ELISA-Based Studies on the Ecology and Epidemiology of Barley Yellow Dwarf Virus in Indiana

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ABSTRACT

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Seasonal occurrence and spread of *Rhopalosiphum padi* and of PAV- and RPV-like isolates of barley yellow dwarf virus (BYDV) were assessed by observation and by enzyme-linked immunosorbent assay from 1981 to 1984 in wheat and oat crops and in oat bait plants exposed periodically at selected sites at the Purdue University Agronomy Farm. Aphid activity and virus infection were much higher in 1981 and 1982 than in 1983 and 1984. Peak virus spread and aphid activity generally occurred in the spring and fall. The results suggested that a major source of BYDV is in exogenous aphid populations moving from distant plants in wind currents, especially in the spring. Transmission from local grasses appears to be sporadic, and less common. In the fall, aphid populations colonizing winter wheat probably are from both distant and local sources, depending on conditions. One such source is corn (maize), but its potential as an oversummering reservoir of virus between wheat crops seems variable. Visual surveys underestimate the occurrence of BYDV, probably because commonly grown cultivars of wheat and oats have been selected for tolerance.

Acquisition of detailed, reliable data on the occurrence of barley yellow dwarf virus (BYDV) in cereals has been limited by difficulties in diagnosing it by observing crop plant symptoms. Accurate diagnosis has hitherto been based on technically demanding vector transmission studies (15). In Indiana, the predominant small grain crops are cultivars of soft red winter wheat (*Triticum aestivum* L.) in which symptoms of BYDV infection are often not distinctive. Although BYDV is known to occur regularly and is widespread, dramatic effects have been noticed only occasionally (e.g., 1), and detailed information on its year-to-year importance and spread is lacking. Enzyme-linked immunosorbent assay (ELISA) now offers a simple means of BYDV detection and identification in cereals and grasses (13).

The purpose of the studies reported here was to improve understanding of the incidence, ecology, and epidemiology of BYDV in Indiana. Further details are available elsewhere (5).

MATERIALS AND METHODS

Identification of virus isolates. Virus standards were the RPV and MAV isolates of Rochow (15) and the P-PAV isolate of Hammond et al (9). Isolates reacting like these in ELISA are referred to here as "RPV-like," "PAV-like," or "MAV-like" in accord with the terminology established by Rochow (e.g., 16). Virus culture (in Clintland-64 oats [*Avena sativa* L.]) and ELISA procedures were as previously described (7,18). The immunoglobulins (Igs) used were from polyclonal antisera produced in rabbits by intradermal or intramuscular immunization with purified virus preparations (12). Their homologous and heterologous behavior in ELISA was as described by Fargette et al (7); that is, in tests with the three virus standards, the P-PAV and RPV Igs reacted only with their homologous antigens, whereas the MAV Ig reacted with both MAV antigen and P-PAV antigen.

Leaf samples for extraction were placed in 95 × 25-mm glass vials and homogenized at 1:10 w/v in 0.1 M phosphate buffer at pH 7.0 (11) with a Polytron homogenizer (Brinkman Instruments Inc., Westbury, NY) with the PT-20-ST probe at setting 6 for 30 sec. Control ELISA reactions with extracts from healthy leaves were usually less than 0.05 $A_{405\ nm}$, and were not visibly yellow. Reactions giving obvious yellow color or absorbances greater than twice the average for healthy control samples in the same experiment were regarded as positive. They were clearly distinguishable and their $A_{405\ nm}$ values ranged up to about 1.5. Evaluation of virus isolates was mostly by use of the P-PAV and RPV Igs, but a few tests were done with MAV Ig. Most tests therefore identified PAV- and RPV-like isolates and did not specifically evaluate other known types of BYDV such as the SGV and RMV isolates of Rochow (17); other surveys (16) suggest that these may be relatively uncommon. PAV- and RPV-like isolates have *Rhopalosiphum padi* L. as a common vector, and this was by far the most common aphid we saw on small grains.

Location of sampling sites. Seasonal occurrence and spread of BYDV was studied at three locations on the Purdue University Agronomy Farm during 1981–1984. Locations (Fig. 1) were: a grass area in Field 11; a wheat/oats area in Field 11; and an area about 1,500 m away comprising the contiguous Fields 72, 73, 74, and 75 assigned to the USDA/ARS-Purdue University Integrated Pest Management Study (IPM). At the IPM location, 36 plots of soft red winter wheat sown with the cultivar Beau were distributed within rotations involving corn, soybeans, and wheat (5). When the IPM plots were established, the area was clear-plowed and the strips of ground separating the plots were sown with fescue (*Festuca* sp.).

Plant sampling. To estimate the amount of BYDV infection occurring in the fall and to check for aphid overwintering, six samples (11 × 11-cm soil cores, each containing several wheat plants) were collected at random from the outside three or four border rows of each wheat subplot in the IPM in March of 1982, 1983, and 1984 (collection of samples from within subplots was precluded by yield trials). These samples, taken before any aphid activity was evident, were kept in an unfumigated greenhouse during 8 wk for observation of any aphids that might have overwintered on the wheat roots, inside leaf sheaths or in the soil. The new wheat growth (which was always asymptomatic) was then harvested and tested for virus by ELISA. In June of 1981, 1982, 1983, and 1984, wheat leaf samples were also collected at random directly from field plants, to estimate the number of infections that had occurred during the entire growing season. The plants sampled

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were categorized as asymptomatic or as having yellow or red coloration likely to indicate BYDV infection. In June 1983, additional samples were also taken specifically from selected plants with yellow or red leaves to determine whether either symptom was diagnostic of BYDV infection.

