VECTOR AND HOST RELATIONS OF NORTH AMERICAN WHEAT STRIATE MOSAIC VIRUS[1]

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Abstract

Wheat striate mosaic virus from wheat in southeastern Saskatchewan was acquired and transmitted by both nymphs and adults of the leafhopper *Endria inimica* (Say) collected in Ontario. The preinfective period of leafhoppers varied from 4–6 to 22–24 days after they first fed on diseased plants. Records of serial transmission by individual insects varied greatly. Some insects infected most test plants on which they were given 2-day feeds during 20 to 30 days after the preinfective period, but subsequently they transmitted irregularly. Some transmitted virus for only a few days. Others transmitted intermittently for several weeks. None of the insects infected any plants on which they fed later than 72 days after feeding on diseased plants even though some lived another 10 to 20 days. Two of 25 insects became infective after feeds as short as 30 seconds on diseased plants, but the percentages of infective insects increased to more than 90% as acquisition access times were increased to 2 or more days. All insects from some inbred lines became infective after 3 days on diseased plants, but 45% of the descendants of one non-transmitting female failed to become infective. The inoculation threshold period on Ramsey wheat test plants was 15 minutes, but the percentage of test plants infected increased from 15% to 88.8% as the test access times were increased to 4 days. The incubation period of the virus in Ramsey wheat seedlings varied from 6 to more than 28 days.

In tests of host reactions, all durum wheat varieties were highly susceptible to the virus. Several of the hard red spring and winter wheat varieties were highly susceptible and a few others were highly resistant or immune, but most were mildly to moderately susceptible. Most varieties of oats and barley and 10 species of wild annual grasses were moderately susceptible. Mild to moderate symptoms also developed on some of the plants in one or more varieties of *Zea mays* L., *Lolium multiflorum* Lam., *L. perenne* L., and *Bromus inermis* Leyss. Four varieties of rye tested did not develop symptoms, nor did any plants in 13 species of perennial grasses, including *Chloris gayana* Kunth, which is susceptible to the Australian wheat striate mosaic virus. *E. inimica* multiplied on wheat and 14 other annual and 21 perennial grass species, many of which are common on the prairies. There was considerable variation in the reactions to the virus of different plants in the variety Ramsey, but there were no inherent variations detected between the virus isolates used for the experiments. The wheat varieties Cappelle-Desprez and Rescue which are highly susceptible to the European type of wheat striate mosaic virus did not become infected with the Canadian isolates tested.

Attempts to transmit the European type of wheat striate mosaic virus with *E. inimica* failed.

Introduction

Wheat striate mosaic was first detected in winter wheat in South Dakota, U.S.A., in 1950, and was shown to be caused by a virus efficiently transmitted by the leafhopper, *Endria inimica* (Say) (Slykhuis 1951, 1953). The characteristic early symptoms of striate mosaic are very fine-lined, parallel, chlorotic dashes and streaks associated with the leaf veins. These symptoms are quite distinct from the wider chlorotic dashes and streaks in the lamina of leaves of wheat infected with the mite-transmitted wheat streak mosaic virus. Other symptoms on susceptible varieties include death of chlorotic leaf areas,

[1]Contribution No. 304.

sometimes brown necrosis, severe stunting, partial sterility of heads, and premature death of plants. Although wheat striate mosiac appeared to cause serious losses in Nebred and Minter winter wheat in southcentral South Dakota, the significance of the disease was difficult to assess because it was usually associated with wheat streak mosaic and in advanced stages the symptoms of the two were difficult to differentiate.

Although wheat striate mosaic probably persists in southcentral South Dakota, it appears to be rare or occurs inconsistently in other areas. Only traces of the disease have been detected in neighboring areas of Nebraska.[2] The presence of the virus in *E. inimica* was suspected in Illinois.[3] The first evidence of significant amounts of the disease outside South Dakota was reported by Timian (1960), who observed symptoms on up to 25% of the plants in durum wheat fields and on fewer plants in hard red spring wheat in northeastern North Dakota in 1959. The disease also affected wheat in neighboring areas of western Minnesota, and southern Manitoba. It was again found in Canada in 1961 when it affected up to 1% of the plants in 29 of 30 fields of spring wheat examined in southeastern Saskatchewan and southern Manitoba (Slykhuis 1961). The ability of the disease to cause severe losses in Ramsey durum and Selkirk wheat was indicated by the severe stunting (30%–50%), reduced seed set, shrivelled seed, and early death of the diseased plants. Also the vector, *E. inimica*, was common on grasses on roadsides and in pastures near the wheat fields. Despite the uniform distribution of the disease in 1961, it was not found in the same areas of Manitoba or Saskatchewan in 1962.

