Interactions Between Maize Mosaic and Maize Stripe Viruses in Their Insect Vector, *Peregrinus maidis*, and in Maize

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ABSTRACT

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Interactions between maize mosaic virus (MMV) and maize stripe virus (MStpV) were studied in two cultivars of maize and in two biotypes of the planthopper vector, *Peregrinus maidis*. Plants previously infected with either virus were partially protected from infection by the other. This interference was more consistent in cultivar Aristogold Bantam Evergreen than in cultivar Golden Cross Bantam and at a temperature of 25.5 C than at 32–33 C. As judged by enzyme-linked immunosorbent assay, the concentration of MStpV antigen was usually higher in plants infected by MStpV alone than it was in plants also infected with MMV. In both *P. maidis* biotypes, access to MMV-infected plants within 0–14 days before or after access to MStpV-infected plants significantly reduced the fraction of insects transmitting MStpV. Also, MStpV transmission was significantly delayed in insects exposed to both viruses. In contrast, access to MStpV-infected plants usually had no effect on the acquisition and transmission of MMV.

Maize mosaic virus (MMV) and maize stripe virus (MStpV) cause distinct diseases of maize (*Zea mays* L.) in tropical and subtropical areas of Africa and North, Central, and South America (6). MStpV, associated with fine (about 3 nm in diameter) filamentous nucleoprotein particles (8), belongs to a new group of plant viruses, the Rice Stripe Virus Group (R. I. Hamilton, *personal communication*); MMV is a rhabdovirus (9). Both viruses are vectored by the same delphacid planthopper, *Peregrinus maidis* Ashmead, and have overlapping plant host ranges and geographical distributions (6,8–10). These properties suggest a high likelihood of natural, mixed infections and the potential for MMV-MStpV interactions in plants, insects, or both. Recently, Lastra and Carballo (11) observed an almost complete displacement of MMV by MStpV throughout Venezuela between 1976 and 1982. However, no MMV-MStpV interaction studies in *P. maidis* or maize have been reported, except for abstracts of the present work (2,4).

In this study, interactions of MMV and MStpV were studied in two cultivars of maize and in two biotypes of *P. maidis*. The possible implications of these interactions on the epidemiology of the two viruses is discussed.

MATERIALS AND METHODS

Viruses and vectors. The MMV isolate was obtained from Hawaii (3). The MStpV isolate was originally collected in Florida and was described by Gingery et al (7). The two biotypes of *P. maidis*, F and H, were obtained from Florida and Hawaii, respectively, and maintained in culture as previously described (8).

MMV-MStpV interaction in maize plants. Exposed or inoculative *P. maidis* were placed on sweet corn (*Z. mays*) cultivar Aristogold Bantam Evergreen or cultivar Golden Cross Bantam at the three- to five-leaf stage. Exposed planthoppers were those that had fed on MMV- or MStpV-infected plants for 1–2 wk at least 2 wk before being used for inoculation. Inoculative planthoppers were exposed ones shown to be virus transmitters by bioassay on maize plants.

During inoculation-access periods (IAPs), the duration of which varied depending on the experiment, plants were maintained in a growth chamber at 25 ± 1 C and 16 hr light/day. Test plants were all the same age and were either healthy or previously infected with MMV (when MStpV was inoculated) or MStpV (when MMV was inoculated). After IAPs, plants were sprayed with insecticide and held 4–5 wk in an insect-containment greenhouse (maximum temperature of 32 or 33 C) or growth chamber (25 ± 1 C) for observation of symptoms. All doubly inoculated plants and all symptomless, singly inoculated plants were assayed by enzyme-linked immunosorbent assay (ELISA) for MStpV and by gel double-diffusion tests for MMV.

MMV-MStpV interaction in *P. maidis*. Planthoppers were maintained at 25 ± 1 C in the growth chamber. For virus acquisition, groups of nonviruliferous, second- to third-instar nymphs were exposed to MMV-, MStpV-, or doubly infected plants for 1–7 days. In some experiments, insects were given sequential acquisition periods. (Doubly infected plants were serologically confirmed to contain both viruses before being used for acquisition feeds.) Planthoppers were then held for 2–3 wk on healthy maize to allow for the virus latent period in the vector before testing them individually for inoculativity by allowing them to feed on a series of four or five maize seedlings (1 wk each). These plants were then held in the greenhouse for 4–5 wk and observed for symptoms. Surviving planthoppers were then tested for MStpV by ELISA. (No serological test sensitive enough to test for MMV in individual planthoppers was available.) Test plants fed on by insects exposed to both viruses were assayed for both serologically.

