Corn Stunt Spiroplasma and Viruses Associated with a Maize Disease Epidemic in Southern Florida

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ABSTRACT

Bradfute, O. E., Tsai, J. H., and Gordon, D. T. 1981. Corn stunt spiroplasma and viruses associated with a maize disease epidemic in southern Florida. Plant Disease 65:837-841.

In 1979 and 1980, a severe disease complex was observed in fall-planted maize in southern Florida. Assays revealed spiroplasmas, presumed to be corn stunt spiroplasmas, in most of the plants. In some plants, maize rayado fino virus, maize stripe virus, maize dwarf mosaic virus (strain B), and novel, straight, tubular viruslike particles (about 720 nm long) were found. Pathogens were found in all plants with diagnostic symptoms and in some plants with only symptoms of a coinfecting pathogen or unidentified symptoms. This is the first evidence of a high incidence of spiroplasmas associated with a severe maize disease in the United States.

Additional key words: *Dalbulus maidis, Exitianus exitiosus, Graminella nigrifrons, Peregrinus maidis*

A severe, viruslike disease outbreak in fall-planted maize (*Zea mays* L.) occurred in southern Florida in 1979 and again in 1980. Maize stripe virus (MStpV) (6,20), maize rayado fino virus (MRFV) (4), and corn stunt virus (14) have been reported in southern Florida. The identity of corn stunt virus has not yet been resolved (16). A similar outbreak of maize disease is not known to have occurred in this area for more than 20 yr.

We describe the disease outbreak and report the results of microscopic, serologic, and vector transmission assays for pathogens in samples from affected plants. Abundant corn stunt spiroplasmas (CSS), three maize viruses, and novel viruslike particles were found but may not account for all symptoms observed.

MATERIALS AND METHODS

Samples and field data. O. E. Bradfute and J. H. Tsai made field observations and selected samples during surveys near Princeton, FL, about 12 km north of Homestead. Further field observations and samples selected from the same area were supplied by D. C. Wrucke, D. R. Wilkinson, and J. A. Wright (Pioneer Hi-Bred International, Inc.) and by K. J. Leonard (Department of Plant Pathology, North Carolina State University, Raleigh). M. B. Lawrence (National Hurricane Center, National Weather Service, NOAA, Coral Gables, FL) interpreted the weather data.

Assays. Spiroplasmas were detected by dark-field light microscopy of expressed leaf sap (4) and by electron microscopy of sections of fixed and embedded leaf samples (3). Virus particles were detected by electron microscopy of negatively stained leaf sap (4). Enzyme-linked immunosorbent assays (ELISAs), as described previously (17), were used to test for MRFV and maize dwarf mosaic virus strain A (MDMV-A) and strain B (MDMV-B). Similar ELISAs were used to test for maize chlorotic dwarf virus (MCDV) and maize chlorotic mottle virus (MCMV) (D. T. Gordon, *unpublished*). Mechanical transmission assays (8) were used to confirm the differentiation between MDMV-A and MDMV-B.

Vector transmission. Colonies of *Peregrinus maidis* (Ashmead), *Graminella nigrifrons* (Forbes), and *Exitianus exitiosus* (Uhler) were established from 1974–1979 collections in the Fort Lauderdale area by J. H. Tsai and identified by F. W. Mead (Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville). Colonies of *Dalbulus maidis* (DeLong & Wolcott) were collected from heavily infested maize and *Tripsacum* spp. at the Fairchild Tropical Garden in Miami on 14 April 1978, and identification was confirmed by F. W. Mead and D. M. DeLong (Department of Zoology and Entomology, Ohio State University, Columbus).

D. maidis, P. maidis, and *E. exitiosus* were reared on maize (*Z. mays* var. *saccharata* 'Guardian') with 12 hr of light per day. *G. nigrifrons* was reared on Tetra-Petkus rye (*Secale cereale* L.) with 16 hr of light per day. All colonies were maintained in an insect-rearing room or growth chamber at 23–27 C. Guardian sweet corn was used for source and test plants.