The above observations indicate that wheat striate mosaic virus is capable of causing serious losses in spring wheat on the prairies, and thus further knowledge of the disease is of practical as well as theoretical interest. Results of experiments done at Ottawa on host and vector relations of wheat striate mosaic virus agreed with and supplemented results of experiments carried out in South Dakota in 1951. The results also indicated further differences between this and other leafhopper-transmitted viruses that cause similar symptoms on wheat and other Gramineae.

Materials and Methods

The virus used in these experiments was obtained from wheat plants collected in southeastern Saskatchewan. The initial transmissions were done with *E. inimica* from Saskatchewan, but all further experiments were done with insects collected in the vicinity of Ottawa, or reared on wheat or brome grass. Eggs of *E. inimica* hatched slowly at moderate greenhouse temperatures, but when temperatures were kept between 24° and 34° C, and if supplementary light was supplied in winter, eggs hatched in 2–6 weeks and a continuing supply of insects was maintained.

Preliminary tests indicated that Ramsey wheat was a suitable test host, and it was generally used in the one- to early two-leaf stage. When groups of

[2]Personal communication from Mr. Robert Staples, Entomology Department, University of Nebraska.

[3]Personal communication from Dr. H. Jedlinski, Field Crops Research Branch, U.S.D.A., University of Illinois, Urbana, Illinois.

insects were used they were caged on the test plants by means of clear plastic cylindrical cages 25 cm high by 10 cm in diameter, with ventilator holes in the sides and with the top end covered with sheer dacron cloth. Single insects were caged on individual wheat plants with cages constructed from clear butyrate tubing 2.3 cm in diameter by 23 cm in length with cloth-covered ventilator holes in the sides.

For experiments on vector–virus relations, leafhoppers were given feeds of specified duration on diseased plants, then individually placed in numbered cages on single test plants and put in a warm (20°–25° C) greenhouse, with supplementary light when necessary for a 16-hour day. The length of time the insects were left on the test plants varied from a few minutes to 7 days, depending on the experiment. Usually each insect was fed on a series of test plants and records were kept of the development of striate mosaic symptoms on every test plant on which each insect fed.

The author has endeavored to use terminology recommended by the Terminology Committee of the Canadian Phytopathological Society (Welsh 1961).

Experiments and Results

Records of Infectivity of E. inimica after Feeding on Diseased Plants

To determine the length of the preinfective period, the efficiency of transmission and the persistence of wheat striate mosaic virus in *E. inimica* after various acquisition access times, groups of non-infective leafhoppers were caged on diseased wheat for periods of 8 hours, 1 day, 2 days, and 4 days, respectively, then sorted according to sex and caged singly on test plants. The caged plants and insects were kept in a greenhouse where the temperature ranged from 18° to 25° C. All insects were transferred to new test plants every 2 days as long as they lived. The development of striate mosaic on the series of test plants on which each insect fed showed the time each insect started to transmit, and indicated its infectivity for the rest of its life. None of the 30 control insects that fed only on healthy plants transmitted the virus, thus showing that the insects were not infective until after they were fed on the source plants. Data presented in Table IA indicate the total numbers of insects alive and the numbers that transmitted the virus at each transfer date and include the records for all insects given access to diseased plants for 8 hours to 4 days. Since a few insects were dead or lost at each transfer date, the total numbers gradually decreased from 120 just after the acquisition period on the diseased plants to one by the 90th day of the test. None of the insects proved infective during the first 6 days after they first fed on diseased plants, but during the 6- to 8-day test, 5% were infective and by the 12- to 14-day test, 74% infected the test plants on which they fed. Fifty percent or more of the insects transmitted the virus during each 2-day test period between 10 and 32 days after they first fed on the virus source, but subsequently the percentage that transmitted diminished. None of the surviving insects transmitted the virus after the 72nd day.

