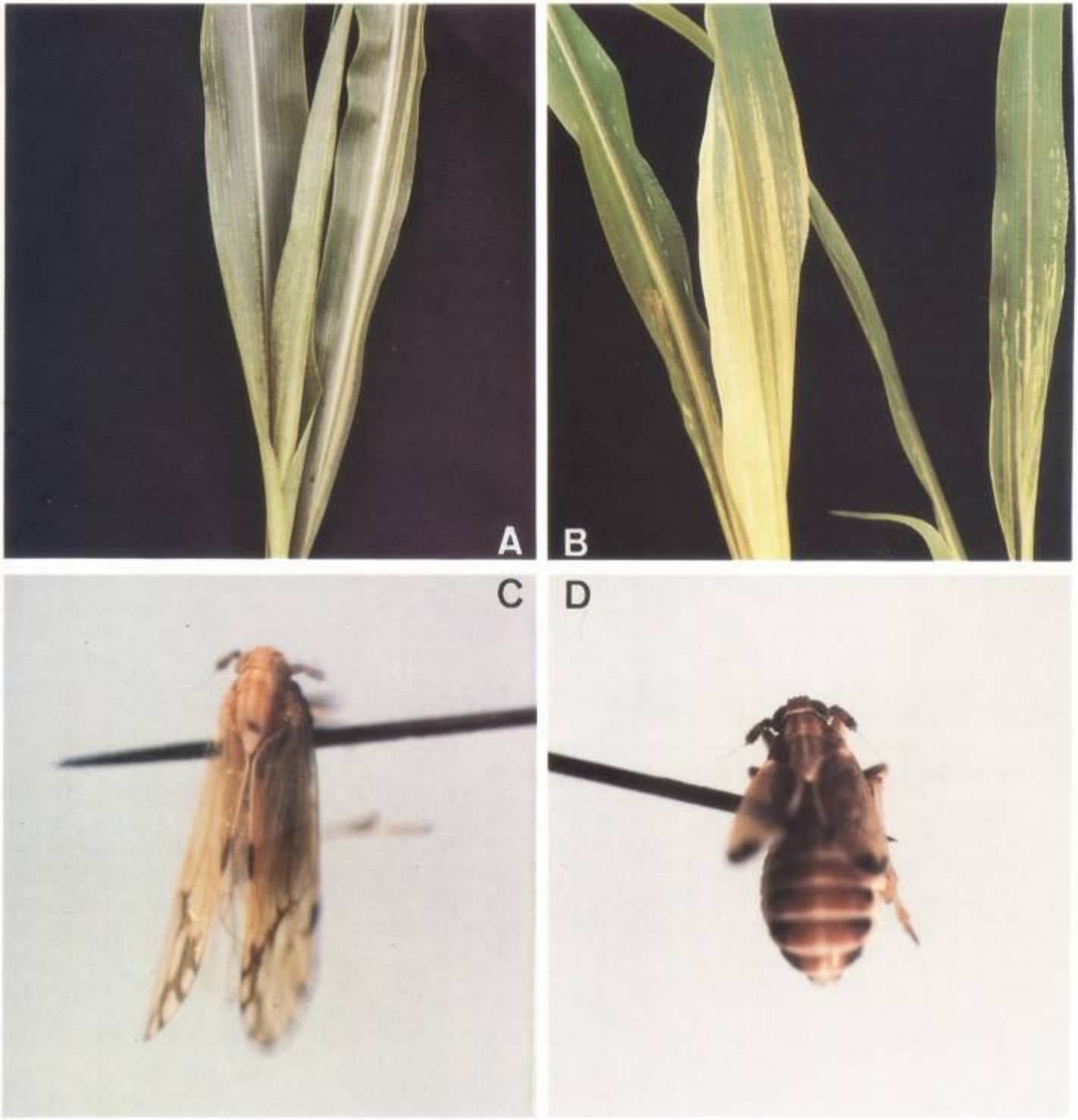

Fig. 1. Maize stripe-affected plants and vector planthoppers. Symptoms of maize stripe on maize showing initial fine chlorotic stripplings (A) and fused chlorosis at leaf base and a "brushed out" appearance (B). Adult of the planthopper *Peregrinus maidis* with long wings (C) or short wings (D).