For transmission tests, third- to fourth-instar nymphs were given acquisition access periods on infected plants or field-collected samples, followed by a 21-day incubation period on healthy maize plants. Insects (5 or 10 per test plant) were then caged for a 5- to 8-day inoculation access period. Plants exposed to insects taken directly from colonies remained healthy.

To determine the latent period and retention period of the disease agent in the vector, insects were transferred singly to healthy maize test seedlings at the two- to three-leaf stage after the acquisition access period. Serial transfers were made daily for 2–3 wk and every 2 days thereafter.

RESULTS

Field observations. Disease was observed in fields separated by as much as 8 km on 27–28 November 1979 and thought to be representative of an estimated 2,000 ha of fall-seeded maize south of Miami. Severity and prevalence varied from slight discoloration of a few plants to total yield loss of all plants in one field. Distribution of affected plants within a field showed no obvious pattern such as increased incidence along a row or edge.

Leaf symptoms that could be readily associated with known diseases included high-contrast chlorotic streaks, symptoms of Rio Grande CSS (Fig. 1); high-contrast rows of fine, unevenly spaced dots and streaks of discoloration along second-, third-, and fourth-order veins, symptoms of MRFV (4); chlorotic stripes

Approved for publication as Journal Article 44-81 of the Ohio Agricultural Research and Development Center, Wooster, and as Florida Agricultural Experiment Station Journal Series Paper 3037.

Accepted for publication 30 July 1981.

0191-2917/81/10083705/$03.00/0

and wide bands parallel to veins, symptoms of MStpV (6,20); and chlorotic mosaic patterns, symptoms of MDMV (13). Symptoms neither diagnostic for a known maize disease nor necessarily associated with a pathogen included diffuse chlorotic mottling (Fig. 2), diffuse interveinal chlorosis resembling magnesium deficiency (Fig. 3), and low-contrast chlorotic streaks at leaf blade bases (Fig. 4).

Few plants with more than one type of symptom were observed. Reddening at leaf tips and margins occurred on most plants regardless of symptoms, except those with mosaic. Although reddening indicates stress, it appeared to be associated with genotype and was not useful in disease diagnosis.

Many affected plants showed little or no stunting. However, only some of the plants with leaf symptoms of CSS infections showed significant stunting or other symptoms of this disease (multiple ears and increased tillering).

Fields planted shortly after 3 September 1979, when Hurricane David (11) passed near the area, were most severely affected. Increased rainfall and cloud cover after the hurricane prevented the application of or removed much of the semiweekly insecticide commonly applied as part of the intensive cultural practices followed in the area. Concurrently, growers noted an unusual abundance of insects in and around seedling maize fields. From growers' descriptions, these insects may have included the leafhopper and planthopper vectors of maize pathogens.

Symptoms of representative plants in five fields were recorded to document the variation in prevalence of symptom types. Symptoms on maize inbreds planted in one entire field on 10 September 1979 were so severe that diagnosis was not attempted. Sixty-two of 100 consecutive hybrid maize plants in the border row of this field showed symptoms (14 with CSS symptoms, two with MRFV symptoms, six with MStpV symptoms, nine with diffuse chlorotic mottling, six with diffuse interveinal chlorosis, and 25 dead or desiccated to the extent that patterns of discoloration were not evident).

