

## Studies of Maize Streak Virus Isolates from Grass and Cereal Hosts in Nigeria

T. MESFIN and N. A. BOSQUE-PÉREZ, International Institute of Tropical Agriculture (IITA), PMB 5320, Ibadan, Nigeria; I. W. BUDDENHAGEN, Department of Agronomy and Range Science, University of California, Davis 95616; and G. THOTTAPPILLY and S. O. OLOJEDE, IITA, Ibadan, Nigeria

### ABSTRACT

Mesfin, T., Bosque-Pérez, N. A., Buddenhagen, I. W., Thottappilly, G., and Olojede, S. O. 1992. Studies of maize streak virus isolates from grass and cereal hosts in Nigeria. *Plant Dis.* 76:789-795.

Maize streak virus (MSV) isolates originating from maize, other cereals, and 18 grass species in Nigeria were characterized based on symptoms, transmission, host range, and serological tests. All isolates could be transmitted to MSV-susceptible sweet corn cv. Golden Bantam using *Cicadulina storeyi* as a vector, but only some could be transmitted to MSV-susceptible maize cv. Pool 16. Differences were observed among isolates in symptom severity (ranging from very mild to severe), average time of symptom appearance, percent transmission to maize, and host range. Of the 24 isolates tested, 18 reacted with an antiserum to a severe MSV maize isolate from Nigeria, four each with antisera to *Panicum maximum* and sugarcane isolates, and none with Digitaria streak virus antiserum. Results suggest that streak found in many grasses in Nigeria is not readily transmissible to susceptible field maize and that some of the weeds most likely to be involved in perpetuating an epidemiologically competent maize strain of MSV are *Axonopus compressus*, *Brachiaria lata*, and *Setaria barbata*.

Maize streak virus (MSV) causes an important disease of maize (*Zea mays* L.) in Africa and neighboring islands of the Indian Ocean. Although MSV infects sugarcane (*Saccharum* sp.) and introduced cereal crops such as barley (*Hordeum* sp.) and wheat (*Triticum* spp.) (23,27), it is not clear how important the disease is in these crops. Indigenous African crops such as sorghum (*Sorghum*

*bicolor* (L.) Moench), African rice (*Oryza glaberrima* Steudel), pearl millet (*Pennisetum americanum* (L.) K. Schum.), and finger millet (*Eleusine coracana* (L.) Gaertn.) also have been reported to become infected with streak virus (23,24), but with the exception of rice, we have never seen these crops naturally infected with MSV in farmers' fields in West Africa. Although similar virus diseases have been observed on pearl millet, wheat, and other graminaceous crops in India (25), their exact relationship to MSV as it occurs in Africa

is unknown. From Vanuatu, a disease of *Digitaria setigera* Roem. & F. W. Schultz (previously reported as *D. sanguinalis* (L.) Scop.), caused by Digitaria streak virus (DSV), has been described (9) and the virus recently referred to as a strain of MSV (20).

MSV is a geminivirus (13) and is transmitted by at least eight leafhopper species in the genus *Cicadulina* (23,28). This African virus has a wide host range within the Gramineae (7) and occurs naturally on various indigenous and introduced grasses (23). MSV has been reported to occur as distinct strains, some of which were considered to be adapted to one particular host species (3,22,27). Isolates from maize, *Panicum maximum* Jacq., and sugarcane from East Africa were reported by Bock et al (3) to be morphologically identical in electron microscopy preparations and serologically related but not identical; the three isolates were considered to be MSV strains by these authors. Ricaud and Felix (22) working in Mauritius reported the occurrence of maize, *Coix lachryma-jobi* L., and sugarcane strains of streak and concluded that the maize and *C. lachryma-jobi* strains were very closely related.

In studies carried out at the Interna-

Accepted for publication 4 February 1992.

© 1992 The American Phytopathological Society

tional Institute of Tropical Agriculture (IITA), Ibadan, Nigeria (14,24), differences have been observed among streak isolates from wild grasses and crops with respect to their transmission to maize and virulence. Pinner et al (20) conducted comparative studies of 24 isolates of MSV derived from different host plants and concluded no adaptation to grass hosts occurred because all isolates could be transmitted to the sweet corn cv. Golden Bantam. Studies using polyclonal and monoclonal antibodies have indicated great diversity among MSV isolates (8,19). Ngwira (17) demonstrated a serological relationship among MSV isolates from Nigeria, Malawi, Uganda, South Africa, and Egypt. Peterschmitt et al (18) recently characterized MSV isolates and concluded that maize isolates from 11 African countries all belonged to the same serotype. Identification of streak virus strains, however, is not easy and information on the epidemiological characteristics of any particular strain is lacking.

Annual and perennial grass hosts that harbor streak virus and its vectors could play a key role in the epidemiology of MSV disease in maize. Severe outbreaks of MSV in maize have been reported from many African countries in the last decade. Maize varieties with a high level of resistance to MSV have been developed at IITA and made available to national research programs across Africa (11). However, little is known in West Africa about the role of indigenous grasses as reservoirs of the virus and about the virulence and economic importance of the various isolates or strains of streak virus.

The objectives of this study were to characterize streak virus isolates collected across Nigeria from a wide range of host plant species based on symptoms, transmission, and host range, and compare these results with serological analysis of the isolates using polyclonal antisera produced against DSV and the maize, sugarcane, and *P. maximum* strains of MSV.

