Transmission of Barley Yellow Dwarf Virus Strains from Northwestern China by Four Aphid Species

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ABSTRACT

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During a 3-yr period, 66 barley yellow dwarf virus (BYDV)-infected wheat plants were collected from 17 localities in Shanxi, Shaanxi, Gansu, and Henan provinces of the People's Republic of China. Four strains of BYDV (GPV, DAV, RPV, and GPDAV) were identified on the basis of differential aphid transmissions. The predominant strain was GPV, which was found in 77.3% of the 66 samples tested. GPV was transmitted nonspecifically by *Schizaphis graminum* and *Rhopalosiphum padi*, but transmission by *S. graminum* was 36.8% more efficient than by *R. padi*. *Macrosiphum avenae* rarely transmitted GPV. This strain was not transmitted by *Acyrthosiphon dirhodum*. DAV was found in 15.2% of the total 66 samples. DAV was transmitted nonspecifically by *S. graminum, M. avenae*, and *A. dirhodum* but was not transmitted by *R. padi*. RPV was found in 4.5% of the samples, RPV was transmitted exclusively by *R. padi*, and GPDAV was found in 3% of the samples. This strain was transmitted nonspecifically by all four aphid species. The vector specificity of GPV and DAV remained constant regardless of the number of aphids used in the tests. *S. graminum* and *M. avenae* apparently acquired and inoculated GPV and DAV strains, respectively, in as short a time as 1 min. Increase in duration of acquisition and inoculation feeding time did not appreciably increase the rate of transmission. Both nymphs and adults of *S. graminum* and *M. avenae* were efficient transmitters of BYDV. The median latent period (LP_{50}) values in both vector species were about the same. The mean retention period of BYDV was 20.1 days in *S. graminum* and 13.9 days in *M. avenae*. There were significant differences in varietal reaction to GPV and DAV among the 24 wheat cultivars tested, ranging from 0.0 to 85.7% infection.

Additional key word: luteoviruses

Barley yellow dwarf virus (BYDV) is the most common and widely distributed cereal virus in the world. It has been reported in Australia (4), Belgium (27), Canada (16), Czechoslovakia (31), England (33), Finland (12), Germany (18), India (15), Israel (11), the Netherlands (17), Sweden (14), and the United States (1,19). Its host range includes about 100 species of Gramineae; no dicotyledonous plants have ever been reported susceptible (24). Among the Gramineae, barley, oats, wheat, rice, corn, and rye are the most economically important hosts of BYDV. Transmission of BYDV is dependent on vector species, virus isolates, test plant species, source plants, and temperature (22). Five isolates of BYDV, namely PAV, MAV, RPV, RMV, and SGV, have been differentiated on the basis of vector specificity and serology in the United States during the past 20 yr (25). Similar isolates have been reported in Canada by Gill (7) and their relationships were based partly on results of aphid transmission tests and partly on cytological reactions (8,9).

BYDV has been known to occur in the People's Republic of China (PRC) for the last two decades (34). The disease reached epidemic proportions in 1966, 1970, 1973, and 1978 over a vast area in China, including Shaanxi, Gansu, Shanxi, Henan, Hebei, and Shandong provinces as well as Ningxia and Nei Monggal (Inner Mongolia) autonomous regions. Other localized BYDV infestations during this period occurred in Liaoning, Jilin, Heilongjiang, Jiangsu, Anhui, Sichaun, Guizhou, and Qinhai provinces as well as Xingjiang and Xizang autonomous regions. Yield losses in wheat caused by BYDV have been estimated at 20–30%. As a result of the Cultural Revolution, no basic research on vector-virus-host relationships was encouraged during that 10-yr period. This paper reports identification of four strains of BYDV from wheat by differential aphid transmissions. We have tentatively designated these strains as GPV, DAV, RPV, and GPDAV. The transmission characteristics of two dominant strains of BYDV are also reported.

