Aphid Transmission of Barley Yellow Dwarf Virus: Inoculation Access Periods and Epidemiological Implications

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ABSTRACT

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In this study, we examined the efficiency of transmission of three isolates of barley yellow dwarf virus (BYDV) from New York by two aphid species for the purpose of assessing the relative importance of these species as vectors. The influence of the duration of the aphid inoculation access period (IAP) on transmission was investigated for RPV and PAV isolates of BYDV transmitted by *Rhopalosiphum padi* and for MAV and PAV isolates transmitted by *Sitobion avenae*. For each aphid–isolate combination, 15 IAPs, ranging from 30 min to 72 hr, were tested. *R. padi* was equally effective at transmitting the RPV and PAV isolates; 33.3 and 24.6% of individual aphids transmitted RPV and PAV, respectively, given a 30-min IAP. For both isolates, 50% transmission required an IAP of approximately 2 hr. In contrast, *S. avenae* was less efficient in transmitting PAV and MAV. Given a 30-min IAP, 1.8% of individual aphids of *S. avenae* transmitted PAV, while 10.0% transmitted MAV. Fifty percent transmission required an IAP of 4-6 hr for MAV and approximately 72 hr for PAV. After a 72-hr IAP, 86.7% of individual aphids of *R. padi* transmitted PAV, but only 53.3% of individual aphids of *S. avenae* had done so. These results suggest that *S. avenae* is likely to play a secondary role in the spread of BYDV when it co-occurs with *R. padi* and when PAV-like isolates predominate. Moreover, these data may help to explain the coincident increase of PAV and decline of MAV in upstate New York during the past several decades.

Additional keyword: persistent transmission.

The epidemiology of barley yellow dwarf virus (BYDV) in small grains in the area of Ithaca, NY, depends on transmission in a persistent, nonpropagative fashion by two predominant aphid vectors: the English grain aphid, *Sitobion avenae* F. (formerly *Macrosiphum avenae*); and the oat-bird cherry aphid, *Rhopalosiphum padi* L. Rochow (13) documented a gradual shift in the prevalence of three common New York isolates of BYDV between 1957 and 1976. He found that the incidence of the MAV isolate, transmitted by *S. avenae*, decreased from 90 to 0% of the BYDV samples; while PAV, transmitted by both *S. avenae* and *R. padi*, increased from 3 to 98%. The RPV isolate, transmitted by *R. padi*, remained consistently at low incidence (0–28%) during this period. Virus samples from oats and wheat show that PAV continues to predominate in this area (A. G. Power, *unpublished data*; 7).

This shift in the prevalence of particular BYDV isolates does not appear to have resulted from any changes in the relative abundance of *S. avenae* and *R. padi* (13), but may have been influenced by more subtle aspects of vector transmission behavior. The spread of persistently transmitted plant viruses like BYDV is largely determined by vector propensity (sensu Irwin and Ruesink [6]), or the probability that a vector will successfully inoculate a plant with a virus. Vector propensity thus includes vector acquisition efficiency, vector activity, and vector inoculation efficiency. Measurements of vector activity estimate the combined effect of vector abundance and the movement of those vectors (6).

It is well documented that species of aphid vectors differ in their ability to transmit various isolates of BYDV (14), but little is known about the temporal aspects of these differences. If aphids are moving rapidly from plant to plant, then differences among BYDV isolates in the feeding periods needed to acquire virus from infected plants or transmit it to healthy plants could lead to the dominance of those isolates that are transmitted more rapidly. Similarly, if aphid species differ in the feeding periods required for transmission of BYDV, then vectors requiring shorter feeding periods are likely to be more efficient vectors.

From previous studies, we have information on the activity of aphid vectors of BYDV (5,10) and on the vector acquisition efficiency for different isolates of BYDV (4). Additional data on the plant access periods required for inoculation of plants with different BYDV isolates are vital for understanding BYDV epidemiology. To evaluate whether differences among aphid species and BYDV isolates in inoculation feeding periods could play a role in the change in isolate prevalence in upstate New York, we compared the inoculation access period (IAP) required to transmit the PAV, MAV, and RPV isolates of BYDV to oats by *S. avenae* and *R. padi*.

MATERIALS AND METHODS

Virus isolates and aphid species. The New York isolates of PAV, MAV, and RPV, previously characterized by Rochow (12),

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were used in this set of assays. All isolates were maintained in Coast Black oats (*Avena byzantina* K. Koch) as described by Rochow (12). MAV is transmitted specifically by *S. avenae*; RPV is transmitted specifically by *R. padi*; and PAV is transmitted by both aphids. The aphids used in these experiments were taken from the clones used by Rochow (12), and the rearing conditions were identical.

