Rice Root Aphid, Rhopalosiphum rufiabdominalis, a Vector of Barley Yellow Dwarf Virus in Illinois, and the Disease Complex

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ABSTRACT

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The rice root aphid, Rhopalosiphum rufiabdominalis, overwintered as viviparae on underground parts of Vermillion wheat (Triticum aestivum) and Hudson barley (Hordeum vulgare) at Urbana, IL, under relatively stable temperatures and transmitted the barley yellow dwarf virus. Hudson barley, Michigan Amber wheat, and Dubois oats (Avena sativa) were good virus sources and indicator test plants. In parallel tests, R. rufiabdominalis and R. padi were equally able to transmit two vector nonspecific isolates. Both aphids, however, failed to transmit the Macrosiphum avenae specific virus isolate. Like the other two isolates, this one was readily transmissible by Sitobion avenae. This brings the total number of aphid species known to be vectors of barley yellow dwarf virus to 18.

Additional key words: epidemiology, winter barley

Barley yellow dwarf (BYD), one of the most serious viral diseases of small grains and grasses, is caused by a luteovirus (37,42) that has been the subject of many studies (3,8,35,42,45). It is transmitted exclusively by aphids. Much attention has been focused on the relationship between virus and vector and the role of aphids in the epidemiology of the disease (38). From four to more than 20 aphid species have been reported to transmit barley yellow dwarf virus (BYDV) (3,12,15,19,35,37,45,56). The number of reports may be explained in part by conflicting taxonomy, independent discoveries of the species, and the data of the various reports (6,7,9,33,44,45,47,49).

This paper reports on winter survival of the rice root aphid, Rhopalosiphum rufiabdominalis (Sasaki), and its role as a vector of BYDV in Illinois. Its efficiency in transmitting three isolates of BYDV is compared with that of Rhopalosiphum padi L. and Sitobion avenae Fab. (syn. Macrosiphum avenae Fab.). I also present the current status of the known

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aphid vectors of BYDV, using the binomials of the classification system of Eastop and Hille Ris Lambers (9). A preliminary account of this study was reported previously (16).

MATERIALS AND METHODS

In March 1961, 12 samples each of winter barley (Hordeum vulgare L. 'Hudson') and winter wheat (Triticum aestivum L. 'Vermillion') were removed from the field at Urbana, IL, before any cereal aphid activity was noticed. They were transplanted into pasteurized, screened soil in 15-cm clay pots and covered immediately with cylindric, plastic cages. The caged plants were incubated in the insectary section of the greenhouse.

Within 2½ wk, colonies of the rice root aphid developed on lower stems and leaves of one of the barley plants and two of the wheat plants. Symptoms typical of BYD developed on the barley plants and on one set of the wheat plants. The aphids were then used in a transmission test.

Newborn nymphs from detached, healthy wheat leaves of the Michigan Amber cultivar were used to establish nonviruliferous cultures of the rice root aphid on leaves of the same cultivar. The cultures were placed on moist filter paper in closed paper cups and incubated in the dark at 25 C. Leaves were changed every 12 hr, and nymphs were transferred to healthy plants. These aphids served as healthy stock cultures. Clones of virusfree R. padi and S. avenae were maintained on Hudson barley as described previously (17,18). Aphids from stock cultures free of BYDV were included as controls in all transmission experiments to monitor for viral contamination.

Detached leaves of Hudson barley, Michigan Amber wheat, or Dubois oats (Avena sativa L.) were used as sources of inoculum. In a preliminary experiment, viruliferous R. rufiabdominalis aphids were taken from transplanted Hudson barley and Vermillion wheat that had symptoms of BYD. In all other experiments, predominantly apterous aphids were allowed to acquire the virus for 2 days at 20 C from comparable portions of leaves in closed paper cups in the dark. Ten aphids were transferred to each indicator test plant in an early oneleaf stage, and each plant was caged immediately after the transfer.

After an inoculation feeding of 4 days at 25 C during the day and 21 C at night, the cages were removed and the plants fumigated in a closed chamber with nicotine (14% nicotine, expressed alkaloid) or lindane, or they were sprayed with a 0.1% aqueous solution of malathion or nicotine sulfate. They were then moved to an air-conditioned enclosure in the greenhouse. Supplemental fluorescent and incandescent lights simulated 16 hr of daylight. Uninfected plants were observed for at least 30 days.

