

Transmission of barley yellow dwarf virus by field collected aphids (Homoptera: Aphididae) and their relative importance in barley yellow dwarf epidemiology in southwestern Idaho

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Summary

Populations of cereal aphids were sampled from 1985–1988 and assayed for transmission of barley yellow dwarf virus (BYDV). *Rhopalosiphum padi*, *Rhopalosiphum maidis*, *Sitobion avenae*, *Metopolophium dirhodum*, *Schizaphis graminum* and *Macrosiphum euphorbiae* collected from host plants transmitted BYDV in bioassays. Of the 1028 *Diuraphis noxia* collected from plants, one may have transmitted BYDV. The isolate involved resembled SGV in serological and biological characteristics, but since it was not recoverable by any of more than 800 *D. noxia* subsequently tested, we suspect it may have been a contaminant.

Among those aphids collected during the autumn from a suction trap adapted for live collection, *R. padi* transmitted BYDV most frequently. Other trapped species which transmitted BYDV included: *R. maidis*, *Rhopalosiphum insertum*, *Macrosiphum euphorbiae*, *Metopolophium dirhodum* and *Ceruraphis eriophori*. An adapted Infectivity Index indicated that *R. padi* is by far the most important vector of BYDV during the autumn sowing season in southwestern Idaho. Male *R. padi* consistently transmitted BYDV more frequently than did females collected during the same period.

Key words: BYDV, barley yellow dwarf, Aphididae, cereals, epidemiology

Introduction

Barley yellow dwarf virus (BYDV) was first characterised by Oswald & Houston (1951) and first confirmed in irrigated winter wheat crops in Idaho in 1978 (Forster *et al.*, 1983). Previous occurrences had no doubt been undetected or undocumented, since the disease has been commonly observed in subsequent years in southern Idaho, and symptomology can be confusing. BYD is also an increasing problem in autumn-sown cereals in Washington (Brown, Wyatt & Hazelwood, 1984). BYDV is actually a complex of viruses which differ in several respects including aphid transmission specificity (Lister, Clement, Skaria & Foster, 1984). The probability of an epidemic developing depends upon many factors, especially aphid transmission characteristics of the isolates present, the intensity of vector flight and the proportion of viruliferous individuals.

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Several species of aphids regularly colonise cereal crops in southwestern Idaho, including *Rhopalosiphum padi* (L.), *Schizaphis graminum* (Rondani), *Rhopalosiphum maidis* (Fitch), *Metopolophium dirhodum* (Walker), *Sitobion avenae* (Fabricius), *Sipha elegans* del Guercio and *Diuraphis* (*Holcaphis*) *frequens* (Walker). *Diuraphis* (*Diuraphis*) *noxia* (Kurdjumov) became established in the area in 1987 (Halbert, Johnston & Stoltz, 1988). Root infesting species including *Forda marginata* Koch, *Geoica* spp. and *Anoecia setariae* Gillette & Palmer are occasionally found on wheat and barley. In addition, other species which normally infest Juncaceae, Cyperaceae or other Gramineae may occasionally feed on wheat or barley. Many of these species have been reported as vectors of BYDV (Jedlinski, 1981).

Diuraphis noxia has been reported to be a vector of BYDV in South Africa (von Wechmar, 1984) but in recent experiments in North America it failed to transmit the standard New York BYDV isolates (Damsteegt, Gildow, Carroll & Hewings, 1988) and several naturally occurring Mexican isolates (Burnett, Mezzalama & Gilchrist, 1988; Gilchrist, Montessoro & Burnett, 1986).

The purpose of this study was to determine what percentage of aphids from natural populations in southwestern Idaho were infective and to compare *D. noxia* with other species as a potential vector. The results are discussed in relation to BYD epidemiology in southwestern Idaho.

Materials and Methods

Collections from host plants

Aphids were collected directly from plants in Canyon county, Idaho in each of four years, 1985–1988. Each year we selected several commercial wheat, barley and maize fields and several stands of volunteer cereals from which a mixture of species was sampled. The species composition varied from year to year. Several stands of *Echinochloa crusgalli* (L.) Beauv. from which *Rhopalosiphum maidis* was collected also were selected. In 1985, collections of *Sitobion avenae* and *Metopolophium dirhodum* were made from *Setaria lutescens* (Weigel) Hubb. and *Phalaris arundinacea* L., respectively. In each case, only one aphid was collected from a given plant so as not to bias the sample by collecting several aphids from an infected plant. Sites were sampled several times during the season.

Each aphid was assayed for its ability to transmit BYDV by placing it on a single oat (*Avena sativa* L.) cv. California Red or, in the case of *Diuraphis noxia* a single barley (*Hordeum vulgare* L.) cv. Luther, seedling for 48–72 h. Plants were then treated with insecticide and held in a greenhouse for at least 3 weeks. Plants deliberately infected with an Idaho isolate of the PAV serotype of BYDV (ID-PAV) and uninfected plants were used as positive and negative controls. Plants were sprayed regularly to prevent spread of BYDV in the greenhouse.

Collection and assay methods for *Anoecia setariae* differed from those for other species. Mature *E. crusgalli* roots were examined for *A. setariae* colonisation. Up to 10 of the aphids from each infested root were placed on roots of oat cv. California Red seedlings (one seedling/colony) in plastic containers containing moist paper towels. Because root aphids are sometimes dependent on ants, two ants attending each colony were added to the containers. After 48 h, the oat seedlings were sprayed and transplanted for observation as in other assays.

