

Aphid Nymphs Transmit an Isolate of Barley Yellow Dwarf Virus More Efficiently than do Adults

C. C. Gill

Research Scientist, Canada Department of Agriculture, Research Station, 25 Dafoe Road, Winnipeg 19, Manitoba.

Contribution No. 427, Canada Department of Agriculture, Research Station.

The technical assistance of J. Marchinko is gratefully acknowledged.

Accepted for publication 3 July 1970.

ABSTRACT

The proportion of 12-hour-old nymphs of the corn leaf aphid, *Rhopalosiphum maidis*, that transmitted an isolate of barley yellow dwarf virus specific for this aphid was consistently larger than the proportion of adults that transmitted. This ratio was higher for acquisition feeding periods of 1 and 2 days than for longer feeding periods.

Apterous adults of *Rhopalosiphum maidis* transmitted the virus to more test seedlings than did alate adults. When aphids were allowed access to the virus source plants as 12-hour-old nymphs, the percentage of plants infected by both alate and apterous adults

was considerably higher than when the aphids acquired virus as adults.

Young nymphs of the greenbug, *Schizaphis graminum*, were also more efficient vectors for this isolate than adults, but there was no significant difference between the efficiency of nymphs and adults of *Macrosiphum avenae* or *Rhopalosiphum padi*. Nymphs of *Rhopalosiphum maidis* were also more efficient vectors than adults for three other *R. maidis*-specific virus isolates, but not for a fourth. Phytopathology 60:1747-1752.

Isolates of barley yellow dwarf virus (BYDV) that are transmitted specifically by the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), were first described from New York by Rochow in 1961 (8). Subsequently, isolates with similar aphid specificity were found in Manitoba (3, 5). An isolate of this type was used in the present study.

The comparative ability of nymphs and apterous and alate adults of viviparous *R. maidis* to transmit the *R. maidis*-specific isolate was investigated. In previous work of this nature with BYDV, Toko & Bruehl (12) found no difference between the ability of nymphs and adults to transmit isolates specific for *Macrosiphum avenae* (Fabricius) or *Rhopalosiphum padi* (Linnaeus). Sana & Shulz (10) reported that transmission of the North Dakota strain was lower and more inconsistent with nymphs of *R. fitchii* (Sand.) than with adults. Dizon (2) found that nymphs of *M. avenae*, *R. padi*, *Schizaphis graminum* (Rondani), and *R. maidis* did not differ significantly from adults of these species in their abilities to transmit a nonspecific isolate, though nymphs appeared to be slightly less efficient than adults. For other circulative, aphid-borne viruses, only two cases are known to the author in which there was a difference in the efficiency of transmission between developmental stages of the aphid. These concern filaree red leaf virus and *M. geranicola* (Hille Ris Lambers) (1), and pea enation mosaic virus and *Acyrtosiphon pisum* (Harris) (= *M. pisi* [Kalt]) (11). In both cases, nymphs were more efficient vectors than adults.

Reports of differences in the ability of alate and apterous viviparous forms (alienicolae) of an aphid species to transmit a virus are also scarce. Dizon (2) found that alate and apterous forms of *M. avenae*, *R. padi*, *S. graminum*, and *R. maidis* did not differ significantly in their abilities to transmit a nonspecific isolate of BYDV.

MATERIALS AND METHODS.—The *R. maidis*-specific

isolate, 6417, examined intensively in this work, was isolated from an individual of *R. maidis* caught on commercial barley in southern Manitoba in 1964. Four other *R. maidis*-specific isolates tested were 6715, 6716, 6719, and 6725 (5). The *M. avenae*-specific isolate used for comparison was 6407 (3). Stocks of these isolates were maintained on oats, *Avena sativa* L. 'Clintland 64', or *A. byzantina* K. Koch 'Coast Black'.