In addition to the isolates from Hudson barley and Vermillion wheat, three other strains of BYDV described elsewhere were used in the study (17,18). Champaign-6 and Southern Illinois-1, which are not specific to a vector and resemble R. padi nonspecific virus isolate (PAV) (18), have different levels and spectra of virulence. The third strain, Macrosiphum avenae specific virus isolate (MAV), is vector specific. It was previously obtained from Rochow (18).

Unless otherwise stated, Dubois oats were used as indicator plants. They were grown in pasteurized, composted soil supplemented with 10-10-10 (N-P-K) fertilizer in 10-cm pots. Four seeds per pot were planted 5 cm apart in a square pattern. When the plants reached an early one-leaf stage, they were selected for uniformity and used in transmission experiments.

RESULTS

The rice root aphid survived the winter of 1960–1961 as viviparae on underground parts of Hudson barley and Vermillion wheat at Urbana. No aphids resembling this species were observed on the plants in the fall. Conditions were very favorable for overwintering during that season. Soil

temperatures at 10 and 20 cm were quite stable, dropping 1 C below the freezing point for only a few days despite much higher fluctuations of air temperature (from 28 to -24 C). In general, winter temperatures were above and precipitation below normal for Illinois (data from the Illinois State Water Survey). The only other report I know of concerning possible overwintering of this species at similar latitudes is that by Palmer (30) from Colorado. Negative observations were made by Kieckhefer (20) in South Dakota.

Of the 12 samples each of barley and wheat removed from the field on 15 March 1961, 1 of barley and 2 of wheat yielded colonies of *R. rufiabdominalis*. The apterae appeared first on lower parts of the stems and then moved progressively up the plants. A few alates developed later at the top of the cages. The apterae appeared darker in color and multiplied at a much lower rate than *R. padi*. These forms can easily be differentiated by long hairs on the antennae and the whole body (7,33).

Typical BYD developed on all eight plants each of Hudson barley, Michigan Amber, and Dubois oats exposed to aphids collected from the Hudson barley and Vermillion wheat plants that showed symptoms of the disease. None of the corresponding uninoculated plants became infected. These infected plants served as a source of inoculum in the next tests with nonviruliferous rice root aphids. In four tests, the rice root aphid readily acquired BYDV and transmitted it to all plants tested (Table 1). Hudson barley, Michigan Amber wheat, and Dubois oats served as satisfactory

sources of inoculum and as indicator test plants. The mean transmissibility rate of 97% indicated that the rice root aphid was an efficient vector.

R. rufiabdominalis transmitted strains Champaign-6 and Southern Illinois-1, which are not vector specific, to Dubois oats at about the same frequency as did R. padi. However, it did not transmit strain MAV, which is specific to the vector S. avenae (Table 2).

None of the 72 control plants exposed to inoculation feeding by nonviruliferous *R. rufiabdominalis* and *R. padi* became infected. At the same time, *S. avenae* readily transmitted the MAV isolate.

DISCUSSION

This report brings the total number of aphid species known to transmit BYDV to 18. A compilation of the reported vectors of BYDV, equated in the standard classification system of Eastop and Hille Ris Lambers (9), is given in Table 3.

The rice root aphid, R. rufiabdominalis. has been reported from different parts of the world (6,7,9,11,21,30,33,47,51,52). It was originally described by Sasaki in 1899 as a pest of rice in Japan (47). The taxonomy of this aphid species has been confusing (6,11,21,30,51,52), and its proper status has not been defined until recently (7.9.33.47). An excellent historical review with synonymy, plant hosts, and world distribution was given by Doncaster (7). As early as 1915, the aphid was reported to be destructive on wheat and rice in Egypt (51). Consequently, the recent discoveries of BYDV in the Mediterranean area on rice (2) and grasses (10) are of special interest.

Table 1. Transmission of a field isolate of barley yellow dwarf virus by *Rhopalosiphum rufiabdominalis* (Sasaki)

Virus source	No. of plants infected/no. inoculated (% infected) ^a			
	Hudson barley	Michigan Amber wheat	Dubois oats	
Hudson barley	31/32 (97)	30/32 (94)	26/32 (81)	
Michigan Amber wheat	31/32 (97)	32/32 (100)	31/32 (97)	
Dubois oats	25/32 (78)	28/32 (88)	28/32 (88)	
Aphid controls	0/32	0/32	0/32	
Plant controls	0/32	0/32	0/32	

^aTotals from four experiments. Each test plant was infested with 10 apterous aphids for 4 days after acquisition feeding on detached leaves with well-expressed symptoms for 2 days at 20 C.