Serological tests. Plants were assayed for MStpV antigen by ELISA according to the method of Nault et al (14), except that the coating antibody was 1.0 μg/ml and the A_{405nm} was determined

with a Bio-Tek Model EL307 EIA Reader (Bio-Tek Instruments, Inc., Burlington, VT). Plant samples were prepared by grinding 0.5 g of leaf tissue in 1 ml of phosphate-buffered saline (PBS)-Tween (0.14 M NaCl, 0.01 M potassium phosphate, pH 7.4, containing 0.02% sodium azide and 0.05% Tween 20) with a mortar and pestle and pressing the extract through two layers of cheesecloth. Planthopper samples were prepared by grinding individual insects in 0.2 ml of PBS-Tween in a glass tissue homogenizer.

Gel double-diffusion tests were done in 0.5% agar in PBS-EDTA (PBS containing 0.02% sodium azide and 0.01 M EDTA) using plant samples prepared as above for ELISA. Plates were incubated overnight at 25 C.

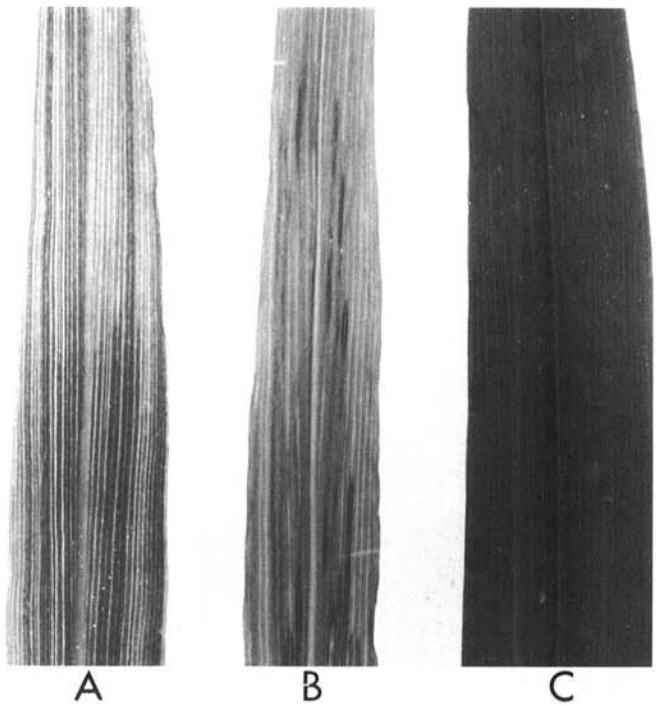

Fig. 1. Advanced symptoms of maize mosaic and maize stripe viruses on maize leaves. **A,** Maize mosaic virus. **B,** Maize stripe virus. **C,** Healthy.

RESULTS

Symptoms on singly and doubly infected plants. On maize inoculated at the three- to five-leaf stage, MMV produced long, nearly continuous chlorotic stripes uniformly distributed over the leaf blade (Fig. 1A). MStpV produced finer, more closely spaced chlorotic stripes that radiated from the basal part of the leaf blade and gradually widened into yellow bands (Fig. 1B). At a later stage of MStpV infection, younger leaves were frequently completely yellow. Symptoms of MStpV infection usually appeared 1 or 2 days earlier than those of MMV. Golden Cross Bantam sweet corn under greenhouse conditions (14.4–32.2 C) first expressed symptoms of MStpV infection at 6.2 ± 0.5 days after inoculation, and of MMV infection at 7.7 ± 0.6 days after inoculation (54 and 38 plants, respectively).

Initially, doubly infected plants usually showed symptoms characteristic of both viruses, i.e., both fine and coarse chlorotic stripes and yellow bands. However, after 3–4 wk, MStpV symptoms appeared to mask those of MMV, and, except for early death, symptoms on older doubly infected plants were indistinguishable from those on plants infected with MStpV alone. In an experiment with Golden Cross Bantam, the fractions of plants that died 5–6 wk after inoculation were 0/11 for MMV-, 2/15 for MStpV-, and 13/19 for doubly infected plants.