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MATERIALS AND METHODS

Aphid species used in this study were *Rhopalosiphum padi* (L.), *Macrosiphum* (=*Sitobion*) *avenae* (Fabricius), *Schizaphis graminum* (Rondani), and *Acyrthosiphon dirhodum* (Walker). Each of these four species (RP, MA, SG, AD, respectively) represented progeny of a single viviparous female originating from Wugong in Shaanxi Province or Gangu in Gansu Province. All stock colonies of virus-free aphids were reared on caged wheat plants (*Triticum aestivum* L.) in an isolated room under 12-hr fluorescent illumination at about 23 C. A group of aphids from each species was also used as controls in the experiments.

A total of 66 infected plants showing BYDV symptoms was collected from 17 localities in Shanxi, Shaanxi, Gansu, and Henan provinces. One to three leaves from each of these 66 infected plants was each divided into four sections, and each section was placed in a separate petri dish containing a given test-aphid species. Four- to 5-wk-old plants inoculated in the first test were selected at random for subsequent tests with the four aphid species; this process was repeated for two to five cycles. All viruses were routinely maintained by serial transmissions by aphids to *Avena nuda* L. at 4- to 5-wk intervals. *A. nuda* seedlings in the two-leaf stage were used as test plants for transmission trials. All insects were starved for at least 2 hr before each test in order to enhance the initiation of feeding.

For vector specificity tests, an acquisition access period of usually 2 days at 22 ± 1 C was followed by transfer of two aphids by means of a camel's hair brush from each detached, infected leaf to each *A. nuda* test seedling for an inoculation access period (IAP) of 2 5 days at 22 ± 1 C. In one test, transfers included five aphids per seedling and 10 aphids per seedling for comparison. In all trials, test insects and plants were sprayed with DDVP (2,2-dichlorovinyl dimethyl phosphate) at the end of the inoculation access period, after which plants were placed on a greenhouse bench for at least 6 wk and observed for symptom development. Symptomatology was the only means used throughout this study to

confirm the experimental results. Occasionally, a few symptomless plants resulting from various transmission trials were selected for aphid-acquisition checks. No transmission ever occurred.

To obtain a more precise comparison between virus strains and aphid species, individual insects were serially transferred to healthy seedlings at 2-hr intervals for 30 hr to determine the median latent period (LP_{50}) using Sylvester's method (28). Retention of BYDV inoculativity by aphids was determined by transfer of test insects, singly at daily intervals, until the death of the insects. For studying transmission characteristics of two dominant strains of BYDV, GPV and DAV, by their vectors *S. graminum* and *M. avenae*, respectively, individual insects were carefully observed and precisely timed during various acquisition and inoculation feeding periods.

RESULTS

Results from 66 samples of BYDV-infected wheat collected from Shanxi, Shaanxi, Gansu, and Henan provinces during 1978–1981 are summarized in Table 1. Four distinct strains of BYDV were detected in northwestern China. The predominant strain was GPV, which was transmitted nonspecifically by both *S. graminum* and *R. padi*, but transmission by *S. graminum* (55.3%) was more efficient than by *R. padi* (18.5%). *M. avenae* rarely transmitted GPV and it was not transmitted by *A. dirhodum*. The second most predominant strain was DAV, which was transmitted nonspecifically by *S. graminum, M. avenae*, and *A. dirhodum* (30.8, 38.1, and 25.0%, respectively) but was not transmitted by *R. padi*. The third strain was RPV, which was transmitted exclusively by *R. padi*. The fourth strain, GPDAV, was transmitted nonspecifically by all four species of aphid tested.

