Dependent Virus Transmission by Rhopalosiphum padi From Mixed Infections of Various Isolates of Barley Yellow Dwarf Virus

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Cooperative Investigation, Agricultural Research Service, U.S. Department of Agriculture, Cornell University Agricultural Experiment Station, and Canada Agriculture, Research Branch. Supported in part by NSF Grant PCM 74-19814.

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Contribution No. 783 of Agriculture Canada, Research Station, Winnipeg, Manitoba.

We thank Irmgard Muller for technical assistance in Ithaca.

Accepted for publication 17 August 1977.

ABSTRACT

ROCHOW, W. F., and C. C. Gill. 1978. Dependent virus transmission by Rhopalosiphum padi from mixed infections of various isolates of barley yellow dwarf virus. Phytopathology 68: 451-456.

Rhopalosiphum padi rarely transmits virus from oats infected only by the MAV isolate of barley yellow dwarf virus (BYDV), but it often transmits MAV, together with the RPV isolate, from plants doubly infected by MAV and RPV. Since previous work on this dependent virus transmission phenomenon was restricted to these two virus isolates, we studied interactions of eight additional BYDV isolates as a way to assess potential relevance of dependent transmission in the field. Six isolates were from collections of oats made in 1968 in fields in New York or Illinois. From all nine combinations of double infections made with the three RPV-like isolates, *R. padi* transmitted each of the three MAV-like ones. Dependent transmission of the paired isolates occurred from 76% of 193 doubly-infected oats. Two BYDV isolates from Canada were used in other experiments. One of the Canadian isolates (isolate 6524) was similar to RPV; the other (isolate 6407) was similar to MAV. In experiments in Ithaca, *R. padi* transmitted either MAV or 6407, together with RPV or 6524, from 81% of 89 doubly-infected plants. In Winnipeg, dependent transmission of MAV in the presence of RPV occurred in five of six cases studied; dependent transmission of isolate 6407 in the presence of isolate 6524 occurred from three of six mixed infections. In almost all tests, *Macrosiphum avenae* transmitted only MAV or MAV-like isolates from the mixed infections. These data show that dependent virus transmission occurs with a range of BYDV isolates, and support the possibility that such virus interactions affect BYDV transmission in nature.

In dependent virus transmission by aphids, the vector transmits a virus only in the presence of a second virus (7, 9). One system of dependent transmission of viruses transmitted by aphids in the circulative manner involves two vector specific isolates of barley yellow dwarf virus (BYDV). *Rhopalosiphum padi* does not regularly transmit the MAV isolate of BYDV from singly-infected plants, but it often transmits MAV, together with the serologically unrelated RPV isolate, from plants doubly infected by MAV and RPV. Previous studies of this system have provided some evidence for heterologous encapsidation as the explanation of this virus interaction and have furnished a useful approach to studies of the mechanism of virus-vector specificity (7). Other considerations of this dependent virus transmission system have focused on the potential for mixed infections in the epidemiology of viruses in nature (9). But all previous studies have involved only RPV and MAV, two characterized BYDV isolates originally collected in New York (5).

If dependent virus transmission by *R. padi* influences virus spread in the field, it must occur with a range of virus isolates and not be unique for the RPV and MAV isolates. Dependent transmission by *R. padi* of MAV in the presence of RPV has been a reproducible, consistent phenomenon in studies conducted at Cornell for many years. Reports from some other locations suggested that a similar interaction did not occur in transmissions from mixed infections of isolates similar to RPV and MAV (3, 15). In Sweden, however, Lindsten (4) described transmissions from mixed infections by *R. padi* and *Macrosiphum avenae* that might be similar to dependent transmission. To study the potential applicability of the dependent transmission phenomenon for BYDV in the field, we made tests of mixed infections with a spectrum of virus isolates collected from several areas in the United States and Canada (10). By making parallel tests with some of the isolates in Ithaca, New York, and in Winnipeg, Manitoba, we also evaluated the role of different clones of aphid species used in the separate laboratories.