During these experiments, we sometimes observed partial recovery, i.e., the gradual recession of symptoms on newly emerging leaves, in MMV-infected plants, especially at warm (> 32 C) greenhouse temperatures (Fig. 2A). Some of these plants also produced new symptomless shoots (Fig. 2B). Serological tests on five such plants were positive for MMV on older, symptomatic leaves and negative on younger, symptomless leaves. The fractions of MMV-infected plants in the greenhouse showing recovery by 4–5 wk after inoculation were 17/85 (20%) for Aristogold and 28/93 (30%) for Golden Cross Bantam. At cooler (growth chamber) temperatures, only 0–5% of MMV-infected plants showed recovery. Recovery in MStpV-infected plants ranged from 5 to 8% in warm greenhouse conditions but was not detected in the growth chamber.

Interactions in maize plants. We assessed interference between MMV and MStpV in maize by determining if prior infection by one of these viruses decreased the probability of infection by the other. We also tested for a reduction in replication of MStpV

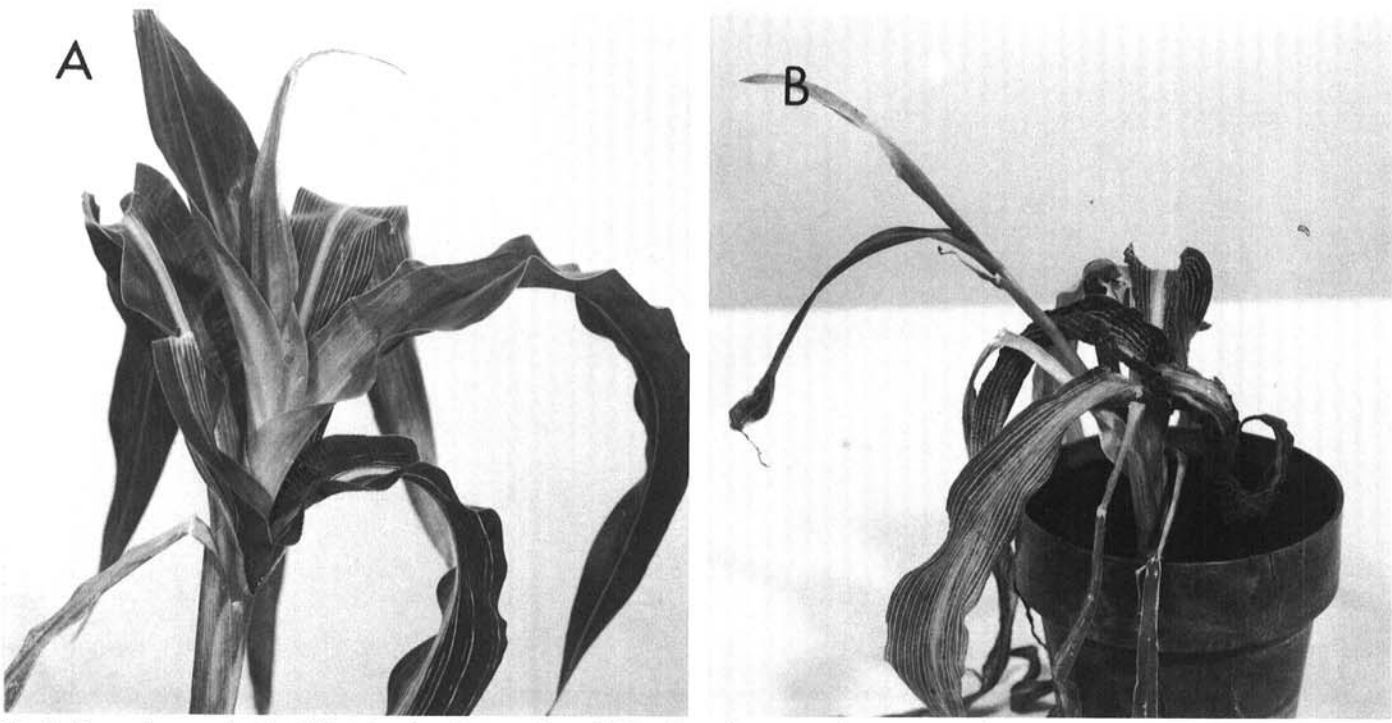

Fig. 2. Two maize mosaic virus-infected maize plants, cultivar Golden Cross Bantam, under warm greenhouse temperature, showing recovery from symptoms. **A,** The emergence of new symptomless leaves. **B,** The appearance of a new symptomless shoot.

caused by infection of MMV.