In May 1984, infections in grass also were assessed by taking cores from between plots in the IPM, and also from the grass area in Field 11 both within and adjacent to the area in which oat bait plants were exposed (see below). Infection in oat crops (cultivar Noble) in several fields at the Agronomy Farm, was also assessed in June 1982 and 1983 by testing randomly-collected leaf samples by ELISA.

Assessment of infection in corn was by sampling corn ears and leaves found to be aphid-infested, predominantly with *R. padi* and *R. maidis* (Fitch), during September 1981 and 1982. These samples were collected from suitable plants selected at random within the first two or three rows of plants from several fields. Nymphs and apterous *R. padi* from individual samples were transferred to individual Clintland 64 oats, which were sprayed with Malathion to kill the aphids after 2 days, then grown for 2-3 weeks in the greenhouse prior to checking by ELISA. This procedure was preferred instead of direct ELISA of leaf tissue because of the uneven distribution of virus within corn plants (9).

Time of virus spread. To investigate when BYDV spread occurred in relation to cropping, 13× 13.5-cm-diameter plastic pots each containing from five to 10 Clintland 64 oat bait plants 10 days old were placed adjacent to the mid-points of opposite sides of each wheat subplot in the IPM area; in sites about 10 m apart in two rows 10 m apart in the grass area of Field 11; and in sites established at similar intervals alongside wheat or oats surrounded by grass in Field 11 (Fig. 1). Thus, 116 pots were exposed at approximately weekly intervals in each of the growing seasons of 1981–1983, with 72 in the IPM, 22 in the Field 11 grass, and 22 by the Field 11 wheat/oats plot. On collection, the presence or absence of *R. padi* on the bait plants was recorded as an estimate of aphid activity during the exposure period. The plants were then sprayed with Malathion, grown for 2 wk in the greenhouse, and the bulked plants from each pot were tested by ELISA.

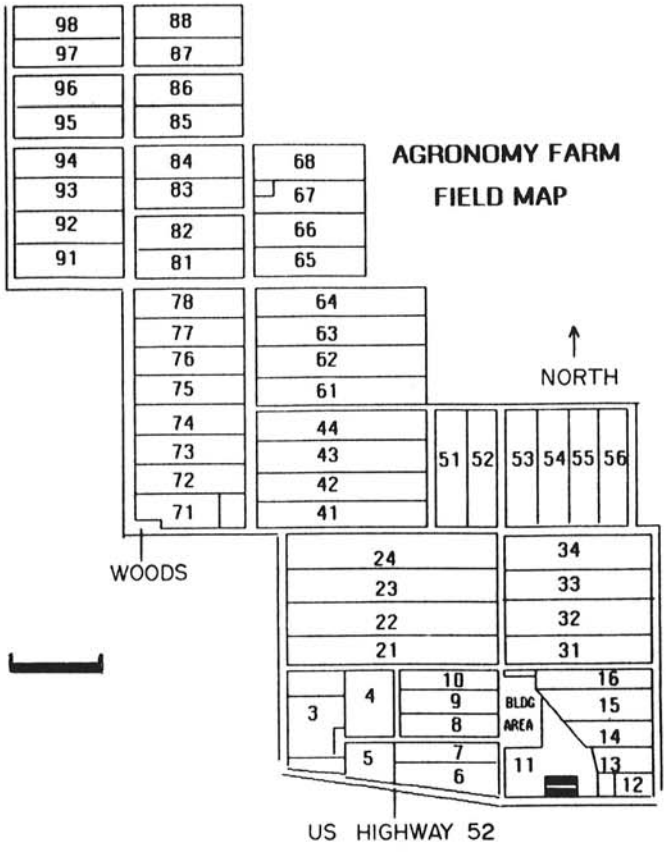


Fig. 1. Plan of the Purdue University Agronomy Farm, showing field locations. The Integrated Pest Management Study (IPM) occupied Fields 72, 73, 74, and 75. Oat bait plants were also exposed in the grass area of Field 11 (i.e., in the area covered by the number "11") and in the wheat and oats alternated between the two plots indicated in black in Field 11. Scale bar = 300 m.

Overwintering of aphids. To check for overwintering aphid eggs on their primary woody hosts, several branches sampled from each of 30 wild *Prunus* spp. from various sites around the Agronomy Farm were brought indoors in the early spring of 1981, placed in containers of water to force new growth, and observed for signs of aphid activity as the buds broke and leaves emerged.

Aphid population estimates. Aphid population variations and activity were not assessed by trapping procedures. However, during part of 1981, population variations for *R. padi* were estimated by counting aphids on small grain and corn samples in the IPM area. Cereal aphid occurrence was also assessed by general observations made during visits to the farm.