## MATERIALS AND METHODS

**Sources of streak virus isolates.** Samples of different plant species showing streak symptoms were collected in 24 sites located in nine states, across the major ecological zones of Nigeria (forest, southern guinea savanna, and northern guinea savanna). Plants were taken from farmers' maize fields and/or from grassland areas surrounding maize fields and from maize fields at IITA. The term "isolate" was given to the virus occurring in each infected plant sample maintained on its original annual or perennial host or on the sweet corn cv. Golden Bantam through transmission by *Cicadulina storeyi* China (= *C. triangula*) without any symptom variation. Plants were kept in pots in an insect-proof greenhouse

and the isolates were maintained by regular transfers. Isolates from 15 sites were characterized in detail. The different plant species with streak symptoms collected were from the following genera: *Axonopus*, *Brachiaria*, *Coix*, *Dactyloctenium*, *Digitaria*, *Echinochloa*, *Eleusine*, *Oryza*, *Panicum*, *Paspalum*, *Pennisetum*, *Rhynchelytrum*, *Rottboellia*, *Setaria*, and *Zea*. Grasses were identified at the species level following the guide by Akobundu and Agyakwa (1).

**Vector species.** Transmission of the different isolates was carried out using *C. storeyi*. Adult *C. storeyi* were obtained from a culture selected for improved transmission efficiency (percentage of vectors = 65) maintained at IITA. The leafhoppers were reared on healthy plants of a local pearl millet variety. All plants used for rearing leafhoppers were grown in pots, under isolation in a greenhouse. Precautions were taken to avoid contamination of the plants by insects or virus.

**Transmission tests.** All transmission work was conducted at IITA. Groups of 75–100 insects were confined for 24 hr on 7- to 10-day-old healthy maize seedlings that were observed later as negative checks. After 24 hr, the insects were collected and given a virus acquisition access period of 48 hr on infected leaves of one of the host plant species. Sections of infected leaves (approximately 16 cm long) were placed in small glass vials (8 cm high) containing water, and cotton wool was placed over the water to prevent the insects from drowning and to keep the leaves in place. The infected leaves and the insects were covered with a polyvinyl chloride (PVC) tube cage (30 cm high × 7 cm diameter) fitted with openings covered with nylon mesh on the top and on two sides.

After the acquisition period, insects were transferred singly to a 1-wk-old healthy maize seedling or, for host range studies, to healthy seedlings of the different plant species used. The insects and seedlings were caged using PVC tubes. After a 48-hr inoculation access period, the insects were removed and the plants were sprayed with insecticide. The inoculated seedlings were kept in a greenhouse for symptom development. All of the acquisition and inoculation tests were done in an environmental chamber maintained at 25 C with a 12-hr photoperiod. Symptom severity and time of appearance of symptoms (latent period) were determined. A graded scale of 0–5 where 0 = no streaking, 1 = very few streaks, 2 = light streaking, 3 = moderate streaking, 4 = severe streaking on at least 60% of leaf area, and 5 = severe streaking on 75% of leaf area or more and stunting (26) was used to evaluate the virulence of the different streak virus isolates. In each experiment, greenhouse evaluation and observation of symptoms was completed by the time maize plants reached

the six-leaf stage.

**Host range studies.** The MSV-susceptible sweet corn cultivar Golden Bantam was used as a test plant for all the streak virus isolates studied. After transmission to cv. Golden Bantam, further transmissions were carried out from this host back to the respective species from which the isolates originated and from Golden Bantam to Golden Bantam. Two other MSV-susceptible cultivars of field maize were used in host range studies of some of the isolates: the open-pollinated tropical variety Pool 16 (seeds produced at IITA) and the temperate hybrid FR 1141 × FR 303 (Illinois Foundation Seed Inc., Matrix, Alexandria, VA.)

Tests were conducted to determine if it was possible to transmit each isolate from the original host species directly to the same species. In addition, transmission tests of virus isolates from *P. maximum* (mild), *Axonopus compressus* (Sw.) Beauv. (mild and severe), *Brachiaria lata* (Schumacher) C. E. Hubb. (severe), and *D. horizontalis* Willd. (mild) to these four grass species were conducted.

The ability of 15 grass species, rice, and pearl millet cv. ex Bornu to become infected with a severe MSV maize isolate from Nigeria was tested. Transmissions back to maize (cv. Pool 16) then were carried out from those hosts that became infected with the severe MSV isolate. Young plants grown from seed or from tillers from healthy plants were used for all tests. Virus acquisition and inoculation were carried out as described above.

**Enzyme-linked immunosorbent assays (ELISA).** The streak virus isolates from the various host plant species were analyzed by two ELISA techniques—direct double-antibody sandwich (DAS) and protein A antibody sandwich (PAS). ELISA tests were carried out with sap extracts from the original hosts.

DAS-ELISA was performed using the techniques described by Clark and Adams (5). One hour after the reaction, absorbance was read at 405 nm using an ELISA reader (Dynatech MR 5000, Guersy, UK). For DAS-ELISA tests, the polyclonal antiserum against an MSV isolate from Nigeria and the conjugate used were prepared by G. Thottappilly, Virology Unit, IITA.

PAS-ELISA tests were carried out following the procedure described by Edwards and Cooper (10). Reactions were stopped after 30 min at room temperature and absorbances were read at 655 nm. Protein A-horseradish peroxidase conjugate was obtained from Sigma (St. Louis, MO). Polyclonal antisera were obtained from P. G. Markham (John Innes Institute, UK) for the following: severe maize isolate from IITA, Nigeria; *P. maximum* isolate from Kenya; sugarcane isolate from South Africa; and DSV from Vanuatu. The production of these polyclonal antisera has

been described by Pinner and Markham (19).