Suction trap collections

Aphids were collected from a suction trap adapted for live collections each year during the autumn planting season in 1985–1988. The trap was built according to the design of

Allison & Pike (1988) and located at Parma, ID. It was 1.5 m high, the same height as the live trap used at Rothamsted (Plumb, 1976). The collection jar had rain wicks and a piece of crumpled cloth inside it to protect the aphids from injury as they landed in the jar. The motor ran continuously, and samples were collected daily except at weekends. Of the aphids taken in the traps, only those species known to feed on Gramineae, Cyperaceae or Juncaceae were tested. Aphid sex and reproduction on indicator plants were recorded. In July, 1988, 286 *D. noxia* and 144 *S. graminum* were collected and assayed, and in June/July 1990, an additional 508 *D. noxia* were collected and assayed during an outbreak of the pest.

An 8 m suction trap, built according to the same design and part of a regional survey system (Pike *et al.*, 1990), is also located at Parma. Samples were collected in a 50/50 mixture of ethylene glycol and ethanol weekly during the growing season during each of the four years (1985–1988).

Biological information

Biological information on life cycles and host plants in Idaho is based on surveys and collections by the authors (Halbert, Sandvol & Bishop, 1990b) unless otherwise stated.

Aphid identification

All aphids were identified by Idaho authors. Voucher specimens are held at the Aberdeen Research and Extension Center, Aberdeen, Idaho.

Results

Collection from host plants

Nine species of aphids were collected from their host plants and tested for BYDV transmission (Table 1). Of these *Rhopalosiphum padi*, *Rhopalosiphum maidis*, *Sitobion avenae*, *Metopolophium dirhodum*, *Schizaphis graminum* and *Macrosiphum euphorbiae* transmitted BYDV. *Diuraphis noxia* may have transmitted once. *Anoecia setariae* and *Sipha elegans* did not transmit BYDV. *Diuraphis frequens*, though regularly found infesting isolated wheat plants, was never abundant enough for a sufficient sample to be collected for an assay. Most of the *Rhopalosiphum maidis* sampled were collected from *Echinochloa crusgalli*, and infectivity was high in comparison with other aphid species. None of the 44 *S. avenae* collected from *Setaria lutescens* transmitted BYDV. One of the 40 *M. dirhodum* collected from *Phalaris arundinacea* transmitted the virus.

To determine how readily *D. noxia* would transmit the single isolate obtained from that aphid species we allowed a colony of *D. noxia* to develop on an infected barley plant. Leaf pieces infested with about 10 aphids were transferred to each of 42 oat cv. California Red and 42 barley cv. Luther indicator seedlings. The aphids moved to the seedlings as the leaf pieces dried. As a positive control, *S. graminum* were allowed to feed on leaf pieces from the same plant for 24 h, after which two of the *S. graminum* were transferred to each of six barley and five oat indicator plants. *Schizaphis graminum* transmitted the virus to four of the barley plants and three of the oat plants. By contrast, *D. noxia* did not transmit the isolate.

Collections from suction trap adapted for live collection

Among those aphids assayed from suction trap collections, *R. padi* transmitted BYDV most frequently and consistently (Table 2). Male *R. padi* transmitted BYDV more frequently than females collected during the same period. The differences in 1985 and 1986 were

Table 1. Barley yellow dwarf virus transmission by aphids collected from plants in southwestern Idaho, 1985-1988

Species	Hosts	1985		1986		1987		1988	
		No. tested	% transmitted	No. tested	% transmitted	No. tested	% transmitted	No. tested	% transmitted
<i>Rhopalosiphum padi</i>	maize, winter grain	1442	1.3	1186	0.7	1464	2.6	393	0.25
<i>Sitobion avenae</i>	maize, spring wheat	408	1.2	390	0.0	332	1.8	—	—
<i>S. avenae</i>	<i>Setaria lutescens</i>	44	0.0	— ^c	—	—	—	—	—
<i>Rhopalosiphum maidis</i>	winter grain, <i>Echinochloa crusgalli</i>	158	26.0	194	9.8	995	14.1	125	6.4
<i>Metopolophium dirhodum</i>	maize, spring wheat	—	—	31	0.0	64	4.7	—	—
<i>M. dirhodum</i>	<i>Phalaris arundinacea</i>	40	2.5	—	—	—	—	—	—
<i>Schizaphis graminum</i>	spring wheat	—	—	32	0.0	240	9.2	—	—
<i>Diuraphis noxia</i>	wheat, barley	—	—	—	—	676	0.1 ^b	352	0.0
<i>Macrosiphum euphorbiae</i>	maize	828	0.5	212	0.0	320	0.3	21	0.0
<i>Anoea setariae</i>	<i>E. crusgalli</i>	—	—	124 ^a	0.0	—	—	—	—
<i>Sipha elegans</i>	spring wheat	—	—	31	0.0	—	—	—	—

^a Represents entire colonies tested.^b One symptomatic plant proved to be infected with an SGV like isolate. *D. noxia* was not able to recover the virus.^c Not screened.