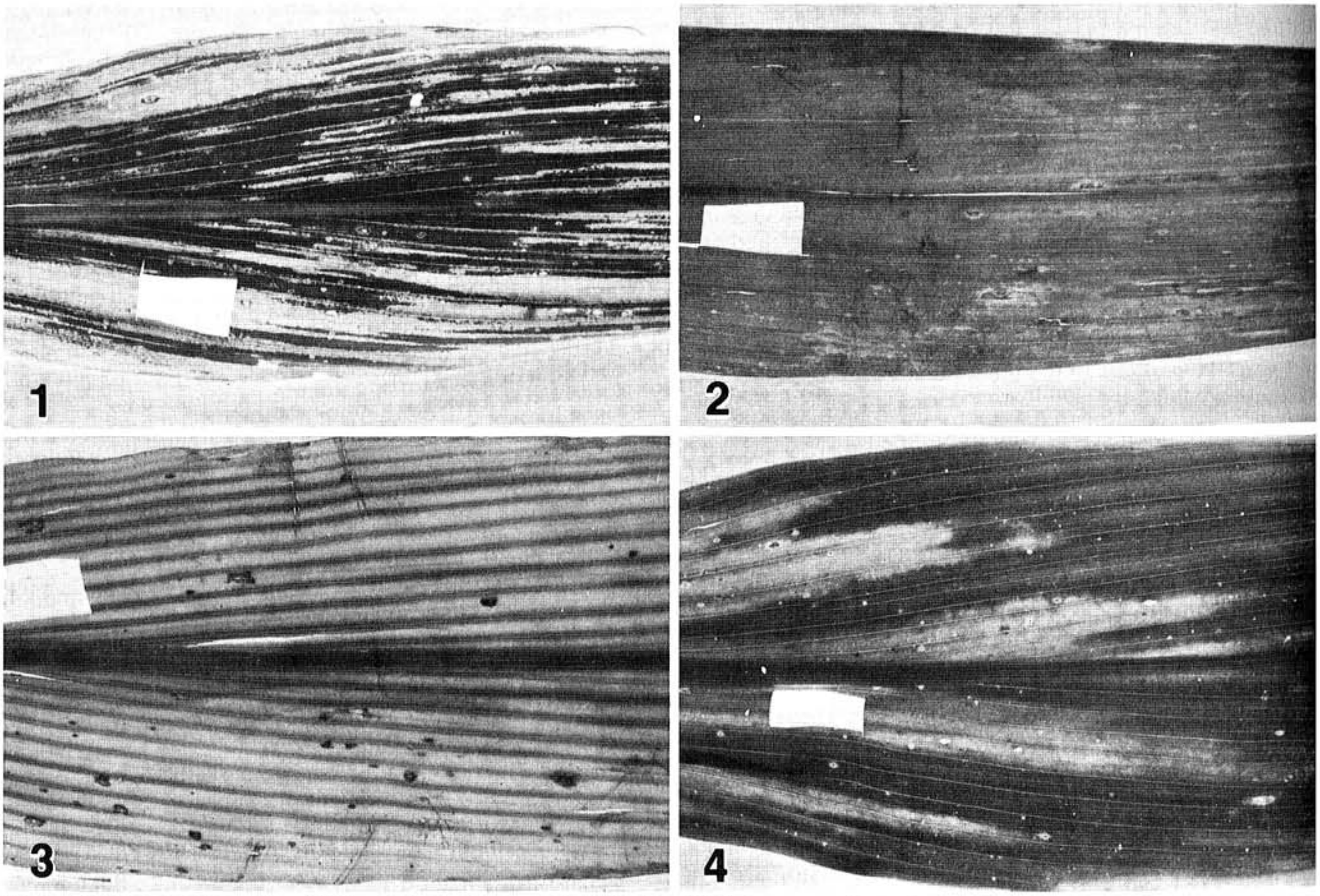
In a second field planted with a single hybrid on three sequential dates, all of 60 plants seeded on 18 September were affected. Of these, 51 showed symptoms of CSS and nine had diffuse chlorotic mottling. Of 30 plants seeded on 23 September, 53% were affected (six with symptoms of CSS and 10 with diffuse chlorotic mottling), and of 30 plants seeded on 28 September, 37% were affected (two with CSS symptoms and nine with diffuse chlorotic mottling).