## RESULTS

### Sources of streak virus isolates.

Twenty-one species of plants with streak symptoms were recorded in Nigeria from 1989 to 1990 (Table 1). Symptoms on these host plants varied from severe to mild (Fig. 1). All hosts are in the family Gramineae. Fifteen of the hosts belong to the tribe Paniceae, including the perennials *A. compressus*, *P. maximum*, *Paspalum conjugatum* Bergius, *P. notatum* Flügge, and *P. scrobiculatum* L., and the annuals *Brachiaria lata*, *B. deflexa* (Schumacher) C. E. Hubb. ex Robyns, *B. distichophylla* (Trin.) Stapf, *D. horizontalis*, *Echinochloa colonum* (L.) Link, *E. stagnina* P. Beauv., *Pennisetum americanum*, *P. polystachion* (L.) Schult., *Rhynchelytrum repens* (Willd.) Hubb.), and *Setaria barbata* (Lam.) Kunth. One of the hosts belongs to the tribe Oryzae (*Oryza sativa* L.), two to the tribe Eragrostideae (the annuals *Eleusine indica* (L.) Gaertn., and *Dactyloctenium aegyptium* (L.) Willd.), one to the tribe Andropogoneae (the annual *Rottboellia cochinchinensis* (Lour.) W. Clayton), and two to the tribe Maydeae (the annuals *C. lachryma-jobi* and *Z. mays*). Of these species, maize, *A. compressus*, *P. conjugatum*, and *P. notatum* are of American origin; *C. lachryma-jobi*, *P. scrobiculatum*, and rice are Asian; *D. aegyptium*, *E. colonum*, and *R. cochinchinensis* are from the Old World Tropics (which presumably includes Africa); and the remaining ones are of African origin (21).

MSV-infected *P. maximum* was most commonly found in the forest zone of Nigeria whereas MSV-infected *A. compressus*, *D. horizontalis*, *Brachiaria* spp., *D. aegyptium*, and *S. barbata* frequently were observed both in the forest and savanna zones of the country. The remaining grass species harboring streak virus were encountered less frequently and sometimes very rarely in the various ecological zones.

**Transmission tests.** All of the isolates tested from the various host plants were found to be transmissible to the sweet corn cv. Golden Bantam using *C. storeyi* as a vector (Table 1). Differences were observed among the isolates in symptom severity, average time of symptom appearance (latent period), and percentage of transmission (Table 1). The isolates from maize, *D. horizontalis*, *D. aegyptium*, *R. repens*, *P. americanum*, *B. distichophylla*, and *E. indica* were transmissible to maize at higher frequencies (over 55%) than were the other isolates. Isolates obtained from maize, *D. aegyptium*, *B. lata*, *A. compressus*, *S. barbata*, and *D. horizontalis* caused severe symptoms on Golden Bantam, rating 4–5 on the 0–5 scale. In contrast, isolates from *P. maximum*, *Echinochloa* spp., *R. cochin-*

*chinensis*, and *Paspalum* spp. showed a lower percentage of transmission and caused milder symptoms on Golden Bantam (ratings of 1–3).

The symptoms observed on maize cv. Golden Bantam caused by the various isolates varied from severe (wide chlorotic streaks diffusing into one another

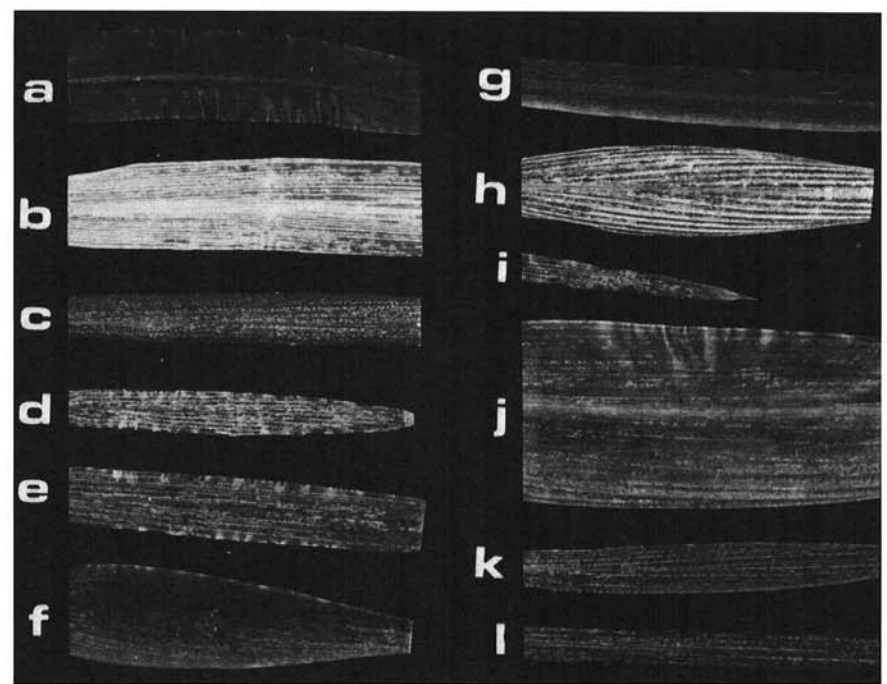
and covering most of the leaf) to mild, consisting of a few small streaks or spots widely dispersed on the leaves. The isolates from *A. compressus* and *B. lata*, which caused severe symptoms on maize and on their original hosts, also induced a marked stunting effect on these hosts. The infection caused by the isolate from

**Table 1.** Transmission of streak virus isolates from different host plant species to maize cv. Golden Bantam using *Cicadulina storeyi* as a vector