Table 2. Transmission of barley yellow dwarf virus by aphids collected in a suction trap during fall planting season (unless otherwise noted), Parma, ID, 1985-1988

Species	Sex	1985 ^a			1986			1987			1988		
		No. tested	% transmitted		No. tested	% transmitted		No. tested	% transmitted		No. tested	% transmitted	
<i>Rhopalosiphum padi</i>	f	699	4.6		1695	5.4		159	3.8		154	1.9	
<i>Rhopalosiphum padi</i>	m	281	9.6		665	10.7		57	5.3		11	9.1	
<i>Sitobion avenae</i>	f	6	0.0		0	—		6	0.0		4	0.0	
<i>Sitobion avenae</i>	m	0	— ^c		0	—		2	0.0		0	—	
<i>Rhopalosiphum maidis</i>	f	47	6.4		22	0.0		25	4.0		36	0.0	
<i>Rhopalosiphum insertum</i>	f	77	5.2		46	2.2		19	0.0		6	0.0	
<i>Rhopalosiphum insertum</i>	m	17	0.0		15	6.7		5	0.0		0	—	
<i>Macrosiphum euphorbiae</i>	f	26	3.8		15	6.7		18	0.0		12	0.0	
<i>Macrosiphum euphorbiae</i>	m	0	—		9	0.0		7	14.3		2	0.0	
<i>Metopolophium dirhodum</i>	f	88	0.0		9	0.0		84	1.2		45	0.0	
<i>Metopolophium dirhodum</i>	m	1	0.0		4	0.0		40	2.5		24	0.0	
<i>Ceruraphis eriophori</i>	f	14	7.1		27	0.0		3	0.0		0	—	
<i>Ceruraphis eriophori</i>	m	2	0.0		10	0.0		7	0.0		0	—	
<i>Schizaphis graminum</i>	f	0	—		0	—		4	0.0		145 ^b	0.0	
<i>Diuraphis noxia</i>	f	0	—		0	—		4	0.0		293 ^b	0.0	
<i>Anoea corni</i>	f	3	0.0		5	0.0		2	0.0		1	0.0	
<i>Ceruraphis viburnicola</i>	f	0	—		0	—		1	0.0		22	0.0	
<i>Ceruraphis viburnicola</i>	m	0	—		0	—		1	0.0		0	—	
<i>Colopha ulmicola</i>	f	0	—		3	0.0		4	0.0		0	—	
<i>Hyalopterus pruni</i>	f	0	—		2	0.0		1	0.0		9	0.0	
<i>Hyalopterus pruni</i>	m	0	—		0	—		2	0.0		6	0.0	
<i>Rhopalomyzus loniceræ</i>	f	0	—		4	0.0		58	0.0		5	0.0	
<i>Rhopalomyzus loniceræ</i>	m	0	—		1	0.0		54	0.0		8	0.0	
<i>Rhopalomyzus poae</i>	f	0	—		1	0.0		11	0.0		0	—	
<i>Rhopalomyzus poae</i>	m	0	—		0	—		1	0.0		3	0.0	
<i>Rhopalosiphum rufiabdominalis</i>	f	0	—		0	—		1	0.0		0	—	
<i>Tetraneura ulmi</i>	f	0	—		1	0.0		0	—		0	—	

^a Published in part in Blackmer & Bishop (1991).^b Most collected during peak flights in July.^c None collected.