RESULTS

Occurrence of BYDV in small-grain crops. Surveys of the 36 wheat plots in the IPM area during 1981, 1982, 1983, and 1984 yielded information on the relative incidence of PAV- and RPV-like isolates of BYDV during those years and also indicated when virus spread had occurred (Table 1). In June 1981, 78% of the wheat plant samples were infected; most contained PAV-like isolates and of the 10% containing RPV-like isolates, 8% were mixed infections by both PAV- and RPV-like isolates. In March 1982, 20% of the wheat plants collected were infected; 13% contained PAV-like isolates and 10% contained RPV-like isolates, with 3% mixed infections. Thus, fall infections in 1981 comprised PAV- and RPV-like isolates about equally. By June 1982, 83% of samples were infected; 82% with PAV-like isolates and 21% with RPV-like isolates, all but 1% of which were in mixed infections with PAV-like

TABLE 1. Incidence of PAV- and RPV-like isolates of barley yellow dwarf virus as detected by ELISA in symptomatic (S), asymptomatic (AS), yellow (Y), or red (R) wheat samples from the Integrated Pest Management Study at the Purdue University Agronomy Farm during 1981–1984[a]

Time of collection	Samples (no.)	Percent ELISA-positive for: PAV[b]	RPV[b]	PAV and RPV	PAV or RPV
June 1981[c]	234 (S)	73	15	12	76
	136 (AS)	82	2	1	83
	Total (S + AS)	76	10	8	78
March 1982[d]	216 (AS)	13	10	3	20
June 1982	360 (S)	99	26	26	99
	144 (AS)	39	6	3	42
	Total (S + AS)	82	21	20	83
March 1983	216 (AS)	24	3	0.5	27
June 1983	101 (S)	50	13	7	56
	259 (AS)	12	8	1	19
	Total (S + AS)	22	9	3	28
June 1983	72 (Y)	21	7	0	28
	72 (R)	93	14	14	93
	Total (Y + R)	57	10	7	60
March 1984	216 (AS)	0	0	0	0
June 1984	14 (S)	29	0	0	29
	202 (AS)	4	0	0	4
	Total (S + AS)	6	0	0	6

[a] S and AS samples were each from randomly collected plants (March) or leaf samples (June). Y and R leaf samples represented individual plants randomly selected from among those with such symptoms.
[b] Data include double and single infections.
[c] June sample results identify infections that occurred in the previous fall or during the spring.
[d] March sample results identify infections that occurred in the previous fall.

isolates. This indicated that most spring 1982 infection had been with PAV-like isolates and that secondary spread of RPV-like isolates was relatively uncommon. In March 1983, 27% of the wheat plants collected were infected, 24% with PAV-like isolates and 3% with RPV-like isolates, with only 0.5% mixed infections. This indicated that most fall 1982 infection had been with PAV-like isolates. By June 1983, infection was assessed at 28%, indicating there had been essentially no further infection in the wheat plots during the spring of 1983. Interestingly, in March 1984, no infections with PAV-, RPV-, or MAV-like isolates were detected; thus, there was no evidence of fall infection having occurred during 1983. Little infection occurred during the following spring also, since in June 1984, only 6% of samples were infected, all with PAV-like isolates. The relatively low number of new infections in wheat during the spring of 1983, the absence of infections in the fall of 1983, and the low numbers of infections in the spring of 1984, were associated with exceptionally low aphid populations observed on the wheat crops in April and May of both years and in September 1983. These observations also correlated with the relatively low proportions of oat bait plants observed to have aphids during these periods (see below). However, BYDV did spread into oats at the Purdue University Farm in 1983. In an oat field (Field 6) surveyed in June, 48% of samples collected at random were infected; 43% with PAV-like isolates, 9% with RPV-like isolates, and 4% with mixed infections (Table 2). Presumably aphids causing these infections arrived too late in the season to cause detectable infections in the maturing wheat. A similar pattern of late aphid arrival occurred in 1984, when very few aphids were observed until after the wheat had headed.

Symptoms as a definitive index of BYDV infection in small grains. Of the wheat samples collected randomly from the IPM area and then grouped as symptomatic and asymptomatic (Table 1), 76% of the symptomatic samples and 83% of the asymptomatic samples collected in June 1981 reacted positively in ELISA; 99% of the symptomatic samples and 42% of the asymptomatic samples collected in June 1982 reacted positively; and 56% of the symptomatic samples and 19% of the asymptomatic samples collected in June 1983 reacted positively. Very few samples collected in June 1984 had symptoms, and ELISA assessment revealed only 29% infection in the symptomatic samples and 4% infection in the asymptomatic samples. The results for additional samplings, done in June 1983 specifically to see if BYDV incidence in wheat was correlated with yellowing or reddening symptoms, indicated 93% infections in plants with reddening symptoms and 28% in those with yellowing symptoms (Table 1).

In similar studies with oats in June 1982, plants with either reddening or browning symptoms were compared with asymptomatic plants by ELISA (Table 2). In three of the fields studied (Fields 7, 11, and 22) all reddened plants were infected with BYDV, but in a fourth (Field 85) only 60% of the reddened plants sampled were infected. Browning symptoms were associated with 80-96% infection. Infections in asymptomatic plants ranged from 20 to 64%, and in three of the fields more than half of the asymptomatic samples contained virus. Tests of oats randomly sampled from Field 6 in June 1983 confirmed that neither reddening or browning were definitive for BYDV (Table 2).

Occurrence of BYDV in corn. In 1981, less than 2% of the samples (2 of 133) from nine corn fields were infected, and all infections were with PAV-like isolates. In 1982, 5% of the samples (4 of 83) from three fields were infected, and again all infections were with PAV-like isolates. All the corn plants that we observed were asymptomatic. Aphid populations did not build up prior to corn senescence in 1983 and 1984, and no test samples were collected.

Occurrence of BYDV in grasses. The grassed divisions between plots in the IPM, and the grass in Field 11 in the area where oat bait plants were exposed, were sampled in May 1984. For samples from the IPM (mainly fescue) the infection rate was 73%, including 40% of PAV-like isolates, 12% of RPV-like isolates, and 8 and 10% of mixed infections containing PAV-like with MAV-like isolates, or PAV-like with RPV-like isolates, respectively. Three percent of the samples were infected with all three of these BYDV types. Results for the Field 11 grass area were strikingly different. In this long-established grass field, which consisted mostly of Kentucky bluegrass (*Poa pratensis* L.), 18% of the samples were infected, all with RPV-like isolates only. All the grasses sampled were asymptomatic.