For both viruses, the rates of infection were usually lower in previously infected plants than in healthy plants (Table 1). This trend was more evident when test plants were exposed to day temperatures of 25.5 ± 1 C (growth chamber; experiments 4 and 5) than when day temperatures rose to 33.3 C (greenhouse; experiments 2 and 3). In three of the five experiments, the inhibitory effect of preinfection with MMV on subsequent infection with MStpV was more pronounced than was the effect of MStpV on MMV (experiments 2, 4, and 5). When the results of the five experiments were combined, the effect of MMV on MStpV was more highly significant ($\chi^2 = 20.3$, $P < 0.001$) compared with that of MStpV on MMV ($\chi^2 = 5.9$, $P < 0.05$). An ELISA test for MStpV antigen allowed us to determine if the above interference also included the inhibition of MStpV replication in MMV-infected plants (Table 2). The results showed a significant reduction in the titer of MStpV antigen in such plants in four of the seven experiments ($P < 0.03$ to < 0.001). A comparable test for MMV replication was not done because of the lack of a suitable MMV assay.

Interactions in the insect vector. To test for interactions between MMV and MStpV in *P. maidis*, we measured the effect of oral acquisition of one virus on the ability to transmit the other. Planthoppers were given various acquisition-access sequences and times on singly and doubly infected plants and then checked individually for their ability to transmit the viruses in four or five successive, week-long bioassay tests. In all five experiments (Table 3), access to MMV-infected plants markedly decreased the

TABLE 1. Effect of prior infection by maize mosaic virus (MMV) or maize stripe virus (MStpV) on subsequent infection by the other virus

Experiment (maximum daily temp. [C])[a]	Maize cultivar (*Peregrinus maidis* biotype)	Inoculated virus[b]	Test plant previously infected with[c]	Plants tested (no.)	Plants infected with[d] (%)	
					MMV	MStpV
1	Golden Cross	MMV	···	18	66.7	···
(32.2)	Bantam	MStpV	···	20	···	70.0
	(F)[e]	MMV	MStpV	18	27.8*	···
		MStpV	MMV	15	···	53.3
2	Aristogold	MMV	···	40	97.5	···
(33.3)	(H)	MStpV	···	40	···	100.0
		MMV	MStpV	30	93.3	···
		MStpV	MMV	27	···	81.5**
3	Golden Cross	MMV	···	40	90.0	···
(33.3)	Bantam	MStpV	···	40	···	97.5
	(H)	MMV	MStpV	28	96.4	···
		MStpV	MMV	21	···	100.0
4	Aristogold	MMV	···	29	82.8	···
(25.5)	(H)	MStpV	···	30	···	100.0
		MMV	MStpV	20	55.0*	···
		MStpV	MMV	19	···	63.2***
5	Golden Cross	MMV	···	28	75.0	···
(25.5)	Bantam	MStpV	···	30	···	100.0
	(H)	MMV	MStpV	20	70.0	···
		MStpV	MMV	20	···	80.0*
Overall		MMV	···	155	85.2	···
		MStpV	···	160	···	95.6
		MMV	MStpV	116	73.3*	···
		MStpV	MMV	102	···	77.5***

[a] Plants were maintained in a greenhouse (Experiments 1–3) or in a growth chamber (Experiments 4 and 5).
[b] Plants were inoculated by placing (five to eight) insects previously exposed to virus-infected plants on each test plant for a 1-day inoculation access period.
[c] These plants were showing symptoms of the indicated virus and had been inoculated 8 days earlier.
[d] Presence of virus was judged by the appearance of symptoms for singly inoculated plants and by serological tests for doubly inoculated plants. *, **, and *** indicate that the fraction of doubly inoculated plants that became infected with a virus is significantly different at $P < 0.05$, < 0.01, and < 0.001, respectively, from the fraction of singly inoculated plants infected with the same virus in the same experiment (χ^2 tests).
[e] F = Florida biotype; H = Hawaii biotype.

TABLE 2. Effect of infection by maize mosaic virus (MMV) on the concentration of maize stripe virus (MStpV) antigen in maize

Maize cultivar	Experiment no.	Inoculation sequence	MStpV antigen concentration in plants infected with[a]		Significance[c] (P)
			MStpV	MMV[b] and MStpV	
Aristogold	1	MMV-MStpV[d]	1.46 (3)	0.48 (5)	0.002**
	2	MStpV-MMV[d]	1.95 (1)	1.36 (5)	0.03*
	3	Simultaneously[e]	0.73 (3)	0.55 (16)	0.11
Golden Cross	1	Simultaneously[e]	0.59 (18)	0.32 (16)	0.001***
Bantam	2	MMV-MStpV[f]	0.47 (4)	0.32 (9)	0.17
	3	MStpV-MMV[f]	0.52 (8)	0.40 (5)	0.20
	4	Simultaneously[e]	1.12 (5)	0.66 (16)	0.02**