The persistence of infectivity of different insects varied greatly, as is illustrated by the records of transmission for 21 insects that lived at least 56 days after they fed on diseased plants (Table IB). After the initial preinfective

TABLE I

Transmission of wheat striate mosaic virus by leafhoppers (*Endria inimica* (Say)) which were given various acquisition access periods on diseased plants, then tested singly by moving to new test plants at 2-day intervals until death

		Days from first access on diseased plants to the start of each 2-day feed on new test plants																																										
		2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78	80	82	84	87	90
		(A) Total insects at each date																																										
No. tested*		120	117	111	109	98	85	82	80	77	75	74	71	67	63	60	56	52	51	51	47	41	39	34	32	30	29	27	26	24	19	17	15	15	14	14	12	10	8	7	7	6	4	3	1
No. transmitting		0	0	5	35	57	63	57	54	52	52	37	46	40	33	35	26	26	24	14	12	7	6	4	6	3	5	7	4	5	5	3	1	0	1	1	0	0	0	0	0	0	0	0	0
% transmission (nearest unit)		0	0	5	32	58	74	70	68	68	68	50	65	60	52	58	46	50	47	27	26	17	15	12	19	10	17	26	15	21	26	18	7	0	7	7	0	0	0	0	0	0	0	0	0
		(B) Transmission records of 21 individuals that lived at least 56 days after the acquisition access periods																																										
	No.																																												
8 hours	37	0	0	0	0	0	0	+	+	+	+	0	+	+	+	+	0	+	+	+	+	+	+	+	+	+	0	+	+	+	0	0	X												
acquisition	51	0	0	0	0	0	+	+	0	+	0	0	+	0	+	+	+	+	0	+	0	+	+	+	+	0	0	0	0	0	0	0	+	0	0	+	0	0	0	0	0	0	0	0	0
access	53	0	0	0	+	+	+	+	+	+	+	+	+	+	0	+	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	X													
	54	0	0	0	0	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	+	+	+	+	+	+	0	0	+	0	0	+	0	0	0	0	0	0	0	X		
	60	0	0	0	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	+	0	+	0	0	0	+	X												
1 day	81	0	0	0	0	+	+	+	+	+	+	+	+	+	+	+	0	0	+	0	0	+	0	0	0	0	0	0	0	X															
acquisition	83	0	0	0	0	0	+	+	+	+	+	0	+	+	+	+	+	+	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	X							
access	85	0	0	0	+	+	0	+	0	+	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
	86	0	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X					
2 days	97	0	0	0	0	+	+	+	+	+	+	+	+	+	+	0	+	+	+	+	+	0	+	0	0	0	0	+	+	+	+	+	0	0	0	0	X								
acquisition	102	0	0	0	0	+	+	+	+	+	+	0	+	+	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X						
access	110	0	0	0	0	+	+	+	+	+	+	+	0	+	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	X															
	111	0	0	0	0	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X														
	112	0	0	0	+	+	+	+	+	0	+	+	+	+	0	0	0	+	+	+	+	+	0	0	+	0	+	+	0	+	+	0	0	0	0	0	0	0	0	0	0	X			
	118	0	0	+	+	+	+	+	+	+	0	0	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X		
	119	0	0	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	+	+	+	+	+	+	+	+	0	0	X														
	120	0	0	0	0	+	+	+	+	+	0	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X								
4 days	123	–	0	0	0	+	+	+	+	0	0	0	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X														
acquisition	124	–	0	0	0	+	+	+	+	+	+	0	+	+	+	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X							
access	137	–	0	0	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	0	0	0	0	0	+	0	0	+	0	0	0	0	0	0	0	X						
	141	–	0	0	+	+	+	+	+	0	+	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	X														

NOTE: A includes all insects fed on diseased plants and alive at the time of each transfer to new test plants, but does not include the 30 noninfective controls which did not infect any test plants.

In B, + = test plants diseased; 0 = no symptoms on test plants; X = insect dead; – = insects still on source plants.

period, some insects infected only a few plants, then stopped transmitting (No. 111). Some insects transmitted intermittently (Nos. 51, 85). A number of others infected nearly all test plants on which they fed from 8 to 40 or more days after the beginning of the acquisition feed, but subsequently either ceased to transmit, or transmitted intermittently. Some failed to infect test plants for periods of several days to 3 weeks, then infected several more test plants. Several insects lived 40 to 60 days after the last time they infected a test plant. Only one insect (No. 51) transmitted the virus as late as 70–72 days after it fed on the virus source, and it lived 20 days longer without transmitting again. The length of the acquisition access period did not appear to affect persistence of infectivity. There was no obvious difference between the transmission records of males and females.

The preinfective periods of different insects, as indicated by the first plants infected in the series on which each insect fed, varied greatly (Table IIA). The first transmissions occurred during the 6- to 8-day access times on test plants, regardless of whether the acquisition access times had been 8 hours or 1, 2, or 4 days. The preinfective periods of most insects was between 8 and 14 days. The longest preinfective periods were 22–24 days, 18–20 days, 14–16 days, and 12–14 days respectively for insects in groups that had been given acquisition access times of 8 hours or 1, 2, and 4 days on diseased plants.