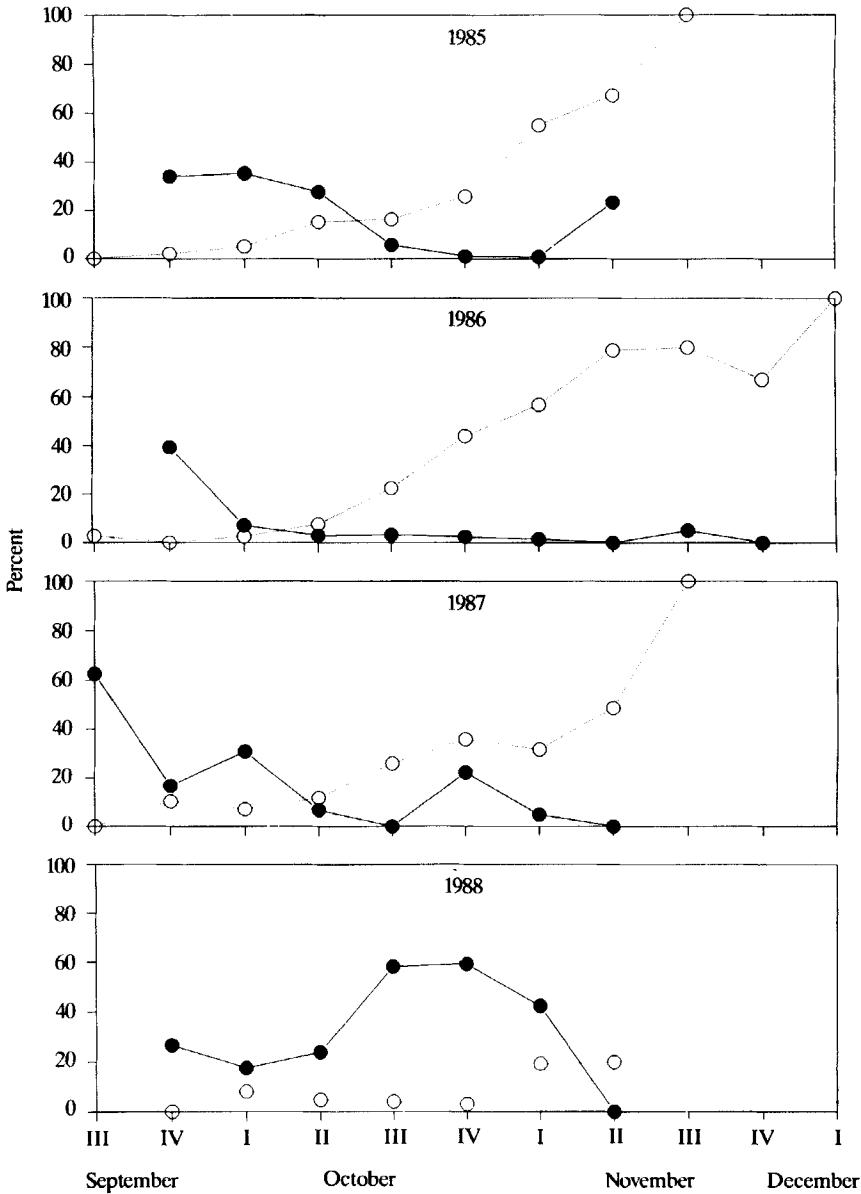


Fig. 1. Percent males (○) and percent females reproducing on indicator plants (●) for *Rhopalosiphum padi* collected in a live collection suction trap for barley yellow dwarf virus infectivity assays in southwestern Idaho in 1985–1988. Roman numerals indicate approximate weeks of the month; e.g., points corresponding to the 1st week of October represent samples collected during the week beginning on the Friday closest to October 1

statistically significant at the 0.01% confidence level using χ^2 analysis. Other common aphids on cereals and maize which transmitted BYDV in these assays included *R. maidis*, *M. dirhodum* and *M. euphorbiae*. Of the species of aphids tested that do not regularly colonise cereal crops or maize, *Rhopalosiphum insertum* (Walker) transmitted BYDV in 1985 and 1986, and *Ceruraphis eriophori* (Walker) transmitted once in 1985. Trapped *D. noxia* never transmitted BYDV.

Table 3. *Barley yellow dwarf virus transmission by Rhopalosiphum maidis and Rhopalosiphum padi collected from reservoir hosts (during interim between cereal harvest and autumn sowing), autumn cereals and a suction trap which operated during autumn planting season, Canyon County, Idaho, 1985–1988*

	% Transmission			
	1985	1986	1987	1988
<i>Rhopalosiphum padi</i>				
maize (reservoir host)	1.2	0.6	2.2	0.0
autumn cereal (planted and volunteer)	2.4	1.3	3.2	0.3
suction trap	6.0	6.9	4.2	2.4
<i>Rhopalosiphum maidis</i>				
<i>Echinochloa crusgalli</i> (reservoir host)	26.3	10.9	17.1	7.0
autumn cereal (planted and volunteer)	—	2.7	7.8	—
suction trap	6.4	0.0	4.0	0.0

Only *R. padi* was collected in sufficient numbers to determine change in reproduction on indicator plants through the season. In every year except 1988, percent reproduction on indicators declined during October, as the proportion of males increased (Fig. 1). In 1985 and 1987 there was an additional peak of reproducing females later in the season. In 1988, females continued to reproduce on the indicators into late October, and males were never a majority of the sample.

To examine potential off-season reservoirs of BYDV, *R. maidis* and *R. padi* transmission data from reservoir hosts in the interim between cereal harvest and emergence of the autumn crop were compared with data during the autumn sowing season (Table 3). Transmission by *R. padi* varied from year to year, but infectivity during drilling season (0.3% – 3.2% for *R. padi* in emerging wheat and barley, and 2.4% – 6.9% for trap collected specimens) was always higher than by *R. padi* collected on maize prior to emergence of the autumn crop (0% – 2.2%). Transmission by *R. maidis* during the sowing season (2.7% – 7.8% for *R. maidis* on emerging wheat and barley and 0% – 6.4% for trap collected specimens) was less than that observed by *R. maidis* collected from *E. crusgalli* during the mid-summer dry season (7.0% – 26.3%).

Survey suction trap collections

Flight activity differed among species and years (Figs 2 & 3). *Sitobion avenae*, *M. dirhodum* and *S. graminum* had single major flights each year as cereals matured. Activity was also sometimes detectable in the autumn. *Diuraphis noxia* was detected for the first time in 1987, and many were trapped in 1988, reflecting heavily infested local fields. There were three periods of detectable activity for *R. padi* in June/July, early September, and early-to-mid October though all peaks were not detectable every year. Data for *R. padi* in 1985 were published in Blackmer & Bishop (1991) and Blackmer (1986). *Rhopalosiphum maidis* is present throughout the season with no particular periods of peak activity.

Discussion

Aphid vectors

Rhopalosiphum padi

Rhopalosiphum padi is holocyclic in Idaho, overwintering on *Prunus virginiana* L.

