Leafhopper Transmission and Host Range of Maize Rayado Fino Virus

L. R. Nault, R. E. Gingery, and D. T. Gordon

Professor, Department of Entomology; research chemist, Agricultural Research, Science and Education Administration, U.S. Department of Agriculture; and professor, Department of Plant Pathology, respectively, Ohio Agricultural Research and Development Center (OARDC), Wooster 44691.

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ABSTRACT

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The leafhoppers, *Dalbulus maidis, D. elimatus, Stirellus bicolor*, and *Graminella nigrifrons*, transmitted a Texas isolate of maize rayado fino virus (MRFV) to 70.0, 25.0, 11.5, and 9.7% of test corn plants, respectively, when 10 insects per plant were used. In one test, groups of five *Baldulus tripsaci* transmitted MRFV to two of six test plants. The leafhopper, *Macrosteles fascifrons*; the aphid, *Rhopalosiphum padi*; and the planthopper, *Peregrinus maidis* did not transmit MRFV. In a comparative test, the transmission rate by single *D. maidis* was 15.0% with a mean latent period of 16.0 days when leafhoppers acquired virus from plants, whereas the rate of transmission for leafhoppers injected with 10 μg of partially purified virus was 77% with a mean latent period of 6.9 days. Transmission efficiencies of male (10.5%) and female (9.2%) leafhoppers were similar. First instar *D. maidis* nymphs acquired and transmitted virus more efficiently (13.5%) than did adults (3.5%). In tests during a period of 2.5 yr, 12.0% (0–20% range) of 1,753 single *D. maidis* transmitted MRFV. When vector male and female leafhoppers were selected for breeding, 38.7% of 98 resultant sib 1 offspring transmitted MRFV. Of the 48 gramineous species or subspecies in 25 genera tested, only *Zea mays* and its teosinte subspecies, *Z. luxurians, Z. diploperennis, Tripsacum australe, Rottboellia exaltata*, and several *Z. mays* × *T. dactyloides* hybrids were susceptible to MRFV. The tropical weed, *R. exaltata*, could serve as an over-seasoning host for MRFV in the southern USA and Latin American countries. The absence of an overwintering host for MRFV may be the only factor preventing spread of MRFV to the U.S. Corn Belt, since an abundant vector, *G. nigrifrons*, is already present.

Maize rayado fino virus (MRFV) was first described in 1969 from Costa Rica (7). Several isolates have since been reported from Mexico and several Central and South American countries (9,15,20,22). Maize rayado fino virus is transmitted by the corn leafhopper, *Dalbulus maidis* (DeLong & Wolcott) (7), and has a restricted host range infecting only corn, *Zea mays* L., and teosinte, *Z. mays* ssp. *mexicana* (Schrad.) Iltis (8,24). Recently, MRFV was identified from diseased corn plants collected from the Rio Grande Valley of Texas and Dade County, Florida (4). It is not known whether MRFV has been recently introduced into the USA or whether it is endemic but of limited distribution. In this paper we report on the leafhopper transmission and host range of a Texas isolate of MRFV and compare these with properties previously reported for isolates from Central and South America and speculate on the potential for MRFV to become a problem in major U.S. corn growing regions.

MATERIALS AND METHODS

Insect rearing. Insects were reared in growth rooms with a temperature range of 23–27 C and 16-hr of light per 24-hr day. The following insect species were reared on the listed hosts: *D. maidis, D. elimatus* (Ball), and *Peregrinus maidis* (Ashmead) on corn; *Baldulus tripsaci* Kramer & Whitcomb on *Tripsacum dactyloides* L. and corn; *Graminella nigrifrons* (Forbes) and *Macrosteles fascifrons* (Stal) on oats, *Avena sativa* L.; *Stirellus bicolor* (Van Duzee) on rye, *Secale cereale* L.; and *Rhopalosiphum padi* L. on barley, *Hordeum vulgare* L.

