Irrigated Corn as a Source of Barley Yellow Dwarf Virus and Vector in Eastern Washington

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ABSTRACT

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Barley yellow dwarf virus (BYDV) causes economic loss in winter grain crops in eastern Washington when seedlings become infected shortly after emergence. Irrigated corn was identified as a reservoir of the virus and its aphid vectors during the interim between summer harvest and fall planting of winter grains. Although foliar symptoms were not associated with BYDV-infected corn plants, 58 and 65% of the corn fields surveyed in the Columbia Basin harbored the virus in 1981 and 1982, respectively. Viruliferous *Macrosiphum avenae* (Aphididae) were present in late June and July, 1980, but the largest aphid populations, which consisted of *Rhopalosiphum padi*, were present in August and September. Sixty-one percent of the *R. padi* collected from corn in 1980 were viruliferous. In 1981, viruliferous *M. avenae* was noted in corn fields in June, while *R. padi* infested 36, 11, and 90% of the corn fields surveyed in July, August, and September, respectively. Virus was recovered from all but one of 75 corn cultivars, hybrids, or lines when experimentally inoculated by *R. padi* in greenhouse studies. Over 50% of the corn tested exhibited foliar symptoms under greenhouse conditions, usually a red discoloration of the leaves. Aphid transmission and ELISA test results suggest BYDV isolates from corn are similar to previously identified vector-nonspecific isolates from wheat fields in Washington.

Additional key words: maize virus, symptomless infection, yellow dwarf.

Barley yellow dwarf virus (BYDV) causes disease in winter wheat and barley grown in the Palouse and Columbia Basin regions of eastern Washington (4,6). A major increase in the frequency of disease incidence has resulted in the need to identify the factors involved in BYDV epidemics.

In eastern Washington, the virus is vectored nonspecifically by four species of cereal aphids common to the area (19). The bird cherry-oat aphid, *Rhopalosiphum padi* L., and the English grain aphid, *Macrosiphum* (*Sitobion*) *avenae* Fabricius, are the most efficient and numerous of the vectors of the nonspecific *padi-avenae* (named for the vector-host combination) viruslike (PAV-like) (17,18) isolates of BYDV found in eastern Washington (3,5,19). Aphid infestations of small grains in eastern Washington increase throughout the spring, decrease by early summer (when small grains mature and dry), and increase again in early fall (2).

The increased incidence of BYDV in fall-planted grains was thought to be associated with an increase in vector populations. However, the naturally sparse weeds that survive arid summer conditions do not support substantial vector populations. Recently, the expansion of irrigation in the Columbia Basin has allowed weeds and certain crops to remain lush throughout July and August. As a direct result of increased irrigation, corn (*Zea mays* L. [sweet, silage, and grain]) acreages have expanded from 14,170 ha (35,000 acres) in 1955 to over 64,777 ha (160,000 acres) in 1980 (22). Because BYDV is known to have a wide host range among gramineous plants (3,4,13,14) and corn remains lush throughout the summer months when winter grains are drying, we hypothesized that corn could be a potential summer carry over source of virus and vector. There are conflicting reports (1,9,12,14,15,20,21,23) concerning the ability of corn to serve as an experimental host of BYDV and it is not known if the aphid vectors are able to colonize corn under field or experimental conditions (7,10,15).

We report here the results of field surveys undertaken in the Columbia Basin to determine if corn was a field crop survival host of BYDV between the summer harvest and fall planting of small grains.

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MATERIALS AND METHODS

Field collections and detection of BYDV. Leaf samples were collected from corn and/or wheat fields in four counties (Adams, Benton, Franklin, and Grant) in eastern Washington throughout the summer and fall in 1980 and 1981. Developing leaves (three or four per plant) were collected randomly from each of five different plants within a field, pooled to constitute a sample, and assayed for BYDV by aphid transmission tests (16). Aphids were likewise collected (5–10 aphids per plant, five plants per field) from infested plants, pooled, and allowed access to greenhouse-grown indicator hosts to determine if they were viruliferous.