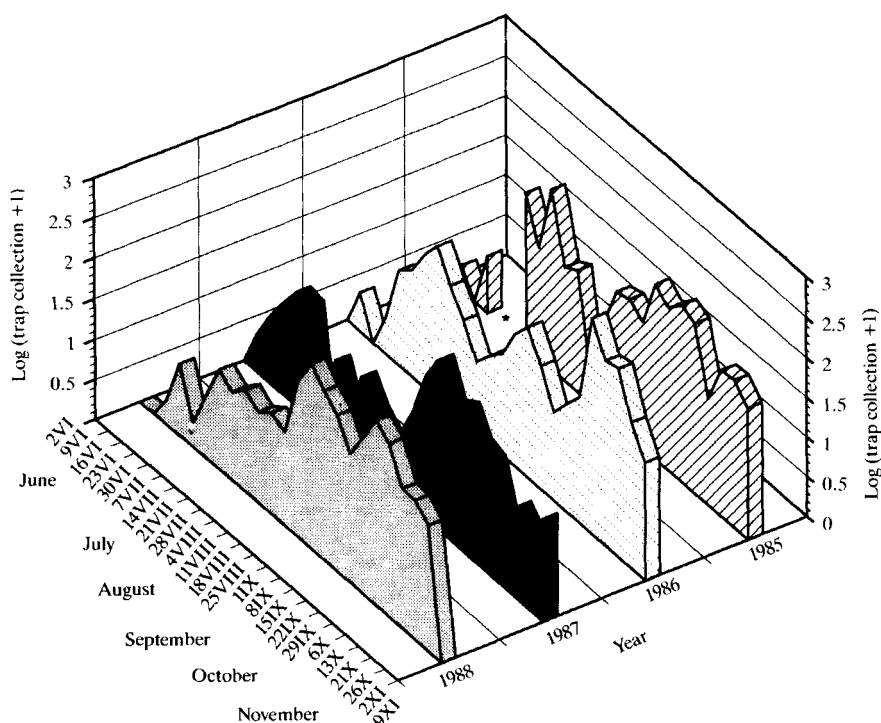


Fig. 2. Numbers of *Rhopalosiphum padi* collected in an 8 m suction trap (Allison & Pike, 1988) at Parma, Idaho, 1985–1988. Asterisk (*) indicates no data due to trap malfunction.

(chokecherry). Large colonies are widespread on chokecherry in early May in Idaho and Washington, though only a small percentage of trees are infested. During the growing season, *R. padi* can be found on wheat and barley during the spring and early summer. Very high populations often occur on maize in August and September (Blackmer, 1986; Blackmer & Bishop, 1991). Maize is the most important reservoir host of *R. padi* during the interim between harvest and emergence of the fall crop (Henry & Dedryver, 1989; Blackmer, 1986; Blackmer & Bishop, 1991; Brown *et al.*, 1984). Timodal flight peaks (Fig. 2) probably reflect emigration from maturing cereals (July) and crowded colonies on maize (September), and fall migration activity (October) (Blackmer & Bishop, 1991). Spring migration is not detectable by the traps.

Virus transmission by *R. padi* from fall cereals and by those captured by the suction trap was consistently higher than by those collected in maize (Table 3). Although maize has been reported as an important reservoir of BYDV in the Pacific Northwestern USA (Brown *et al.*, 1984; Halbert *et al.*, 1990a), France (Henry & Dedryver, 1989), Italy (Coccano & Peressini, 1989) and the midwestern United States (Clement, Lister & Foster, 1986), its role in Idaho may be more limited. Most maize in southwestern Idaho is harvested for silage in early to mid-September. Irrigation water is turned off mid-August to allow the crop to dry slightly prior to harvest. Emigrant *R. padi* colonise emerging volunteer wheat and barley and a very few early autumn-sown fields in early to mid-September. Most autumn sowing occurs in October and November which is too late for colonisation by emigrants from maize.

Maize is the major reservoir for *R. padi* during the August – September dry season and may also be important as an overwintering host of BYDV; however, other plants such as