In a third field, seeded on 21 September, 25% of 400 plants examined were affected (14 with CSS symptoms, nine with MRFV symptoms, three with MStpV symptoms, one with MDMV symptoms, and 73 with diffuse chlorotic mottling). In a fourth field, seeded on 3 October, 34% of 200 plants showed symptoms (33 with CSS symptoms, one with MRFV symptoms, one with MStpV symptoms, and 33 with diffuse interveinal chlorosis). Diffuse interveinal chlorosis was associated with only one of the two genotypes in this field.

In a seedling field planted 23–24 October, only MStpV symptoms (in less than 1% of the plants) and a reddening resembling phosphorus deficiency were observed. This reddening is common on maize seedlings grown on the coral-derived soils (pH 7.8–8.2) of the area but is normally not observed in older plants.

Johnsongrass (*Sorghum halepense* (L.) Pers.), weed host of MDMV-A and MCDV (9), and itchgrass (*Rottboellia exaltata* L.), weed host of MStpV (12) and MRFV (18), were found in and around several affected maize fields. Itchgrass has become more common in this area in the last few years.

Assays. Results of microscopic and serologic assays conducted at Wooster (Table 1) were similar to results of vector transmission assays conducted at Fort



Figs. 1–4. Close-ups of leaves from field-collected maize in southern Florida. (**1**) High-contrast chlorotic streaks, typical symptom of Rio Grande corn stunt spiroplasma. (**2–4**) Unidentified symptoms: (**2**) Diffuse chlorotic mottle. (**3**) Diffuse interveinal chlorosis. (**4**) Low-contrast streaks at blade base. (Note locations of samples removed for microscopic examination.)

Lauderdale on separately collected samples (Table 2). Most samples contained spiroplasmas in microscopic tests or had the transmission characteristics and symptom development of CSS in transmission tests. In addition, many plants contained viruses, and plants with multiple infections were common.

Spiroplasmas or CSS were found in all plants with CSS symptoms and in many plants with MRFV and unidentified symptoms. Some plants having the same genotype but different symptoms (Figs. 1, 2, and 4) contained spiroplasmas without evidence of coinfecting pathogens.

Numerous spiroplasma cells in helical form were seen in sections, 0.2–0.3 μm thick, of phloem sieve elements (Fig. 5). Higher magnification of thinner sections, 0.05–0.07 μm thick, of the same tissue revealed ribosomes and DNA fibrils bounded by a single membrane, which are typical of spiroplasma ultrastructure (Fig. 6).

CSS was transmitted by three species of leafhoppers found in Florida, *D. maidis*, *G. nigrifrons*, and *E. exitiosus*; transmission efficiencies after a 5-day acquisition access period were 88.2% (30/34), 23.8% (5/21), and 30% (6/20), respectively. The average latent period in 18 *D. maidis* was 15.8 days, with a range of 11–23 days, after a 3-day acquisition access period. The retention period in *D. maidis* averaged 30.4 days, with a range of 6–45 days. The minimum incubation period in the plant was 24 days at 29–31 C day temperature. Leaf samples randomly selected from four experimentally infected plants had symptoms typical of CSS (Fig. 1) and were infected with spiroplasmas, as detected by dark-field light microscopy.

MRFV was found in all plants with MRFV symptoms (including those with multiple symptoms), in some plants with only CSS symptoms, and in other plants with only unidentified symptoms. In assays of samples collected in 1979 and 1980 (Table 1), MRFV was indicated by the presence of small, isometric, viruslike particles with substructure similar to virus particles previously identified as MRFV (4). The virus was identified by

Table 1. Association of pathogens with symptoms in Florida maize disease epidemic: Microscopic and serologic assays