Virus-free clones of the English grain aphid, *M. avenae*, the rose grass aphid, *A. dirhodum* (Walker), the cherry oat aphid, *R. padi*, the corn leaf aphid, *R. maidis*, and the greenbug, *S. graminum*, were reared on caged barley, *Hordeum vulgare* L., as previously described (3). The clone of the quackgrass aphid, *Sipha kurdjumovi* (Mordvilko), was reared on caged quackgrass, *Agropyron repens* (L.) Beauv., under the same conditions. The two clones of *R. maidis*, clone 3 and clone 5, were started from aphids collected in the field in southern Manitoba in 1964. Most tests were conducted with clone 3. Aphids from these colonies were tested regularly to ensure that they were free from virus. Viruliferous aphid colonies of *R. maidis* or *M. avenae*, carrying their specifically-transmitted virus isolates, were reared in the same way as the virus-free colonies, but in separate growth cabinets to avoid contamination.

Virus isolate 6417 was characterized by comparing the ability of apterous adults of five species of aphids to transmit the virus in each of eight trials. A sixth aphid, *S. kurdjumovi*, was included in four of the trials. In each trial, *Briza maxima* L. was used for the virus source plants. This grass had proved to be a good indicator for this isolate, and the concn of virus appeared to be high (unpublished data). The source plants were inoculated by caging 15 viruliferous *R. maidis* for 2 days on each seedling at the two- or three-leaf stage in the greenhouse. The aphids were killed by spraying with the insecticide tetraethylpyrophosphate (TEPP). The

remainder of the procedure, using the detached, split leaf method was the same as that previously described (3), except that two or four lots of 15 aphids each were transferred from each dish to Clintland oat seedlings for a 5-day inoculation feeding period, each lot being caged on a separate seedling.

To determine the time when plants inoculated with isolate 6417 were most suitable for use as virus source material for aphids, one flat each of Herta barley and Clintland oats was seeded in a growth cabinet at 20 C. Sixty seedlings in each flat were inoculated with the virus at the two-leaf stage by caging 15 viruliferous individuals of *R. maidis*-clone 3 on each seedling. After 2 days, the aphids were sprayed with TEPP. Four plants of each cereal were taken at random daily from the 4th to the 15th day after the start of the inoculation feeding. The second and third leaves of each plant were detached, placed in a petri dish, and infested with virus-free apterous adults of *R. maidis*-clone 3. After 1 day at 15 C, 12 feeding aphids were removed from each dish and caged individually on Clintland oat seedlings grown in wooden flats of soil in the greenhouse. After 5 days, the aphids were sprayed with TEPP.

In subsequent experiments comparing transmission of isolate 6417 by nymphs and adult aphids or by adult apterae and alatae, and in most of the experiments involving daily serial transfers of individuals of *R. maidis* on test plants, Herta barley, or occasionally Clintland oats, grown four seedlings to a 5-inch pot and inoculated as described above, were used as the virus source plants 8 days after their inoculation. For tests with isolate 6407, each plant of the same cultivar was inoculated with 10 viruliferous individuals of *M. avenae*, and these were used as virus source plants 6 days after the start of the inoculation access feeding (4). Aphid nymphs with an average age of 12 hr were obtained by placing virus-free apterous or alate adults on healthy, detached barley leaves in petri dishes at 18 C. The nymphs were collected from the dishes 24 hr later for use as test aphids. Most of these nymphs were in the first instar. Aphids approx 10 days old were obtained by placing 12-hr-old virus-free nymphs on healthy, caged Herta barley in a growth cabinet at 20 C. After 10 days, the mature forms were removed for use as test aphids. These young adults had just reached the reproductive stage. Alate and apterous forms of *R. maidis* and *M. avenae* usually alternated between generations. In a few experiments, virus-free test aphids (young nymphs and adults) were selected from regular nonviruliferous colonies.