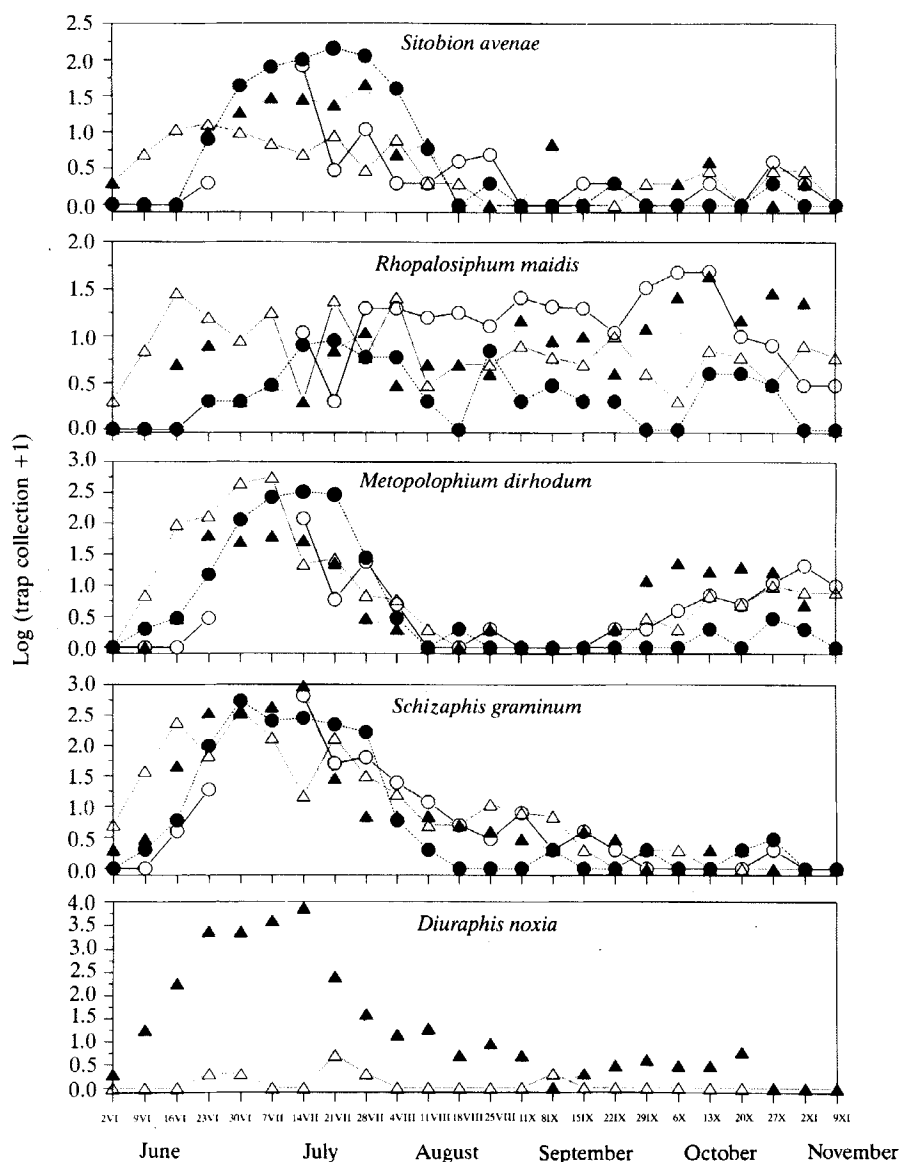


Fig. 3. Numbers of *Sitobion avenae*, *Rhopalosiphum maidis*, *Metopolophium dirhodum*, *Schizaphis graminum* and *Diuraphis noxia* collected in an 8 m suction trap (Allison & Pike, 1988) at Parma, Idaho in 1985 (○), 1986 (●), 1987 (△) and 1988 (▲).

volunteer wheat and barley are probably more important virus inoculum sources for *R. padi* that colonise autumn-sown cereal crops because of timing and higher infectivity of *R. padi* in volunteer cereals. Similarly, Plumb, Lennon & Gutteridge (1982) suggested that *R. padi* from volunteer cereals are more likely to transmit BYDV than those from maize because of low concentrations of BYDV in maize as measured by ELISA. Data from France (Gillet *et al.*, 1990) suggest that BYDV is carried from maize to cereal volunteers in September – October and from the latter to the autumn cereal crop in November – December; however, the increase in infectivity through the autumn season was not as evident as it is in Idaho. They also found much more yearly fluctuation in maize infection,

Table 4. Relative importance of potential vectors of barley yellow dwarf virus in southwestern Idaho, Autumn, 1985-1988

	1985			1986			1987			1988		
	No. probable vectors in suction trap ^a	% contribution to total	No. probable vectors in suction trap	% contribution to total	No. probable vectors in suction trap	% contribution to total	No. probable vectors in suction trap	% contribution to total	No. probable vectors in suction trap	% contribution to total	No. probable vectors in suction trap	% contribution to total
<i>Rhopalosiphum padi</i>	91	75.8	148	97.1	36	83.7	17	100.0				
<i>Rhopalosiphum maidis</i>	21	17.5	0	0.0	4	9.3	0	0.0				
<i>Rhopalosiphum insertum</i>	6	5.0	4	2.6	0	0.0	0	0.0				
<i>Metopolophium dirhodum</i>	0	0.0	0	0.0	1	2.3	0	0.0				
<i>Sitobion avenae</i>	0	0.0	—	—	0	0.0	0	0.0				
<i>Macrosiphum euphorbiae</i>	1	0.8	1	0.3	2	4.7	0	0.0				
<i>Ceruraphis eriophori</i>	1	0.8	0	0.0	0	0.0	—	—				
<i>Diuraphis noxia</i>	— ^b	—	—	—	0	0.0	0	0.0				
<i>Schizaphis graminum</i>	—	—	—	—	0	0.0	0	0.0				
Total	120	99.9	153	100.0	43	100.0	17	100.0				

^a This value is similar to the Infectivity Index (Plumb, Lennon & Gutteridge, 1982). It is calculated by multiplying the number collected in the 8 m survey trap from 10 September until flights ceased by the transmission rate obtained in bioassays of aphids collected in the 1.5 m trap adapted for live collection.

^b No transmission data because none were collected in the live collection trap.

both in terms of percent infection and predominant serotypes, than we did. More study is needed on the role of maize in BYD epidemiology.

Virus transmission by male *R. padi* collected in the trap was always higher than by females. This result differs from European reports (Leather, 1982; Tatchell, Plumb & Carter, 1988; McGrath & Bale, 1989; Gillet *et al.*, 1990) but the reason for this is unknown. Perhaps North American *R. padi* males have evolved a higher propensity to feed on grain because favourable overwintering sites are sparse.

Reproduction on oat plants decreased over time in 1986 and 1987 (Fig. 1), suggesting that, at least by the end of the season, most females collected in the trap were gynoparae. The timing of this change is similar to that observed by Tatchell & Parker (1990). The level of transmission by females collected in late fall was as high as that of females collected earlier in the season, indicating that gynoparae are probably transmitting BYDV in Idaho.

Sitobion avenae

Sitobion avenae is holocyclic on cereals in southwestern Idaho, and fundatrices can be found in winter wheat in March. Maximum populations occur on the heads of maturing spring sown wheat and barley, and the major single yearly flight peak reflects emigration from these crops as they senesce (Fig. 3). *Sitobion avenae* colonises maize briefly during mid-summer. It has been postulated that *S. avenae* carries PAV-like variants from winter grain to maize where *R. padi* acquires them and transmits them to fall cereals to complete the cycle (Brown *et al.*, 1984). About half of our isolates collected from maize were not transmissible by *S. avenae*, suggesting that much of the BYDV in maize in the years we sampled was transmitted to the crop by *R. padi*. Sporadic colonies of *S. avenae* can be found on maturing heads of *Setaria lutescens*, but the ephemeral nature and small size of the colonies make it unlikely that *S. lutescens* is an important interim reservoir for *S. avenae* vectored BYDV. Serological analysis of isolates obtained in 1987 and 1988 did not reveal any unquestionable MAV-like isolates, and infectivity of field collected *S. avenae* was low (Tables 1 and 2). Our observations differ markedly from Balež (1990) who reported that *S. avenae* was evidently the major vector in an outbreak in Yugoslavia. In Great Britain (Plumb & Carter, 1991; Barker, 1990) and France (Gillet *et al.*, 1990; Henry & Dedryver, 1989), *S. avenae* plays a minor role in the autumn because populations are low at that time. This is similar to our observations in Idaho.