Symptom[a]	Plants assayed (no.)	Positive assays (no.) CSS[b]	MRFV[c]	MStpV[d]	STVLP[e]
		Plants seeded in fall 1979[f]			
CSS	15	15	1	0	0
MRFV	5	3	5	0	1
MStpV	5	1	0	5	0
DCM	31	18	4	0	2
DIVC	14	8	0	0	4
CSS + MRFV	2	2	2	0	1
CSS + DCM	1	1	0	0	1
MRFV + MStpV	1	1	1	1	1
MRFV + DIVC	1	1	1	0	1
DCM + DIVC	4	4	0	0	2
Subtotal	79	54	14	6	13
		Plants seeded in fall 1980			
CSS	16	16	4	NT	3
DCM	6	6	1	NT	1
DIVC	23	21	5	NT	16
LCBS	3	3	1	NT	1
Subtotal	48	46	11	···	21

[a] Corn stunt spiroplasma (CSS), maize rayado fino virus (MRFV), maize stripe virus (MStpV), diffuse chlorotic mottle (DCM), diffuse interveinal chlorosis (DIVC), low-contrast basal streaks (LCBS).

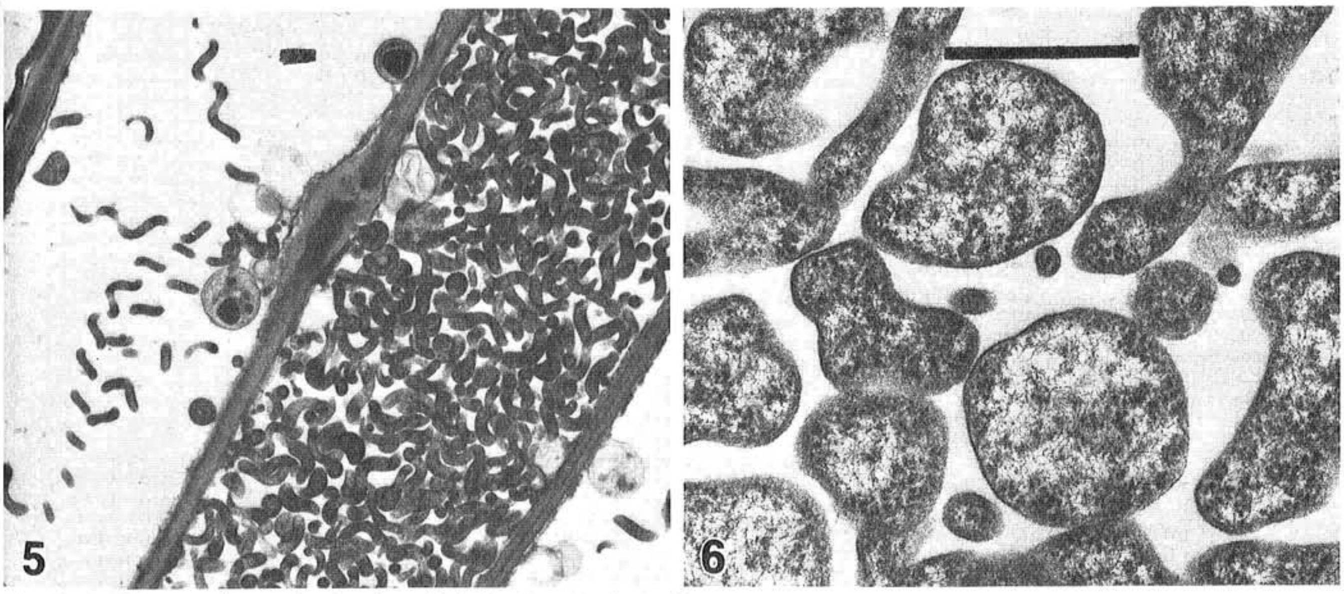
[b] CSS detected by dark-field light microscopy and confirmed by electron microscopy.

[c] MRFV detected by enzyme-linked immunosorbent assays (ELISAs) in samples collected in 1979 and detected as small, isometric virus particles by leaf-dip electron microscopy in samples collected in 1979 and 1980.

[d] MStpV detected by the presence of unique subcellular inclusions. Samples collected in 1980 were not tested (NT) for MStpV.