In experiments involving daily serial transfers of aphids on test plants, 12-hr-old nymphs and 10-day-old adults were caged on separate groups of four virus source plants each, while 10-day-old apterous and alate adults were caged on one group of four source plants for an acquisition feeding period of 2 days in a growth cabinet at 15 ± 1 C. Aphids were then removed from different parts of the source plants and caged individually on the first group of test seedlings at the two-leaf stage. These were grown one to a 3-inch pot in a growth cabinet at 20 ± 1 C. After 24 hr, each aphid

was transferred to a second caged test seedling at the two-leaf stage. This transfer was continued at daily intervals until the aphid died or the experiment was concluded.

Transmission by 12-hr-old nymphs and 10-day-old apterous adults was compared by caging each separately on one pot of four virus-infected Herta plants for the acquisition feeding period. In some experiments, leaves from the source plants were detached, each leaf was split lengthwise into two parts, and each part was placed in a separate petri dish containing moist sand. Nymphs were transferred to one dish and adults to the other for the acquisition feeding. For the inoculation feeding, aphids were transferred from the source material to individually-caged Clintland oat test plants at the two-leaf stage in a growth cabinet at 20 C. The plants were then incubated for symptom expression at about 18 C.

When the ability of apterous or alate adults to transmit was compared, the test aphids were selected from healthy colonies and the two forms were caged on a single pot of four Herta barley source plants for the acquisition feeding.

When determining the ability of different developmental stages of *R. maidis* to transmit *R. maidis*-specific isolates other than 6417, leaves of Clintland oats, grown in the greenhouse and infected with the respective isolate, were detached from plants showing early symptoms. Each leaf was split into two parts, the parts were placed in separate petri dishes and 12-hr-old nymphs of clone 5 were transferred to one dish and young apterous adults to the other dish. After a 2-day acquisition feeding period, aphids were caged in groups of three on Clintland oats for a 2-day feeding period, and were then sprayed with TEPP.

Fluorescent lamps in the growth cabinets provided about 1,400 ft-c of illumination at soil level on a 16-hr daily photoperiod. Greenhouse temp were regulated for 20 C, but occasionally temp rose to higher values for short periods. Final readings for the number of infected test plants were made 4 weeks after inoculation.

RESULTS.—*Transmissibility of virus isolate 6417 by apterous adults of six species of aphids.*—*Rhopalosiphum maidis*-clone 3 was the most efficient vector in each trial. *Schizaphis graminum* transmitted the virus occasionally, and transmissions by *R. padi* were rare. Clone 5 of *R. maidis* was included in one of the trials, and proved as efficient as clone 3. The total numbers of plants infected out of the total inoculated by the six aphid species in the eight trials were *R. maidis*, 19/32; *S. graminum*, 4/32; *R. padi*, 2/30; *M. avenae*, 0/30; *A. dirhodum*, 0/30; and *S. Kurdjumovi*, 0/14. Symptoms of this isolate on Clintland oats were mild. This, together with the pattern of transmission by the aphid species, indicates that isolate 6417 belongs to the *R. maidis*-specific strain (5, 9).

Transmissibility of virus isolate 6417 from cereals at different times after their inoculation.—The percentages of *R. maidis* that transmitted isolate 6417 to the test plants at different times after inoculation of the virus source plants are shown in Fig. 1. The transmission