00032-949X/78/000 075$03.00/0

MATERIALS AND METHODS

Ten isolates of BYDV were used in the studies in Ithaca. The MAV isolate, which originated in New York, previously has been described and characterized (5, 14). Four additional isolates, considered similar to MAV because they were transmitted regularly by *Macrosiphum avenae* (Fabricius) but only rarely transmitted by *Rhopalosiphum padi* (Linnaeus), were used. One of them, isolate 6407, originated in Canada and has been described elsewhere (1). The other three MAV-like isolates, which will be called A, B, and C, were from collections made near Ithaca, New York in June, 1968 (12). The RPV isolate of BYDV, transmitted specifically by *R. padi*, originated in New York and has been described previously (5, 14). In Canada another isolate similar to RPV (isolate 6254) also was previously studied and characterized (1). Three additional RPV-like isolates came from collections made by H. Jedlinski in Illinois in 1968 (12); these will be referred to as isolates D, E, and F.

Virus isolates regularly used in studies in New York were maintained by periodic transfer to Coast Black oats (*Avena byzantina* C. Koch), the test plant used in all Ithaca experiments. The six additional isolates (A to F) had been stored in infected oat tissue in a freezer from 1968 until 1974. At the start of these experiments, the six frozen samples were extracted in a Waring Blendor in 0.1 M neutral potassium phosphate buffer. Virus was concentrated from each of the samples by centrifugation, and the concentrated preparation was used in membrane feeding assays to recover virus (14). All 10 isolates were maintained by serial transfers during the 2-yr course of these studies. Two or more aphid species were used for each transfer to provide frequent tests of the stability of the vector specificity of each isolate (5). Results of such transfers and of controls for various experiments illustrate the relative vector specificity of the isolates (Table 1).

The basis for identification of the virus isolates in transmission studies was usually the transmission pattern in a comparative test, using opposite halves of a detached oat leaf from an infected plant in the greenhouse. One half of a leaf was infested with *M. avenae*, the opposite half with *R. padi*. Clones of aphids used in Ithaca were the same as those used in all previous studies. Aphids were given a 2-day acquisition feeding period at 15 C in the dark. The inoculation test feeding period was in a growth chamber at 21 C for 5 days. Groups of about 10 aphids were placed on each of three seedlings for each treatment. Severity of symptoms observed during 4 wk in the greenhouse sometimes aided identification of the isolates because doubly-infected plants usually had more severe symptoms than singly-infected ones.

In Winnipeg, the virus isolates used were MAV, RPV, 6407, and 6524. Procedures were similar to those described for tests in Ithaca except that groups of five aphids were placed on each of three seedlings for each treatment, and the inoculation feeding took place in a greenhouse. Clones of aphids were those initiated in 1964 (1).

RESULTS

Tests in Ithaca.—In one series of experiments we studied interactions of the six isolates that originated from collections in Illinois or New York in 1968 (12). Three of the isolates (A, B, and C) were similar to MAV; the other three (D, E, and F) were similar to RPV. In each of two experiments groups of oats were inoculated with the RPV-like isolates and the MAV-like ones in the nine possible combinations. Parallel transmission tests were made from leaves of such doubly-inoculated plants to oat seedlings by means of *R. padi* and *M. avenae*. Then additional parallel tests of virus transmitted to those seedlings were made with the two vectors. These additional tests permitted identification of the isolate or

TABLE 1. Parallel transmission tests with *Rhopalosiphum padi* and *Macrosiphum avenae* of 10 isolates of barley yellow dwarf virus from leaves of oats

Location of tests	Virus isolate	Number of plants that became infected over number infested with aphids of species shown[a]	
		R. padi	*M. avenae*
Ithaca	MAV	1/45	45/45
	A	2/45	45/45
	B	0/45	45/45
	C	1/45	45/45
	6407	2/57	57/57
	RPV	45/45	0/45
	D	42/42	2/42
	E	45/45	8/45
	F	45/45	0/45
	6524	57/57	1/57
	APHID CONTROLS	0/99	0/99
Winnipeg	MAV	0/24	24/24
	6407	0/42	41/42
	RPV	30/30	4/30
	6524	37/42	0/42
	APHID CONTROLS	0/18	0/18