[a] Plants were assayed 4 wk after inoculations were completed. Values are the average A_{405nm} value of plant samples tested; numbers of plants assayed are in parentheses, duplicates of each sample were done.
[b] Presence of MMV confirmed by gel double-diffusion test.
[c] Differences between the two means in each experiment were evaluated with a Student's t-test.
[d] Each plant was inoculated using one inoculative insect/plant, 2-day inoculation access period (IAP); the two inoculations followed one another immediately.
[e] MMV and MStpV simultaneously inoculated using five to eight MMV-exposed insects and five to eight MStpV-exposed insects per plant; 1-day IAP.
[f] For each inoculation sequence there were 4 days between individual inoculations and five to eight exposed insects were used with a 1-day IAP.

transmission of MStpV, regardless of whether the access to MMV-infected plants occurred before, after, or simultaneously with, access to MStpV-infected ones. In contrast, the transmission rates of MMV in reciprocal tests was largely unaffected by access to MStpV-infected plants. Results were similar for simultaneous acquisition from doubly infected plants (experiments 1–3) or sequential acquisition from singly infected ones (experiments 4 and 5). Interference with MStpV transmission by MMV is also shown in Figure 3, where the weekly transmission percentages of MMV and MStpV by *P. maidis* after single and sequential acquisitions are plotted.

This seemingly one-way interference of MMV with MStpV in *P. maidis* occurred in both biotypes, even though biotype H transmitted MStpV separately much more efficiently than it did

TABLE 3. Transmission of maize mosaic virus (MMV) and maize stripe virus (MStpV) by *Peregrinus maidis* after acquisition-access periods on MMV-, MStpV-, or doubly infected plants

Experiment[a] (*P. maidis* biotype)	Acquired virus(es)	AAP[b] (days)	Insects tested (no.)	Insects transmitting[c] (%)		Insects doubly inoculative[d] (%)
				MMV	MStpV	
1 (F)[e]	MMV	1	54	3.7		
	MStpV	1	50		10.0	
	MMV + MStpV[f]	1	81	2.5	4.9	0.0
2 (F)	MMV	3	51	5.9		
	MStpV	3	50		28.0	
	MMV + MStpV[f]	3	70	7.1	5.7***	1.4
3 (F)	MMV	7	43	18.6		
	MStpV	7	18		16.7	
	MMV + MStpV[f]	7	40	27.5	5.0**	5.0
4 (F)	MMV	14	59	32.2		
	MStpV	14	60		40.0	
	MMV, MStpV[g]	14	58	25.9	6.9***	1.7
	MStpV, MMV[g]	14	60	35.0	16.7**	3.3
5 (H)	MMV	7	51	35.3		
	MStpV	7	51		88.2	
	MMV, MStpV[g]	14	51	43.1	15.7***	7.8
	MStpV, MMV[g]	14	51	43.1	13.7***	5.9
	MMV, MStpV[h]	14	51	54.9*	58.8**	33.3
	MStpV, MMV[h]	14	51	41.2	19.6***	17.6

[a] Maize cultivar was Golden Cross Bantam in Experiment 4 and Aristogold Bantam Evergreen in other experiments.
[b] AAP = Acquisition-access period.
[c] Two weeks after acquisition, insects were placed individually on a new maize test plant each week for four consecutive weeks. Viruses transmitted to test plants were determined 4–5 wk after exposure to insects by symptomatology and/or serology. *, **, and *** indicate that the fraction of insects transmitting a virus after acquisition from a plant infected with both viruses (Experiments 1–3) or from two plants, each infected with a different virus (Experiments 4 and 5) was significantly different at $P<0.05$, <0.01, and <0.001, respectively, from the fraction transmitting the same virus following acquisition from a singly infected plant in the same experiment (χ^2 tests).
[d] Insects transmitting both MMV and MStpV; these insects are also included in the columns MMV and MStpV.
[e] F = Florida biotype; H = Hawaii biotype.
[f] Acquisition from doubly infected plants.
[g] Sequential AAPs of 7 days for each virus.
[h] AAPs of 7 days for each virus with a 7-day period between AAPs.