Transmission studies. Insects were given access to infected plants for varying lengths of time, usually 24–96 hr to allow for incubation of virus in the insects, before transfer to corn plants for 14–21 days. Unless otherwise indicated, mid-instar (third or fourth) insects were used for virus acquisition. Test insects were then transferred at the rate of one to 10 per sweet corn test plant in a series of two to four consecutive, 3- to 4-day inoculation access periods. Test plants were sprayed with insecticide and placed in a greenhouse for symptom development. In tests to determine latent periods of virus in vectors, insects were confined singly to plants with plexiglass tube cages that covered whole plants or with clip-on leaf cages. In these tests, insects were transferred daily.

The method for preparation of partially purified MRFV extracts was previously reported (11). These extracts were injected into insects (.025 μl/insect) by machine-pulled glass needles.

Host plant range. We selected species from the major Gramineae assemblages (29), grasses common to southern and Corn Belt states, and the major cereal grains to test as susceptes to MRFV. We also concentrated on species considered to be close relatives of corn. Seeds of test species were germinated in 10-cm-diameter plastic pots and plants were thinned to 1–12 per pot. At least four pots of each species were tested. *Dalbulus maidis*, injected 1 wk earlier with a partially purified virus preparation, were placed 10 per pot for a 48-hr inoculation access period. Plants were then held in a greenhouse for 3–4 wk for symptom development. Inoculated plants as well as uninoculated controls were checked for presence of MRFV by enzyme-linked immunosorbent assay (EIA) as described previously (22). As a check for inoculativity of leafhoppers, eight corn plants each were exposed to 10 *D. maidis* for each experiment.

RESULTS

Insect transmission. Various leafhopper species were given a 48-hr acquisition access period (AAP), a 2- to 3-wk incubation period (IP) and then serially transferred, 10 insects per test plant, for a 4-day inoculation access period (IAP). From 440 to 620 leafhoppers of each species were tested. The leafhopper species and percent transmission were *D. maidis* (70.0%), *D. elimatus* (25.0%),

S. bicolor (11.5%), *G. nigrifrons* (9.7%) and *M. fascifrons* (0%). In a single test, groups of five *B. tripsaci* transmitted MRFV to two of six test plants; however, the colony of this leafhopper died out before further tests could be conducted. In other tests, insects were injected with a concentrated, partially purified virus preparation. Following a 1-wk IP, insects were serially transferred, five per test plant, for a 1-wk IAP. The insect species and ratios of infected to exposed test plants were *D. maidis*, 16/16; *G. nigrifrons*, 6/16; *M. fascifrons*, 0/16; *P. maidis*, 0/8; and *R. padi*, 0/16.

When *D. maidis* were given a 48-hr AAP and then singly transferred to test plants for 28 daily serial passages at 23 C, the minimum, maximum, and mean latent periods were 10, 20, and 16 days, respectively (Table 1). When MRFV was injected directly into leafhoppers, the transmission rate increased as the latent period decreased. Increasing the dose of injected virus increased the rate of transmission and decreased the latent period (Table 1).

In further tests with *D. maidis*, first instar, mid instar (third or fourth), and adults were compared for transmission efficiency. Insects were given a 48-hr AAP, 13-day IP, and then tested singly on test plants for a 4-day IAP. The experiment was repeated four times with 50 insects in each age and sex class for each trial. First and mid-instar leafhoppers were better vectors than adults, and transmission efficiency was nearly equal for both sexes (Table 2).

Over a period of 2.5 yr, single *D. maidis* transmitted MRFV to 12.0% of 1,753 test plants. Transmission ranged between 0 and 20%. Two virgin females and three virgin males were selected to establish a new colony after each had transmitted MRFV in single-insect transmission studies. Approximately 20–30 progeny resulted from these crosses. These siblings were allowed to mate, and their progeny (sib 1) were compared for MRFV transmission with nonselected *D. maidis* from the stock colony. The insects were given a 4-day AAP, a 17-day IP, and then placed singly for 4 days on test plants for IAP. Nonselected *D. maidis* transmitted MRFV to 14 of 100 test plants, whereas the sib 1 progeny transmitted to 38 of 98 ($\chi^2 = 15.7$).