Table 2. Comparison of transmissibility of three barley yellow dwarf virus strains by *Rhopalosiphum rufiabdominalis* (RR), *R. padi* (RP), and *Sitobion avenae* (SA)

Virus strain	No. of plants infected/no. infested with aphid shown (% infected) ^a			
	RR	RP	SA	
BYDV Champaign-6	35/36 (97)	36/36 (100)	33/36 (92)	
BYDV Southern Illinois-1	35/36 (97)	36/36 (100)	32/36 (89)	
MAV	0/36 (0)	0/36 (0)	34/36 (94)	
Aphid control	0/36	0/36	0/36	

^aTotals from three experiments. Each of the indicator test plants was infested with 10 predominantly apterous aphids for 4 days after acquisition feeding on detached leaves of Hudson barley or Dubois oats with well-expressed symptoms for 2 days at 20 C.

Old records in the United States indicate that the aphid was found on various hosts in California (11), Florida (52), South Carolina (21), and Colorado, Kansas, and Nebraska (30). In a more recent list, Smith and Parron (47) extended the number of states to 26.

Although species of *Prunus* are reported as primary overwintering hosts (7) of the rice root aphid, all known observations in this country have been of viviparae on secondary hosts. A remarkable characteristic of this aphid vector, from the standpoint of the etiology of plant luteo viruses, is a very wide host range that includes members of the Compositae, Cyperaceae, Gramineae, Iridaceae, Leguminosae, Malvaceae, Onagraceae, Orobanchaceae, Papaveraceae, Plytrichaceae (Bryophyta), Rosaceae, Solanaceae, and Umbelliferae.

Survival of the rice root aphid during the winter in Illinois and subsequent recovery of BYDV (Table 1) could be attributed to relatively stable temperatures below the soil. The transmissibility of the three virus isolates to winter Dubois oats (Table 2) is comparable to that of R. padi. The failure of R. rufiabdominalis to transmit MAV, which is specifically vectored by S. avenae, makes this relationship comparable to the vector specific one described by Rochow (38). It also lends support to the conclusion of Doncaster (7) that R. padi, R. insertum (Walker), and the rice root aphid are closely related. Further, Paliwal (29) recently reported that R. rufiabdominalis transmits BYDV isolates regularly transmitted by Rhopalosiphum species but does not transmit those regularly transmitted by Sitobion and Schizaphis species. This finding is of special interest in terms of the virus-vector relationship of the two distinct virus groups.

Most studies on aphid dynamics have considered the problem of BYDV from the standpoint of aerial aphid biology. Aphid species vary in their ability to transmit BYDV (4,14,24,25,38,53). Within species, different forms (25,34,38), stages, and clones (38) vary in their ability to transmit the virus. Closely associated with aphid variability is that of vector specificity, which is linked to both the virus (39) and the vector (13,36,41).

The underground biology and dynamics of R. rufiabdominalis, R. insertum, and Rhopalomyzus poae (Gill.) as they relate to the transmission of BYDV have been neglected. Common associations of different species in a complex as viviparae below the soil level may be unnoticed (7,20,30,44,49). The soil may favor survival when aerial conditions are extreme, as when temperatures stay above or below certain threshold levels for long periods in summer or winter. These associations may be of special interest to the epidemiology of BYDV. They may explain some severe outbreaks of the disease without the conspicuous presence of vectors in the field. Fall mass migrations of *R. rufiabdominalis* viviparae from voluntary wheat to the new wheat planted in the fall (30) may explain the appearance of the disease in circular patches of varying size with practically all plants being infected or in dense infections confined to the borders (5,39,43). The ability of the aphid to survive as subterranean alienicolae late into winter in the northern areas of the United States (20) and to overwinter as far north as Colorado (30) and Illinois on

secondary hosts may provide a link in BYDV epidemiology from summer to winter crops. Furthermore, the wide host range of *R. rufiabdominalis* (7,9,47) and its possible association in complexes (8) may account for acquisition and spread of mixtures of strains. The *R. padi* specific virus isolate (RPV), which is related to such complexes (8), was shown by Terry (50) to be readily acquired and transmitted via tops and roots. Other luteo viruses (8,40) could be favored in their dissemination by dependent

transmissions (42).