Origin of isolate	Number of plants challenged	Percent transmission	Latent period (days)	Symptom severity <sup>a</sup>
<i>Axonopus compressus</i> A <sup>b</sup>	21	52	5	4
<i>A. compressus</i> B	15	40	7	2
<i>Brachiaria lata</i> A	31	42	7	4
<i>B. lata</i> B	12 <sup>b</sup>	50	9	3
<i>B. deflexa</i>	20	40	7	3
<i>B. distichophylla</i>	16	62	6	3
<i>Coix lachryma-jobi</i>	33	27	8	3
<i>Dactyloctenium aegyptium</i>	20	60	5	5
<i>Digitaria horizontalis</i> A	32	59	7	4
<i>D. horizontalis</i> B	12	50	5	3
<i>Eleusine indica</i>	22	59	5	3
<i>Echinochloa colonum</i>	23	18	7	3
<i>E. stagnina</i>	12	25	7	3
<i>Oryza sativa</i>	20	50	7	3
<i>Paspalum conjugatum</i>	26	38	6	2
<i>P. notatum</i>	30	33	5	3
<i>P. scrobiculatum</i>	32	31	6	2
<i>Panicum maximum</i>	35	37	12	1
<i>Pennisetum americanum</i>	30	66	6	2
<i>P. polystachion</i>	12	41	8	2
<i>Rhynchelytrum repens</i>	25	64	6	3
<i>Rottboellia cochinchinensis</i>	39	23	6	3
<i>Setaria barbata</i>	20	40	6	4
<i>Zea mays</i>	60	75	4	5

<sup>a</sup> Based on a scale of 0–5, where 0 = no streaking, 1 = light streaking, and 5 = severe streaking on 75% or more of the leaf area and stunting.

<sup>b</sup> A = severe isolate; B = mild isolate.



**Fig. 1.** Symptoms of maize streak virus isolates in their original hosts. a = Healthy maize, b = MSV-infected maize, c = *Panicum maximum*, d = *Axonopus compressus* severe, e = *A. compressus* mild, f = *Brachiaria lata*, g = *Pennisetum americanum*, h = *Setaria barbata*, i = *Dactyloctenium aegyptium*, j = *Coix lachryma-jobi*, k = *Digitaria horizontalis*, l = *Eleusine indica*.

*P. maximum* on maize cv. Golden Bantam was very mild and sometimes symptoms developed in the first three or four leaves only and did not appear in subsequent leaves. On the basis of symptom severity on cv. Golden Bantam, most of the isolates showed an intermediate aggressiveness between the severe isolates from maize and *D. aegyptium* (rating 5) and the mild isolate from *P. maximum* (rating 1) (Table 1).

Different plants of *B. lata*, *D. horizontalis*, *A. compressus*, and *S. barbata* were observed to have either mild or severe streak symptoms. When isolates from these were transmitted to maize cv. Golden Bantam, they produced either

severe or mild symptoms as observed in the original host. This implies there are distinct severe and mild streak isolates infecting these species.

We also observed streaklike symptoms on *Andropogon gayanus* Kunth, but we were not able to transmit any virus from this host into maize using *C. storeyi* as a vector.

**Host range.** The results of the host range studies with three maize cultivars revealed differences in the transmissibility of some of the isolates (Table 2). All isolates could be transmitted to Golden Bantam using *Cicadulina* leafhoppers, but isolates from *P. maximum*, *Paspalum* spp., *C. lachryma-jobi*, *O. sa-*

*tiva*, and *P. americanum* could not be transmitted from their original hosts to maize cultivars Pool 16 and FR 1141 × FR 303. The isolates from *R. cochinchinensis* and *R. repens* infected cvs. Golden Bantam and FR 1141 × FR 303 but not Pool 16. Golden Bantam was confirmed useful for distinguishing streak isolates by symptom expression as reported by Pinner et al (20). Most of the isolates, when transmitted back from maize to their original host species, not only caused infection but also symptoms similar in severity to the ones observed initially on the original host. Isolates originating from *B. deflexa*, *B. distichophylla*, *E. colonum*, *P. maximum*, *P. scrobiculatum*, and *R. repens* could not be transmitted back from maize to their original host. Attempts to transmit streak isolates directly from infected *P. scrobiculatum*, *P. conjugatum*, and *E. colonum* to healthy plants of the original host species were not successful (Table 3). All isolates were readily transmissible on Golden Bantam with the exception of the isolate from *P. maximum* (Table 3).

The severe MSV maize isolate was transmissible to 10 of the 17 grass and crop species tested, but on five of the species (i.e., *B. deflexa* and *P. americanum*), the symptoms were mild (Table 4). In the case of *B. deflexa*, transmission from this host back to maize cv. Pool 16 resulted in severe symptoms. In contrast, transmission of the maize isolate from *E. indica*, *P. americanum*, and *P. scrobiculatum* back to maize cv. Pool 16 resulted in mild symptoms. It is possible the maize "isolate" is a mixture of a severe and a mild isolate and, for reasons that are not yet clear, some hosts can become infected only with the mild isolate. Pinner et al (20) reported they derived a mild isolate of streak from a severe MSV isolate obtained from IITA.

It was not possible to transmit the severe MSV maize isolate to some grasses, notably *P. maximum* and *D. aegyptium* (Table 4). Bock et al (3) reported an MSV maize isolate to cause mild transient streak in sugarcane and no infection on *P. maximum*.

The results of grass-to-grass transmissions are summarized in Table 5. It was possible to transmit all five grass isolates tested to *A. compressus* and *D. horizontalis*, whereas none could be transmitted to *P. maximum* except the *P. maximum* isolate. The *D. horizontalis* mild isolate and the *P. maximum* isolate were transmissible to *B. lata*. The *A. compressus* mild isolate was transmissible to *D. horizontalis*, but the severe *A. compressus* isolate was not.