In another experiment, during a period when greenhouse temperatures were warmer (19°–35° C), the preinfective period of some insects was between 4 and 6 days after the start of a 4-day acquisition access period on diseased wheat, and most insects transmitted for the first time between the 6th and 12th day (Table IIB). It appears that temperatures may influence the length of the preinfective period.

Percentages of Insects Becoming Infective after Different Acquisition Access Times

Different experiments were carried out to ascertain the relationship between access times on diseased plants and the percentage of insects that became infective. The insects were starved for about 1 hour before the shorter acquisition access times on the virus source, but not before access times of 8 hours or longer. Also, for the shorter feeds, the insects were observed individually and the time required for stylet penetration noted. The percentage of insects that transmitted the virus is based on the numbers alive 14 days after the start of acquisition access periods, by which time the preinfective

TABLE II

Preinfective periods of individual *E. inimica* after different acquisition access times on diseased wheat

Acquisition access time	No. insects with indicated preinfective periods in days*									
	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18–20	20–22	22–24
(A) 8 hr	0	1	1	8	2	1	0	0	1	1
1 day	0	1	5	3	6	0	0	2	0	0
2 days	0	1	9	9	2	1	0	0	0	0
4 days	0	2	16	5	1	0	0	0	0	0
(B) 4 days	3	29	36	26	9	5	2	0	0	0

*Calculated from the start of the acquisition feeds to the period when the insects were fed on test plants.

TABLE III

Acquisition access times in relation to infectivity of *E. inimica*

Acquisition access time	No. insects infective/No. tested in different expts.*				Total infective	
	I	II	III	IV	No.	%
0	0/23	0/18	0/14	0/37	0/92	0.0
15 sec				0/33	0/33	0.0
30 "				2/25	2/25	8.0
1 min			1/9	2/30	3/39	7.7
5 "			3/18	4/23	7/41	17.0
15 "			9/16	7/24	16/40	40.0
30 "		11/22	7/15		18/37	48.6
1 hr		12/22	9/19		21/41	51.2
2 "		13/20	6/17		19/37	51.4
4 "		12/18	8/16		20/34	58.8
8 "	16/21	9/18			25/39	64.1
16 "			14/17		14/17	82.4
1 day	17/22				17/22	77.3
2 "	21/23				21/23	91.2
3 "		62/64			62/64	96.9
4 "	20/20	83/85		72/79	175/184	95.1

*The numbers infective are based on the insects still alive 14 days after the start of the acquisition access times.

period of most of the vectors had passed. Since some insects transmitted irregularly, an insect that infected any test plant in a series is counted as a vector.

The combined results of the four experiments in which different acquisition access times were used (Table III) indicate an increase in numbers of insects transmitting from 8% (2 out of 25) for insects that had fed for 30 seconds, to over 90% for insects that fed for 2 days or more on diseased plants. In some tests, all insects in some groups that had 3 or 4 days access on diseased plants became infective.

Acquisition and Transmission of Wheat Striate Mosaic Virus by Nymphs

Nymphs in the first to third instars were fed on diseased wheat for 1 week then transferred to healthy wheat on which they were left for 1 week. Thirty nymphs were then caged singly on wheat seedlings and transferred to new test plants at 2-day intervals. Each time the insects were transferred they were examined to note when they became adult. The record of symptoms on test plants showed that 10 of the 30 insects tested transmitted the virus to one or more test plants in the series on which they fed before they became adults, while 1 did not transmit until it became adult. Two nymphs infected four different test plants before molting and emerging as adults. All insects that transmitted while nymphs continued to transmit after they became adults, then several of them infected an additional five test plants in a series before the test was discontinued.

To compare the abilities of nymphs and adults to acquire and transmit the virus, both nymphs and adults were fed on diseased wheat for 4 days before being caged singly on test plants. They were transferred to new test plants every 2 days until the 20th day of the test. Of the insects still alive on the 12th day after they had first fed on diseased plants, the numbers that transmitted the virus were 27 out of 33, or 81.8%, of those that were nymphs at

the time they were removed from the diseased plants, 54 out of 55 or 97.7% of those that were adult female, 39 out of 40 or 97.5% of those that were adult male when they were removed from the diseased plants.