Occurrence of virus vectors in the field. No aphids or aphid eggs were seen on the twigs from wild *Prunus* spp. forced in early spring, 1981. Likewise, no evidence of aphids was seen on the wheat plants brought in the greenhouse from the IPM in March 1982 and 1983.

TABLE 2. Incidence of PAV- and RPV-like isolates of barley yellow dwarf virus as detected by ELISA in oats sampled at the Purdue University Agronomy Farm in June 1982 and 1983

Sampling time	Field number	Symptom category	Percent ELISA-positive for:[a] PAV[b]	RPV[b]	PAV and RPV	PAV or RPV
June 1982	7	Red	100	44	44	100
		Brown	80	16	16	80
		Asymptomatic	64	8	8	64
	11	Red	100	24	24	100
		Brown	88	12	12	88
		Asymptomatic	16	14	10	20
	22	Red	100	16	16	100
		Brown	96	12	12	96
		Asymptomatic	52	8	0	60
	85	Red	60	0	0	60
		Brown	80	0	0	80
		Asymptomatic	52	16	16	52
June 1983	6	Symptomatic	63	15	7	71
		Asymptomatic	18	4	0	22

[a] Based on tests of 25 plants in each symptom category, sampled at random from Fields 7, 11, 22, and 85 (see Fig. 1), and of 52 and 48 symptomatic and asymptomatic plants, respectively, sampled at random from Field 6.
[b] Data includes double and single infections.

TABLE 3. Surveys of the abundance of *Rhopalosiphum padi* from plants sampled at random from within and around the Integrated Pest Management Study area at the Purdue University Agronomy Farm during 1981

Sampling dates	Numbers of *R. padi*/100 culms or stems[a] Volunteer wheat	Volunteer oats	Corn	IPM winter wheat
August				
3	5	50	0	–
11	4	52	0	–
17	10	60	0	–
24	12	73	2	–
31	30	97	40	–
September				
8	63	43	43	2
21	103	–	c.150[b]	40
24	40	–	c.200	93
28	–	–	c.500	106
October				
6	–	–	c.1,000	110
13	–	–	c.200	93
20	–	–	c.100	95
26	–	–	42	103
November				
2	–	–	–	115
9	–	–	–	119
16	–	–	–	79
23	–	–	–	52
30	–	–	–	13

[a] Minuses mean no plants were available to sample at these times.
[b] The values for corn between 21 September and 20 October are approximate.

Counts of *R. padi* made in 1981 within and around the area of IPM indicated that volunteer wheat and oats, and also corn plantings, served as bridging hosts for aphid populations between winter wheat crops (Table 3). The development of very large populations of *R. padi* along with *R. maidis* on maturing corn coincided with population buildup of *R. padi* on winter wheat seedlings. A similar pattern of population development on corn and winter wheat occurred in 1982 but not in 1983 or 1984.

Occurrence of vectors on, and virus in, bait plants. Based on the occurrence of *R. padi* on oat bait plants when collected, high levels of aphid activity developed suddenly in late April and later subsided in late May-June in both 1981 and 1982 (Fig. 2). However, by this assessment, aphid activity was less overall in 1983 and was more erratic and spread more evenly over the season than in the previous two years. Aphid activity was less evident in April and May 1983 than in 1981 and 1982, and peak activity was observed in June. In both 1981 and 1982, major peaks of aphid activity were indicated in the fall, with a minor peak in August, between wheat crops. Results in 1983 indicated an aphid activity peak in late September, with peaks also in early and late August, between wheat crops.

The patterns of aphid activity indicated at each specific location (IPM, Field 11 grass, Field 11 grains) were similar in many respects to that seen overall (Fig. 2). However, in 1981, 1982, and 1983, spring peaks of aphid activity were more obvious on the bait plants exposed near grain crops than on those exposed in grass. Observing aphids on bait plants only during collection provided an estimate of aphid establishment, rather than aphid visitations, during each exposure period. However, ELISA estimates of BYDV infection in all three of those years often followed approximately the same trends as this estimate of aphid activity. The most notable exception was the occurrence of large numbers of infections in late August 1981 when few aphids were seen. Rainfall records for this period indicated that aphids alighting on the plants may have been washed off by heavy rains before the plants were collected (5). This effect may also explain some of the disparities between ELISA results and aphid activity estimates that occurred during June 1981. A reverse situation occurred in the fall of 1982 when large proportions of bait plants had aphids when collected, but relatively few infections were recorded. This indicates that large populations of nonviruliferous aphids can develop and spread in the fall season, perhaps from corn. The best correspondence between the estimates of aphid activity and infection occurred at the IPM location in 1983. In all three years, and at each exposure site, PAV-like isolates were overall much more prevalent in the bait plants than RPV-like isolates (Table 4). Infections with RPV-like isolates were distributed sporadically over the season, although about one-half of those occurring in 1981 occurred in the October-November exposure period, and such infections also predominated in April 1983 (Fig. 2).

Because some of the observations suggested that (especially during the spring) aphids became established less readily on bait plants exposed in grass than on those exposed in grain crops, aphid occurrence on grass bait plants was directly compared with occurrence on oat bait plants. One pot each of young transplants of red fescue (*Festuca rubra* L.) and Kentucky bluegrass (*P. pratensis* 'Wabash') were exposed alongside each oat bait plant pot from 6 to 10 June 1983. A total of 24% of the oat bait pots exposed during this period had aphids when collected, and about 12% contained infections, whereas no aphids were seen on the grass bait pots and no infections were detected in them.