4 hr. The minimum incubation period (IP) in both nymphs and adults was 4 to 5 days. The average retention of MStV by 2nd and 3rd instars was 13.7, 13.2, and 15.8 days after 48, 72, and 98 hr AAP as compared to 3.7, 5.5, and 6.5 days retention by adults. MStV could also be transmitted by sap injection, hemolymph injection and transovarial passages (131). The rate of transovarial transmission was reported as high as 33.3% (131) propagative in *P. maidis* and 59% (57). In a time course study, no 32 K protein was detected in *P. maidis* until 8 days after the beginning of a 5-day AAP on MStV-infected plants. The percentage of MStV-positive *P. maidis* increased over time indicating multiplication of MStV in *P. maidis* (49). These data suggest that the MStV is propagative in *P. maidis*.

Biology of MStV vector, *P. maidis*

P. maidis is pantropical species (9) and has been recorded from most tropical regions (130). In general,

there are 5 instars, however, the number of instars varied depending on the temperatures. The nymphal development time and adult longevity were also temperature dependent. Developmental times for each instar varied from 10 to 24.3 days for instars one through four at 10 C, 7.7 to 13.5 days for instars one through five at 26.7 C, and 1.9 to 16.8 days for instars one through four at 32.2 C. Both male and female longevities were highest at 15.6 C and lowest at 10 C. Number of eggs laid per day per female was (mean ± SD) 605 ± 2.5, number of eggs per female per life was (mean ± SD) 605 ± 190.1 preoviposition period was 3 to 6 days, and the oviposition period was 11 to 48 days. The optimal temperatures for *P. maidis* are 21.1 C and 26.7 C (130).

It was found that several spot characteristics such as the number of tarsomers on the metatarsi, the number of pits on each side of pronotum, the number of teeth on the second tarsomere, and metatibial spurs can be used to identify *P. maidis* instars (130). *P. maidis* was reported to utilize such plant hosts as *Sorghum bicolor* (L.), *Pennisetum typhoides* (Burm.) Stapf and Hubb, *Echinochloa colonum* (L.) Link, and *Paspalum scrobiculatum* L. (28,121). We have found that this insect bred on *S. bicolor, Rottboellia exaltata, Tripsacum dactyloides* (Tsai and Falk, unpublished).

MAIZE MOSAIC VIRUS

Maize mosaic was first reported in 1914 in Hawaii (86). It is considered a serious disease in the tropics and subtropics, and has been speculated as a possible cause of the collapse of Mayan civilization (23). The rhabdovirus morphology of maize mosaic virus (MMV) was not known for nearly 40 years (72). MMV is also transmitted by *P. maidis* in a persistent manner. Maize mosaic has often been confused with maize stripe in the literature because of their similarity. MMV has been reported in Central and South America, Mexico, India, Mauritius, Reunion, Madagascar, and Tanzania (10,71,119). Although the rhabdovirus infections of maize in the U.S. were found in Texas, Alabama, Louisiana, and Mississippi (18,39,135), positive vector identification and serological relationship to MMV were only done with Florida isolate of MMV (18,44).

Symptomatology and host range

Initial symptoms of maize mosaic are light-green to yellow long stripes along the midrib, these stripes elongate to form the distinct, even, chlorotic stripes between and along the veins extending from the base of the leaf to the tip (Fig. 2). All commercial maize hybrids tested in Venezuela were susceptible to MMV (89), and all U.S. mainland sweet corn inbreds, hybrids, and cultivars tested in Hawaii were susceptible to MMV (14). Other plants such as *R. exaltata, Septaria vulpiseta* Roem. E. Schult, *S. verticilliflorum Z. mays mexicana* Iltis and *Sorghum* sp. *Axonopus compressus* Beauv. are susceptible to MMV (10,48,51,89). Yield losses of more than 50% under glasshouse and field conditions were recorded (10).

Properties of MMV

Various sizes of MMV virions have been reported. Dimensions of 255 × 90 nm for negatively stained partially purified preparations, and 242 × 48 nm for particles in thin sections of MMV-infected tissues have been reported for Venezuelan isolate (89); 224 × 68 nm and 234–325 × 63 nm have been reported for purified virions and those in MMV-infected cells, respectively, for the Florida isolate (18,44); and deminsions of 204 × 67 nm for bullet-shaped particles, 245 × 80 nm for bacilliform particles have been reported for the Hawaiian isolate of MMV (102).