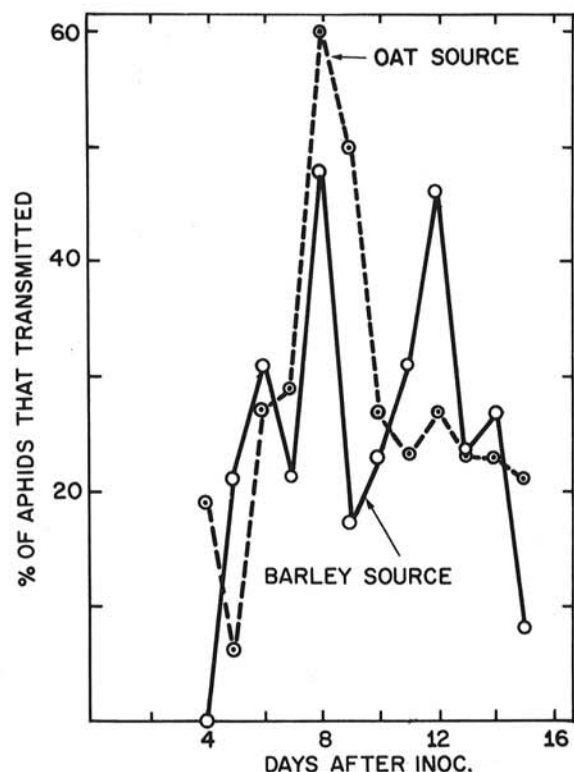


Fig. 1. The percentage of *Rhopalosiphum maidis* that transmitted barley yellow dwarf virus isolate 6417 from Herta barley or Clintland oats to Clintland oats when the aphids were allowed access to the virus source plants at different time intervals after their inoculation. Test aphids were allowed access to the virus source material for 1 day, then were caged singly on the test seedlings for 5 days.

curves for Herta barley and Clintland oat source plants both reached a max 8 days after the start of inoculation. A second major peak for barley at 12 days coincided with a small peak for oats. Symptoms on barley and oat source plants started to appear on the 11th day after inoculation. In subsequent experiments, Herta barley and Clintland oats were, therefore, used as virus source plants on the 8th day after inoculation.

Transmission of the R. maidis- and M. avenae-specific virus isolates when the vectors were transferred daily to successive test seedlings.—When apterous adults of *R. maidis* were allowed to feed first on source plants infected with isolate 6417 and were then transferred successively to new test plants at daily intervals in a preliminary trial, only a very low percentage of test plants became infected. In a second trial of this kind, virus transmission by *R. maidis* and *M. avenae* was compared after each aphid had fed on its respective specific isolate. Three individuals of *R. maidis* that were tested fed on 9 or 10 plants/sequence, and each of three others fed on 20 plants. Five of the six aphids transmitted once only; the other transmitted twice. Only 10% of 71 test plants became infected. The transmission pattern appeared to be random. On the other hand, six individuals of *M. avenae*, each of which fed

on 20 plants/sequence, transmitted isolate 6407 with only occasional lapses, and 92% of 96 test plants became infected. In this trial, the virus source plants were Clintland oats; the test plants were Herta barley. Several other trials with isolate 6417 and *R. maidis* were conducted in which *B. maxima* was used as the source plant and either Clintland oats or *Cynosurus echinatus* L. were the test seedlings. Although few aphids lived longer than 10 days on the test seedlings, transmission patterns were similar to those in the other experiments with this isolate. Occasionally an individual transmitted on the 1st day. This indicated that lack of transmission was not due to the need for a long latent period in the aphid.

A second trial, in which Clintland oats were both virus source material and test seedlings, was conducted with *M. avenae* and isolate 6407. The pattern of transmission was similar to that for the same isolate in the first trial. Eighty-nine per cent of 96 test plants became infected. These high rates of infection, resulting from daily aphid transfers to successive test seedlings, confirm the results of Rochow (7) in a similar type of experiment for *M. avenae* and an *M. avenae*-specific isolate derived from New York.

Transmission of virus isolate 6417 by nymphs and adults of R. maidis.—The poor transmission obtained with isolate 6417 in the previous experiments with adults of *R. maidis* prompted an investigation of the ability of young nymphs to transmit this isolate. Two trials were conducted with the detached, split leaf method. The aphids were allowed to feed on the detached leaves for 2 days, then single aphids were transferred to individually caged test seedlings for a 5-day period. The number of test plants that became infected out of the number infested with aphids in the first trial was 33/60 for nymphs and 4/38 for adults; in the second trial, 45/58 for nymphs and 15/59 for adults.

Effect of varying the length of the acquisition or the inoculation feeding period on the transmission of virus isolate 6417 by nymphs and adults of R. maidis.—Three trials were conducted in which the acquisition feeding period was varied from 1 to 6 days and the inoculation feeding period was 5 days. The aphids were caged on the virus source plants for the acquisition feeding. The results in Table 1 indicate that in each experiment, more nymphs transmitted virus to the test seedlings than did adults for each of the acquisition feeding periods. The ratios of the proportion of plants infected by nymphs to the proportion infected by adults was greatest for the 1- and 2-day acquisition feeding periods.