TABLE 4. Patterns of transmission of maize mosaic virus (MMV) and maize stripe virus (MStpV) by doubly inoculative *Peregrinis maidis*[a]

Acquisition treatment[b]	Insect no.	Virus transmitted during week[c]					Acquisition treatment	Insect no.	Virus transmitted during week				
		3	4	5	6	7			3	4	5	6	7
Week 1: MStpV	1	*S*	*M* + *S*	M + S	M + S		Week 1: MMV	17		*M*	*M* + *S*	.	.
Week 2: MMV	2	–	*M*	S	.	.	Week 3: MStpV	18		*M* + *S*	.	M + S	.
	3	–	M	*M* + *S*	–			19		*M* + *S*	.	.	.
Week 1: MStpV	4		–	*M* + *S*	.	.		20		M	*M* + *S*	M + S	.
Week 3: MMV	5		–	–	M	*M* + *S*		21		–	–	*M* + *S*	.
	6		–	–	*M* + *S*	.		22		M	*M* + *S*	.	.
	7		–	–	*M* + *S*	–		23		M	*M* + *S*	.	.
	8		–	–	M	*M* + *S*		24		M	*M* + *S*	.	.
	9		–	–	M	*M* + *S*		25		M	*M* + *S*	.	.
	10		*S*	S	M + S	*M* + *S*		26		*M* + *S*	M + S	*M* + *S*	.
	11		*S*	S	*M* + *S*	–		27		*M*	M + S	*M* + *S*	.
	12		S	*M* + *S*	.	M + S		28		M	*M* + *S*	.	.
Week 1: MMV	13	*S*	*M* + *S*	M + S	.			29		M	–	*M* + *S*	*M* + *S*
Week 2: MStpV	14	M	M	M	*M* + *S*			30		M	*M* + *S*	M + S	.
	15	M	M	*M* + *S*	.			31		M	*M* + *S*	–	–
	16	*M* + *S*	.	.	.			32		*M* + *S*	M + S	.	.
								33		*M*	M	*M* + *S*	–

[a] Planthoppers from Experiment 5 in Table 3 that transmitted both viruses; maize cultivar was Aristogold Bantam Evergreen.
[b] Acquisition-access period = 7 consecutive days per virus.
[c] Individual insects were placed on a new maize test plant each week for four consecutive weeks. Viruses transmitted to test plants were determined 4 wk after exposure to insects by symptomatology and/or serology. M = Symptoms of MMV, S = symptoms of MStpV; *M* and *S* = symptoms confirmed by serology; – = no symptoms; . = test plant or insect died.

MMV (Table 3). Biotype F transmitted MMV and MStpV separately with similar efficiencies. However, the percentage of insects that became doubly inoculative was 0–5% in biotype F and 5.9–33.3% in biotype H. For biotype H, this percentage was higher when a week elapsed between two 1-wk feedings on diseased plants than if the two feedings immediately followed each other ($P <$ 0.1–$<$ 0.01).

Weekly transmission by doubly inoculative insects (biotype H) was monitored to see if the sequence or timing of virus acquisitions affected the patterns of MMV or MStpV transmission (Table 4). Of the 33 insects monitored, 18 transmitted the first-acquired virus (14 MMV and four MStpV) 1–3 wk before the second-acquired virus, six transmitted the second-acquired virus first (five MMV and one MStpV), and nine began transmitting both viruses during the same week. Whether transmitted alone or with MMV, a significant delay in MStpV transmission was detected in insects exposed to both viruses in either sequence. The mean latent period for MStpV in these insects was 2.44 ± 0.12 wk, compared with 1.86 ± 0.07 wk for insects that had had access only to MStpV (means different at $P <$ 0.001). On the other hand, the latent periods of MMV in insects after single-virus or double-virus acquisition feedings were similar, 2.94 ± 0.15 wk and 2.83 ± 0.12 wk, respectively. It is interesting to note that the latent period of singly acquired MMV (2.94 wk) was significantly longer than that of singly acquired MStpV (1.86 wk) ($P <$ 0.001).