Both the perinuclear accumulation of virus particles in the infected cells (14) and the presence of particle in the cytoplasm of epidermal, mesophyll, and vascular parenchyma cells and phloem and xylem elements of infected plants have been reported (89,102). The granular masses were found to surround the nuclei of the peidermal strips of MMV infected leaves and roots using light microscopy (113).

The virions of MMV have been purified using modifications of the methods developed for sonchus yellow net virus by Jackson and Christie (80). MMV virions contained a single-stranded RNA of Mr 4.2×10^6 (44). MMV virons contain three major structural proteins of Mr 75,000, 54,000, and 30,000 as analyzed by SDS-PAGE. The Mr 75,000 and 30,000 proteins were determined as G and M proteins, respectively, whereas Mr 54,000 protein was determined as an N protein (44). Lastra and Carballo (90) identified two additional proteins, L protein of Mr 150,000 and N_s protein of Mr 45,000 as determined by PAGE analysis. The Florida isolate of MMV is serologically related to Venezuelan MMV (44), and the three isolates of MMV from Mauritius were also related to Venezuelan MMV (10).

Characteristics of MMV transmission by *P. maidis*

MMV is solely transmitted by *P. maidis* in a persistent-propagative manner. The rate of MMV transmission by *P. maidis* by means of plant acquisition ranged from 5 to 42% (46,89). *P. maidis* was able to acquire MMV in less than 15 min. The IP in *P. maidis* was 9 and 12 days for three strains of MMV in Mauritius (10). Carter (26) found that the IP of MMV ranged from 11 to 29 days. Others have reported IP of 16–58 days (70) and 14–31 days (103). The virus persisted in *P. maidis* and the patterns of transmission were often erratic (46,103). The median incubation period (IP_{50}) was 13.5 and 14.8 days for Florida isolate

of MMV (46). The efficiency of MMV transmission by *P. maidis* could be increased from 20–43% by injection with either purified MMV or with sap from MMV-infected corn plants (46,89).

The detection of MMV in individuals of *P. maidis* was dependent on inoculum concentrations (46). The total number of MMV-postive *P. maidis* decreased with decreasing injection inoculum concentrations (25, 2.5 and 0.25 μg/ml). The average absorbance value for MMV-positive *P. maidis* increased with time at all three concentrations, indicating multiplication of MMV in *P. maidis*. Evidence for MMV multiplication in *P. maidis* was also originally suggested by thin section electron microscopy (73). The interaction between MMV and MStV *in vitro* has been demonstrated (7).

MAIZE RAYADO FINO VIRUS

Maize rayado fino was first reported in El Salvador in the 1960's (8). Later Gamez (50,51) demonstrated a Costa Rican isolate of maize rayado fino virus (MRFV) transmission by *Dalbulus maidis*. This disease has also been found in Uruguay, Brazil, Colombia, Panama, Guatemala, Honduras, Nicaragua and Mexico (52,53), Peru (110), Venezuela (91), Ecuador (20) and the U.S. (15). Yield losses in Central America may be up to 40–50% of early infected plants. Losses and incidences may reach 100% for newly introduced cultivars (52). All maize cultivars tested were susceptible to MRFV in Central, South and North America (51,52,53,122).

Symptomatology and host range

Symptoms on the inoculated maize first appear 7–14 days after inoculation as a few rows of fine, unevenly spaced chlorotic dots or short stripes along the secondary and tertiary veins at the basal portions of the young leaves (Fig. 3). The discolorations range from chlorosis to complete bleaching. The dots become more numerous and fused longitudinally on succeeding leaves as chlorotic stipple stripes. Symptoms on young plants are always more pronounced than the old plants. However symptoms tend to fade gradually in most inoculated plants. Only *Zea mays* and its teosinte subspecies, *Z. luxurians, Z. diploperennis, Tripsacum australe, Rottboellia exaltata,* and several *Z. mays* × *T. dactyloides* hybrids were susceptible to MRFV (109).

Properties of MRFV

MRFV can be readily extracted from infected tissue with simple procedures (51,52). The Texas and Florida isolates of MRFV were recently purified by means of chloroform clarification, rate-zonal centrifugation, and isopyncnic banding in CsCl (48,56). Antiserum prepared with a Costa Rican isolate MRFV reacted with Brazilian corn streak virus and virus del rayado Colombian del maiz (82,101). MRFV particles are isometric, 22–33 nm in diameter and contain a single-stranded RNA genome (2.4×10^6 daltons)(56).