Rhopalosiphum maidis

There are two common forms of *R. maidis* in Idaho, an eight chromosome form on maize and a 10 chromosome form on barley, *Echinochloa crusgalli*, and other grasses. Both forms can sometimes be found in low numbers on wheat in the autumn (Blackman, Halbert & Carroll, 1990). Of the two, the maize form is much less abundant and is only found relatively late in the season. *Rhopalosiphum maidis* is assumed to be anholocyclic (Blackman & Eastop, 1984), though a recent report indicates that it can overwinter on *Prunus cornuta* in Pakistan (Remaudière & Naumann-Etienne, 1991). Its overwintering site in Idaho is unknown. Surveys of fall barley indicate that *R. maidis* is not cold hardy, but it is sometimes one of the first species to appear in the spring.

The most consistently colonised plant in the interval between harvest and emergence of the autumn crop in our survey was the annual grass *E. crusgalli*, and *R. maidis* collected from this plant transmitted BYDV more frequently than any other species. Most BYDV isolates tested from *E. crusgalli* were RMV serotypes, of which many were vector non-specific (Halbert *et al.*, 1992). The non-specific ID-RMVs are probably carried from *E. crusgalli* to winter wheat by *R. maidis* in the autumn. Colonies of *R. maidis* on winter wheat

in the autumn are usually small and ephemeral, but ID-RMV can occasionally be recovered from wheat (Halbert *et al.*, 1992). *Rhopalosiphum maidis* is seldom found on winter wheat in the spring, so we suspect the virus is transmitted in the spring by other species from winter wheat to spring barley. Above ground parts of *E. crusgalli* are rarely colonised by species other than *R. maidis*, and root aphids found on *E. crusgalli*, including *Forda marginata*, *Geoica setulosa* (Passerini) and *Anoecia setariae*, are probably unimportant vectors due to inefficient transmission (Orlob, 1966) and predominantly spring and early summer flight activity in Idaho. Thus, we postulate that *R. maidis* moves the virus from barley to *E. crusgalli* to complete the cycle.

Rhopalosiphum maidis differed from other species in not having peak periods of flight (Fig. 1). It is possible that the continuous flight activity of *R. maidis* is responsible for its high infectivity because of increased opportunity for season-long virus distribution.

Unlike *R. padi*, transmission by *R. maidis* collected in the autumn was less than by those collected from dry season reservoir hosts (Table 3). The lower transmission frequency may be because some of the *R. maidis* collected in the autumn were emigrating from plants which are poorer hosts of BYDV than *E. crusgalli* or because *E. crusgalli* plants become senescent in the autumn, and virus titre is probably very low.

The high rate of infectivity of *R. maidis* in Idaho differs from findings in Europe, where *R. maidis* is apparently not an important vector (Signoret, 1990), although it has been reported as capable of transmitting some European isolates (Barker, 1990; Loi *et al.*, 1990). In some parts of South America, *R. maidis* may be an important vector (Araya, 1990). RMV serotypes have been reported both from Montana (Yount & Carroll, 1983) and Washington (Halbert & Pike, 1985b) in the northwest USA.

Metopolophium dirhodum

Metopolophium dirhodum is holocyclic in Idaho with rose (*Rosa* spp.) as a winter host. There is one major flight peak per year, coinciding with emigration from maturing cereal crops in mid-June to mid-July (Fig. 3). A much smaller peak in October and November reflects flights of autumn migrants. The main dry season host is *Phalaris arundinacea*, where *M. dirhodum* is often found in association with colonies of *Rhopalomyzus* (*Judenkoa*) *loniceræ* (Siebold). Collections from *P. arundinacea* were made only in 1985, when one of 40 transmitted BYDV. In 1987, *M. dirhodum* transmitted BYDV at a low rate, but *R. loniceræ*, though collected in moderate numbers, did not transmit. More data are needed to determine what role, if any, *R. loniceræ* plays in epidemiology of *M. dirhodum* transmitted BYDV isolates.

Plants with BYDV-like symptoms obtained from assays with *M. dirhodum* and tested by ELISA gave weak RMV reactions or no reaction; however, *M. dirhodum* transmitted field isolates of RMV and PAV and the ID-MAV laboratory isolate (Halbert *et al.*, 1992). Burnett & Mezzalama (1990) report that *M. dirhodum* transmitted MAV is common in Mexico, and Barker (1990) reported that *M. dirhodum* transmits a British MAV-like isolate. *Metopolophium dirhodum* and *M. dirhodum* transmitted BYDV can be abundant in fall cereals in the Pacific northwestern states (Halbert & Pike, 1985a), but this has not been observed in Idaho. Similarly, few if any MAVs were found in our surveys (Halbert *et al.*, 1992). If either the aphid or MAV-like isolates become abundant in the fall, the roles of *P. arundinacea* and *R. loniceræ* in BYD epidemiology should be re-examined.