DISCUSSION

Systematic exposure of oat bait plants in three areas of the Purdue University Agronomy Farm provided data on the dynamics of aphid activity and virus spread through several years in different field environments. Thus, the IPM area provided a background for wheat in typical crop rotations, the Field 11 wheat/oats area provided a cereal monoculture environment, and Field 11 grass provided a typical permanent grass area. In an earlier survey (7), about 50% of Field 11 grass samples from around the wheat/oat plots were infected with BYDV, almost all isolates being RPV-like. In our May 1984 survey of Field 11 grass around the area where the bait plants were exposed, 18% of samples were infected with RPV-like isolates and none with PAV-like isolates. Since the IPM area was cleared of vegetation prior to establishing the IPM (fall, 1980), there were no sources of BYDV within that area prior to the outset of the current work. But, for the Purdue University Farm as a whole, as elsewhere in Indiana, the earlier survey (7) again indicated nearly 50% of the grass sampled was a BYDV reservoir, mostly of RPV-like isolates. Therefore, it is of considerable interest that the predominating BYDV found in the bait plants was PAV-like and that this was true of all locations.

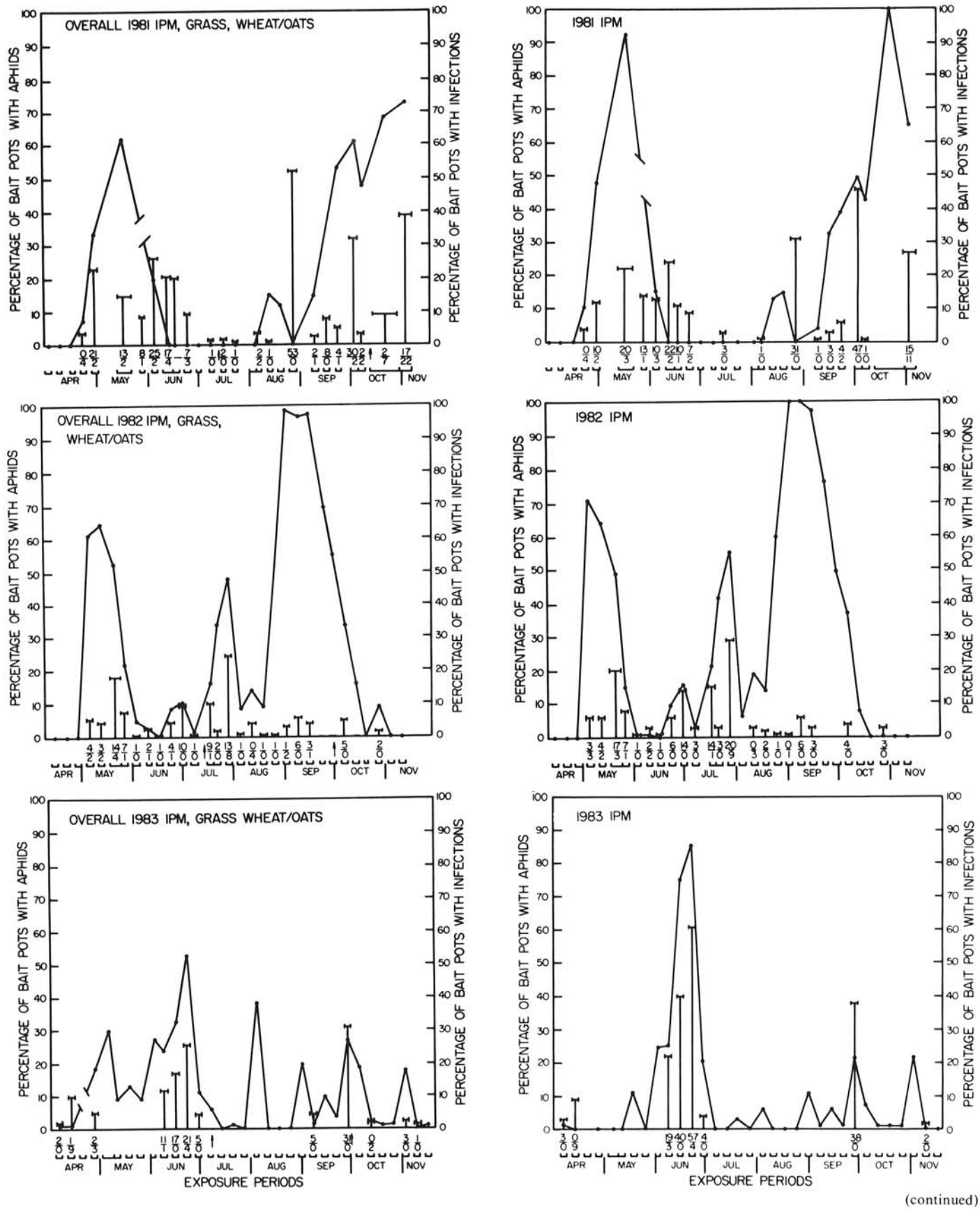
Overall, around 80% of infections detected in oat bait plants were with PAV-like isolates. Infections with RPV-like isolates occurred sporadically, but in 1981 about one-half occurred in the fall. PAV-like isolates also predominated over RPV-like isolates in wheat and oat crops sampled throughout the farm. RPV- and PAV-like isolates were about equally common in infections that took place in the fall of 1981 in the IPM wheat, but the large increase in infections in spring 1982 was mainly of PAV-like isolates, and by June 1982 essentially all the RPV-like isolates diagnosed were associated with PAV-like isolates. Therefore, secondary spread of RPV-like isolates in the spring of 1982 seems to have been much less significant than exogenous infections with PAV-like isolates. Although comparable data for the fall-winter period of 1980 are lacking, those for infections measured in June 1981 were similar to those of June 1982, and the bait plant observations indicated that PAV-like isolates predominated in infections occurring in spring 1981. It is, therefore, tempting to speculate that most RPV-like infections detected in the IPM wheat crop in June 1981 also took place in the previous fall.