Two capsid proteins were found in each component. Leon and Gamez (92) suggested that the Costa Rican isolate of MRFV had one major capsid protein and possibly a minor protein. The two capsid proteins (ca Mr 29,000 and 22,000) of the Florida isolate of MRFV were compared by one-dimensional peptide mapping after digestion with *Staphylococcus aureus* V-8 protease and showed an indistinguishable set of polypeptides (48). The irregular inclusions and granular inclusions in the parenchyma and phloem cells of leaf sheaths, lef veins and roots were used for diagnosis of MRFV infection (113).

Characteristics of MRFV transmission by *D. maidis*

MRFV is transmitted by *D. maidis* in a persistent manner. A protracted incubation period in the vector is required. The rate of MRFV transmission by *D. maidis* was usually low ranging from 10–34% (50,51,85,109). Nymphs were more efficient transmitters than the adults (109). The average IP in *D. maidis* was 15 days (15), 16 days (109), 12.5 days (60) and 13.8 days (Tsai and Falk, unpublished). The average retention period in *D. maidis* was 20.2 days (15); 16.5 days (Tsai and Falk, unpublished). The infectivity of partially purified MRFV was demonstrated by vector injection and membrane feeding (51). Gonzales and Gamez (60) were first to suggest that MRFV multiplies in *D. maidis*. Later Nault *et al.* (109) demonstrated that the transmission rate for *D. maidis* injected with partially purified MRFV was dosage dependent. Using ELISA tests, MRFV was shown to multiply in *D. maidis* in a time course study (56,118). The Texas isolate of MRFV has also been experimentally transmitted by *D. elimatus, Stirellus bicolor,* and *Graminella nigrifrons* (109) MRFV was reported to be pathogenic to *D. maidis* and *D. elimatus* (11).

CORN STUNT SPIROPLASMA

Corn stunt is one of the most economically important diseases of maize in the U.S., Mexico, and Central and South America (17,108). Corn stunt was first named by Kunkel (87). Over the next three decades, corn stunt was thought to be caused by several strains of a virus based on symptomatology and vector transmission (62,98,108). The helical morphology of the causal agent of Rio Grande corn stunt (96) was subsequently established (31,35,133) and was named as corn stunt spiroplasma (CSS) (*Spiroplasma kunkelii*). CSS is transmitted naturally by *Dalbulus maidis* (DeLong and Wolcott), and *D. elimatus* (Ball), and experimentally by *Graminella nigrifrons* (Forbes), *G. sonora* (Ball), *Stirellus bicolor* (Van Duzee), *Exitianus*

exitiosus (Uhler), and *Euscelidius variegatus* (Kirsch.) (36,62,64,111).

During 1978–1980, the CSS played a dominant role in the epidemic in south Florida as part of the disease complex (21,38,129); the infection of CSS in the diseased field samples in 1979 and 1980 reached 68.4 and 98.5%, respectively (21). In recent years the incidence of CSS has declined and MStV is the prominent pathogen (47).

Symptomatology and host range

The initial symptoms of Rio Grande corn stunt showed characteristic small chlorotic stripes that developed at the leaf bases of new leaves after about 25–30 days. The chlorotic stripes become fused and extended further toward the leaf tips in the older leaves with green spots and stripes on a chlorotic background (Fig. 4). The infected plants had much shorter internodes and a proliferation of secondary shoots in leaf axils. The reddening on leaves varied depending on the corn genotype and environmental conditions. The plant hosts of CSS are *Z. mays, Z. mays mexicana* (Schrad.) Iltis, *Z. diploperenis* Iltis, Doebley and Guzman, *Z. perennis* (Hitchc.) Reeves and Mangelsd, *Z. mays* × *Tripsacum floridanum* Porter ex Vasey L., and *Z. luxurians* (Durieu and Ascherson) Bird (36,105,108). In addition, *Vicia faba* L., *Catheranthus roseus* (L.) G. Don, and *Lolium perenne* L. were reported to be susceptible to CSS (25,100). Radish (*Raphanus sativus*), mustard (*Sinapis alba*) and spinach (*Spinacia oleracea*) were also reported as experimental hosts for CSS (99).