Inoculation Access Time in Relation to Infection of Test Plants

Adult *E. inimica* that had been reared on diseased wheat were used in an experiment to determine the relation of feeding time to the infection of Ramsey wheat test plants. Insects were placed in each of four plastic tubes 2.3 cm in diameter by 46 cm long, with one end plugged with cotton wool. Wheat test plants in the one- to early two-leaf stage were removed from the soil and the roots wrapped in polyethylene to prevent drying. A test seedling was inserted into each tube, and cotton was packed around the stem to prevent the escape of the leafhoppers and hold the seedling in place. The insects in the tube were then shaken onto the plant and observed until one or more of them began to feed; then feeding was timed. For feeds of 1 or more hours, the insects were shaken onto the plant and left undisturbed for the required period. To terminate the feed, the tube was tapped or shaken to dislodge the insects. The seedling was removed and planted in a pot of soil, and another seedling inserted into the tube for the next test feed. The numbers of plants infected out of the total number on which infective insects fed for each specified time indicate a general increase from 15% for 15-minute feeds to 88.8% for 4-day access periods on the test plants (Table IV). No infections resulted from feeds as short as 1 minute or 5 minutes.

Tests for Transovarial Transmission

To test for transovarial transmission of wheat striate mosaic virus, eggs laid in test plants by infective female *E. inimica* were transferred to healthy plants that were then kept in a warm, saturated atmosphere to induce hatching. The nymphs that emerged were transferred singly to Ramsey wheat seedlings to be tested individually for infectivity. At least 129 nymphs hatched from eggs laid by females that had fed on diseased plants were tested, but none of them proved infective.

TABLE IV

Inoculation feeding time of viruliferous *E. inimica* on Ramsey wheat seedlings in relation to infection with wheat striate mosaic virus

Length of test access time	Nos. of single plants infected/tested	% of single plants infected
1 min	0/20	0.0
5 "	0/24	0.0
15 "	13/87	15.0
30 "	12/69	17.4
1 hr	10/39	25.6
2 "	11/49	22.2
4 "	25/40	62.5
8 "	30/57	52.6
16 "	41/69	59.5
1 day	8/10	80.0
4 "	8/9	88.8

Further evidence that the virus is not transovarially transmitted was obtained in a test of perennial grasses as hosts of both virus and leafhoppers. Adult insects known to be infective laid eggs in all the grasses tested. Nymphs that hatched and fed on grasses that were immune to the virus were not infective, but those that hatched on susceptible grasses that got infected with virus became infective. Thus it is evident that nymphs from eggs laid by infective females were not infective until after they had fed on diseased plants.

Variations in Vector Efficiency of Different Inbred Lines of Insects

Although in some experiments 100% of the insects became infective during 4 days on diseased plants, in certain experiments a few individuals did not become infective. The progeny of several infective and also some non-infective females were reared as separate inbred lines and tested as vectors. They were given a 3-day feed on diseased wheat, then individually caged for weekly periods on each of a series of test plants. The percentages of insects that transmitted virus were calculated on the basis of insects alive at the end of the second week of the test (Table V). All insects in four of the cultures acquired and transmitted the virus. These insects were descendants of females that had been proved able to transmit the virus. Only 55.5% of the individuals in another culture that originated from a female that had failed to become infective proved able to transmit the virus. This culture of insects was accidentally destroyed before further tests could be done, but the above results indicate that it is possible to select strains of *E. inimica* that are not efficient vectors.

TABLE V

Percentage of vectors in different inbred lines of *E. inimica*

Female parent of colony	No. vectors/No. tested	% vectors
12CII, good vector	13/13	100
3–23, good vector	12/12	100
3–53, good vector	4/4	100
14–91, non-vector	10/18	55.5
14–108, non-vector	15/17	88.2
14–14, vector	18/18	100

Incubation Period of the Virus in Ramsey Wheat

In one of the experiments, in which infective insects were given 2-day feeds on single test plants, the plants were kept in the greenhouse at temperatures ranging from 18° to 25° C and examined for symptoms at 2-day intervals during the first 4 weeks after the inoculation feeds. A final examination was made at the end of 6 weeks. Records of the dates on which symptoms were first recognized on each of 454 plants show that the symptoms developed over a very extended period with no predominant peak days (Table VI). About 75% of the plants developed symptoms between the 8th and 24th days. Most of these plants became severely chlorotic, stunted, necrotic, at least partially sterile, and many died prematurely. Symptoms developed so late on some plants (28–42 days) that only the flag leaf showed fine chlorotic streaks while other leaves matured normally.