As evidenced by bait plant observations, spring aphid activity was relatively reduced in the grass area compared with that in the cereal areas. This is consistent with aphid establishment being due to the arrival of winged (alate) aphids seeking favorable sites to settle, and showing preference for leaves of young cereal plants rather than grass. Similar preference was also exhibited when pots of young grass transplants were exposed in June 1983 alongside oat bait plants. Despite such preference, however, BYDV infection accumulated in the newly sown grass between plots in the IPM area during the 4 yr of the study. These infections were predominantly with PAV-like isolates just as was the case in the cereal plants sampled. This strongly suggests that a change in the predominating BYDV isolates has taken place and that long-established grasses acquired their RPV-like isolates some time ago. Similar changes in the predominating isolates of BYDV have been documented in detail for cereals over the last 20 yr elsewhere in the United States (16). Apparently, *R. padi* did not overwinter on its primary hosts (*Prunus* spp.) in the Agronomy Farm area, nor did it overwinter in wheat even in the exceptionally mild winter of 1982–1983. Conceivably, however, it could have overwintered in grasses then,

TABLE 4. Percentages of PAV- and RPV-like isolates of barley yellow dwarf virus in the infections detected by ELISA in all the oat bait plants exposed in three locations at the Purdue University Agronomy Farm during the 1981, 1982, and 1983 growing seasons

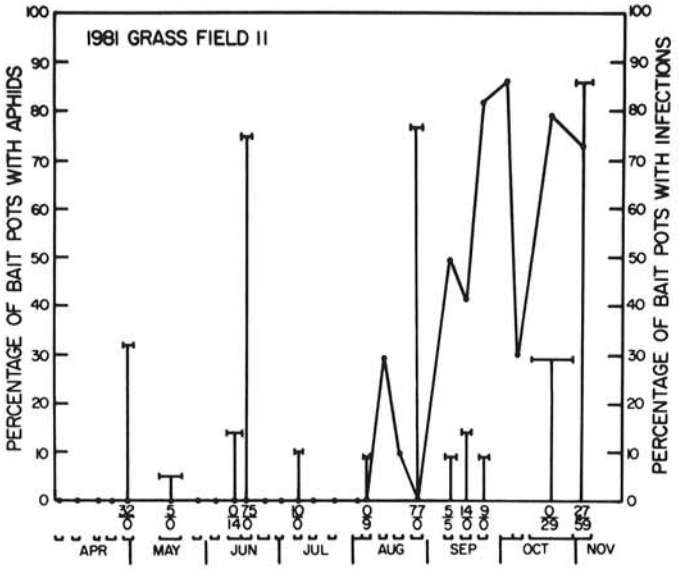
Season	Isolate type	Location[a] IPMS wheat	Field 11 cereals	Field 11 grass	All
1981	PAV[b]	87	90	70	84
	RPV[b]	15	13	30	18
	PAV and RPV	2	3	0	2
1982	PAV[b]	82	67	73	79
	RPV[b]	21	33	27	23
	PAV and RPV	3	0	0	2
1983	PAV[b]	89	71	89	84
	RPV[b]	13	33	11	18
	PAV and RPV	2	4	0	2

[a] For locations see Figs. 1 and 2.
[b] Data includes double and single infections.



(continued)

Fig. 2. Aphid activity and seasonal spread of barley yellow dwarf virus as indicated by observations on pots of oat bait plants exposed in the Integrated Pest Management Study area (IPM), Field 11 grass area, and Field 11 wheat/oats area at the Purdue University Agronomy Farm, during 1981, 1982, and 1983 (see Fig. 1, and ref. 5). Solid lines represent percentages of bait pots with plants that had aphids present at the time of collection. Vertical bar lines represent percentages of pots in which infections were detected. The length of the line across the top of each bar indicates the length of the exposure period. Arrows indicate the harvest and planting dates of the winter wheat in the IPM study. Fractions along horizontal axes summarize percentages of bait pots with PAV-like infections (numerators) and RPV-like infections (denominators). Data for aphid occurrence are not available for the 26–29 May exposure period in 1981.