An ELISA test for MStpV was carried out on each of 56 planthoppers that survived the 4-wk bioassay tests (Table 5). The ELISA and bioassay results agreed for all insects (10) that had had access to only MStpV and for 12 of 13 insects that had had access to both viruses, but transmitted only MStpV. For these insects, positive ELISA values (A_{405nm}) for MStpV transmitters averaged 0.718 ± 0.153, whereas negative values for MStpV-unexposed nontransmitters averaged 0.020 ± 0.002. Negative ELISA values for most doubly exposed insects that did not transmit MStpV averaged 0.018 ± 0.001, which is not significantly different from that of MStpV-unexposed insects. However, very low positive ELISA values were observed in 12 doubly exposed insects, eight of which did not transmit MStpV to test plants, one of which transmitted MStpV alone, and three of which transmitted both MMV and MStpV. These low positive values averaged 0.032 ± 0.001, which is significantly higher than the ELISA values of MStpV-unexposed insects ($P <$ 0.001). This indicates a low titer of MStpV in these doubly exposed insects, suggesting that acquisition of MMV may interfere with MStpV multiplication in the vector.

In the above tests with biotype H, doubly inoculative insects transmitted MStpV to significantly fewer test plants (79/134; 59%) than did insects exposed only to MStpV (111/137; 81%) ($\chi^2 = 15.8$; $P <$ 0.001). On the other hand, doubly inoculative insects transmitted MMV to more plants (87/134; 63%) than did insects exposed only to MMV (30/63; 48%) ($\chi^2 = 4.04$, $P <$ 0.05).

DISCUSSION

Most plant virus interference studies have been done with mechanically transmissible viruses, and there are only a few such studies with nonmechanically transmissible viruses. (Neither MMV nor MStpV is mechanically transmissible.) Autrey (5) reported that the leafhopper-borne maize streak virus (a geminivirus) unilaterally protected maize plants against MMV in Mauritius. Rochow et al (15) reported unilateral interference between serologically related isolates of barley yellow dwarf virus in the aphid, *Sitobion avenae* Fabricius. Lindsten (12) reported that oat dwarf tillering disease, caused by oat sterile dwarf virus, a rhabdovirus, unilaterally suppressed oat striate and red disease, caused by the European wheat striate mosaic virus, probably a member of the same virus group as MStpV (1), in the delphacid planthopper vector, *Javesella pellucida* Fabricius. This is a possible parallel to the interference between MMV and MStpV in *P. maidis* reported here.

In the present work, interference between MMV and MStpV in maize plants was more evident in cultivar Aristogold Bantam Evergreen than in cultivar Golden Cross Bantam and at a temperature of 25.5 C than at 32.2–33.3 C. The partial recovery from MMV infection at the higher temperatures, particularly in the latter cultivar, may have reduced the interference exerted on MStpV by MMV under such conditions.

A much more pronounced influence of MMV on MStpV (but not the reverse) was observed in their common vector, *P. maidis*. The dominance of MMV over MStpV in the vector was demonstrated even in biotype H, which normally transmitted MStpV more than twice as efficiently as MMV. This marked interference in the vector was apparently independent of the acquisition process because it was observed even in insects that had been given access to MStpV-infected plants as long as 2 wk before access to MMV-infected plants. The mechanism of this