[e] Straight, tubular, viruslike particles (STVLP) detected in leaf-dip electron microscopy.

[f] One sample was positive for maize dwarf mosaic virus (MDMV) strain B by ELISA, leaf-dip electron microscopy, and mechanical transmission assay. All samples collected in 1979 were negative for MDMV strain A, maize chlorotic dwarf virus, and maize chlorotic mottle virus by ELISA.



Figs. 5 and 6. Electron micrographs of sections of a field-collected maize leaf from southern Florida. Spiroplasmas are shown in phloem sieve elements, confirming the presence of spiroplasmas detected by dark-field light microscopy in maize with symptoms shown in Figures 1–4. (**5**) Section (0.2–0.3 μm thick) showing the helical morphology typical of spiroplasmas. (**6**) Section (0.05–0.07 μm thick) showing the ribosomes, net of DNA fibrils, and single plasma membrane typical of spiroplasma ultrastructure. (Scale bar represents 0.5 μm.)

ELISA in plants collected in 1979; those collected in 1980 were not tested.

Transmission assays with *D. maidis* (Table 2) were positive for MRFV in all samples with MRFV symptoms from both years, including samples of *R. exaltata* and maize with multiple symptoms. MRFV was transmitted by *D. maidis* and *G. nigrifrons* after a 4-day acquisition access period with transmission efficiency of 53.3% (16/30) and 10% (2/20), respectively. The latent period in 11 *D. maidis* averaged 16.3 days, with a range of 12–22 days after a 5-day acquisition access period. The retention period in *D. maidis* ranged from 1 to 23 days, averaging 12.4 days. The minimum incubation period in the plant was 10 days at 29–31 C day temperature.

In samples collected in 1979, MStpV was detected by the presence of a unique subcellular inclusion (O.E. Bradfute and J. H. Tsai, *unpublished*) in all plants with MStpV symptoms, including one plant with multiple symptoms. *P. maidis* transmission tests were positive for MStpV in all samples from both years with MStpV symptoms, including samples of *R. exaltata* and maize with multiple symptoms. MStpV was transmitted by *P. maidis* similarly to earlier reports (6,20).

One sample collected in 1979, with mosaic symptoms and flexuous rod viruslike particles, was positive for MDMV-B by ELISA and by mechanical transmission assay. In 1979, all samples were negative for MDMV-A, MCDV, and MCMV by ELISA. In 1980, ELISA and tests for mechanically transmitted viruses were not performed.

Finally, straight, tubular, viruslike particles (Fig. 7) were found by electron microscopy of negatively stained preparations of some plants of all symptom types except MStpV alone. The particles were estimated to measure about 720 × 13 nm (mean of 30 particles).

DISCUSSION

This is the first demonstration of spiroplasmas associated with a major maize disease outbreak in the United States. Previously, CSS had been identified in only a few maize plants with symptoms resembling corn stunt; MCDV, rather than CSS, was most frequently associated with major disease outbreaks (1,4,8,9). The remaining reports of diseases resembling corn stunt did not describe pathogen morphology but relied on *D. maidis* transmission and symptomatology to identify the pathogen as corn stunt virus or corn stunt agent (8,9,16).

We presume that most, if not all, of the spiroplasmas found in our assays were CSS, based on diagnostic leaf symptoms in both field and experimentally inoculated plants and persistent transmission by three of the five leafhopper species previously reported to be CSS vectors (15,16). Serologic assays, however, were not done. Our studies confirm *D. maidis* as the most efficient vector, but the average latent period of CSS in *D. maidis* (15.8 days) was significantly shorter than has been reported in other studies (21.2 ± 2.2 days [16] or 19.0 ± 2.0 days [15]). The differences may reflect differences in CSS isolates or biotypes of *D. maidis*.