[a]In Ithaca each Coast Black oat seedling was infested with about 10 aphids; in Winnipeg, five aphids per plant were used.

isolates transmitted by each of the vectors from the original doubly-infected plants. In every test of the nine mixed infections, *R. padi* transmitted RPV-like isolates together with MAV-like ones from some of the plants. For some virus combinations, this dependent transmission of MAV-like isolates occurred in nearly all of the 13 tests made of each mixed infection (Table 2). Of the total of 117 doubly-inoculated plants tested, dependent transmission by *R. padi* of an MAV-like isolate in the presence of the RPV-like one occurred from 79 (68%); only RPV-like isolates were transmitted by *R. padi* from the other 38 plants (Table 2).

In parallel tests of the nine mixtures with *M. avenae*, results were similar to those of previous tests of mixtures of RPV and MAV; *M. avenae* recovered only MAV-like isolates from essentially all of the plants tested. In only one of 90 tests was there evidence for transmission by *M. avenae* of both the MAV- and RPV-like isolates (Table 2). This probably is simply an illustration of the relative nature of the specificity; it represents an occasional transmission of RPV-like isolates by *M. avenae*, as happens sometimes from singly-infected plants (Table 1).

Results of these experiments (Table 2) suggested that there may be quantitative differences in the likelihood of dependent virus transmission among the nine different mixed infections. It is likely that interaction might occur more often with some virus variants than with others. On the other hand, the original tests had been done in two major series of experiments in 1974, one of which began in April, and the other in August. Since high summer temperatures in the greenhouse reduce titer of some virus isolates, especially of RPV, it also seemed likely that fluctuating environmental factors during the tests brought about variation of results among the nine treatments. To evaluate these possibilities, we did an additional series of experiments with four of the nine mixed infections. We duplicated the two mixed infections from which *R. padi* had transmitted both viruses from almost all plants (A + D, and A + E); we also studied the two mixtures from which the lowest level of dependent

TABLE 2. Comparative tests with *Rhopalosiphum padi* and *Macrosiphum avenae* for dependent virus transmissions from double infections of three isolates (A, B, C) similar to MAV and three isolates (D, E, F) similar to RPV

Isolates in mixed infection	No. of plants (of 13 tested) from which *R. padi* transmitted virus isolate or isolates shown[a]			No. of plants (of 10 tested) from which *M. avenae* transmitted virus isolate or isolates shown		
	"RPV" only	"MAV" only	"RPV + MAV"	"RPV" only	"MAV" only	"RPV + MAV"
A + D	0	0	13	0	10	0
A + E	1	0	12	0	10	0
A + F	6	0	7	0	10	0
B + D	9	0	4	0	10	0
B + E	3	0	10	0	9	1
B + F	8	0	5	0	10	0
C + D	4	0	9	0	10	0
C + E	3	0	10	0	10	0
C + F	4	0	9	0	10	0

[a]Virus isolates transmitted from the mixed infections by *R. padi* were identified in 144 comparative transmissions in which *R. padi* transmitted virus to 432 of 432 plants; *M. avenae* transmitted virus to 299 of 432 plants. Virus isolates transmitted from the double infections by *M. avenae* were identified in 123 comparative transmissions in which *M. avenae* transmitted virus to 367 of 369 plants; *R. padi* transmitted virus to 19 of 369 plants. None of 168 plants infested as controls became infected. Inoculation test feedings were at the rate of 10 aphids per plant.