Two other trials were conducted in the same way, except that the acquisition feeding period was constant at 5 days and the inoculation feeding period on the test seedlings was varied from 12 hr to 6 days. Again, in each experiment and for each treatment, more nymphs transmitted virus than did adults (Table 2).

Transmission of virus isolate 6417 by nymphs and adults of other aphid species.—In the first series of trials, nymphs and adults of *S. graminum*, *R. padi*, and *M. avenae* were compared. The test aphids were young

TABLE 1. Transmission of barley yellow dwarf virus isolate 6417 by nymphs and apterous adults of *Rhopalosiphum maidis* allowed different acquisition feeding periods

Acquisition feeding period, days	No. plants infected							
	Trial 1		Trial 2		Trial 3		Totals	
	Nymphs	Adults	Nymphs	Adults	Nymphs	Adults	Nymphs	Adults
1	8 ^a	0	11	3	11	3	30	6
2	13	6	11	6	17	4	41	16
3	14	5	18	7	15	9	47	21
4	15	11	16	8	14	11	45	30
5	13	10	17	7	17	13	47	30
6	18	8	19	12	16	6	53	26

^a Each value, except the totals, indicates the number of plants infected of 20 test seedlings, with one aphid/seedling. The inoculation feeding period was 5 days.

nymphs and apterous adults selected from nonviruliferous aphid colonies. The acquisition feeding periods were 1, 2, and 3 days, and the inoculation feeding period on the test plants was 5 days. Twenty individual aphids of each stage were tested for each acquisition feeding period. For each treatment, more nymphs of *S. graminum* transmitted virus than did adults, the total transmissions for all three treatments being 15 for nymphs and 9 for adults. The only transmissions by *R. padi* were three by adults for the 1-day acquisition feeding and one by a nymph for the 3-day feeding. No transmission occurred in the trial with *M. avenae*. Groups of five *R. maidis* nymphs transmitted virus from leaves detached from the source plants to each of three Clintland oat plants for each group of four virus source plants used in these trials. This confirmed the presence of BYDV in the source plants.

In three further experiments with *S. graminum*, young adults from a nonviruliferous colony and 12-hr-old nymphs were allowed to feed for 2 days on the virus source, using the detached, split leaf method. The numbers of test plants that became infected out of 20 infested with nymphs or adults were, respectively, 14 and 7, 14 and 3, and 9 and 0 in the three experiments.

Transmissions of virus isolate 6417 by apterous or alate adults or nymphs when transferred daily to successive test seedlings.—In these trials the virus source plants were Herta barley and the test seedlings Clintland oats. The object was to compare the transmission patterns of nymphs and adults when the aphids were

removed serially on the test seedlings, and to compare the rate of transmission by adults that had fed on the source plants as young nymphs compared with that of aphids that had fed on the source plants when 10 days old. Trial 1 (Table 3) compares the serial transmission patterns obtained for 12-hr-old aphids and 10-day-old apterae when aphids in these stages were allowed to feed on the source plants. Only the results for aphids that fed on 10 or more plants are shown. Six aphids that acquired virus while 10 days old transmitted to 25% of 77 test seedlings. Five aphids that acquired virus while 12 hr old transmitted to 41% of a total of 64 test plants. There was variation in the ability of individual aphids of both developmental stages to transmit virus. Four of the aphids that acquired virus when 12 hr old matured as alatae; the other matured as an aptera. Survival of these individuals after reaching maturity was poor. Nevertheless, if transmissions during the nymphal stages only are considered, 57% of 35 test plants became infected, which is appreciably higher than the 25% that became infected when fed on by aphids that acquired virus when 10 days old.