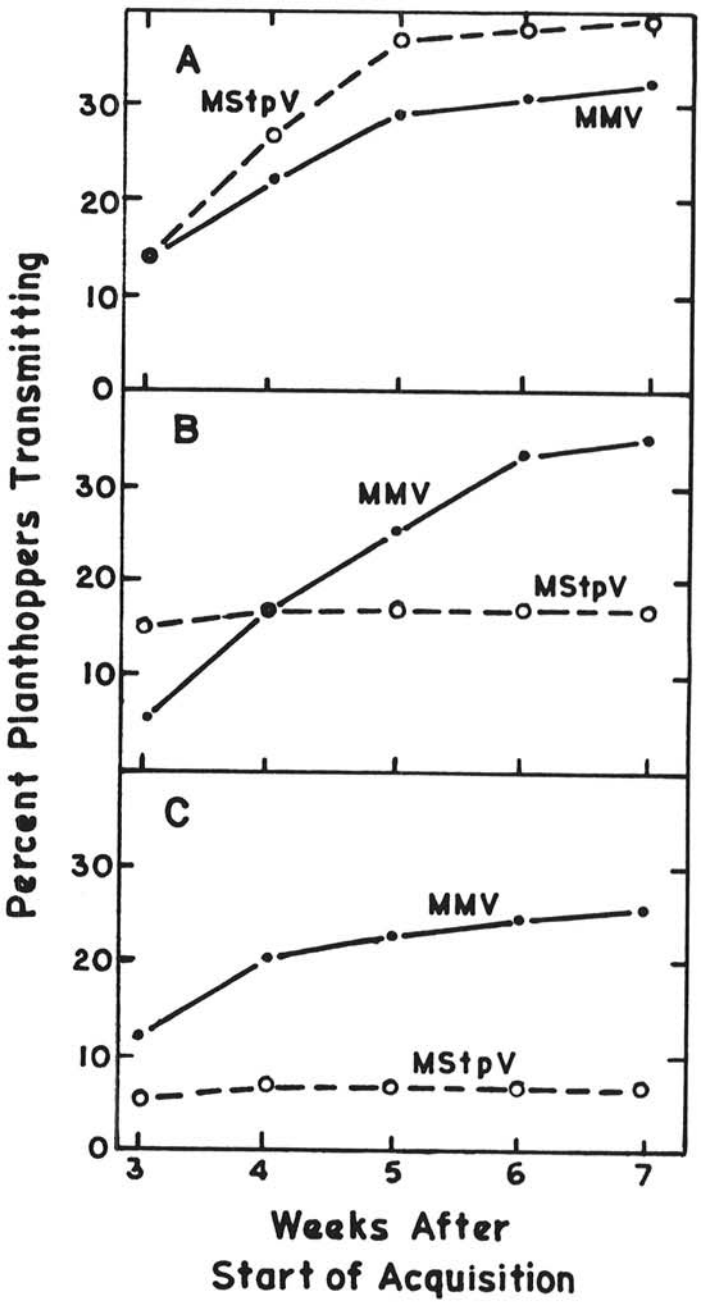

Fig. 3. Percentage of individual *Peregrinus maidis* (biotype F) transmitting maize mosaic virus (MMV) or maize stripe virus (MStpV) to maize seedlings during five consecutive weekly bioassay tests following two 1-wk acquisition access periods (AAP) on source plants. Sixty insects were tested for each treatment. **A,** Single-virus acquisition: MMV or MStpV for 2 wk. **B,** Double-virus acquisition: Week 1 = MStpV, week 2 = MMV. **C,** Double-virus acquisition: Week 1 = MMV, week 2 = MStpV. Viruses transmitted to test plants were determined by symptomatology and/or serological assay 4–5 wk after removing planthoppers.

TABLE 5. Comparison between bioassay and enzyme-linked immunosorbent assay (ELISA) test for MStpV in insects that survived the 4-wk bioassay tests (Table 3, Experiment 5)

Acquisition treatment[a]	Collective result of bioassay tests[b]	Number of insects tested by ELISA	Insects with ELISA values (no.)[c]		
			Negative	Low positive	High Positive
Control (MStpV-unexposed)	–	4	4	0	0
MStpV only	MStpV	6	0	0	6
MMV and MStpV	–	12	8	3	1
	MMV	14	9	5	0
	MStpV	13	0	1	12
	MMV + MStpV	7	1[d]	3	3

[a] Details of single-virus or double-virus acquisitions are given in Table 3.
[b] Transmission of either or both viruses to test plants in four successive weekly tests; – = no transmission detected.
[c] ELISA (A_{405nm}) values were: negative = 0.017–0.024; low positive = 0.031–0.074; high positive = 0.259–1.897.
[d] This insect (number 11 in Table 4) transmitted MStpV alone to the first two test plants, both MMV and MStpV to the third, and neither to the fourth.

interference is not known. However, the results obtained here suggest that MMV probably interferes with multiplication of MStpV both in the host plant, as demonstrated by the ELISA tests, and in the vector, as demonstrated by a longer latent period and a lower titer of MStpV in doubly exposed insects. The general agreement between ELISA and bioassay tests indicated that MMV-MStpV interference in the host plant probably contributed little to the results of experiments on interference in the vector. This is probably because the four or five successive weekly test plants used to measure inoculativity increased the chances of detecting MStpV in bioassay tests and because MMV has a more significant effect on MStpV in the vector than in plants.

Interference between MMV and MStpV in maize and *P. maidis* may influence the epidemiology of these two viruses in nature. Our findings suggest a competitive advantage of MMV over MStpV, in seeming contradiction to the displacement of MMV by MStpV in Venezuela (11). However, it is likely that many factors influence the MMV-MStpV interactions in nature. Such factors might include: 1) transovarial transmission of MStpV in *P. maidis* (7) (MMV has not been shown to be so transmitted); 2) a higher rate of recovery, at higher temperature, of plants infected with MMV compared with those infected with MStpV; and 3) differential pathogenicity of MMV and MStpV toward *P. maidis*, perhaps similar to that shown for maize mollicutes in *Dalbulus* leafhoppers (13).

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