The presence of MRFV and MStpV is not surprising, but they appeared to be more prevalent, and the disease they produced in combination with CSS appeared to be more severe, than previously recognized (4,20). In this study, a Florida isolate of MRFV was transmitted by *D. maidis* and *G. nigrifrons* with about the same latent period in *D. maidis* as the Texas isolate of MRFV (4,15). However, this latent period in *D. maidis* is longer than that reported for the Costa Rican strain (7) but shorter than that reported for the Colombian strain (maize rayado Colombiano virus) (19).

The occurrence of MDMV-B in southern Florida is not surprising, because of its previously established distribution (9), but has not been reported before to our knowledge. Because both johnsongrass (host reservoir) and the appropriate insect vectors are found in the area, it is surprising that MDMV-A and MCDV are not known to cause significant maize diseases in southern Florida as they do in many other regions of the southeastern United States (9). Difficulty in maintaining colonies of aphid vectors of MDMV during periods of high temperature in southern Florida (J. H. Tsai, *unpublished*) may reflect a sensitivity of the aphids to high temperature and may account for the low incidence of MDMV.

The straight, tubular, viruslike particle is novel in maize and is presumed to be a new virus. Similar particles 532 nm long

Table 2. Association of pathogens with symptoms in Florida maize disease epidemic: Vector assays

Symptom[a]	Plants assayed (no.)	Positive assays (no.)		
		CSS[b]	MRFV[c]	MStpV[d]
Plants collected in fall 1979				
CSS	9	9	0	0
MRFV	4 (2)[e]	0	4 (2)	0
MStpV	3 (4)	0	0	3 (4)
CSS + MRFV	2	2	2	0
CSS + MStpV	5	5	0	3
US	12	9	1	0
Subtotal	35 (6)	25	7 (2)	6 (4)
Plants collected in 1980				
CSS	4	4	0	0
MRFV	3 (1)	0	3 (1)	0
MStpV	2 (3)	0	0	2 (3)
CSS + MRFV	3	3	3	0
CSS + MStpV	7	5	0	3
US	9	7	0	1
Subtotal	28 (4)	19	6 (1)	6 (3)

[a] Corn stunt spiroplasma (CSS), maize rayado fino virus (MRFV), maize stripe virus (MStpV), unidentified symptoms (US).
[b] CSS detected by *Dalbulus maidis* transmission followed by development of diagnostic symptoms for CSS.
[c] MRFV detected by *D. maidis* transmission followed by development of diagnostic symptoms for MRFV.
[d] MStpV detected by *Peregrinus maidis* transmission followed by development of diagnostic symptoms for MStpV.
[e] Numbers in parentheses refer to samples taken from infected *Rottboellia exaltata* L.

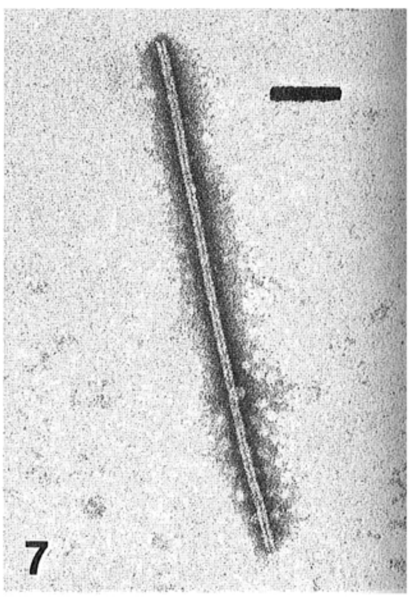

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Fig. 7. Electron micrograph of leaf-dip preparation from a field-collected maize leaf from southern Florida, showing a novel, straight, tubular, viruslike particle about 720 nm long. These particles were found in plants with CSS symptoms and in plants with unidentified symptoms. (Scale bar represents 100 nm.)

have been reported in algae (5), but we are unaware of any virus particle of this morphology and approaching this length in higher plants. However, the particle was not clearly associated with a particular symptom in this study.