In the same trial, 10-day-old alatae were also tested for their ability as vectors. Of the aphids that fed on 10 or more plants, only one of nine alatae transmitted virus, while all six of the apterous forms transmitted, indicating the possibility that 10-day-old alatae were less efficient vectors than 10-day-old apterae. The single alate adult that transmitted fed on 20 plants and infected numbers 7, 11, and 13 in the sequence.

TABLE 2. Transmission of barley yellow dwarf virus isolate 6417 by nymphs and apterous adults of *Rhopalosiphum maidis*, allowed different inoculation feeding periods

Inoculation feeding period, days	No. plants infected					
	Trial 1		Trial 2		Totals	
	Nymphs	Adults	Nymphs	Adults	Nymphs	Adults
0.5	4 ^a	1			4	1
1	6	4	9	5	15	9
2	6	4	17	7	23	11
3	14	5	15	8	29	13
4	8	5	14	12	22	17
5	15	8	18	10	33	18
6	11	6	16	6	27	12

^a Each value, except the totals, indicates the number of plants infected of 20 test seedlings, with one aphid/seedling. The acquisition feeding period was 5 days.

TABLE 3. Frequency of transmission of barley yellow dwarf virus isolate 6417 by individuals of *Rhopalosiphum maidis* when nymphs or apterous adults were allowed to feed on the virus source for 2 days, then were transferred daily to successive seedlings of Clintland oats

Trial	Aphid stage	Aphid No.	Day of transfer ^a																				
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
1	Adult (10-day old)	1	—	—	P	P	P	P	—	P	—	—	—	—	P	— ^d							
		2	—	—	—	—	—	—	P	P	—	— ^d											
		3	—	—	—	—	—	—	P	P	—	—	—	— ^d									
		4	—	—	P	—	—	—	—	—	—	—	— ^d										
		5	—	—	—	—	—	—	P	P	P	P	P	P	—	—	—	—	—	—	P	—	—
		6	—	—	P	—	—	—	—	—	—	—	— ^d										
	Nymph (12-hr old)	1	—	—	P	P	—	—	P ^x	—	P	— ^d											
		2	P	P	P	P	P	P	P	P ^{xx}	P	P	P	P	—	— ^d							
		3	—	P	—	—	P	P	—	— ^x	P	— ^d											
		4	—	—	—	—	—	—	—	— ^x	—	—	—	—	—	—	—	P	—	—	—	—	—
2	Nymph (12-hr old)	1	P	P	—	—	—	—	— ^x	P	—	P	P	P	—	—	—	—	P	—	—	—	—
		2	—	—	—	—	—	—	P	— ^x	—	P	—	—	—	—	—	—	—	—	—	—	—
		3	P	P	—	P	P	—	— ^{xx}	P	P	—	P	P	P	P	P	P	—	P	P	—	—
		4	—	—	—	—	—	—	—	P ^x	—	P	—	—	P	—	—	—	—	—	—	—	—
		5	P	—	—	P	P	—	P	— ^x	P	P	P	P	—	P	P	—	P	P	— ^d		
		6	P	P	—	P	P	P	P	— ^x	P	P	P	P	P	P	P	P	—	—	—	—	P
		7	—	P	—	—	—	P	—	— ^x	P	P	—	P	—	P	—	—	—	—	—	—	—
		8	P	P	P	—	P	—	P	P	P ^x	P	P	P	P	P	—	P	P	—	—	—	— ^d
		9	—	—	—	P	P	—	—	— ^x	—	—	—	—	—	—	—	—	—	—	—	—	— ^d
		10	P	—	P	P	—	—	—	— ^x	—	P	P	P	P	P	P	P	P	—	—	—	— ^d

^a P = plant infected; — = plant not infected; d = aphid died on the plant; x = aphid matured as an aptera on this plant; xx = aphid matured as an alata on this plant.

The results of further tests, in which apterous and alate adults were compared as vectors, are given in the next section.