**ELISA.** In DAS-ELISA, the antiserum to a severe MSV isolate from Nigeria reacted with sap extracts from 18 of the 24 isolates to varying degrees (Table 6). The isolates originating from maize, *A. compressus*, *B. lata*, *D. hori-*

**Table 2.** Transmission<sup>a</sup> of streak virus isolates to selected maize cultivars using *Cicadulina storeyi* as a vector

Isolate	Maize cultivar		
	Golden Bantam	Pool 16	FR 1141 × FR 303
<i>Axonopus compressus</i> A <sup>b</sup>	+	+	+
<i>Brachiaria lata</i> A	+	+	+
<i>B. lata</i> B	+	+	+
<i>B. deflexa</i>	+	+	+
<i>B. distichophylla</i>	+	+	+
<i>Coix lachryma-jobi</i>	+	-	-
<i>Dactyloctenium aegyptium</i>	+	+	+
<i>Digitaria horizontalis</i> B	+	+	+
<i>Eleusine indica</i>	+	+	+
<i>Oryza sativa</i>	+	-	-
<i>Paspalum conjugatum</i>	+	-	-
<i>P. notatum</i>	+	-	-
<i>P. scrobiculatum</i>	+	-	-
<i>Panicum maximum</i>	+	-	-
<i>Pennisetum americanum</i>	+	-	-
<i>Rhynchelytrum repens</i>	+	-	+
<i>Rottboellia cochinchinensis</i>	+	-	+
<i>Setaria barbata</i>	+	+	+
<i>Zea mays</i>	+	+	+

<sup>a</sup> + = Positive transmission (at least one plant positive); - = negative transmission.

<sup>b</sup> A = severe isolate; B = mild isolate.

**Table 3.** Transmission<sup>a</sup> of streak virus isolates to the original host plant species from which they were derived, from maize back to the original host, and from maize to maize using *Cicadulina storeyi* as a vector

Isolate	From original host to original host	From maize to original host	From maize to maize <sup>b</sup>
<i>Axonopus compressus</i> A <sup>c</sup>	8/12 <sup>d</sup>	3/9	+
<i>A. compressus</i> B	7/15	NT	+
<i>Brachiaria lata</i> A	6/14	2/10	+
<i>B. deflexa</i>	4/8	0/10	+
<i>B. distichophylla</i>	9/15	0/10	+
<i>Coix lachryma-jobi</i>	9/20	2/10	+
<i>Dactyloctenium aegyptium</i>	2/8	NT	+
<i>Digitaria horizontalis</i> B	8/23	5/12	+
<i>Eleusine indica</i>	9/14	3/10	+
<i>Echinochloa colonum</i>	0/13	0/10	+
<i>Oryza sativa</i>	4/15	2/10	+
<i>Paspalum conjugatum</i>	0/12	NT	+
<i>P. notatum</i>	NT	NT	+
<i>P. scrobiculatum</i>	0/18	0/10	+
<i>Panicum maximum</i>	6/15	0/10	-
<i>Pennisetum americanum</i>	21/35	5/12	+
<i>Rhynchelytrum repens</i>	2/10	0/2	+
<i>Rottboellia cochinchinensis</i>	2/10	1/10	+
<i>Setaria barbata</i>	15/25	7/15	+

<sup>a</sup> + = Positive transmission (at least one plant positive); - = negative transmission. NT = not tested.

<sup>b</sup> Cv. Golden Bantam to Golden Bantam.

<sup>c</sup> A = severe isolate; B = mild isolate.

<sup>d</sup> Number of plants infected/number of plants challenged.

zontalis, *D. aegyptium*, *R. repens*, and *S. barbata* gave a strong reaction. The isolate from *P. maximum*, although recognized by the antiserum to MSV from maize, gave a weak reaction. In contrast, no reaction was observed with sap extracts from *C. lachryma-jobi*, *P. conjugatum*, *P. scrobiculatum*, *P. americanum*, and *P. polystachion*.

In PAS-ELISA, polyclonal antisera raised against the panicum, maize, and sugarcane strains and DSV were tested against the sap extracts of 21 isolates. The anti-maize MSV antibody reacted with 18 of the isolates (Table 6), but it gave a weak reaction to isolates from *P. maximum*, *P. conjugatum*, and *P. americanum*. The isolates from *P. scrobiculatum*, *C. lachryma-jobi*, and *P. polystachion* did not react with the anti-maize MSV antibody. In general, the reactions of the different isolates against the two maize MSV antisera (one prepared at IITA and the other at John Innes Institute but both prepared using MSV-infected maize from Nigeria) were similar.

Only the isolates from *P. maximum* and *P. americanum* gave a strong reaction with panicum antiserum. The sugarcane antiserum reacted weakly with isolates from maize, *P. americanum*, *P. polystachion*, and *C. lachryma-jobi*. Only the *P. americanum* isolate cross-reacted with antisera from maize, panicum, and sugarcane (Table 6). None of the isolates tested reacted positively with the antiserum from DSV.

## DISCUSSION

From the studies on transmission, host range, and symptoms and from ELISA results, it was apparent that the streaklike virus symptoms on maize and various grass hosts observed in Nigeria were caused by streak viruses. The symptoms induced on maize and on the grasses were similar or identical to those described by Fajemisin et al (12), Bock (2), Rossel and Thottappilly (24), and Pinner et al (20). Differences in virulence were observed among the isolates tested. Similar results have been reported by Peterschmitt et al (18) working with MSV grass isolates from Réunion. Although all isolates tested could infect cv. Golden Bantam, symptoms varied from severe to mild. Pinner et al (20) reported similar findings. In our studies, the isolates from maize, *A. compressus*, *B. lata*, *D. horizontalis*, *D. aegyptium*, and *S. barbata* were the most virulent on cv. Golden Bantam. The *P. maximum* isolate would infect only cv. Golden Bantam and it was so mild it was not possible to maintain it using maize-to-maize transmission; it resulted in symptoms that became milder as maize plants matured. Similar findings by Pinner et al (20) were explained by the inability of the virus isolate to sustain replication at the rate of cell division.