Orlob (24) regarded root aphids as having a minimal role in the spread of BYDV in nature; however, he did not consider all the species involved and the possibilities of viral phenotypic mixing or dependent transmission. For example, Terry (50) demonstrated that under controlled conditions R. rufiabdominalis acquires and transmits BYDV via roots, but the virus is confined to the roots and requires special dark treatments to spread systemically. Similar treatments

Table 3. Aphids reported as vectors of barley yellow dwarf virus

Aphid speciesa	Name reported	Reference
1. Anoecia corni (Fabricius)	Anoecia corni (Fab.)	A'Brook and Dewar (1)
2. Aulacorthum circumflexum (Buckton)	Amphorophora circumflexa (Buct.)	Heinze (15)
2. Automium circumytexum (Dueston)	Macrosiphum circumflexa (Buct.)	Heinze (15)
	Muzus circumflexus (Buct.)	Watson and Mulligan (54)
	Neomyzus circumflexus (Buct.)	Watson and Mulligan (55)
	Siphonophora circumflexa (Buct.)	Heinze (15)
3. Ceruraphis eriophori (Walker)	Ceruraphis eriophori (W.)	Kennedy et al (19)
4. Metopolophium albidum (Hille Ris Lambers)	Metopolophium albidum (H.R.L.)	A'Brook and Dewar (1)
5. Metopolophium dirhodum (Walker)	Acyrthosiphon (M.) dirhodum (Walker)	Kennedy et al (19)
	Macrosiphum dirhodum (Walker)	Oswald and Houston (26,28)
	Metopolophium dirhodum (Walker)	Watson and Mulligan (54,55)
6. Metopolophium festucae (Theobald)	Metopolophium festucae (Theobald)	Plum (31)
7. Metopolophium frisicum (Hille Ris Lambers)	Metopolophium frisicum (H.R.L.)	A'Brook and Dewar (1)
8. Myzus persicae (Sulzer)	Myzus persicae (Sulz.)	Smith (48)
9. Rhopalomyzus poae (Gillette)	Rhopalosiphum poae (Gill.)	Orlob (23)
10. Rhopalosiphum insertum (Walker)	Rhopalosiphon annuae (Östl.)	Heinze (15)
(Rhopalosiphum fitchii (Sand.)	Bruehl and Toko (4)
		Orlob and Arny (25)
		Bruehl (3)
		Smith and Richards (49)
11. Rhopalosiphum maidis (Fitch)	Aphis maydis (Fitch)	Heinze (15)
	Rhopalosiphum (Aphis) maidis (Fitch)	Oswald and Houston (26,28)
12. Rhopalosiphum padi (Linnaeus)	Anuraphis padi (L.)	Heinze (15)
	Rhopalosiphon padi (L.)	Rademacher and Schwarz (32
	Rhopalosiphum padi (L.)	Watson and Mulligan (54)
	Rhopalosiphum prunifoliae	Moore (22)
•	Rhopalosiphum prunifoliae (Fitch)	Oswald and Houston (26,28)
13. Rhopalosiphum rufiabdominalis (Sasaki)	Rhopalosiphum rufiabdominalis (Sasaki)	Jedlinski (16)
14. Schizaphis graminum (Rondani)	Schizaphis graminum (Rond.)	Gill (14)
	Toxoptera graminum (Rond.)	Oswald and Houston (27)
	Toxoptera graminum (Rond.) =	
	Schizaphis graminum (Rond.)	Rochow (34)
15. Sipha elegans (del Guercio)	Sipha agropyrella (H.R.L.)	Smith (48)
16. Sitobion avenae (Fabricius)	Macrosiphum avenae (Fab.)	Slykhuis et al (46)
	Macrosiphum granarium (Kby.)	Oswald and Houston (26,28)
	Sitobium avenae (Fab.)	Watson and Mulligan (55)
	Sitobium avenae (F.)	Heinze (15)
17. Sitobion fragariae (Walker)	Macrosiphum fragariae (Walk.)	Fritzsche et al (12)
	Sitobium fragariae (Walker)	Watson and Mulligan (54)
	Sitobion fragariae (Walker)	Watson and Mulligan (55)
18. Sitobion miscanthi (Takahashi)	Sitobium avenae s-sp. miscanthi	
	(Takahashi)	Butler et al (5)
	Macrosiphum (S.) avenae miscanthi	Kennedy et al (19)

^a According to the classification of Eastop and Hille Ris Lambers (9).

are required with soilborne mosaic virus transmitted via roots by *Polymyxa graminis* (Led.). Fall infections, however, readily become systemic in the spring after growth resumes.

Rochow (38) reviewed six possible interactions among vectors, plants, and viruses and emphasized that all individual variations should be studied to understand the epidemiology of BYDV. These variations should include the biology and dynamics of any aphid vector associations below the soil, which become especially important when considering effective BYD control measures based on integrated pest management.

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