Host range. Several corn inbreds, Oh28, Oh43, Mo17, and B73, were susceptible to MRFV, as were the primitive Mexican races, Conico, Tuxpeno, and Jala. The hybrid sweetcorn, Aristogold Bantam Evergreen, produced diagnostic symptoms and was used in all tests as a virus source and test plant. All the annual teosintes tested were highly susceptible. These included the races Central Plateau and Chalco, *Z. mays* ssp. *mexicana* (Schrad.) Iltis, Balsas, *Z. mays* ssp. *parviglumis* Iltis & Doebley var. *parviglumis*, from Mexico, Huehuetenango, *Z. mays* ssp. *parviglumis* Iltis & Doebley var. *huehuetenangensis*, from Guatemala, and the "Guatemala teosinte," *Z. luxurians* (Durieu) Bird. The other suscepts in our tests were the perennial teosinte, *Z. diploperennis* Iltis, Doebley & Guzman, *T. australe* Cutler & Anderson, and *Rottboellia exaltata* L. Although *Tripsacum dactyloides* was not susceptible to MRFV, all of several *T. dactyloides* crosses with Oh43, Mo17, and B73 inbred corn were susceptible. Symptoms in the above MRFV hosts were similar to those reported in corn for the Texas isolate (4,21). Symptoms in *Z. diploperennis* and *T. australe* were mild or absent. Presence of MRFV was confirmed by EIA and transmission of virus from these hosts back to corn with *D. maidis*. During the course of these tests, *D. maidis* transmitted MRFV to 62 of 64 corn test plants.

None of the following grass species developed symptoms and all were negative for MRFV by EIA: ORYZOIDS—*Oryza sativa* L.; FESTUCOIDS—*Agropyron repens* (L.) Beauv., *Avena sativa* L., *Bromus japonicus* Thunb. ex Murr., *B. secalinus* L., *Lolium perenne* L., *Oryzopsis microcarpa* Pilger, *Phalaris platensis* Parodi, *Secale cereale* L., *Setaria faberi* Herrm., *S. magna* Griseb., *S. viridis* (L.) Beauv., and *Triticum aestivum* L.; CHLORIDOIDS—*Eleusine indica* (L.) Gaertn., *Eragrostis diffusa* Buckl., *E. lugens* Nees, *E. mexicana* (Hornem.) Link, and *Sporobolus asper* (Michx.) Kunth; PANICOIDS—*Digitaria decumbens* Stent, *D. ischaemum* (Schreb.) Schreb. ex Muhl., *Echinochloa crusgalli* (L.) Beauv., *Panicum capillare* L., *P. dichotomiflorum* Michx., *P. maximum* Jacq., *P. miliaceum* L., *P. virgatum* L., and *Paspalum notatum* Fluegge; ANDROPOGONOIDS—*Andropogon gerardii* Vitm., *Coix lacryma-jobi* L., *Cymbopogon citratus* (DC.) Stapf., *Heteropogon contortus* (L.) Beauv. ex Roem & Schult., *Ischaemum indicum* (Houtt.) Merr., *I. rugosum* Salisb., *Sorghum bicolor* (L.) Moench, *S. halepense* (L.) Pers., *Tripsacum dactyloides* L., *T. lanceolatum* Rupr., *T. latifolium*, Hitch., *T. maizar* Hernandez X. & Randolph, *T. pilosum* Scribn. & Merr., *T. zopilotense* Hernandez X. & Randolph, and *Zea perennis* (Hitch.) Reeves & Mangelsdorf.