Transmission assays. Transmission assays were done for each of four aphid–isolate combinations: *R. padi* transmitting RPV; *R. padi* transmitting PAV; *S. avenae* transmitting PAV; and *S. avenae* transmitting MAV. For each experiment, aphids were allowed a 72-hr acquisition access period on excised leaves (11) from Coast Black oats infected with the appropriate isolate. Aphids were then caged individually on 6-day-old oat seedlings and allowed access for periods of 0.5, 1, 1.5, 2, 4, 6, 8, 10, 12, 16, 20, 24, 36, 48, or 72 hr. In addition, an IAP of approximately 6 days (144 hr) was used as a control to determine maximum transmission rates with ample time for inoculation. Twenty test plants with a single aphid per plant were used for each IAP, and the entire experiment was repeated three times, for a total of 60 test plants per IAP for each aphid–isolate combination.

At the end of the IAP, aphids were removed from the test plants and all plants were fumigated with DDVP (O,O-dimethyl O-[2,2 dichlorovinyl] phosphate) in a closed chamber. Test plants were placed in a greenhouse and disease symptoms were evaluated weekly for 3 wk after the initial onset of symptoms. Plants with questionable symptoms were tested for virus with the enzyme-linked immunosorbent assay (ELISA) procedures described by Rochow (15).

Data analysis. The percentage of aphids transmitting, based on 20 aphids for each IAP, was used as the transmission value, which was then transformed by using the arcsine transformation for proportional data. For each aphid–isolate combination, the three experiments were treated as replicates. A two-level nested ANOVA was used to compare the transmission patterns of: (1) RPV and PAV transmitted by *R. padi* (Table 1); (2) MAV and PAV transmitted by *S. avenae* (Table 2); and (3) PAV transmitted by *R. padi* and *S. avenae* (Table 3). For comparisons 1 and 2, replicate experiments were nested under isolate, and the effect of isolate was tested with the variance between replicate experiments as the error term. The effect of IAP and the interaction between IAP and isolate were tested with the residual error. For comparison 3, replicate experiments were nested under aphid species, and the effect of aphid species was tested by using the variance between replicate experiments as the error term. The effect of IAP and the interaction between IAP and aphid species were tested with the residual error.

TABLE 1. Analysis of variance for the transmission of the NY-RPV and NY-PAV isolates of barley yellow dwarf virus by *Rhopalosiphum padi*

Source of variation	df	MS	*F*	*P*
Isolate	1	0.126	0.50	0.519
error 1[a]	4	0.253	...	...
IAP[b]	14	0.256	10.74	0.000
Isolate*IAP	14	0.017	0.69	0.771
residual error[c]	56	0.024	...	...

[a] Error 1 is the variance between replicates nested within isolate. Degrees of freedom include those for replicate (df = 2) and those for isolate* replicate (df = 2).
[b] Inoculation access period.
[c] Residual error includes variance attributable to IAP*replicate (df = 28) and isolate*IAP*replicate (df = 28).

TABLE 2. Analysis of variance for the transmission of the NY-MAV and NY-PAV isolates of barley yellow dwarf virus by *Sitobion avenae*

Source of variation	df	MS	*F*	*P*
Isolate	1	2.124	7.08	0.056
error 1[a]	4	0.300	...	...
IAP[b]	14	0.298	16.61	0.000
Isolate*IAP	14	0.037	2.08	0.028
residual error[c]	56	0.018	...	...

[a] Error 1 is the variance between replicates nested within isolate. Degrees of freedom include those for replicate (df = 2) and those for isolate* replicate (df = 2).
[b] Inoculation access period.
[c] Residual error includes variance attributable to IAP*replicate (df = 28) and isolate*IAP*replicate (df = 28).

RESULTS

R. padi was equally effective in transmitting the PAV and RPV isolates, and the effect of increasing IAP was similar for the two isolates (Fig. 1). An IAP of 30 min resulted in a fairly high frequency of transmission for both isolates (24.6 and 33.3% for PAV and RPV, respectively). After a 2-hr IAP, approximately 50% of the aphids had successfully transmitted virus (47.1 and 58.6% for PAV and RPV, respectively). Given a 6-day IAP, 93.0% of *R. padi* transmitted RPV, while 87.0% transmitted PAV. The length of the IAP significantly affected the proportion of aphids transmitting both isolates ($P < 0.001$; Table 1). There were no significant differences ($P = 0.519$; Table 1) between the two isolates in overall transmission or in the length of the IAP required for transmission (i.e., the shape of the curves in Fig. 1) as indicated by the nonsignificance of the interaction term, isolate*IAP ($P = 0.771$; Table 1).