TABLE 3. Comparative tests with *Rhopalosiphum padi* and *Macrosiphum avenae* for dependent virus transmissions from double infections of two isolates (A, B) similar to MAV and three isolates (D, E, F) similar to RPV

Isolates in mixed infection	No. of plants (of 19 tested) from which *R. padi* transmitted virus isolate or isolates shown[a]			No. of plants (of three tested) from which *M. avenae* transmitted virus isolate or isolates shown		
	"RPV" only	"MAV" only	"RPV + MAV"	"RPV" only	"MAV" only	"RPV + MAV"
A + D	4	0	15	0	3	0
B + D	2	0	17	0	2	1
A + E	0	0	19	0	3	0
B + F	3	0	16	0	3	0

[a]Identification of the virus isolates transmitted from doubly-infected plants by *R. padi* was done in 84 comparative transmissions in which *R. padi* transmitted virus to 252 of 252 plants, and *M. avenae* transmitted virus to 230 of 252 plants. For tests of virus isolates transmitted from the doubly-infected plants by *M. avenae*, *M. avenae* transmitted virus in all 23 tests to 69 of 69 plants; *R. padi* transmitted virus in parallel tests to 5 of 69 plants. None of 78 plants infested as controls became infected. All plants were infested with about 10 aphids for inoculation test feeding.

transmission occurred (B + D, and B + F, see Table 2). Two separate series of experiments were begun in January and March, 1975. When data from all of these additional tests were summarized (Table 3), it was clear that dependent transmission of the MAV-like isolates by *R. padi* was no more likely to occur from one of the mixed infections than from another. *Rhopalosiphum padi* transmitted both kinds of isolates from 67 (88%) of the 76 doubly-inoculated plants that were tested. Although there may be quantitative differences among virus combinations in these mixed infections, we think the more likely basis for variations in the initial tests (Table 2) was the high greenhouse temperatures during the summer months when those tests were done. At any rate, the data clearly show that the phenomenon occurs often enough for dependent transmission to be a potential factor in nature, which was our original concern.

In another series of experiments in Ithaca, we tested mixed infections of the two isolates (isolates 6524 and 6407) that originated from collections in Canada (1). In five initial tests, some dependent transmission of 6407 in the presence of 6524 occurred in each test. From a total of 33 doubly-inoculated plants, *R. padi* transmitted both viruses from 20 of the plants. In the various comparative tests that enabled identification of these cases of dependent virus transmission, *R. padi* transmitted virus to 158 of 162 test plants; *M. avenae* transmitted virus to 114 of 162 plants. In parallel tests of 31 doubly-infected plants, only isolate 6407 was transmitted by *M. avenae*. In these experiments *M. avenae* transmitted virus to 167 of 167 test plants; *R. padi* transmitted virus in the parallel tests to 3 of 168 plants. None of 42 plants that were infested as controls in these tests became infected. Because this level of dependent virus transmission by *R. padi* was below that of previous tests with RPV and MAV (6, 8), we made additional tests to avoid the high

TABLE 4. Comparative tests in Ithaca with *Rhopalosiphum padi* and *Macrosiphum avenae* for dependent virus transmission from oats doubly infected with combinations of RPV, MAV, and two similar isolates from Canada (isolates 6524 and 6407)

Isolates in mixed infection	No. of plants (of 14 tested) from which *R. padi* transmitted virus isolate or isolates shown [a]			No. of plants (of eight tested) from which *M. avenae* transmitted virus isolate or isolates shown		
	"RPV" only	"MAV" only	"RPV + MAV"	"RPV" only	"MAV" only	"RPV + MAV"
6524 + MAV	2	0	12	0	8	0
RPV + 6407	0	0	14	0	8	0
6524 + 6407	2	0	12	0	8	0
RPV + MAV	0	0	14	0	8	0

[a]Virus isolates transmitted from the mixed infections by *R. padi* were identified in 56 comparative transmission tests in which *R. padi* transmitted virus to 167 of 168 plants; *M. avenae* transmitted virus to 156 of 168 plants. The isolates recovered from the mixed infections by *M. avenae* were identified in 32 comparative tests in which *M. avenae* transmitted virus to 96 of 96 plants; *R. padi* transmitted virus to 0 of 96 plants. None of 90 plants infested as controls became infected. For inoculation test feedings, each plant was infested with about 10 aphids.