Properties of CSS

CSS is a motile, helical, cell wall-free prokaryote as seen by phase contrast or dark field microscopy of plant juice or hemolymph and abdominal smears from leafhopper vectors (35). It is a phloem limited organism. CSS is highly resistant to penicillin, but sensitive to antibodies in vitro tests (27), and treatment of inoculated plants with tetracycline antibiotic caused remission of symptoms and interfered with leafhopper transmission (63). The helical cell of CSS is bounded by a trilaminar membrane. When CSS is cultured in vitro, rounded bodies 0.4–0.6 um in diameter were found to connect to helical cells. The motility of CSS was observed as translational movement (36). CSS was first isolated in an artificial medium (30), and subsequently was cultured and subcultured (31,133). The successful culture and subculture depended on the mothod of isolation, incubation temperature, atmospheric conditions, pH, osmotic pressure of the culture medium and composition of medium (36,38).

CSS was reported to be pathogenic to *D. elimatus* and *D. maidis* (65). The pathogenicity of CSS to *D. maidis, D. elimatus, D. gelbus, D. guevarai, D. quinquenotatus, D. tripsacoides* and *Baldulus tripsaci* by shortening the longevity of leafhoppers has been demonstrated (93,94,112). Other effects of CSS on leafhopper survival and fecundity (93,94,112), development rates (93) have also been studied.

CSS is not only related to Spiroplasma citri, but also to spiroplasmas from honey bees, flower nectar, and ticks. Like other spiroplasmas, it can be infected by spiroplasma virus (36).

Characteristics of leafhopper transmission

CSS is transmitted by *D. maidis* in a persistent and propagative manner (3,95,111,129). Other vectors include *D. elimatus, D. grievarai* (DeLong), *G. nigrifrons, G. sonora, S. bicolor, E. exitosus, Cicadulina mbila* (Naude), *Macrosteles sexnotatus* (Fallen), *E. variegatus* (64,99,105,111). *D. maidis* is the most efficient vector of CSS (4,87,88,93) with an AAP of 15 min and 7 days, 15 and 100% of the test insect transmitted CSS, respectively (99). CSS transmission could also be achieved by injection of the vector with either sap extracted from the infected plant or cultured CSS and membrane feeding (31,35,99). 100% transmission efficiency of *D. maidis* following injection and membrane feeding has been reported (2,3,4). The IP_{50} in *D. maidis* was 19 and 21.2 days (105,108), 17.5 to 21.2 days (129), and 14.3 days (3,4). The length of IP was negatively related to the length of AAP (3,4). The retention periods of CSS by *D. maidis* were variable ranging from 88 days (88), 42 days (3,4), to 45 days (129).

D. guevarai was reported to be a more efficient vector of a Mexican isolate of CSS than *D. maidis* (116). The rates of CSS transmission by *D. elimantus, E. exitiosus, G. nigrifrons,* and *S. bicolor* after a 4-day AAP were at 80, 84, 20, and 61%, respectively (105). The transmission rate of a Jamaican isolate of CSS by *C. mbila, E. variegatus* and *M. sexnotatus* were at 60, 3.8 and 2%, respectively (99).

Biology of CSS and MBSM vector, *D. maidis*

There is little information available concerning the ecology and biology of *D. maidis* since it was reported as a vector of the corn stunt pathogen (87,107). Davis (33) performed a brief study on the biology of *D. maidis* at six temperatures and found that *D. maidis* adult longevity at 70 °F was 26–51 days and the average number of eggs produced per female per life was 151. Females failed to lay eggs at 55 ° and 65 °F. Tsai (128) studied the life history of *D. maidis* at 10, 15.6, 26.7, and 32.2 C. The average development times for instars I-V ranged from 11.6 to 33.6 days at 10 C, 6.3 to 13.3 days at 15.6 C, 2.5 to 3.8 days at 26.7 C, and 2.4 to 4.4 days at 32.2 C. Both male and female (Fig. 5) longevities were greatest at 15.6 C and lowest at 32.2 C. Oviposition data obtained at 15.6 and 26.7 C.