S. avenae was a more effective vector of MAV than of PAV (Fig. 2). After an IAP of 30 min, the percentage of aphids that transmitted PAV was only 1.8%; whereas, 10.0% transmitted MAV. Fifty percent of the aphids transmitted MAV given a 4- to 6-hr IAP, but this rate of transmission required an IAP of 72 hr for PAV. After a 6-day IAP, 90.4% of the aphids transmitted MAV, but only 71.0% transmitted PAV. The difference between

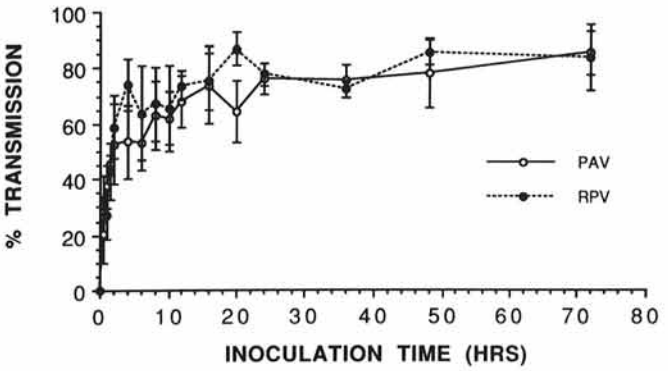

Fig. 1. The percentage of transmission of the NY isolates RPV (dashed line) and PAV (solid line) of barley yellow dwarf virus (BYDV) by *Rhopalosiphum padi* as a function of the inoculation access period. Each data point represents the percentage of 60 test plants that became infected with BYDV after inoculation by a single aphid. Error bars represent standard errors.

TABLE 3. Analysis of variance for the transmission of the NY-PAV isolate of barley yellow dwarf virus by *Rhopalosiphum padi* and *Sitobion avenae*

Source of variation	df	MS	*F*	*P*
Aphid species	1	2.487	12.29	0.025
error 1[a]	4	0.202	...	...
IAP[b]	14	0.206	13.59	0.000
Aphid*IAP	14	0.016	1.07	0.406
residual error[c]	56	0.015	...	...

[a] Error 1 is the variance between replicates nested within aphid. Degrees of freedom include those for replicate (df = 2) and those for aphid* replicate (df = 2).
[b] Inoculation access period.
[c] Residual error includes variance attributable to IAP*replicate (df = 28) and aphid*IAP*replicate (df = 28).

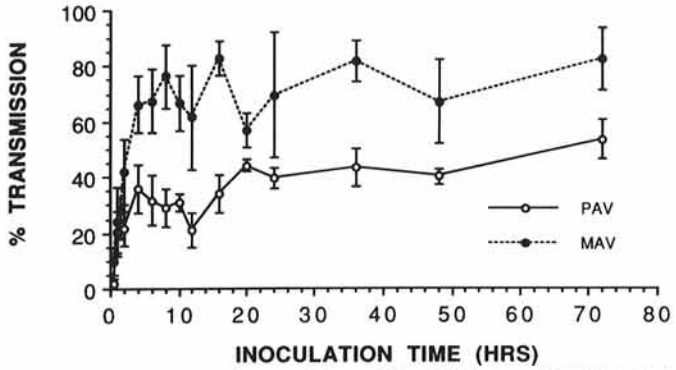

Fig. 2. The percentage of transmission of the NY isolates MAV (dashed line) and PAV (solid line) of barley yellow dwarf virus (BYDV) by *Sitobion avenae* as a function of the inoculation access period. Each data point represents the percentage of 60 test plants that became infected with BYDV after inoculation by a single aphid. Error bars represent standard errors.

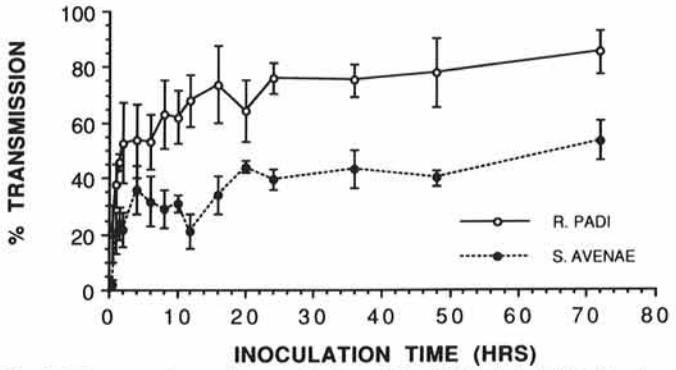

Fig. 3. The percentage of transmission of the NY isolate PAV of barley yellow dwarf virus (BYDV) by *Rhopalosiphum padi* (solid line) and *Sitobion avenae* (dashed line) as a function of the inoculation access period. Each data point represents the percentage of 60 test plants that became infected with BYDV after inoculation by a single aphid. Error bars represent standard errors.

isolates in the proportion of aphids transmitting, independent of IAP, was weakly significant ($P = 0.058$; Table 2). The significant IAP by isolate interaction ($P = 0.033$; Table 2) indicated that there was a difference in the length of the IAP necessary for transmission of the two isolates. That is, the shape of the transmission curves in Figure 2 differed significantly.