TABLE 1. Transmission of maize rayado fino virus by single *Dalbulus maidis* serially transferred to corn (*Zea mays* L.) test plants at daily intervals for 28 days

Method of acquisition[a]	Transmission[b] (%)	Min.-Max.[c] latent periods (Days)	Mean ± SD[c] latent period (Days)
Plant	15	10–20	16.0 ± 3.5
Injection (1 μg)	36	6–17	10.7 ± 3.5
Injection (10 μg)	77	3–12	6.9 ± 3.0

[a] Plant; leafhoppers exposed to MRFV infected seedlings for 48 hr; leafhoppers injected with 1 or 10 μg MRFV.
[b] Transmission rate based on 61, 25, and 22 leafhoppers, respectively, for the three treatments.
[c] Latent periods based on 9, 9, and 17 leafhoppers, respectively, for the three treatments.

TABLE 2. Effect of age and sex on efficiency of *Dalbulus maidis* transmission of maize rayado fino virus

	Instar of vector			
Sex	First	3rd–4th	Adult	Mean
Male	15.0 ± 5.4[a]	14.5 ± 6.1	2.0 ± 2.4	10.5 ± 7.6
Female	13.5 ± 2.2	9.5 ± 5.0	5.0 ± 3.6	9.2 ± 5.0
Mean	14.3 ± 4.2	12.0 ± 6.0	3.5 ± 3.4	9.9 ± 6.6

[a] Each value is percent ± standard deviation for 200 leafhoppers tested in four trials.

DISCUSSION

Dalbulus maidis was confirmed as a vector of MRFV. In addition, we have shown that the closely related *D. elimatus* and *B. tripsaci*, as well as the unrelated deltocephaline leafhoppers, *G. nigrifrons* and *S. bicolor*, are vectors. Injection of partially purified MRFV increased the rate of transmission by *D. maidis* and *G. nigrifrons* and decreased the mean latent period of virus in *D. maidis*. The effect of injection on the latent period in *G. nigrifrons* was not determined. Banttari and Zeyen (1) recorded a similar increase in transmission rate and decrease in latent period for oat blue dwarf virus (OBDV) in *M. fascifrons* when virus was injected into leafhoppers. Needle injection of MRFV into *M. fascifrons*; the aphid, *R. padi*; or the planthopper, *P. maidis*, did not render these insects vectors. Previously, *P. maidis* was shown not to be an MRFV vector (23).

Gonzalez and Gamez (10) reported a mean latent period of 12.5 days for a Costa Rican MRFV isolate at 25 C in *D. maidis*, compared to 16.0 days for our isolate at the same temperature. Rico de Cujia and Martinez-Lopez (24) reported a longer mean incubation period of 23 and 24 days at 22 and 26 C, respectively, for the maize rayado Colombiano virus (MRCV), which recently was shown to be serologically related to the Texas MRFV isolate (Gordon and Martinez-Lopez, *unpublished*). Gonzalez and Gamez (10) reported no difference in the transmission ability of third–fourth instars compared to adults, whereas we found early instars as well as third–fourth instars to be more efficient than adults. Also, Gonzalez and Gamez (10) found females to be more efficient vectors than males, whereas we did not find a difference for our isolate nor did Martinez-Lopez (19) for MRCV.

Transmission of MRFV by *D. maidis* is clearly under genetic control. In a single selection, with known vectors as parents, we tripled the transmission rate of our isolate. Paniagua and Gamez (23) noted similar effects for their Costa Rican isolate with

controlled matings of *D. maidis,* but when these selected populations mated randomly, the transmission rate dropped to the normal level after several generations. Martinez-Lopez (19) reported an increase in transmission rate from 10% to 20–25% for selected vectors of MRCV. Apparently, phenotypic expression of enhanced MRFV transmission does not confer a selective advantage in laboratory colonies or perhaps even in the field. Our relatively low (12%) average transmission rate compares to a similar rate (10%) reported by Martinez-Lopez et al (20) for field-collected leafhoppers in Colombia.