Of the 66 samples tested, 77.3% contained a virus similar to GPV (Table 1). This strain was widely distributed in most plain areas of Shaanxi, southern Gansu, southern and central Shanxi, and central Henan provinces. DAV was only found in 15.2% of the samples and was distributed only in the high elevations of central Shaanxi, eastern Gansu, and northern Shanxi provinces. RPV and GPDAV were found in only three and two samples, respectively. Their distribution was rather limited; the former was found in the Taibei San Mountain and Meixian in Shaanxi Province and the latter was found in Taibei San Mountain and Longxian in Shaanxi Province.

To test the stability and distinctive nature of the predominant strains, GPV and DAV, we increased the number of test aphids from two to five and 10 per plant for each of the four aphid species. These results showed that the vector specificity of these two strains remained constant regardless of the numbers of aphids used (Table 2). *R. padi* transmitted GPV but not DAV, and *A. dirhodum* transmitted DAV but not GPV.

Because *S. graminum* and *M. avenae* were the most efficient vectors of GPV and DAV, respectively (Table 1), we conducted another series of experiments to elucidate the vector-virus-plant relationship. The transmission characteristics of GPV and DAV by these two aphid species are summarized in Table 3. It is interesting to note that both strains

Table 1. Summary of transmission of four strains of barley yellow dwarf virus by four aphid species during 1978–1981

Strain	Collection site	No. samples	No. test plants infected/no. plants infested by indicated aphid species[a]							
			SG	Percent	RP	Percent	MA	Percent	AD	Percent
GPV	Northern Shaanxi	3	47/62	75.8	15/69	21.7	2/63	3.2	0/71	0.0
	Central Shaanxi	39	501/883	56.7	159/907	17.5	50/861	5.8	0/880	0.0
	Southern Shaanxi	1	56/114	49.1	4/115	3.5	0/114	0.0	0/115	0.0
	Eastern Gansu	5	52/112	46.4	46/114	40.4	11/113	9.7	0/116	0.0
	Central Shanxi	1	19/31	61.3	15/30	50.0	0/27	0.0	0/33	0.0
	Northern Shanxi	1	43/93	46.2	10/90	11.1	0/94	0.0	0/97	0.0
	Central Henan	1	16/32	50.0	1/29	3.4	0/31	0.0	0/30	0.0
Total		51	734/1327	55.3	250/1354	18.5	63/1303	4.8	0/1342	0.0
Percent		77.3								
DAV	Central Shaanxi	4	32/157	20.4	0/169	0.0	79/161	49.1	49/158	31.0
	Eastern Gansu	5	34/109	31.2	1/112	0.9	42/112	37.5	28/108	25.9
	Northern Shanxi	1	56/130	43.1	0/130	0.0	30/123	24.4	21/126	16.7
Total		10	122/396	30.8	1/411	0.2	151/396	38.1	98/392	25.0
Percent		15.2								
RPV	Central Shaanxi	3	0/32	0.0	20/31	64.5	0/32	0.0	0/31	0.0
Total		3								
Percent		4.5								
GPDAV	Central Shaanxi	2	17/32	53.1	9/41	22.0	21/30	70.0	19/21	90.5
Total		2								
Percent		3.0								
Healthy insects			0/236	0.0	0/228	0.0	0/230	0.0	0/233	0.0

[a]SG = *Schizaphis graminum*, RP = *Rhopalosiphum padi*, MA = *Macrosiphum avenae*, and AD = *Acyrthosiphon dirhodum*. A total of 656 healthy plants was used as uninoculated controls throughout this test period; none of the control plants developed BYDV symptoms.

apparently were acquired and inoculated by their respective vectors in as little as 1 min. Increase in duration of acquisition feeding period and inoculation feeding period did not appreciably increase the rate of transmission. Nymphs were as efficient vectors as adults in either species. There was a definite latent period of the virus in its vectors. The LP_{50} values in the vector species were 19.4 and 17.7 hr for nymphs and adults of *S. graminum* and 20.8 and 16.6 hr for nymphs and adults of *M. avenae* (Table 3). The virus could be retained until the death of the insect, with a mean of 20.1 and 13.9 days in *S. graminum* and *M. avenae*, respectively (Table 3).