TABLE VI

Incubation periods of wheat striate mosaic virus in individual Ramsey wheat plants

Days after inoculation by insects	Plants showing first symptoms on indicated dates	
	Number	% of total
4	0	0.0
6	14	3.1
8	21	4.6
10	58	12.8
12	53	11.7
14	32	7.0
16	36	7.9
18	38	8.4
20	31	6.8
22	37	8.2
24	40	8.8
26	18	4.0
28	14	3.1
28–42	62	13.6
Totals	454	100.0%

Variability in Reaction of Ramsey Wheat Plants to the Virus

Ramsey durum wheat appeared to be one of the most susceptible varieties of wheat, hence it was regularly used as a test host, but there was considerable variability in the incubation period and severity of symptoms even on this variety. Such variability could result if the sources of virus being used included a mixture of strains that differed in virulence, or if the wheat test plants varied in susceptibility. To determine the cause of the variability in symptom severity, two plants with mild, two with moderate, and two with severe symptoms were selected from Ramsey wheat plants of similar age and infected about the same time by different individual insects. Twenty non-infective *E. inimica* were caged on each of the diseased plants and also on a healthy plant for 4 days, then the insects from all groups were caged singly for 2 days on each of a series of test plants. The transmission of virus by each insect was recorded and in addition the severity of symptoms that developed on each test plant was rated as mild, moderate, or severe (Table VII). The

TABLE VII

Variations in severity of wheat striate mosaic symptoms on Ramsey wheat infected by *E. inimica* that acquired virus from Ramsey wheat plants with mild, moderate, or severe symptoms

Symptoms on source plant	Insects transmitting		No. plants with symptoms		
	No.	%	Mild	Moderate	Severe
1 Severe	13/13	100	7	27	69
2 Severe	15/15	100	8	33	88
3 Moderate	11/13	84.6	4	12	58
4 Moderate	14/16	87.6	18	49	43
5 Mild	9/12	75.0	5	20	45
6 Mild	8/9	88.8	4	13	33
7 Healthy wheat	0/15	0.0	0	0	0

TABLE VIII

Grass hosts of wheat striate mosaic virus and *E. inimica*

Grass species	Common name or variety	No. samples	Striate symptoms	*E. inimica* nymphs hatched on grass	
				App. No.	Infective
Wild annuals					
Avena fatua L.	Wild oats	1	++	50	Yes
Bromus arvensis L.		1	+	50	Yes
B. japonicus Thunb.	Japanese chess	1	+	20	Yes
B. secalinus L.	Chess	1	++	20	Yes
B. tectorum L.	Downy chess	2	++	70	Yes
Digitaria sanguinalis (L.) Scop.	Crabgrass	2	+	20	Yes
Echinochloa crusgalli (L.) Beauv.	Barnyard grass	1	++	20	Yes
Eragrostics cilianensis (All.) Lutati	Stink grass	1	+++	50	Yes
Panicum capillare L.	Witch grass	2	+++	70	Yes
Setaria verticillata (L.) Beauv.	Bur bristlegrass	2	0	20	No
S. viridis (L.) Beauv.	Green bristlegrass	3	0	70	No
S. viridis (L.) Beauv.	Green bristlegrass	1	+	70	Yes
Cultivated annuals					
Panicum miliaceum L.	Broomcorn millet	1	++	70	Yes
Cultivated biennials					
Lolium multiflorum Lam. (Italian ryegrass)	S22-Britain	1	++	70	Yes

Perennials					
Agropyron cristatum (L.) Gaertn.		1	0	20	No
A. intermedium (Host.) Beauv.		2	0	80	No
A. repens (L.) Beauv.		3	0	70	No
A. smithii Rydb.		2	0	20	No
Agrostis alba L.		1	0	70	No
Bromus inermis Leyss.	Canadian	1	0	20	No
	Lincoln	1	0	50	No
	Manchar	1	+	80	Yes
	Saratoga	1	0	50	No
	Wisconsin 55	1	+	20	Yes
Dactylis glomerata L.	S26(Britain)	1	0	50	No
	S37(Britain)	1	0	50	No
Elymus virginicus L.		1	0	70	No
Festuca elatior L.		1	0	20	No
F. rubra L.		1	0	20	No
Lolium perenne L.	Norlea	3	+	80	Yes
Phleum pratense L.	Climax	1	0	50	No
	Drummond	1	0	80	No
	Medon 1206	1	0	80	No
Poa compressa L.		1	0	20	No
P. pratensis L.	Delta	1	0	80	No

\+ = Few plants infected.
++ = About 50% plants infected.
+++ = Nearly all plants infected, symptoms clear.

results showed a higher percentage transmission by insects fed on severely diseased plants than by those that fed on plants that had mild or moderate symptoms. However, the symptoms on the test plants ranged from mild to severe regardless of the severity of symptoms on the source plants. Also, symptoms caused by the same insects on different source plants on which they fed varied considerably in rate of development and severity. These observations indicate that differences in symptoms were not caused by inherent differences in the virus in the different source plants.