1981 GRASS FIELD II
PERCENTAGE OF BAIT POTS WITH APHIDS
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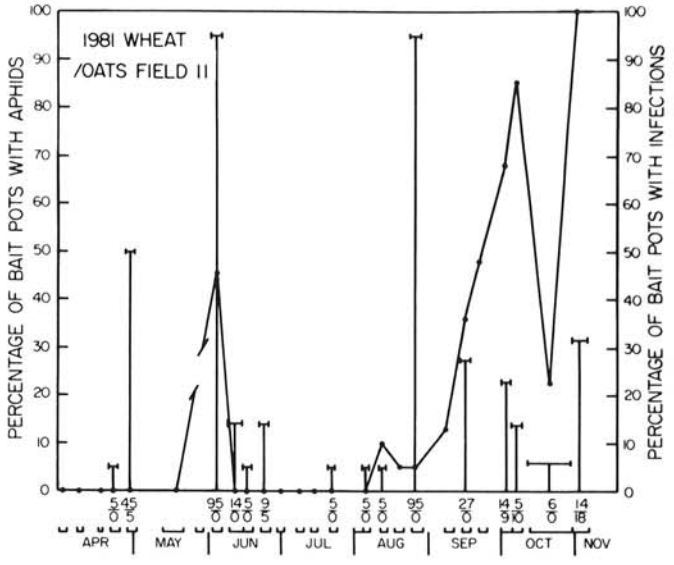
1981 WHEAT
/OATS FIELD II
PERCENTAGE OF BAIT POTS WITH APHIDS
PERCENTAGE OF BAIT POTS WITH INFECTIONS
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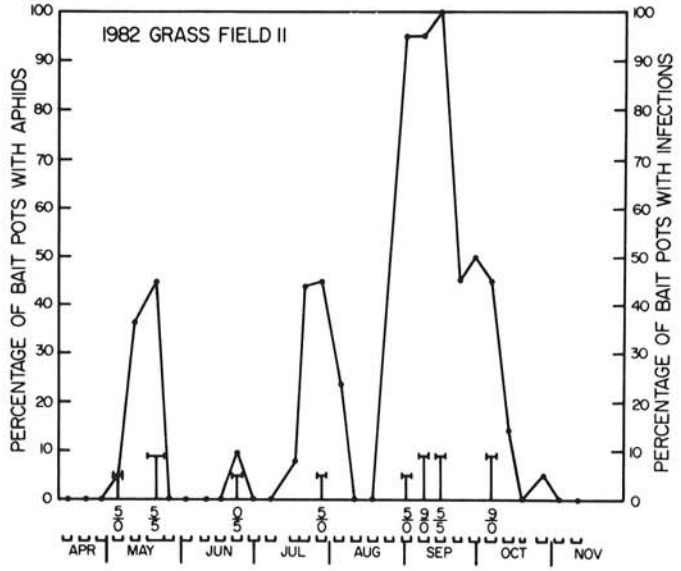
1982 GRASS FIELD II
PERCENTAGE OF BAIT POTS WITH APHIDS
PERCENTAGE OF BAIT POTS WITH INFECTIONS
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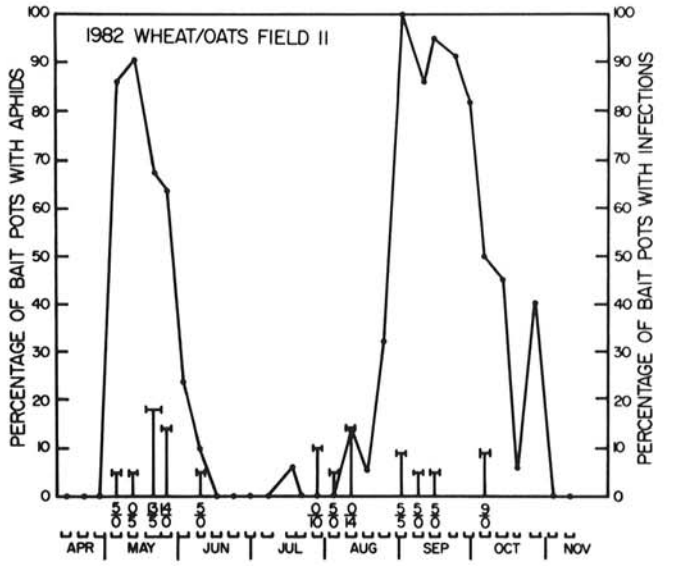
1982 WHEAT/OATS FIELD II
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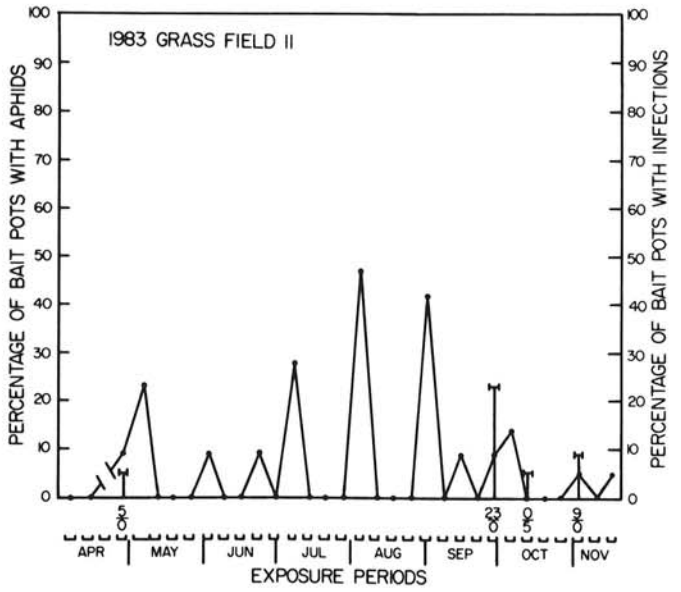
1983 GRASS FIELD II
PERCENTAGE OF BAIT POTS WITH APHIDS
PERCENTAGE OF BAIT POTS WITH INFECTIONS
APR
MAY
JUN
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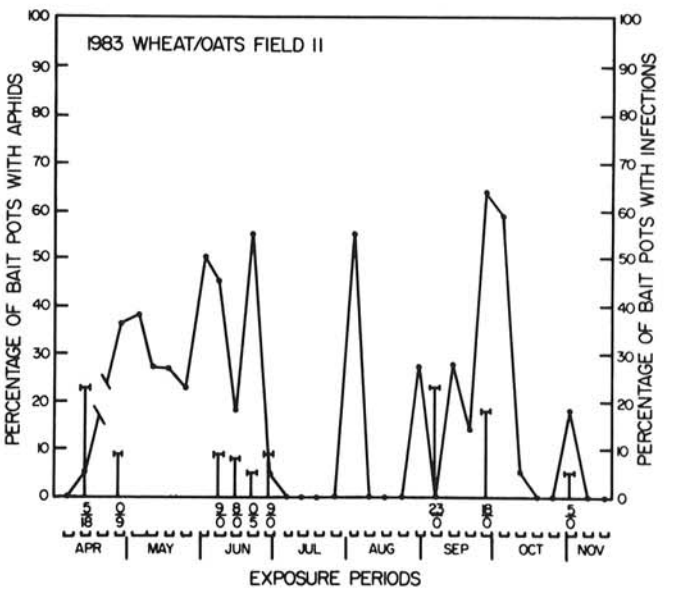
EXPOSURE PERIODS