Another series of experiments was carried out in greenhouses to study the virus-host plant relationships. Twenty-four cultivars of wheat were used for inoculation trials. Each test plant was inoculated by two or three aphids. The first 10 cultivars in Table 4 were commonly grown in northwestern China. The results of X^2 test showed that seven cultivars differed significantly in reaction to the main strains of BYDV (Table 4).

DISCUSSION

We have identified four strains of BYDV from infected wheat in northwestern China based on results of comparative transmission tests with four aphid species. Isolates similar to GPV were predominant in the major wheat-growing areas. *S. graminum* was the predominant vector species throughout this region. This insect was not only the most numerous in this vast plain but also was the most efficient vector (Table 3). Therefore, it apparently played a major role in severe outbreaks of barley yellow dwarf in 1966, 1970, 1973, and 1978 when the weather was favorable in the preceding year (6). A similar isolate (SGV) was reported in Canada (7) and New York (13). This isolate was very rare in Canada because of low vector transmission efficiency; only 13% of individual *S. graminum* and 2% of *R. padi* transmitted SGV (7). Although *R. padi* was not an efficient vector of GPV in China, the importance of *R. padi* in spread of BYDV cannot be underestimated because this insect was a predominant oversummer species, thus providing an adequate inoculum for subsequent crops.

The second important strain in China was DAV, but its distribution was limited to high elevations. *M. avenae*, the most efficient vector of DAV, was also most numerous in the mountain regions. Because of different ecological conditions at high elevations, the compositions of flora and insect fauna are more complex in this region. Therefore, such variables as fluctuating populations of different aphid species and interactions among viruses, aphids, and host plants contribute to the complex nature of the epidemiology of BYDV. One reason for the limited distribution of DAV could be simply the effect of temperature. The generally higher temperature at low elevations could affect the transmission efficiency of the aphid vector. Rochow (23) reported that temperature had a marked effect on transmission of the RMV isolate of BYDV. The answer to this question rests on future experimental proof.

The third and less common isolate,

Table 2. Comparative studies on the stability of two strains of barley yellow dwarf virus using different numbers of aphids allowed a 2-day acquisition access period

Strain	No. aphids per plant	No. test plants infected/no. plants infested by indicated aphid species[a]							
		SG	Percent	RP	Percent	MA	Percent	AD	Percent
GPV	2	14/22	63.6	1/22	4.5	0/9	0.0	0/17	0.0
	5	6/10	60.0	0/9	0.0	0/10	0.0	0/8	0.0
	10	20/30	66.7	7/30	23.3	1/28	3.6	0/28	0.0
Total		40/62	64.5	8/61	13.1	1/47	0.2	0/53	0.0
DAV	2	7/24	29.2	0/19	0.0	1/9	11.1	6/20	30.0
	5	11/15	73.3	0/11	0.0	3/11	27.3	2/11	18.2
	10	11/11	100.0	0/11	0.0	11/11	100.0	10/11	90.9
Total		29/50	58.0	0/41	0.0	15/31	48.4	18/42	42.9

[a]SG = *Schizaphis graminum*; RP = *Rhopalosiphum padi*; MA = *Macrosiphum avenae*; AD = *Acyrthosiphon dirhodum*.

Table 3. Transmission characteristics of the GPV and DAV strains of barley yellow dwarf virus by *Schizaphis graminum* (SG) and *Macrosiphum avenae* (MA)