Survival of the aphids in a second trial, in which only 12-hr-old aphids were tested, was good, and the results of the transmissions by 10 aphids, each of which fed on 19 or 20 plants, are shown in Trial 2 (Table 3). Again, the number of transmissions by individuals was variable, ranging from 2 to 14 infected plants/aphid. The 10 aphids infected 43% of a total of 196 test plants. During the nymphal stages, which fed on the first seven plants in the sequence, 42% of 70 plants became infected; during the adult stage, which fed on plants 9 to 20, 45% became infected. The proportion of test plants infected during the first part of the adult stage, plants 9 to 15, was higher (53%) than the second part for plants 16 to 20, when only 22% became infected. All except one of these aphids were alatae. The pattern of transmissions in a third trial in which 12-hr-old nymphs again were tested was similar to the pattern in the second trial. All aphids in the third trial were alatae.

Transmission of virus isolate 6417 by apterous and alate adults of R. maidis.—Individuals of *R. maidis*-clone 3 were used in each of the five trials. The results in Table 4 show that in each experiment, more apterae transmitted virus than alatae. The difference between the number of plants infected by each aphid form was significant ($P < .05$) when the acquisition and inoculation feeding periods were 2 and 4 days, respectively, but not when the feeding periods were 5 days each ("Student" t-test). This, therefore, confirms the results in the preceding section that apterous adults of

R. maidis are more efficient vectors for isolate 6417 than alate adults.

Transmission of R. maidis-specific virus isolates, other than 6417, by nymphs and adults.—Twenty test seedlings were infested with each aphid stage in each trial. The numbers of test plants infected by nymphs and adults, respectively, for isolate 6715 were 4 and 0, 3 and 0, and 6 and 0, in three trials; for isolate 6716: 2 and 2, 2 and 2, and 10 and 2, in three trials; for isolate 6719: 4 and 0 in one trial; and for isolate 6725: 11 and 2, and 10 and 2, in two trials. Nymphs were therefore more efficient vectors than adults for three isolates, but in only one of three trials for isolate 6716.

DISCUSSION.—The differences found between nymphs and apterous and alate adults of *R. maidis* as vectors for isolate 6417 were in the proportion of aphids that transmitted virus (Table 1) and in the frequency of transmissions that resulted from individual aphids

TABLE 4. Transmission of barley yellow dwarf virus isolate 6417 by apterous and alate adults of *Rhopalosiphum maidis*

Acquisition feeding period, days	Inoculation feeding period, days	Plants infected	
		Apterae	Alatae
5	5	19/30 ^a	10/30 ^a
5	5	12/30	8/30
2	4	10/60	3/60
2	4	8/60	0/60
2	4	17/60	5/60

^a Number of test plants infected out of total number exposed.

when moved serially on test plants (Table 3). It is possible that the latent period of the virus in the nymphs was also shorter than in the adults because the ratio of the number of plants infected by nymphs to the number infected by adults was highest with the shorter acquisition feeding periods of 1 and 2 days (Table 1).

Different feeding habits may account at least partly for the differences in the ability of nymphs and apterous and alate adults of *R. maidis* to transmit isolate 6417. Nevertheless, nymphs and adults of several aphid species have proved to be equally efficient as vectors for other strains of BYDV (2, 12). A difference in the virus-vector relationship between the stages or forms of the aphid may be involved. For example, adults, particularly alatae, were poor vectors when the mature individuals were allowed to feed on the virus source, but the ability of adults to transmit virus was much greater when they fed on the virus source as 12-hr-old nymphs. Perhaps the condition of the gut wall in nymphs is more favorable for the passage of virus into the haemolymph than in adults.

No tests were made with older instars of *R. maidis* to determine how their ability as vectors compared with that of nymphs in the first instar. Results from the experiments involving daily transfers of the nymphs to new test plants confirmed that isolate 6417 is of the circulative type (6), because the aphids continued to transmit after each moult.