Reactions of Cereal Varieties

The reactions of 172 varieties and selections of wheat, 19 of oats, 11 of barley, 4 of rye, and 3 of corn, on which infective *E. inimica* had been caged for 1 week, were reported previously (Slykhuis 1962). The development of symptoms differed greatly on different varieties of wheat. All nine durum varieties were highly susceptible. Some of the plants of most varieties and selections of winter and hard red spring wheat developed slight to moderate symptoms, while a few did not develop symptoms. The most susceptible varieties of spring wheat included Cadet, Lake, Prelude, Redman, Regent, Renown, and Selkirk. No symptoms have developed on any plants of Chinook, Rescue, Thatcher, or Willet, even though six tests were done including 60 to 120 plants of each of these varieties. The most susceptible winter wheat varieties were Minter, Nebred, and Winalta. No symptoms developed on Atlas, Cappelle-Desprez, Cheyenne, or Frisco. It is interesting to note that two wheat varieties, Rescue and Cappelle-Desprez, which did not develop symptoms, were highly susceptible to the European type of wheat striate mosaic virus (Slykhuis and Watson 1958). All varieties of oats tested developed symptoms, but Victory was the only one that developed severe striate, stunting, and necrosis. Ten barley varieties developed faint to moderate chlorotic symptoms, and only Montcalm did not develop symptoms. Neither Dominant, Horton, Petkus, nor Sangaste rye developed symptoms. Some of the Gaspe Flint corn plants developed pronounced striate mosaic symptoms and were severely stunted.

Annual and Perennial Grasses as Hosts to the Virus and Vector

In addition to the above cereals, 11 species of wild annuals, 1 cultivated annual, 1 biennial, and 14 perennial grasses were tested as hosts of the virus and *E. inimica*. Each grass was grown in 6-in. clay pots, 8 to 15 plants per pot. Two seedlings of Ramsey wheat were also planted in each pot to check the infectivity of each lot of insects. The plants were caged, 10 infective *E. inimica* were introduced and the pots were placed in the greenhouse where the temperature during May and early June frequently reached 37° C. Within 15 days after the insects were introduced, Ramsey wheat plants in all pots had developed symptoms of striate mosaic, indicating that insects on all the grasses were infective. All the Ramsey wheat plants were removed, but the insects were left on the grasses until the 30th day. As, by that time, nymphs were hatching from eggs laid by adults, all adults were removed. Ten nymphs from each grass were then caged for 7 days on healthy Ramsey wheat seedlings to determine if they were infective. Three weeks later 10 more insects from

each grass were similarly tested for infectivity. The caged grasses were examined for symptoms of striate mosaic and the relative abundance of nymphs produced on each grass species was recorded (Table VIII). Striate mosaic symptoms developed on some plants of 11 of the 12 species of annual grasses tested, and on the biennial, *Lolium multiflorum* Lam. In contrast, most perennial grasses were not infected. Only a few plants of Manchar and Wisconsin brome grass and perennial ryegrass developed mild to moderate symptoms. *E. inimica* nymphs emerged on all grasses. They were abundant on the following perennial grasses: *Agropyron intermedium* (Host.) Beauv., *A. repens* (L.) Beauv., *Agrostis alba* L., *Bromus inermis* Leyss. (Manchar), *Lolium perenne* L., *Phleum pratense* L., *Poa pratensis* L. The only nymphs that proved infective were those that emerged on grasses that developed striate mosaic symptoms, thus none of the grasses proved to be symptomless carriers. Nymphs from eggs laid by infective females in grasses immune to the virus were not infective, thus giving further evidence against transovarial transmission of this virus.