Aphid transmission tests were conducted as virus infectivity assays of detached leaf pieces by using nonviruliferous, apterous *R. padi* from greenhouse-maintained colonies. Stock aphid colonies were maintained on barley (*Hordeum vulgare* L. 'Luther') and assayed periodically to ensure they remained virus-free. Cultivar Luther barley was used as the BYDV indicator host in all tests. Indicator barley seedlings were grown in 8.0-cm-diameter plastic pots in a greenhouse isolated from aphid colonies and inoculated plants. Detached leaf pieces were analyzed by confining 10–20 *R. padi* with pooled samples in aerated plastic containers for a 24-hr acquisition-access period (16). Intact leaf pieces, with the feeding *R. padi*, were transferred to pots containing barley seedlings and caged. Aphids were allowed a 3-day inoculation-access period and seedlings were fumigated with Pirimor WP50 (ICI Americas, Inc., Wilmington, DE 19897). Inoculated barley seedlings were transferred to a separate greenhouse (18–25 C), placed under fluorescent lights (7,000 lux, 16 hr/day) and observed periodically during a 3-wk period for symptom development (8,19). Indicator barley was fertilized regularly (10 ml per pot) with ammonium sulfate 34-0-0 (20 cc/L). Greenhouses were fumigated weekly with nicotine sulfate (applied as smoke bombs) to eliminate migrant aphids.

The infectivity of field-collected aphids was tested by pooling

apterous aphids (collected 5–10 aphids per plant, five plants per field) and placing them directly on healthy indicator seedlings. Barley indicators were handled in the same manner as described for detached leaf-piece assays.

Strain identification. The field-derived isolates of BYDV from corn were characterized by aphid transmission tests to determine vector specificity and by serological comparison with four BYDV strains from New York (NY) (17).

Characteristically, some BYDV strains (and isolates) are transmitted 'specifically' (exclusively) by a single aphid species (eg, *M. avenae* transmits the MAV-; *R. maidis* Fitch, the RMV-; *R. padi*, the RPV-; and *Schizaphis graminum* Rondani, the SGV-strain(s), respectively) while *R. padi, M. avenae*, and other grain aphids transmit the PAV (named for the vector-host combination, *padi-avenae*) strain of BYDV in a nonspecific manner (17). Vector specificity tests in which corn isolates were experimentally transmitted were conducted by using greenhouse-maintained colonies of either *M. avenae, R. padi*, or *S. graminum*. The same methods and feeding times described above were used. *R. maidis* was unavailable at the time and, therefore, was not included in the test.

Additionally, corn isolates were tested serologically by W. F. Rochow at Cornell University, Ithaca, NY; he used the enzyme-linked immunosorbent assay (ELISA) procedure (17,18) and antisera prepared against four NY-strains of BYDV. Difficulty in detecting BYDV in corn tissue by ELISA was experienced in the past (W. F. Rochow, *personal communication*). To facilitate identification of our corn isolates, virus was transferred from field- and greenhouse- inoculated corn leaves to barley (a host commonly used in ELISA testing) (17,18) by *R. padi* transmission. Fresh leaves and acetone powders prepared from fresh or frozen corn or barley leaves also were tested.

Experimental virus transmission to corn. Corn seeds for experimental transmission tests were supplied by commercial seed companies, the USDA Regional Plant Introduction Station (Ames, IA 50011), or the USDA National Seed Storage Laboratory (Ft. Collins, CO 80523). Seeds of inbred lines were obtained from W. K. Wynn, University of Georgia, Athens 30602. Five seeds were planted per 15-cm-diameter clay pot in commercially prepared potting soil and thinned to three seedlings per pot. Following a 24-hr acquisition-access period on detached leaves of BYDV-infected cultivar Luther barley, viruliferous *R. padi* (10–20 per pot) were transferred to corn seedlings (three- to four-leaf stage) and caged. Aphids were killed by fumigation 3 days later and inoculated plants were maintained in the greenhouse (18–25 or 25–30 C) for 4–8 wk. A balanced fertilizer plus Zn and Mn was applied as needed and plants were observed periodically for symptom development. Inoculated corn plants were back-indexed to healthy barley indicators using detached corn leaf-pieces and *R. padi* (10–20 per plant) with the same feeding times described above. Each corn cultivar was tested three times with at least 10 plants per experiment (2).

RESULTS

Survey of corn for BYDV in 1980. BYDV was recovered from 39, 86, and 50% of the fields sampled in July, August, and September, respectively (Table 1). All plants from which BYDV was recovered were symptomless. At no time were symptoms like those described in BYDV experimentally inoculated corn (1,9,12,15,20,21,23) observed on field-grown corn. Virus was recovered from fields in all four counties surveyed.