Nine isolates could not infect the maize

**Table 4.** Transmission of a severe MSV maize isolate to 17 plant species and from them back to maize using *Cicadulina storeyi* as a vector

Test plant species	From maize <sup>a</sup> to test plant	Symptoms on test plant	Symptoms on maize
<i>Axonopus compressus</i>	+ <sup>b</sup>	Severe	Severe
<i>Brachiaria lata</i>	+	Severe	Severe
<i>B. deflexa</i>	+	Mild	Severe
<i>B. distichophylla</i>	+	Severe	Severe
<i>Coix lachryma-jobi</i>	+	Severe	NT
<i>Dactyloctenium aegyptium</i>	—	...	...
<i>Digitaria horizontalis</i>	+	Mild <sup>c</sup>	Severe
<i>Eleusine indica</i>	+	Mild	Mild
<i>Echinochloa colonum</i>	—	...	...
<i>Oryza sativa</i>	—	...	...
<i>Paspalum scrobiculatum</i>	+	Mild	Mild
<i>Panicum maximum</i>	—	...	...
<i>Pennisetum americanum</i>	+	Mild	Mild
<i>Pennisetum polystachion</i>	—	...	...
<i>Rhynchelytrum repens</i>	—	...	...
<i>Rottboellia cochinchinensis</i>	—	...	...
<i>Setaria barbata</i>	+	Severe	Severe

<sup>a</sup> Zea mays cv. Pool 16.

<sup>b</sup> + = Positive transmission (at least one plant positive); — = negative transmission. NT = not tested.

<sup>c</sup> Some plants had severe symptoms.

**Table 5.** Host range of five streak virus grass isolates from Nigeria

Source of isolate	Test plant			
	<i>Axonopus compressus</i>	<i>Brachiaria lata</i>	<i>Digitaria horizontalis</i>	<i>Panicum maximum</i>
<i>A. compressus</i> , mild	8/12 <sup>a</sup>	1/8	3/11	0/9
<i>A. compressus</i> , severe	7/15	1/17	0/13	0/10
<i>B. lata</i> , severe	5/6	6/14	0/8	0/9
<i>D. horizontalis</i> , mild	6/6	3/8	8/23	0/9
<i>P. maximum</i> , mild	4/15	3/9	0/8	6/15

<sup>a</sup> Number of plants infected/number of plants challenged.

**Table 6.** Serological reactions<sup>a</sup> of 24 streak virus isolates

Isolate	DAS-ELISA <sup>b</sup> antiserum		PAS-ELISA <sup>c</sup> antiserum		
	Maize	Maize	Panicum	Sugarcane	Digitaria
<i>Axonopus compressus</i> A <sup>d</sup>	++++ <sup>c</sup>	+++	—	—	—
<i>A. compressus</i> B	+++	++	—	—	—
<i>Brachiaria lata</i> A	++	+	+/-	—	—
<i>B. lata</i> B	+	NT	NT	NT	NT
<i>B. deflexa</i>	+	+	—	—	—
<i>B. distichophylla</i>	+	+	—	—	—
<i>Coix lachryma-jobi</i>	—	—	+	+	—
<i>Dactyloctenium aegyptium</i>	+++	+++	—	—	—
<i>Digitaria horizontalis</i> A	++	++	—	—	—
<i>D. horizontalis</i> B	+	NT	NT	NT	NT
<i>Eleusine indica</i>	+	+	—	—	—
<i>Echinochloa colonum</i>	+	+	—	—	—
<i>E. stagnina</i>	+	+	—	—	—
<i>Oryza sativa</i>	+	+	—	—	—
<i>Paspalum conjugatum</i>	—	+/-	—	—	—
<i>P. notatum</i>	+	+	—	—	—
<i>P. scrobiculatum</i>	—	—	—	—	—
<i>Panicum maximum</i>	+/-	+/-	++	—	—
<i>Pennisetum americanum</i>	—	+/-	++	+/-	—
<i>P. polystachion</i>	—	—	—	+/-	—
<i>Rhynchelytrum repens</i>	++	+	—	—	—
<i>Rottboellia cochinchinensis</i>	—	NT	NT	NT	NT
<i>Setaria barbata</i>	+++	++	—	—	—
<i>Zea mays</i> (infected)	+++	+++	—	+/-	—
<i>Zea mays</i> (healthy)	—	—	—	—	—

<sup>a</sup> ELISA (enzyme-linked immunosorbent assay) tests carried out using sap extracts from the original host; readings taken after 1 hr.

<sup>b</sup> Double-antibody sandwich ELISA.

<sup>c</sup> Protein A ELISA.

<sup>d</sup> A = severe isolate; B = mild isolate.

<sup>e</sup> +++++ = Positive in 1/5, 1/25, 1/625, and 1/1,250 dilutions; +++ = positive in 1/5 and 1/25 dilutions; ++ = positive in 1/5 dilution only; + = positive in 1/5 dilution but weak; +/- = positive in 1/5 dilution after several hours. NT = not tested.



cultivar Pool 16, known to be susceptible to MSV as it occurs in farmers' fields in West Africa. Pool 16 and FR 1141 × FR 303 are immune to some MSV isolates in spite of their susceptibility to others. Thus, some isolates appear to be adapted to their grass hosts (or to a group of grass hosts) as earlier reported by Bock et al (3). The significance of these observations is that many streak isolates in West African grasses would not be a source of maize-infecting streak in the field. More research is needed with a broader range of maize cultivars to confirm these results.

Some isolates could not be transmitted from maize back to their original host or from maize to maize (i.e., *P. maximum* isolate). It was not possible to retransmit three grass isolates to the host species from which they were derived. The failure to transmit could be attributable to virus/host interactions that may prevent the virus from establishing or perhaps from replicating effectively and/or to vector feeding behavior. Similar results have been reported by Pinner et al (20). Some *Cicadulina* species are known to be more successful at acquiring and transmitting MSV than others (6). Further studies on the interaction of different streak virus isolates, their host plants, and feeding behavior of vector species are underway and will be reported elsewhere.