1983 WHEAT/OATS FIELD II
PERCENTAGE OF BAIT POTS WITH APHIDS
PERCENTAGE OF BAIT POTS WITH INFECTIONS
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
EXPOSURE PERIODS

thus accounting for the earlier appearance of infections in the oat bait plants in 1983 than in 1981 and 1982 and the relative predominance of RPV-like isolates in April 1983 infections (Fig. 2). Also, vector aphids may have overwintered in 1982–1983 in southern Indiana. Symptoms of BYDV were unusually common on wheat there and also in Kentucky early in 1983, suggesting unusual aphid activity, either through extension of the Fall 1982 and Spring 1983 periods of activity, or the early development of aphid populations from overwintering aphids.

In 1981 and 1982, aphid activity was indicated on bait plants suddenly in late April, subsiding in late May-June. This rapid onset of activity in spring, together with disparity between the virus types found in local grasses and cereals themselves, suggests that BYDV was spread into the crop at that time from a distance. A mechanism for this influx exists in the low-level jet winds which have been invoked to explain movement of *Schizaphis graminum* (Rondani) northwards from southern states (10), and also as the basis of spread of maize dwarf mosaic virus to sweet corn crops in Minnesota, far from reservoir hosts (20), as well as spread of BYDV itself elsewhere (8,14,19). Virus spread was less in 1983 than in 1981 and 1982, and the spring peak of aphid activity was delayed. This may have been associated with unusual weather conditions, including a more northerly location of the interface between major cold and warm air masses than usual, affecting the pattern of low-level jet winds.

Regarding other possible reservoirs of BYDV for spread to small grains, our surveys in September of 1981 and 1982 did reveal low percentages of infection in local corn plantings, when both corn and volunteer wheat and oats carried substantial populations of *R. padi*. Therefore, in the fall, there is the potential for virus spread back to wheat crops from infected corn as well as from volunteer wheat and oats and from grasses. Aphid populations did not build up on corn prior to its senescence in 1983 or 1984, so this is not a regular occurrence. When it does happen, however, because corn is so widely grown, even low percentages of infection could be important in BYDV epidemiology. Moreover, corn is senescing, with concommitant pressure for aphid migration, at the same time that sprouting winter wheat provides a suitable host for aphids moving from corn plants. Such migrations could be from local sources, or conceivably also over long distances, should meterological conditions encourage long distance spread from ripening northern corn crops to more southerly winter wheat plantings. Such patterns of long distance movement might be expected as the interface between cold and warm air masses moves south during the fall, as was suggested long ago as a factor in fungal spore dispersal (3).

In summary, the epidemiology of BYDV in central Indiana is clearly complex, but a major source of infection is likely to be in aphid populations moving from distant crops in wind currents, especially in the spring. Aphid overwintering seems rare, and virus transmission from local grasses is probably sporadic. Aphid populations in the fall could include components from both distant crops and local sources, especially corn crops, whenever appropriate population build-up occurs on these. The importance of grasses as a reservoir, and of corn as an oversummering host for both virus and vector, seems variable and difficult to resolve. Detailed investigation of such problems requires much more information on vector populations and dynamics, based on a systematic program of aphid trapping. By comparison with the situation in other parts of the world, such information is surprisingly sparse for the USA.

Finally, our surveys of BYDV occurrence in grain crops confirm that symptomatic appearance is a poor guide to infection (6). In wheat, leaf reddening was a better index of infection than leaf yellowing but disease-associated yellowing and browning was probably readily confused with senescence. Depending on the year, anything from 4 to 83% of asymptomatic wheat plants proved to be infected as assessed by ELISA. It is also significant that fall infections (as estimated in March of the following years) showed no obvious symptoms, even when ELISA estimated 27% infection was present. Fall infection has the most serious economic effect on winter wheat (2,4), so this is the more important type of infection to detect. The lack of symptoms in Beau wheat probably reflects that an incidental selection for BYDV tolerance has gone on in midwestern wheat breeding programs over years, because of the prevalence of the viruses involved. In oats also, although symptoms were a much better index of infection, many asymptomatic plants proved to be infected. BYDV occurred in each of the years from 1981 to 1984, and is probably often much more frequent and widespread in midwestern wheat and oats than indicated by visual surveys, because commonly grown cultivars have been selected for tolerance.

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