TABLE 5. Virus transmission by aphids fed through membranes on mixtures of a virus preparation (made from oats doubly infected by isolates 6524 and 6407 of BYDV) and one of three antisera, and identification of the isolates recovered from the plants that became infected by means of the membrane-fed aphids

Antiserum	No. of plants that became infected over no. infested with 10 aphids of species shown		No. of plants from group at left tested and found to be infected by virus isolate or isolates shown[a]			
	R. padi	*M. avenae*	No.	Only isolate 6524	Only isolate 6407	Isolates 6524 + 6407
MAV	9/12		9	4	0	5
MAV		2/12	2	0	2	0
RPV	0/12					
RPV		12/12	2	0	2	0
HO	9/12		9	3	0	6
HO		12/12	2	0	2	0
None	24/24		6	4	0	2
None		24/24	4	0	4	0
Aphid controls	0/24	0/24	...	...	...	...

[a]Identification of the 11 cases of transmission of only isolate 6524 from the treated preparations was made in tests in which *R. padi* transmitted virus to 33 of 33 plants and *M. avenae* transmitted virus to 0 of 33 plants. The ten cases of recovery of only isolate 6407 from the preparations were identified in transmission tests in which *M. avenae* transmitted virus to 27 of 30 plants and *R. padi* transmitted to 1 of 30. The 13 examples of recovery of both viruses by *R. padi* from the treated preparations were identified in comparative transmissions in which *R. padi* transmitted virus to 39 of 39 plants and *M. avenae* also transmitted virus to all 39 plants. None of 60 plants infested as controls became infected.

greenhouse temperatures that also occurred during these initial experiments with the Winnipeg isolates.

In further tests of the Winnipeg isolates in Ithaca, we made mixed infections of RPV, MAV, and the two Winnipeg isolates to provide the four possible combinations of double infections. From almost all of the mixed infections, *R. padi* transmitted both RPV or isolate 6524 together with MAV or isolate 6407. These dependent transmissions occurred from 52 of 56 plants tested (Table 4). In parallel tests of the doubly-inoculated plants with *M. avenae*, however, only MAV or isolate 6407 was recovered (Table 4). It is possible that isolate 6524 is a less efficient helper virus than RPV, but it would take many more tests to evaluate reproducibility of any such small difference (Table 4).

Our current concept of the mechanism of the dependent transmission of MAV by *R. padi* from mixed infections is based on heterologous encapsidation. During simultaneous replication of the two viruses, some nucleic acid of MAV apparently becomes incorporated into virus particles that contain the protein capsid of RPV. Thus, *R. padi* transmits the heterologously encapsidated MAV nucleic acid along with RPV virions from mixed infections. Evidence for this mechanism came from tests of virus purified from doubly-infected plants. When such virus preparations were treated with MAV antiserum, and aphids then fed through membranes on the treated preparations, *M. avenae* did not transmit virus; MAV in the preparation had been neutralized by the specific antiserum. But from the same preparations *R. padi* transmitted both RPV and MAV to many test plants (6). We did one experiment with virus prepared from mixed infections of isolates 6524 and 6407 to obtain information on the mechanism for the dependent transmission of these two isolates from mixed infections. We made a virus preparation as previously described from 1,700 g of tissue of oats doubly infected with isolates 6524 and 6407 (6, 14). Portions of the concentrated preparation were then incubated with antiserum specific for MAV, for RPV, or for a concentrate of healthy oats (HO) as an antiserum control. Phosphate buffer was used as an additional control. Reaction mixtures were assayed by permitting both *R. padi* and *M. avenae* to feed through membranes on the treated virus preparations. We did not have enough of the virus preparations to make a preliminary assay of virus titer, and thus could only estimate the antiserum dilution (1:5) to use to neutralize virus. Because the virus titer in the preparation was higher than we anticipated, MAV in the preparation was not completely neutralized by the MAV-specific antiserum (Table 5). Despite this qualification, data from this preliminary experiment suggest that the heterologous encapsidation mechanism probably occurs also for these two isolates from Winnipeg. The relative numbers of dependent transmissions by *R. padi* were comparable regardless of whether most of the MAV had been neutralized or not (Table 5). These data also suggest that the two Canadian isolates are similar serologically to the RPV and MAV isolates since the RPV antiserum completely neutralized isolate 6524 and the MAV antiserum greatly reduced transmission of isolate 6407 (Table 5).