Fig. 2. Symptoms of maize mosaic showing elonged chlorotic stripes between the veins. Note that these stripes do not fuse together.
Fig. 3. Symptoms of maize rayado fino showing fine and unevenly spaced dots and stipplings at the basal portions of young leaves.
Fig. 4. Symptoms of corn stunt showing fused chlorotic stripes and shortened internodes.
Fig. 5. Adult of *Dalbulus maidis* (male on the right; female on the left).

respectively, showed that the number ($x \pm SD$) of eggs per female per day was 3.62 ± 1.09 at 15.6 C and 14.18 ± 3.55 at 26.7 C, the number ($x \pm SD$) of eggs per female per life was 402.33 ± 140.03 at 15.6 C and 611.08 ± 164.96 at 26.7 C. Eggs were seldom laid within 24 hours after adult emergence. Adult longevities ($x \pm SD$) between mated females and unmated females at 15.6 and 26.7 were 111.0 ± 14.5 days for mated, and 180.0 ± 26.1 days for unmated at 15.6 C, and 45.5 ± 15.8 days for mated and 112.0 ± 16.5 days for unmated at 26.7 C. Pitre (114) reported that the nymphal development time on corn ranged from 11 to 16 days and the average adult longevity was 12.2 and 12.1 days for females and males, respectively. Besides corn, teosinte, *Euchlaena mexicana* and gamma grass, *Tripsacum dactyloides* were also reported as alternate

hosts of *D. maidis* (12,115). The mean nymphal development time on *T. dactyloides* was 15.4 and 15.3 days and the average adult longevity was 33 and 11.6 days for females and males, respectively (114). Tsai (128) also tested *T. dactyloides, T. dactyloides* var. *meridonale, T. floridanum, Rottboellia exaltata, Secale cereale,* and *Avena sativa* as alternate hosts for *D. maidis* and found that only *T. dactyloides* var. *meridonale* was suitable for rearing *D. maidis.*

MAIZE BUSHY STUNT MYCOPLASMA

In 1955, Maramorosch described two types of corn stunt from Mexico. The first type was designated as Rio Grande corn stunt originally described Kunkel (88) from Texas. The second type was designated as Mesa Central corn stunt which is now believed to be a nonhelical mycoplasma, the maize bushy stunt mycoplasma (MBSM)(16,105). Maramorosch (97) futher demonstrated the difference of these two agents by means of cross protection between maize bushy mycoplasma and CSS. Based on symptomatology, the Louisiana and Mississippi corn stunt agents could also be MBSM (32,62,64). However the proof of their identity and relationship awaits culture of the MBSM and serological study.

Symptomatology and host range

Inoculated plants initially develop a marginal yellow and orange color of the older leaves. The symptoms on subsequently developed leaves are characterized by marginal chlorosis, tearing, shortening and twisting of young leaf tips. Numerous tillers develop at the base of the plant and at leaf axils. Sweet corn cultivars such as "Aristogold" and "Aritogold Bantam Evergreen" hybrids develop extensive leaf reddening, and more basal and auxillary shoots as compared to "Guardian" sweet corn (Fig. 6). Only maize and three races of *Z. mays L. mexicana* (Schrod.) Iltis are known to be susceptible to MBSM (105).

Biology of MBSM

MBSM is a phloem limited pathogen and is similar in morphology and ultrastructure to that of yellows diseases of plants. Granados (62) demonstrated the occurrence of Louisiana corn stunt agent both in vectors and plants. MBSM was pathogenic to leafhopper vectors; it reduced the longevity of *B. tripsaci, D. maidis, D. quinguenotatus, D. tripsacoides, D. guzmani, D. longulus, D. guevarai* (106). Recently, cloned DNA probes for detecting MBSM from the experimentally inoculated corn and infectious *D. maidis* were developed (38).

Transmission characteristics of MBSM by leafhopper vectors

MBSM is transmitted by *D. maidis* in a peristent and propagative manner. It is also transmitted by *D. elimatus, Baldulus tripsaci, G. nigrifrons,* and *G. sonorus* (62,64,66,105). The rate of MBSM transmission