The small number of plants assayed per field during the general survey did not allow for an estimation of infection frequencies within individual fields. Therefore, during August 50 additional samples were collected randomly from within each of seven corn fields (identified as virus sources during the July surveys). Based upon aphid transmission tests, the incidence of BYDV occurrence in each field (F) was F8, 24%, F9, 56%; F10, 63%; F11a, 6%; F11b, 64%; F15N, 4%; and F115, 34%.

Survey of corn for BYDV vectors in 1980. In eastern Washington, the two most common and efficient vectors of BYDV to wheat are *R. padi* and *M. avenae* (20). In early July, low levels of alate and apterous *M. avenae* (2–10 per plant) were noted in 82% of the surveyed corn fields (three- to five-leaf stage). Apterous *M. avenae* infestations were limited to mid-stalk regions of corn plants. In contrast, *R. padi* (alate and apterous) was observed on corn (2–10 per plant) in only two of the 23 fields surveyed in July, and infested both stalks and the undersides of corn leaves (Table 1).

In early August, *M. avenae* was no longer observed in corn fields, but by mid-August *R. padi* had heavily colonized the corn stalks and ear sheaths (over 1,000 per ear) in 93% of the fields surveyed (Table 1). Both alate and apterous aphids were present and 90% were viruliferous as determined by assay on cultivar Luther barley. In September, some of the corn had been harvested, but *R. padi* was present in all remaining corn fields (Table 1), and 38% of collected aphids were viruliferous. Unharvested corn fields remained lush and continued to support *R. padi* alate and apterous aphids until harvest or death of the plants due to frosts in late September. During July, 1980, *R. maidis*, the corn leaf aphid heavily infested one corn field in Adams County. Corn leaf aphids were not viruliferous and no virus was recovered from the corn leaves by *R. padi* in transmission tests. *R. maidis* is occasionally found in eastern Washington, but previous work by Seybert and Wyatt (19) demonstrated this aphid to be an inefficient vector of Washington PAV-like isolates of BYDV.

Movement of virus and vectors in wheat. The 1980, dryland winter and spring wheat crops in eastern Washington were not

TABLE 1. Occurrence of barley yellow dwarf virus (BYDV) in corn and wheat leaves and of two grain aphid species in corn fields in eastern Washington during 1980–1981

	BYDV infection						
	Corn		Wheat		Aphid collections from corn fields		
Collection date	Samples collected[a] (no.)	Infected (%)	Samples collected (no.)	Infected (%)	Samples collected[b] (no.)	*M. avenae* (%)	*R. padi* (%)
1980							
July	23	39	6	0	23	82	8
August	15	86	...[c]	...	15	0	93
September	9	50	11	63	8	0	100
1981							
March	...	...	31	55	...	...	...
June	9	77	...	...	9	100	0
July	50	54	4	100	11	0	36
August	11	63	...	...	2	0	11
September	3	100	...	...	30	0	90

[a] Each leaf sample consisted of a composite of three to four leaves per plant collected randomly from five plants per field.
[b] Aphid samples consisted of five aphids per plant collected randomly from five plants per field and pooled.
[c] Not collected.

heavily infected with BYDV. Symptoms were associated with less than 15% of observed fields (*unpublished*); therefore, eastern Washington dryland wheat fields were probably not the primary source of virus inoculum for subsequent infections occurring in Columbia Basin corn or wheat.

Occasionally, late spring wheat is planted adjacent to irrigated corn sites in the Columbia Basin; when this occurred, those spring wheat fields were sampled. In July, 1980, *M. avenae* was observed in only one of six (17%) such wheat fields and virus was not recovered from any sample by aphid transmission tests. *R. padi* was not observed in Columbia Basin spring wheat fields in July or August, 1980 (Table 1).

Winter and spring grain crops are dry by midsummer and winter wheat for the following crop is planted in late August and September. Upon emergence of winter wheat seedlings in September 1980, *R. padi* was noted in 73% of the early-planted fields (Table 1). Virus was recovered from 63% of the fields sampled and from 45% of the *R. padi* that were collected.

Mild fall and winter weather conditions during 1980–1981 permitted low levels of *R. padi* (one to two aphids per 3,000 seedlings) populations to overwinter in wheat seedlings in the Columbia Basin (*unpublished*).