Tests in Winnipeg.—In one trial, groups of oats were inoculated either with RPV or MAV as controls, or with both isolates. Good evidence was obtained that *R. padi* transmitted both RPV and MAV from five of the six doubly-inoculated oats and that *M. avenae* transmitted only MAV from these plants (Table 6), thus confirming the results of earlier experiments with these two isolates (6) in which different clones of aphids were used.

In another trial similar to that above but with isolates 6524 (*R. padi*-specific) and 6407 (*M. avenae*-specific), transmission of both isolates by *R. padi* from the doubly inoculated plants was less evident than with MAV and RPV (Table 6). Thus, in the 27 comparative transmissions used to identify the viruses that had been transmitted by *R. padi* from plants doubly inoculated with isolates 6524 and 6407, 78 of 81 (96%) plants became infected after being infested with *R. padi* and only 18 of 81 (22%) became infected after being infested with *M. avenae*. With RPV and MAV, however, 35 similar identification tests for virus transmitted by *R. padi* from doubly-inoculated plants resulted in values of 104 of 105 (99%) test plants becoming infected and 72 of 105 (69%) becoming infected after being infested with *R. padi* and *M. avenae*, respectively.

In previous studies with isolates 6524 and 6407 (3) no dependent transmission was detected in limited trials when *R. padi* transmitted virus from oats doubly inoculated with these two isolates. Therefore, it seems

TABLE 6. Comparative tests in Winnipeg with *Rhopalosiphum padi* and *Macrosiphum avenae* for dependent virus transmissions from double infections of MAV and isolate 6407 (similar to MAV), and RPV and isolate 6524 (similar to RPV)

Isolates in mixed infection	No. of plants (of six tested) from which *R. padi* transmitted virus isolate or isolates shown[a]			No. of plants (of six tested) from which *M. avenae* transmitted virus isolate or isolates shown		
	"RPV" only	"MAV" only	"RPV + MAV"	"RPV" only	"MAV" only	"RPV + MAV"
RPV + MAV	1	0	5	0	6	0
6524 + 6407	3	0	3	0	6	0

[a]Virus isolates transmitted from the mixed infections by *R. padi* were identified in 62 comparative transmissions in which *R. padi* transmitted virus to 182 of 186 plants; *M. avenae* transmitted virus to 90 of 186 plants. Virus isolates transmitted from the double infections by *M. avenae* were identified in 59 comparative transmissions in which *M. avenae* transmitted virus to 169 of 177 plants; *R. padi* transmitted virus to 10 of 177 plants. None of 15 plants infested as controls became infected. For inoculation test feedings, each plant was infested with five aphids.

that under conditions at Winnipeg, dependent transmission may occur only occasionally with isolates 6524 and 6407. The use of different aphid clones, five aphids per plant, and other variables in tests with these two isolates may account for the apparent differences between results in Winnipeg and Ithaca.

DISCUSSION

Results of these tests for dependent transmission of MAV-like isolates of BYDV by *R. padi* support the hypothesis that the phenomenon could be important in nature. Dependent transmissions occurred from all mixtures among ten different isolates of BYDV tested. The isolates originated from collections in widely separated geographical areas. The tests were carried out in separate laboratories with distinct clones of *R. padi* under somewhat different conditions. Although this work shows that the dependent transmission phenomenon has wide potential applicability for BYDV, the results do not mean that such virus interactions are necessarily operating in nature.