Treatment Minutes	No. plants infected/no. plants tested							
	GPV transmitted by SG				DAV transmitted by MA			
	Second instar	Percent	Apterous adult	Percent	Second instar	Percent	Apterous adult	Percent
AFP[a]								
1	4/10	40	5/10	50	3/10	30	4/10	40
5	5/10	50	6/10	60	5/10	50	5/10	50
10	6/10	60	4/10	40	5/10	50	6/10	60
20	6/10	60	7/10	70	5/10	50	6/10	60
40	6/10	60	6/10	60	6/10	60	6/10	60
50	4/10	40	7/10	70	7/10	70	6/10	60
60	8/10	80	9/10	90	6/10	60	7/10	70
IFP[b]								
1	4/10	40	3/10	30	3/10	30	6/10	60
5	5/10	50	6/10	60	4/10	40	6/10	60
10	7/10	70	6/10	60	5/10	50	5/10	50
20	6/10	60	7/10	70	5/10	50	5/10	50
30	8/10	80	8/10	80	5/10	50	6/10	60
40	8/10	80	7/10	70	6/10	60	6/10	60
50	7/10	70	7/10	70	6/10	60	7/10	70
60	8/10	80	9/10	90	7/10	70	8/10	80
Min. LP	<14 hr		<14 hr		<14 hr		<14 hr	
LP_{50}	19.4 hr		17.7 hr		20.8 hr		16.6 hr	
Max. LP	20 hr		20 hr		24 hr		28 hr	
Min. retention	10 days				7 days			
Max. retention	31 days				19 days			
$\bar{x}$ retention	20.1 days				13.9 days			

[a]AFP = Acquisition feeding period.
[b]IFP = Inoculation feeding period (all test insects were given a 48-hr AFP).

similar to RPV, was transmitted specifically by *R. padi*. This isolate is related to the PAV-like isolate of BYDV in the United States by means of enzyme-linked immunosorbent assay. Again, this strain and its vector were mainly found at high elevations. The vector specificity of DAV seems to be more pronounced than the RPV isolate reported in the United States (22). The RPV isolate in the United States was also transmitted efficiently by *S. graminum*. It appears that different biotypes of aphids, especially *S. graminum*, show a great deal of variation in ability to transmit BYDV, ranging from inactive to active vectors of the virus (20,22). *S. graminum* transmits the same isolate as does *R. padi* in the United States (26).

Another less common and nonspecific strain was GPDAV, which was transmitted by all four aphid species. This nonspecific strain appeared distinctive and similar to the PAV isolate in the United States (3,23,29). Experiments are now in progress using purified virus of BYDV (J. H. Tsai et al, *unpublished*) to determine the distinctive nature and stability of different strains of BYDV in the PRC. Special emphasis will be placed on the study of GPV and DAV strains. These strains, using the enzyme-linked immunosorbent assay technique, appear related to MAV (W. F. Rochow, *personal communication*) but can only be distinguished on the basis of vector specificity and vector relationships (22). A possible explanation for relatedness of GPV and DAV to MAV could be that they share a common vector, *M. avenae*; therefore, they have some antigens in common with MAV. This phenomenon is not uncommon. Serological tests may indicate a similarity in viruses once thought to be unrelated. Rochow and Duffus (25) described this evolution of understanding in various isolates of BYDV in the United States when they showed that three isolates (RPV, PAV, and MAV) of BYDV are also serologically related to beet western yellows virus, which was once thought to be totally distinct and different. Ultimately, the serological relationships among the strains of BYDV as well as other luteoviruses will be studied. Until this can be done with the strains of BYDV in China, it is better to consider the strains as being distinct and to distinguish them on the basis of their vector specificity. Ideally, parallel vector transmission tests would be done to complement results from serological tests, and evidence from both sources should enable us to draw a conclusive determination on the relationships in this group.

Several workers have found *S. graminum* to be an efficient vector of BYDV, and others have found it erratic (22). Our results indicate that *S. graminum* apparently acquired and inoculated GPV in as little as 1 min, which is much shorter than the 1–5 days reported earlier (8,13). The reasons for such low acquisition and inoculation feeding period thresholds could be: 1) The test aphids had gone through many selection processes with only the most efficient transmitters kept in culture. 2) The distribution of BYDV in the infected plants may not be restricted to the phloem as has been suggested. It is possible that small numbers of virus particles may be scattered throughout the mesophyll cells and the aphid could acquire the virus from these cells as well. Future ultrastructural studies are needed to answer this question. 3) Possibly, a nonpersistent virus coexists with BYDV in the infected plants. To resolve this issue, all future test results will have to be verified by enzyme-linked inmunosorbent assay.