Other authors (3,16,27) have reported difficulties in transmitting isolates from grasses to maize. Rossel and Thottappilly (24) indicated they were unable to transmit streak isolates from *B. mutica*, *R. cochinchinensis*, and *P. maximum* to maize. Markham et al (15) and Pinner et al (20) were unable to transmit the sugarcane isolates from South Africa and Mauritius to sugarcane and the *Coix*-infecting isolate from *C. lachryma-jobi* to *C. lachryma-jobi* or from maize to *C. lachryma-jobi*. We were, however, able to transmit a *C. lachryma-jobi* isolate back to its original host in nine of 20 attempts.

By using polyclonal antisera derived separately from maize and *P. maximum*, we were able to distinguish two distinct strains among the streak isolates tested. These are the maize strain and the *P. maximum* strain. Our results are in agreement with those of Bock et al (3), Rossel and Thottappilly (24), and Pinner et al (20). The isolates from *P. maximum* and *P. americanum* belong to the *Panicum* strain; neither infected cvs. Pool 16 or FR 1141 × FR 303, and both resulted in mild symptoms in cv. Golden Bantam. The isolate from *C. lachryma-jobi* reacted with antisera to strains from panicum and sugarcane but not to the maize strain, thus, it appears not to be serologically related to the maize MSV isolate from Nigeria. This is in contrast with reports by Ricaud and Felix (22), indicating the maize and *C. lachryma-jobi*

streak strains from Mauritius were closely related. Isolates from *P. scrobiculatum*, *R. cochinchinensis*, and *P. polystachion* appear not to be serologically related to the maize MSV isolate from Nigeria either. In spite of differences in virulence depending on the host origin of the isolate, all other isolates studied were found to be serologically related to the maize strain; this also was confirmed by their other biological properties.

None of the isolates tested reacted positively with the antiserum from DSV. Peterschmitt et al (18) reported crude extracts from *D. setigera* (= *D. sanguinalis*) infected with DSV did not react with antiserum to MSV from maize from Réunion. It is probable that this is a distinct virus and not a strain of MSV as reported before (19). Pinner et al (20) were unable to transmit the Vanuatu DSV to maize cv. Golden Bantam even when *Cicadulina* leafhoppers were injected with concentrated pure virus. The vector of DSV is not *Cicadulina* sp. but *Nesochlutha declivata* (Julia and Dollet cited by Pinner et al) (20). In view of the close relationship between maize streak virus and its *Cicadulina* vectors in Africa (23), this gives further credence to the idea that DSV is a distinct virus in spite of its reported serological relationship to some MSV isolates (9,20).

As it occurs in maize, MSV is a new-encounter disease (4) that followed the reunion of maize, introduced to Africa from the Americas approximately 400 yr ago, and streak virus, an endemic African virus of indigenous grasses (23,27). Presumably, only some of the original streak strains were capable of naturally infecting maize. Infection events probably happened independently in various locations in the African continent, followed by further selection/host adaptation in those locations and further spread (4). With the expansion of maize cultivation in the continent, epidemics then followed and occur periodically.

Weed grass hosts are normally considered to be reservoirs of streak virus and to pose a potential threat to susceptible maize. It appears, however, that the streak occurring in many grasses in Nigeria (representative of lowland ecologies of West Africa) is of strains not readily transmissible to susceptible field maize. Peterschmitt et al (18) suggested the importance of alternate hosts of MSV may be less than originally thought because grasses might be infected by avirulent or not very aggressive strains. Although 18 of 24 isolates we tested from different crop and grass hosts reacted to some degree with the IITA MSV antiserum in DAS-ELISA tests, only half of the isolates could infect a susceptible tropical field maize cultivar (Pool 16). Based on the results of host range, symptom severity, and serology of the isolates we tested, it appears that some of

the grass weeds most likely to be involved in perpetuating an epidemiologically competent maize strain of MSV in Nigeria are *A. compressus*, *B. lata*, and *S. barbata*. These are common weeds in many parts of Nigeria, and we have confirmed that they harbor MSV inoculum under field conditions and can become infected with the severe MSV maize isolate under controlled conditions. In addition, some of them are known to be hosts of the leafhopper vectors.

Other grasses to which we were able to transmit the severe MSV maize isolate, such as *B. deflexa* and *B. distichophylla*, might also be of epidemiological importance, but more research is needed to determine if they harbor the MSV maize strain under natural field conditions. The epidemiological role of *D. aegyptium* remains unclear; although this species was found to harbor a severe streak isolate easily transmissible to maize cv. Golden Bantam and which reacted with MSV maize antisera, attempts to transmit to it a severe MSV maize isolate failed. Similarly, *D. horizontalis* was confirmed to harbor a severe streak isolate, but transmission of the severe MSV maize isolate to this host gave varied results. In addition, transmission to *D. horizontalis* of other severe MSV isolates originating from *A. compressus* and *B. lata* failed.

Based on serology and/or transmission results the streak isolates tested from *C. lachryma-jobi*, *P. maximum*, *Paspalum* spp., *Pennisetum* spp., *R. cochinchinensis*, and *R. repens* appear too distantly related to MSV from maize to be important in relation to MSV disease in the field. Understanding survival of grasses harboring maize-competent MSV and vectors during the dry season (November to April) particularly in "fadamas" (low lying fields with residual moisture) will be of critical importance for understanding MSV ecology and epidemiology. Although much more remains to be understood on MSV epidemiology and vector ecology/behavior in the field, we believe our results are of significance from the point of view of suggesting the potential for and limitations of the spread of the disease within and between the different plant species and then onto maize crops.

#### ACKNOWLEDGMENTS

We thank P. G. Markham for providing antisera; H. W. Rossel, D. Florini, and M. Winslow for reviewing the manuscript; and C. W. Agyakwa for assistance in identification of the grass species.