In the absence of direct data on the role of dependent transmission of isolates of BYDV in nature, we can only speculate on the potential significance of mixed infections. An important role for mixed infections among isolates of BYDV, which has recently been discussed elsewhere (9), seems possible for several reasons. Mixed infections of distinct isolates of BYDV are common in certain situations, such as in winter grains in New York (12, 13). The RPV isolate is not the only isolate of BYDV that can serve as a helper virus; other similar interactions occur with additional isolates and additional aphid vectors (8, 9). The serological relationship between RPV and other Luteoviruses, such as beet western yellows virus, suggests a range of potential interactions that extends beyond the barley yellow dwarf disease (2, 11).

One of the remarkable aspects of the results described here is the similarity in variants of BYDV collected in Manitoba and in New York. This similarity in the vector transmission patterns among different variants identified at the two locations has been in surprising agreement and has shown an amazing consistency when one considers the many variables that can affect interactions among plant viruses, aphid vectors, and susceptible hosts. The serological similarities of the isolates from Winnipeg with those from New York illustrate another feature of this agreement in consistency and stability of the variants of BYDV collected from the field.

LITERATURE CITED

1. GILL, C. C. 1967. Transmission of barley yellow dwarf virus isolates from Manitoba by five species of aphids. Phytopathology 57:713-718.
2. DUFFUS, J. E., and W. F. ROCHOW. 1977. Neutralization of beet western yellows virus by antisera against barley yellow dwarf virus. Phytopathology 67:45-49.
3. HALSTEAD, B. E., and C. C. GILL. 1971. Effect of inoculation of oats with paired combinations of barley yellow dwarf virus isolates. Can.J. Bot. 49:577-581.
4. LINDSTEN, K. 1964. Investigations on the occurrence and heterogeneity of barley yellow dwarf virus in Sweden. Lantbrukshögsk. Annaler 30:581-600.
5. ROCHOW, W. F. 1969. Biological properties of four isolates of barley yellow dwarf virus. Phytopathology 59:1580-1589.
6. ROCHOW, W. F. 1970. Barley yellow dwarf virus: Phenotypic mixing and vector specificity. Science 167:875-878.
7. ROCHOW, W. F. 1972. The role of mixed infections in the transmission of plant viruses by aphids. Annu. Rev. Phytopathol. 10:101-124.
8. ROCHOW, W. F. 1975. Barley yellow dwarf: Dependent virus transmission by Rhopalosiphum maidis from mixed infections. Phytopathology 65:99-105.
9. ROCHOW, W. F. 1977. Dependent virus transmission from mixed infections. Chapter 10. Pages 253-273 *In* K. F. Harris and K. Maramorosch, eds. Aphids as virus vectors. Academic Press, New York. 559 p.
10. ROCHOW, W. F., and C. C. GILL. 1976. Dependent virus transmission by Rhopalosiphum padi of various isolates of barley yellow dwarf virus. Abstr. 199 *in* Proc. Am. Phytopathol. Soc. 3:247.
11. ROCHOW, W. F., and J. E. DUFFUS. 1977. Relationships between barley yellow dwarf and beet western yellows viruses. Phytopathology 67:51-58.
12. ROCHOW, W. F., and H. JEDLINSKI. 1970. Variants of barley yellow dwarf virus collected in New York and Illinois. Phytopathology 60:1030-1035.
13. ROCHOW, W. F., and I. MULLER. 1974. Mixed infections of barley yellow dwarf virus isolates in winter grains. Plant Dis. Rep. 58:472-475.
14. ROCHOW, W. F., A. I. E. AAPOLA, M. K. BRAKKE, and L. E. CARMICHAEL. 1971. Purification and antigenicity of three isolates of barley yellow dwarf virus. Virology 46:117-126.
15. TOKO, H. V., and G. W. BRUEHL. 1959. Some host and vector relationships of strains of the barley yellow-dwarf virus. Phytopathology 49:343-347.