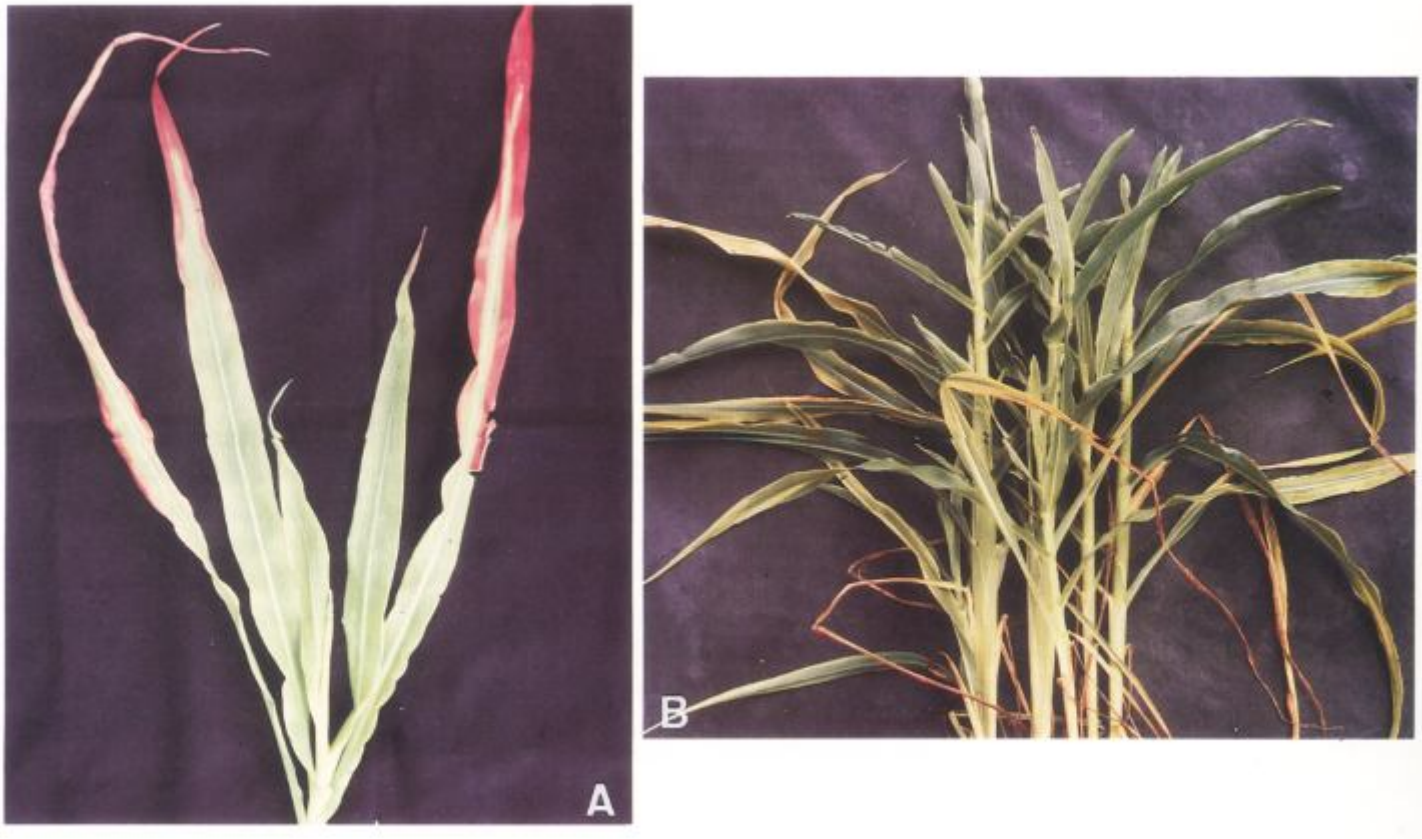

Fig. 6. Symptoms of maize bushy stunt showing leaf reddening (A) and excessive tillering and marginal chlorosis, tearing, shortening and twisting of young leaf tips (B).

by *D. maidis* ranged from 43.9 to 88.9% (105,129), wheras it was transmitted by *D. elimatus* and *G. nigrifrons* at 58.8 and 8.2%, respectively (105). The mean IP for Texas isolate of MBSM in *D. maidis* was 24.2 and 25.5 days (105,129) and IP_{50} for Florida isolate of MBSM in *D. maidis* was 28 days (129). The minimum IP for the Louisiana isolate of corn stunt was 17 to 22 days for *D. maidis,* 14 to 15 days for *D. elimatus* and 22 to 26 days for *G. nigrifrons* (64). The minimum IP for Mississippi isolate was 12 days for *D. maidis* and 15 to 18 days for *G. nigrifrons* (32). The average retention time for Texas and Florida isolates of MBSM was 32.6 and 34.5 days, respectively (129). Under field conditions, plants were often found to be doubly-infected with CSS and MBSM (34,38,108). However, the symptoms of MBSM in the doubly-infected plants always developed earlier than those of CSS as the incubation period for MBSM in corn was 18.9 days compared to 43.3 days for CSS (108).