Pathogens were detected in all plants displaying diagnostic symptoms, but the high incidence of masked infections in plants with symptoms of another pathogen or an unidentified disorder was unexpected. Relatively few plants with multiple infections had symptoms of more than one pathogen. The presence of spiroplasmas in most (but not all) plants displaying unidentified symptoms is not understood, but several possibilities should be considered individually or in combination: 1) CSS, or strains thereof, may induce a wider range of symptoms under field conditions or in different genotypes than has been described for experimental transmissions. If these unidentified symptoms resulted from late infections, lower spiroplasma titers in some plants could have escaped detection. 2) The unidentified symptoms may be the result of nonpathogenic stress, and the prevalence of masked spiroplasma infections may be the same in symptomless plants as in plants with unidentified symptoms (the prevalence of spiroplasmas in symptomless plants was not determined). 3) The unidentified symptoms may be induced by pathogens not detected in this study, such as an undescribed spiroplasma or the mycoplasmalike organism (MLO) associated with maize bushy stunt (MBS) disease (2,16). *D. maidis* is also a vector of this MLO, which is difficult to detect in the presence of CSS. Additional evidence for involvement of the MBS-associated MLO in this disease outbreak is inconclusive at present (O. E. Bradfute and J. H. Tsai, *unpublished*).

The nature of CSS transmission, limited vector specificity and host range, and extended latent period in the vector and incubation period in the host (16 and this study) may help explain this disease outbreak. *D. maidis*, the most efficient CSS vector of the three leafhopper species (locally collected biotypes) in this study, is the least common species in Florida. The site and date of collection of *D. maidis* suggest a possible introduction on imported plant material more than 18 mo before the outbreak. However, the first appearance of the outbreak, in maize that would have been in the seedling stage immediately after Hurricane David, suggests the presence of abundant CSS-inoculative vectors coinciding with that weather system. Introduction of many CSS-inoculative vectors from the Caribbean Islands or some other area of Florida is a possibility. David was unusually intense as it passed over the island of Hispaniola before reaching Florida (11). The reduced insect control immediately after David would have allowed the vectors more time to inoculate maize seedlings. However, the recurrence of significant disease in the fall of 1980 suggests a local source of vectors and a local overseasoning host. Since *Zea* spp. are the only natural hosts of CSS, a recent increase in summer-grown maize in southern Florida could be the most probable source of CSS, as well as other pathogens and vectors. Because much of this summer crop generally does not receive as intense management nor as much insecticide as fall-seeded maize, vectors and pathogens could have increased enough to cause the outbreak.

The possible spread of pathogens associated with this outbreak to other maize-growing regions of the United States has been previously discussed (4,9,15,16,18). CSS and MRFV are limited by less efficient vectors and by the lack of an overseasoning host in all but the most southern regions of the country. Johnsongrass, reported as a host of MStpV in Australia (10), could act as an abundant overseasoning host for this virus in other regions of the United States, but *P. maidis*, the only known vector of MStpV, is rarely reported in temperate regions.

Within Florida, future incidence and spread of the pathogens found in this study will probably depend on trends in the practice of growing maize throughout the year. The lower efficiency of *D. maidis* and *G. nigrifrons* in transmitting MRFV relative to CSS may account for the lower incidence of MRFV and result in slower spread. The recent spread of itchgrass, commonly infected with MStpV and rarely infected with MRFV (J. H. Tsai, *unpublished*), will probably also affect the spread of these viruses in maize.

ACKNOWLEDGMENTS

We thank Ruth Tennant, Joanne Downs, N. J. Ko, and L. S. Negi for technical assistance and Pioneer Hi-Bred International, Inc. for providing funds for travel to collection sites. Appreciation is extended to F. W. Mead and D. M. DeLong for identifying the test insects; to D. C. Wrucke, D. R. Wilkinson, J. A. Wright, and K. J. Leonard for collecting maize samples; to M. B. Lawrence for interpreting weather data; and to the Asgrow Seed Co. for providing seed of sweet corn.

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