Schizaphis graminum

Schizaphis graminum is probably holocyclic in Idaho, with eggs deposited on winter cereals. Oviparae are present in autumn cereal crops. The single flight peak reflects

emigration from maturing grain (Fig. 3). Outbreaks of SGV serotypes have occurred in the autumn in eastern Idaho (Forster, Bishop & Sandvol, 1990), and transmission by *S. graminum* can also be important in western Idaho (Table 1). Several serotypes, including SGV, PAV and RMV, are transmitted by *S. graminum* (Halbert *et al.*, 1992). The importance of *S. graminum* in the epidemiology of BYD in Idaho depends upon its abundance during the autumn sowing season. Autumns in which high *S. graminum* populations coincide with low infectivity have not been observed in Idaho. *Schizaphis graminum* is not a very important vector in Europe (Signoret, 1990) or Great Britain (Barker, 1990) but can be in South America (Araya, 1990).

Diuraphis noxia

Diuraphis noxia is a new pest in North America (Stoetzel, 1987) and was first found in Idaho in a suction trap sample in June, 1987. No holocyclic overwintering has been observed, though a few oviparae have been reported (Kiriak *et al.*, 1990). There is only a single major flight peak, which reflects emigration from maturing grain (Fig. 3), but heavy colonisation of autumn sown wheat has been observed (Halbert *et al.*, 1988).

Although *D. noxia* has been reported as a vector of BYDV in South Africa (von Wechmar, 1984) and Morocco (El Yamani & Hill, 1991), at best, *D. noxia* is a very poor vector of BYDV in southwestern Idaho. Only one of over 1800 *D. noxia* tested transmitted BYDV, and *D. noxia* was not able to recover that isolate. The possibility of infection of the original plant by a contaminant aphid species cannot be excluded. Alternatively, von Wechmar (1984) reports that the presence of *Rhopalosiphum padi* virus (RhPV), an aphid enterovirus, is an important component of *D. noxia* transmission of BYDV. Possibly the single aphid which transmitted BYDV in our experiments was infected with RhPV.

Additional evidence indicating that *D. noxia* is of negligible importance as a vector of BYDV was given by the spring outbreaks of *D. noxia* in southwestern Idaho in 1988 and 1990. Had a *D. noxia* transmissible isolate of BYDV been present, some of the 645 and 508 *D. noxia* tested in 1988 and 1990, respectively, should have transmitted the virus. Since that did not occur we conclude that *D. noxia* is not at present important in the epidemiology of BYDV in southwestern Idaho.

Rhopalosiphum insertum

Rhopalosiphum insertum is holocyclic in Idaho, overwintering on *Crataegus* and *Malus*. Occasional transmission by autumn forms was observed, and *R. insertum* was able to transmit isolates of the ID-PAV, ID-RPV and ID-RMV serotypes (Halbert *et al.*, 1992); however, *R. insertum* does not usually feed on grain (Blackman, Eastop & Brown, 1990; Jedlinski & Voegtlin, 1986) and thus is probably not an important vector of BYDV in cereal crops. Our single collection from cereals was taken on barley roots near Parma, Idaho on 19 June 1987.

Macrosiphum euphorbiae

Macrosiphum euphorbiae is holocyclic in Idaho, overwintering on rose. Heavy populations can develop on maize toward the end of the season. It transmits BYDV infrequently and should not be considered an important vector in southwestern Idaho. Three symptomatic plants obtained from assays with *M. euphorbiae* were tested by ELISA. Of these, one was a PAV serotype, one gave a weak RMV reaction, and one was negative by ELISA (Halbert *et al.*, 1992).

Other species

Sipha elegans and *A. setariae* never transmitted BYDV in our experiments and were never very abundant on cereals or maize. *Ceruraphis eriophori* though reported to be a vector (Jedlinski, 1981), transmitted BYDV only once in our studies. Though it is reported from both wheat and barley in Idaho (Gittins, Bishop, Knowlton & Parker, 1976), it is certainly not common on these plants, and we expect it is of little importance in epidemiology of BYD in grain.

None of the 130 *Rhopalomyzus lonicerae* tested transmitted BYDV. Because this species is restricted to *P. arundinacea* as a secondary host, it could be epidemiologically significant only if a BYDV variant transmissible by both *M. dirhodum* and *R. lonicerae* were prevalent.

Relative importance indices

Plumb, Lennon & Gutteridge (1982) multiplied transmission rates obtained from live trapping at 1.5 m by numbers of aphids collected in the standard Rothamsted Insect Survey Trap at 12.2 m to obtain a measure of risk of virus infection (an estimate of the number of probable vectors collected in the survey trap). This value, cumulated over the season was called the Infectivity Index. We calculated this index for species transmitting in Idaho (using Allison & Pike (1988) traps, our survey and live traps being 8 m and 1.5 m high respectively) and determined the percent each species comprised of the total probable vectors (Table 4). Based on these calculations, *R. padi* was by far the most important vector during the autumn planting season in each of the four years.

Gillet *et al.* (1990) made the point that since proportionally more autumn migrants (which are inefficient vectors in Europe) are collected at 12.2 m than at 1.5 m, infectivity is not comparable. In contrast to this, autumn migrants of *R. padi* in Idaho probably transmit BYDV at least as efficiently as alate exules, so the discrepancy would not be great. We think that any index of potential vectors designed for southwestern Idaho must include autumn migrants, at least until it is known whether they feed on cereal crops under natural conditions.

Conclusions

- 1) *Rhopalosiphum padi* was the most important vector of BYDV during the autumn planting season in southwest Idaho in each of four years.
- 2) Male *R. padi* collected from a suction trap transmitted BYDV more frequently than females collected concurrently.
- 3) *Diuraphis noxia* is at best a very poor vector of BYDV in southwestern Idaho.
- 4) *Echinochloa crusgalli* is a summer dry season reservoir for *Rhopalosiphum maidis* (10 chromosome form) and RMV.

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