The superior levels of transmission attained by *M. avenae* with isolate 6407 may result partly from a high concn of this virus in the source plants as compared with the concn for isolate 6417. Indeed, in purification work with different strains of BYDV, Rochow experienced difficulty in obtaining concn of virus of an *R. maidis*-specific isolate to match those for an *M. avenae*-specific isolate when Coast Black oats were used as the virus source material (9).

Transmissions of isolate 6417 obtained in serial transfers by *R. maidis* were slightly lower when Herta barley was used as the test plant than when oats or other grass species were used. We have found, however, that barley is usually a better host for *R. maidis* than is oats. Therefore it appears that differences in host preference by the aphid do not account for the differences in levels of transmission for isolates 6407 and 6417. Clintland oats was preferred to barley as a test plant for isolate 6417 because symptoms of this isolate on barley were much milder than on oats.

It was significant that nymphs of *S. graminum*, like those of *R. maidis*, transmitted isolate 6417 more efficiently than adults. On the other hand, the use of nymphs did not improve transmission of this isolate by *R. padi* or *M. avenae*.

Results from the limited testing of other *R. maidis*-

specific isolates with nymphs and adults suggests that other isolates of this type may have vector relations similar to those found for 6417. In routine work with BYDV, we have experienced more difficulty in obtaining successful transfers of *R. maidis*-specific isolates from one plant to another than with most other strains of the virus. This may have resulted, in part at least, from the general practice of using adults as vectors.

If isolates with vector-virus relationships like those of 6417 are common, it is probable that attempts to isolate BYDV from field crops would be more successful if young nymphs rather than adults of *R. maidis* were used. Proof of infection by transmission of the virus with aphids is all the more important with the milder isolates of BYDV such as those of the *R. maidis*-specific type, since recent work has indicated that symptoms on a high proportion of barley infected naturally with *R. maidis*-specific isolates, may be masked (*unpublished data*).

LITERATURE CITED

- ANDERSON, C. W. 1951. The insect vector relationships of the filaree red-leaf virus, with special reference to a latent-period difference between nymphs and adults in *Macrosiphum geranicola* (Lambers). *Phytopathology* 41:699-708.
- DIZON, R. L. 1968. Seasonal temperature effects on the transmission of barley yellow dwarf virus by four cereal aphids. Ph.D. Thesis. Penn. State Univ. 143 p.
- GILL, C. C. 1967. Transmission of barley yellow dwarf virus isolates from Manitoba by five species of aphids. *Phytopathology* 57:713-718.
- GILL, C. C. 1969. Cyclical transmissibility of barley yellow dwarf virus from oats with increasing age of infection. *Phytopathology* 59:23-28.
- GILL, C. C. 1969. Annual variations in strains of barley yellow dwarf virus in Manitoba, and the occurrence of greenbug-specific isolates. *Can. J. Bot.* 47:1277-1283.
- KENNEDY, J. S., M. F. DAY, & V. F. EASTOP. 1962. A conspectus of aphids as vectors of plant viruses. Commonwealth Inst. Entomol., London. 114 p.
- ROCHOW, W. F. 1959. Transmission of strains of barley yellow dwarf virus by two aphid species. *Phytopathology* 49:744-748.
- ROCHOW, W. F. 1961. A strain of barley yellow dwarf virus transmitted specifically by the corn leaf aphid. *Phytopathology* 51:809-810.
- ROCHOW, W. F. 1969. Biological properties of four isolates of barley yellow dwarf virus. *Phytopathology* 59:1580-1589.
- SANA, D. L., & J. T. SHULZ. 1962. Barley yellow dwarf transmission by instars of *Rhopalosiphum fitchii* and *Toxoptera graminum*. 17th Ann. Meeting North Central Branch Entomol. Soc. Amer. Proc. 17:95.
- SIMONS, J. N. 1954. Vector-virus relationships of pea-eneation mosaic and the pea aphid *Macrosiphum pisi* (Kalt.). *Phytopathology* 44:283-289.
- TOKO, H. V., & G. W. BRUEHL. 1959. Some host and vector relationships of strains of the barley yellow-dwarf virus. *Phytopathology* 49:343-347.