CONCLUSION

All five tropical corn pathogens included in this chapter are transmitted by the auchenorrhyncha vectors in a persistent-propagative manner (127). In the last two decades, a great deal of progress has been made on the etiology, purification and culture of these corn pathogens which makes a detailed analysis of the mechanisms of their transmission possible. In spite of available information on the interrelations between corn pathogens, the insect vectors, and the host plants, our knowledge of the pathogenic mechanisms involved in any one of these five diseases of corn is very minimal. It is imperative that future studies emphasize research on elucidating the mechanisms of pathogenicity of corn pathogens in corn which will ultimately yield fundamental information of practical importance.

It has been shown that the transmission of these pathogens by their insect vectors is a dynamic process which is affected by biotic and abiotic factors such as temperature and humidity, pathogen strains, intrinsic vector specificity and efficiency, vector biotypes and species, acquisition methods, acquisition access period, inoculation access period, and host plant species. These factors alone or in combination can affect the epidemiology and severity of the diseases. Hence it is important that the biology, ecology and epidemiology of each disease be thoroughly studied with disease control in mind.

Since the relationship of vector-pathogen-plant is such a complex system, with so many variables mentioned above, each set of factors requires careful analysis, and generalizations can only serve as guidelines for other researchers. Recently we have begun to use MStV- *P. maidis* system to characterize the MStV genome and to compare MStV replication and gene expression in its plant and insect hosts (42,76,77,78). Hopefully it would lead to development of novel control strategy.

In recent years, highly specific antisera have been prepared to MStV, MMV, MRFV and CSS. The development of ELISA, immunological analysis of Western blots and nucleic acid hybridization techniques should enable us to understand more fully about the distribution and patterns of migration as well as seasonal fluctuations of infectious vector populations, to search more efficiently for possible new host(s) and vector(s) and to assess the role of alternate hosts and secondary vector(s) in the epidemiology of these corn diseases. Hopefully they will lead to development of more effective and practical disease control measures.

Disease and/or pest control is the ultimate goal of each researcher. The complexity of insect-transmitted corn pathogens makes them more difficult to control. The most widely employed practice at present time is integrated pest management (5). However, the most promising control measure is the use of resistant or tolerant varieties. To date the only successful example in developing the major breeding program for both dent and sweet corn resistant to MMV is done by Brewbaker (22). No corn lines immune to MStV, MRFV, CSS, MBSM are available. This poses a tremendous challenge for maize genetists and breeders to identify the gene(s) responsible for the resistance in maize germplasm. Any fruitful results will probably have to come from the concerted effort of molecular biologists, plant breeders, plant pathologists and vector entomologists.

Finally, we must be aware of the advances in biotechnology. Its promise is so powerful that it cuts across disciplines of biological sciences and offers us a promising tool to address the complex problems of maize. By using the techniques of protoplast fusion, in vitro plant culture and recombinant DNA technology, one should be able to hybridize corn with the perennial relatives of maize among *Zea* and *Tripsacum* spp. which are tolerant or immune to CSS and MBSM, or perhaps with other sexuany incompatible monocotyledon species as well as to develop better control of the pests. Biotechnology potentially cuts down the time required for corn variety breeding and propagation, and it provides maize researchers with a good method for protecting and exchanging germplasm.

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摘　　要

James H. Tsai[1], Bryce W. Falk[2]. 1993. 熱帶地區玉米之病毒與菌質體病害．植病會刊 2:203-217.
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玉米生長在不同的生態環境，有多種不同的病原與媒介昆蟲。熱帶地區就已鑑定五種玉米病毒、一種螺旋菌質體及一種菌質體病原。這些病原爲玉米矮化病毒 A 與 B、玉米條紋病毒、玉米細條紋病毒、玉米花紋病毒、玉米矮化螺旋菌質體和玉米叢矮菌菌質體。

關鍵詞：玉米病毒、玉米菌質體病害。