R. padi was a more effective vector of PAV than was *S. avenae* (Fig. 3). While the shape of the transmission curve was similar for the two aphids and the IAP by aphid species interaction was not significant ($P = 0.404$; Table 3), the proportion of aphids transmitting PAV was higher for *R. padi* than for *S. avenae* ($P = 0.026$; Table 3).

DISCUSSION

Our results demonstrate subtle and significant differences in the IAP required for successful transmission of the three NY isolates of BYDV by different aphid vectors. Overall, *R. padi* was clearly a more effective vector than *S. avenae*, transmitting both RPV and PAV after relatively short IAPs. A previous study, comparing feeding behavior of *R. padi* and *S. avenae* on oats by using electronic monitoring, showed that *S. avenae* spent twice as long in salivation and sheath formation and half as long in contact with the phloem (19). A comparison of *R. padi* and *Schizaphis graminum* (Rondani) indicated that *R. padi* penetrated the phloem and established committed phloem ingestion more rapidly than *S. graminum* (8). This rapid phloem contact allows *R. padi* to effectively transmit virus during relatively short IAPs. For *R. padi*, there was only a slight, nonsignificant tendency for the specific RPV isolate to be transmitted more rapidly than the nonspecific PAV isolate.

In comparison with *R. padi*, *S. avenae* requires a much longer IAP to transmit either MAV or PAV, and it is a much more efficient vector of MAV than PAV. In a previous investigation based on electronic monitoring of 17 aphids, Scheller and Shukle (17) reported no difference in virus transmission of PAV and MAV by *S. avenae*. In contrast, our findings, based on 1,560 single aphids transmitting each isolate, indicate significant differences in the transmission of these two isolates. Scheller and Shukle (17) also estimated that an absolute minimum IAP of 17 min would be required for *S. avenae* to transmit MAV to oats. That estimate is consistent with our data, which showed that 10% of aphids transmitted MAV after an IAP of 30 min. The data presented here indicate that an IAP between 6 and 8 hr would be required for 50% transmission of MAV; whereas, the previous study estimated an IAP of 83 min for 50% transmission (17). Furthermore, we found that 50% transmission of PAV would require 2–3 days. It is possible that the differences between these two sets of experiments were due to the different aphid clones used. However, Rochow and Eastop (16) found little difference between clones of *R. padi* or between clones of *S. avenae* in the transmission of major BYDV isolates.

A separate investigation has demonstrated that *S. avenae* is less efficient than *R. padi* in acquiring BYDV from plants, especially when virus titer is low (4). The relatively long IAP required by *S. avenae* appears to interact with inefficient acquisition and high aphid movement rates (10) in the field to produce a rather ineffective vector. Studies of the local movement of *S. avenae* in grain fields show that individual aphids, including nonwinged forms, move relatively often between plants (5,10). Although vector activity is usually assumed to result in increased virus spread, this is only true if vectors remain on plants long enough to transmit the virus (9). Mark-recapture studies with *S. avenae* indicate that individuals are likely to encounter between 2 and 6 tillers per day under normal field conditions (10). At this movement rate, many aphids would not stay on plants long enough to transmit either MAV or PAV. Thus, to estimate vector propensity of grain aphids, it is essential to examine the plant-access periods required for virus transmission in the context of aphid movement rates in the field.

The requirement of long feeding periods for virus transmission combined with high movement rates reduce the probability of significant virus spread by *S. avenae* in oats, despite the fact that it is an abundant vector species. Data presented here suggest that this inefficient transmission may be one factor that contributes to the decline in MAV incidence. Although transmission of PAV by *S. avenae* is even less efficient than that of MAV, spread of PAV is enhanced by extremely efficient transmission by *R. padi*. Because these data were based on transmission to oats, it is not clear whether *S. avenae* is an equally ineffective vector in wheat.

Data presented here on relative inoculation efficiency, in combination with the data on acquisition efficiency (4), suggest that *S. avenae* is likely to play a secondary role in the spread of PAV in oats wherever this aphid co-occurs with *R. padi*. *S. avenae* will be a particularly ineffective vector of BYDV in regions where PAV-like isolates predominate, as they currently do in California (3), Indiana (1), New York (13), Pennsylvania (2), and Washington (18).

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