#### LITERATURE CITED

1. Akobundu, O. I., and Agyakwa, W. C. 1987. A Handbook of West African Weeds. International Institute of Tropical Agriculture, Ibadan, Nigeria. 521 pp.
2. Bock, K. R. 1974. Maize streak virus. No. 133 in: Descriptions of Plant Viruses. Commonw. Mycol. Inst./Assoc. Appl. Biol., Kew, England. 4 pp.
3. Bock, K. R., Guthrie, E. J., and Woods, R. D. 1974. Purification of maize streak virus and its

- relationship to viruses associated with streak diseases of sugarcane and *Panicum maximum*. *Ann. Appl. Biol.* 77:289-296.
4. Buddenhagen, I. W. 1977. Resistance and vulnerability of tropical crops in relation to their evolution and breeding. *Ann. N.Y. Acad. Sci.* 287:309-326.
  5. Clark, M. F., and Adams, A. N. 1977. Characteristics of the microplate method of enzyme-linked immunosorbent assay for the detection of plant viruses. *J. Gen. Virol.* 34:475-483.
  6. Dabrowski, Z. T. 1987. Some parameters affecting suitability of *Cicadulina* species for resistance screening to maize streak virus (MSV). *Insect Sci. Its Appl.* 8:757-764.
  7. Damsteegt, V. D. 1983. Maize streak virus: I. Host range and vulnerability of maize germ plasm. *Plant Dis.* 67:734-737.
  8. Dekker, E. L., Pinner, M. S., Markham, P. G., and van Regenmortel, M. H. V. 1988. Characterization of maize streak virus isolates from different plant species by polyclonal and monoclonal antibodies. *J. Gen. Virol.* 69:983-990.
  9. Dollet, M., Accotto, G. P., Lisa, V., Menissier, J., and Boccardo, G. 1986. A geminivirus, serologically related to maize streak virus, from *Digitaria sanguinalis* from Vanuatu. *J. Gen. Virol.* 67:933-937.
  10. Edwards, M. L., and Cooper, J. I. 1985. Plant virus detection using a new form of indirect ELISA. *J. Virol. Methods* 11:309-319.
  11. Efron, Y., Kim, S. K., Fajemisin, J. M., Mareck, J. H., Tang, C. Y., Dabrowski, Z. T., Rossel, H. W., Thottappilly, G., and Buddenhagen, I. W. 1989. Breeding for resistance to maize streak virus: A multidisciplinary team approach. *Plant Breeding* 103:1-36.
  12. Fajemisin, J. M., Cook, G. E., Okusanya, F., and Shoyinka, S. A. 1976. Maize streak virus epiphytotic in Nigeria. *Plant Dis. Rep.* 60:443-447.
  13. Harrison, B. D. 1985. Advances in geminivirus research. *Annu. Rev. Phytopathol.* 23:55-82.
  14. International Institute of Tropical Agriculture (IITA). 1984. Pages 42-43 in: IITA Annual Report for 1983. Ibadan, Nigeria.
  15. Markham, P. G., Pinner, M. S., and Boulton, M. I. 1984. The transmission of maize streak virus by leafhoppers, a new look at host adaptation. *Bull. Soc. Entomol. Suisse* 57:431-432.
  16. McClean, A. P. D. 1947. Some forms of streak virus occurring in maize, sugar-cane and wild grasses. *Sci. Bull. S. Afr. Dep. Agric. Tech. Serv.* 265. 39 pp.
  17. Ngwira, P. 1988. Serological differentiation of MSV isolates and epitope characterization of the MSV capsid protein. M. S. thesis. Ohio State University, Columbus, OH. 79 pp.
  18. Peterschmitt, M., Reynaud, B., Sommermeyer, G., and Baudin, P. 1991. Characterization of maize streak virus isolates using monoclonal and polyclonal antibodies and by transmission to a few hosts. *Plant Dis.* 75:27-32.
  19. Pinner, M. S., and Markham, P. G. 1990. Serotyping and strain identification of maize streak virus isolates. *J. Gen. Virol.* 71:1635-1640.
  20. Pinner, M. S., Markham, P. G., Markham, R. H., and Dekker, E. L. 1988. Characterization of maize streak virus: Description of strains; symptoms. *Plant Pathol.* 37:74-87.
  21. Purseglove, J. W. 1972. *Tropical Crops Monocotyledons*. Longman, England. 607 pp.
  22. Ricaud, C., and Felix, S. 1978. Strains of streak virus infecting sugarcane. Pages 449-457 in: *Proc. Congr. Int. Soc. Sugarcane Technol.*, 16th. F. S. Reis and J. Dick, eds. Impress, Sao Paulo.
  23. Rose, D. J. W. 1978. Epidemiology of maize streak disease. *Annu. Rev. Entomol.* 23:259-282.
  24. Rossel, H. W., and Thottappilly, G. 1985. *Virus Diseases of Important Food Crops in Tropical Africa*. International Institute of Tropical Agriculture, Ibadan, Nigeria. 61 pp.
  25. Seth, M. L., Raychaudhuri, S. P., and Singh, D. V. 1972. Bajra (pearl millet) streak: A leafhopper-borne cereal virus in India. *Plant Dis. Rep.* 56:424-428.
  26. Soto, P. E., Buddenhagen, I. W., and Asnani, V. L. 1982. Development of streak virus resistant maize populations through improved challenge and selection methods. *Ann. Appl. Biol.* 100:539-546.
  27. Storey, H. H., and McClean, A. P. D. 1930. The transmission of streak disease between maize, sugarcane and wild grasses. *Ann. Appl. Biol.* 17:691-719.
  28. Webb, M. D. 1987. Species recognition in *Cicadulina* leafhoppers (Hemiptera: Cicadellidae), vectors of pathogens of Gramineae. *Bull. Entomol. Res.* 77:683-712.