Gamez (8,9) and Gonzalez and Gamez (10) suggested that MRFV multiplies in its *D. maidis* vector. However, Black (3) observed that evidence for multiplication of plant viruses in their vectors is clear only for viruses with large particles. This infers that ability to multiply in both plant and insect cells can only be conferred by the genome of large viruses; these would include the plant reoviruses and rhabdoviruses. Nevertheless, Banttari and Zeyen (2) have provided conclusive evidence that OBDV, with an isometric particle similar in size to MRFV, multiplies in its vector, *M. fascifrons.* The transmission patterns for OBDV (1) and MRFV are similar. Both viruses have prolonged latent periods in their vectors that are shortened by injecting virus into the abdominal cavity. These latent periods are in contrast to shorter ones reported for other small, isometric viruses; eg, the aphid-borne pea enation mosaic (28), barley yellow dwarf (25), beet western yellows (5) , potato leaf roll (6), leafhopper-borne beet curly top (17), and maize streak (27) viruses. Evidence for multiplication of these viruses in their vectors is negative or of uncertain interpretation. While the long latent period of MRFV in *D. maidis* suggests multiplication, proof awaits direct evidence from future studies.

Earlier, Gamez (8) and Paniagua and Gamez (23) reported that MRFV has a restricted host range, including only maize and annual teosinte. We also report a restricted host range but have extended it to include several *Z. mays* subspecies, *Z. luxurians*, *Z. diploperennis, R. exaltata,* and *T. australe*. None of the tested cereal grains or annual or perennial weeds common to the Corn Belt were susceptible to MRFV. Although the perennial diploid, *Z. diploperennis* (14), was susceptible, symptoms were very mild. Therefore, the species may be a source of tolerant germplasm. This source may be important considering the susceptibility of the Mexican race Tuxpeno and the severe effects of MRFV on this host which has been considered to be one of the ancestors of the U.S. Corn Belt dent corns (18). The perennial tetraploid, *Z. perennis*, does not readily cross with diploid corn and, therefore, its resistance may be difficult to incorporate into commercial hybrids.

In our host range studies we experienced the same difficulties reported by Gamez (8) and Paniagua and Gamez (23) with respect to survival of *D. maidis* on experimental plants. Inoculative leafhoppers only survived well on *Zea* and *Tripsacum* species. It was predicted earlier(21) that the oligophagous *G. nigrifrons* would be a better vector than *D. maidis* for host range studies. Unfortunately, this was not the case. In a comparative test *G. nigrifrons* failed to transmit MRFV to *R. exaltata*, whereas *D. maidis* successfully inoculated four of 16 test plants; yet the former species survived the entire test-feeding period while the latter did not.

A significant finding is the susceptibility of *R. exaltata* to MRFV. This species was introduced into the Western Hemisphere from tropical Asia and is considered to be one of the world's most serious weeds (13). The genus *Rottboellia* is related to maize (12,18) and this may explain its susceptibility to MRFV. Although *R. exaltata* is an annual, it may be an important alternate host for MRFV because it flowers year round and produces viable seed throughout the season. Some seed may germinate immediately while others show varying degrees of dormancy which results in staggered germination. *Rottboellia exaltata* is found in the Gulf Coast states where it is a problem in the production of sugarcane (*Saccharum officinarum* L.) (13). It is also an alternate host for the *P. maidis*-transmitted maize stripe and maize mosaic viruses in Venezuela (16). Another potential overseasoning host for MRFV is *T. australe*, a species which is widespread in South America (18).

Current and potential distributions of MRFV in the USA will be dictated by availability of vectors and alternate hosts. The efficient *D. maidis* vector and *R. exaltata* host overlap in their distributions along the southern edges of the Gulf Coast states. Maize rayado fino virus may, therefore, occur in southern states other than Texas and Florida. As long as MRFV maintains its limited host range and is efficiently transmitted only by *Dalbulus* species, it is likely that its distribution in the USA will not expand. However, should strains develop that are efficiently transmitted by the abundant and widely distributed *G. nigrifrons* (26) and that adapt to an equally abundant and widely distributed perennial such as johnsongrass, then MRFV could become an important corn pathogen in this country.

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