Attempts to Transmit European Wheat Striate Mosaic Virus with E. inimica

Italian ryegrass plants infected with the European type of wheat striate mosaic virus were obtained from Dr. M. A. Watson, Rothamsted Experiment Station, England. About 40 non-infective *E. inimica* were caged for 1 week on the diseased ryegrass, then tested for weekly periods on each of a series of wheat test plants including Rescue, Cappelle-Desprez, and Ramsey over a 5-week period. None of the test plants became infected, thus indicating that *E. inimica* is not a vector of the European type of wheat striate mosaic virus.

Discussion

A virus disease of Gramineae in North America (Slykhuis 1953), in Europe (Slykhuis and Watson 1958), and in Australia (Grylls 1963) has been named "wheat striate mosaic." This name indicates that wheat is a major host and that the characteristic mosaic pattern includes extremely fine parallel chlorotic streaks. It would be presumptuous to assume, despite the similarities in symptoms, that these diseases are caused by identical or even closely related viruses. The vectors of the North American and Australian viruses, *E. inimica* and *Nesoclutha obscura* Evans respectively, are leafhoppers (superfamily Cicadoideae) whereas the vector of the European virus, *Delphacodes pellucida* (Fab.), is a fulgorid (superfamily Fulgoroidea). It is not yet known whether any one of these vectors can transmit more than one of the three viruses. In tests at Ottawa, the European virus was not transmitted by *E. inimica*. The two leafhopper-transmitted viruses do not appear to be transovarially transmitted by their vectors, but the fulgorid-transmitted European virus is. The three viruses have several hosts in common including wheat, oats, barley, and ryegrass, but even here it is interesting, and for experimental purposes important, to note differences in varietal reactions. Rescue and Cappelle-Desprez wheat were susceptible to the European virus in tests in England, but they were immune to the Canadian isolates of wheat striate mosaic virus. The Australian virus infects *Chloris gayana*, but this grass was

not infected in a test with the Canadian virus. Unless later findings prove similarities in important characteristics, the diseases in the different geographic areas must not be considered identical.

A high vector efficiency of *E. inimica* is indicated from results showing that the percentage of insects that become infective with the Canadian collection of wheat striate mosaic virus increased from about 8% to nearly 100% as the time of the acquisition feed was increased from 1 minute to 3 or 4 days. However, there was evidence that strains of insects could be selected that were not efficient vectors. If non-vector lines can be selected they will be useful in studying insect–virus relations, as well as the heredity of vector ability.

The existence of a preinfective period of about 6 to 22 days and the persistence of a high level of infectivity of most leafhoppers for at least 5 weeks can be interpreted as evidence for virus multiplication in the insects, or can be subject to other interpretations (Bawden 1950). The eventual loss of infectivity of the longer-lived leafhoppers could be interpreted as evidence that the virus does not multiply in the leafhoppers, and hence that the reservoir of virus acquired during the initial feed on diseased plants became depleted. Such loss of infectivity could result from some change in the insects as they aged, making them unable to introduce the virus into the plants even if they were viruliferous. Also it is possible that the virus multiplies during the preinfective period after acquisition, but the rate of multiplication diminishes and even stops at a later stage and hence virus content of the leafhoppers drops from depletion or gradual inactivation. Since the virus content of *E. inimica* can be assayed by mechanical transmission of liquid extracts into non-infective leafhoppers (Lee 1963), it will be possible to determine whether or not the changes in infectivity of insects are correlated with changes in their virus content.

Since some insects failed to infect several test plants in a series but later infected other plants, it appears that such insects must release virus intermittently rather than steadily during feeding. Intermittent transmission could be related to changes in the virus content of insects, or merely to irregularities in the mechanism of virus release.

A noteworthy feature of the host relationships of wheat striate mosaic virus is the great difference in reactions of different varieties of wheat. Such variations in susceptibility could be of practical significance in that the widespread use of highly susceptible varieties could result in increased damage from the disease, whereas resistant or immune varieties could reduce or eliminate losses. It is also apparent that experimental test varieties must be selected with care. Even varieties rated as highly susceptible may contain plants with considerable resistance. Variability in Ramsey, which was used as the standard test variety, probably contributed to the wide variation in the incubation period of the virus in test plants.

Despite considerable variation in the severity of symptoms on test plants, there was no evidence that different pathogenic strains of the virus occurred among the isolates used in these experiments. Perhaps the virus occurs on the Canadian prairies only in seasons when infective leafhoppers enter the area from the south. The virus appeared to be indigenous in southcentral

South Dakota where it was found in wheat each year it was sought, hence more variation in the virus could be expected in such an area. The possibility of significant variations in pathogenicity should be investigated further to indicate the probable effectiveness of host resistance as a means of disease control.

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