On the basis of vector specificity and vector-virus-host relationship, the BYDV strains in China are distinctively different from those reported in the United States (25). We did not detect any difference in transmission efficiency between nymphs and adults of *S. graminum* and *M. avenae* as reported in North America (30). Other workers, however, have reported that nymphs of *S. graminum* are better transmitters than adults (8,10).

We have demonstrated that *M. avenae* and *A. dirhodum* are efficient vectors of the DAV strain. *M. avenae* have also been reported to be relatively efficient vectors of a BYDV isolate in Canada (7). The LP_{50} of DAV in *M. avenae* (20.8 and 16.6 hr for nymphs and adults, respectively) is much shorter than the 65.5 and 44.5 hr reported by van der Broek and Gill (32). Rochow (21) reported that the latent period of BYDV in *M. avenae* and *R. padi* ranged from 1–5 days when the AAP was 12 hr or less.

Several wheat cultivars showed high levels of resistance or tolerance to GPV and DAV infections (Table 4). These are similar to the varietal reactions to BYDV infection in oats (2,5). This information is very important in breeding for resistance or tolerance and in understanding the host-virus interactions.

Table 4. Reactions of commonly grown wheat cultivars to the GPV and DAV strains of barley yellow dwarf virus inoculated by *Schizaphis graminum* and *Macrosiphum avenae*[a]

Variety	No. plants infected/no. plants inoculated				χ^2value[b]
	GPV	Percent	DAV	Percent	
Luochuan 70-1	15/85	17.7	3/93	3.2	8.29[c]
Luosun 701	13/58	22.4	3/60	5.0	5.82[d]
Sanjianmai	13/52	25.0	19/49	38.8	1.16
Juansun 6	25/62	40.3	25/62	40.3	0.0
Shijajuan Red	18/64	28.1	10/60	16.7	1.46
Luofulin 13	21/56	37.5	46/62	74.2	4.57[e]
Xiaoyin 5	15/63	23.8	3/60	5.0	6.54[d]
Xiyu 7	22/59	37.3	45/58	77.6	5.34[d]
6811(2)-16	16/43	37.2	12/49	24.5	0.93
Fensan 189	32/63	50.8	43/68	63.2	0.57
77L5/22-5	15/20	75.0	8/23	34.8	2.10
Zhenzhou 761	7/25	28.0	4/31	12.9	1.34
Fujuang Jinfei 30	24/29	82.8	9/28	32.1	4.12[e]
F49-70	7/17	41.2	2/21	9.5	3.18
Weimai 4	14/26	53.9	3/30	10.0	6.49[d]
Zhong 4	1/26	3.9	0/26	0.0	0.0
Jiantou	18/21	85.7	0/22	0.0	0.0
Luochuan 70-24	15/26	57.7	6/29	20.7	3.37
Dai 541	11/23	47.8	10/19	52.6	0.04
Nanketa	18/27	66.7	12/31	38.7	1.43
Yanan 11	20/26	76.9	12/25	48.0	1.05
Yanan 15	9/14	64.3	6/10	60.0	0.0
Yanan 17	17/29	58.6	9/31	29.0	2.12
Yanan 70-77	23/27	85.2	13/29	44.8	2.18

[a] Three to six replicates; a total of 110 plants from the first 10 varieties was inoculated by healthy insects as control but none of them developed BYDV symptoms.
[b] χ^2 Test performed with one degree of freedom.
[c] $\alpha < 0.01$.
[d] $\alpha < 0.025$.
[e] $\alpha < 0.05$.

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