Shortly after the growth of winter wheat seedlings resumed in March, 1981, BYDV symptoms were noted in over half of the basin and surrounding dryland wheat fields (*unpublished*). In late March, 1981, BYDV was recovered from 55% of surveyed fields (Table 1).

Survey of corn in 1981. *M. avenae* was observed in nine of nine corn fields in late June, 1981 (Table 1). Most *M. avenae* were viruliferous and BYDV was recovered from 77% of the fields by aphid transmission tests with *R. padi*. *M. avenae* was not observed on corn for the remainder of the 1981 year.

Unlike the summer of 1980, however, *R. padi* was not observed in corn fields until July and only 36 and 11% of the corn fields surveyed were infested with aphids in July and August, respectively. By early September, *R. padi* was present in 27 of 30 surveyed corn fields (Table 1). The increase in population levels of *R. padi* occurred after the onset of cooler temperatures following a prolonged, hot summer.

BYDV was recovered from corn fields sampled in June (77%), July (54%), August (63%), and September (100%), 1981 (Table 1).

Strain identification. To determine if the Washington BYDV corn isolates were similar to any of five previously described BYDV small grain strains (17,18,20) the corn isolate was compared to the Washington PAV-like strain (20) and NY-derived BYDV strains (17,18) by aphid transmission tests (2,17) and/or serological testing (17,18).

In aphid transmission tests the corn isolate was transmitted with high (70%), medium (30%), and low (20%) efficiency from corn samples to cultivar Luther barley by *R. padi, M. avenae*, and *S. graminum*, respectively (2).

Based on ELISA testing, mild PAV-like homologous reactions occurred with barley leaves (fresh) to which three corn isolates were transferred by *R. padi*, and with fresh greenhouse-inoculated, BYDV-infected corn leaves (Table 2). Because infectivity tests required a 3-wk waiting period, no fresh field-inoculated corn leaves were available for ELISA testing. A strong PAV-like reaction occurred in acetone powder preparations of BYDV-infected barley leaves, but not in similarly prepared greenhouse-(fresh) or field-inoculated (frozen) corn leaves (Table 2).

Susceptibility of corn cultivars to BYDV. Many corn cultivars are resistant to BYDV isolates (1,9,12,15,20,21,23). Therefore, 20 corn cultivars commonly grown in the Columbia Basin and 52 additional cultivars, lines, or hybrids were tested for susceptibility to the Washington BYDV wheat isolate in greenhouse aphid transmission tests. Using *R. padi* as the vector, virus was transferred to and recovered from all 20 inoculated basin-grown cultivars and from 51 of the 52 other cultivars. The virus was recovered both from leaves present at the time of inoculation and from those that developed following inoculation (2). Therefore, infection appeared to be systemic in all cases. Symptoms were observed in 39 of 72 inoculated cultivars and were generally consistent with those described previously on greenhouse-inoculated corn plants (1,15,20,21,23). Symptoms observed in infected corn plants were: reddening or yellowing of leaf tips, chlorotic flecking of leaf tips, or rarely, chlorotic spotting. Red discoloration of leaves, the most common symptom, occurred 3–4 wk after inoculation when greenhouse temperatures were 25–30 C. When plants were maintained at 18–25 C, foliar discoloration was more intense and developed sooner (in 2–3 wk). Discoloration began at the tips of the oldest (first to fourth) leaves and progressed about halfway down the leaf toward the stalk. Symptoms were limited to the lower three or four leaves and were never observed on newly developing leaves in the whorl.

The following cultivars developed red leaf symptoms: Aunt Marys (5610), DeKalb 640, F-G4141A (Funks), Golden × Bantam (PI233315), Golden Beauty (Lilly Miller [L.M.]), Golden Beauty (PI233332), Golden Sunshine (PI230313), Hrvattaca-KI (PI184281), Improved Golden Bantam (L. M.), Improved Spancross (L. M.), Mohave (PI218187), P10097 (Pioneer), P40452 (Pioneer), PI193487, PI213701, PI232979, Rainbow (Burpee), Rainbow Flint (PI213775), Shohoko (PI303908), Stowell's Evergreen (5628), Stowell's Evergreen (Burpee), Sunglow (L. M.), SX189 (P.A.G.), SX-397 (P.A.G.), Tom Thumb (PI217512), Winnebago (PI213772), and Zuni Blue (PI213799).

The following inbred lines also developed red leaf symptoms: B37-N, B37-T, M017-N, M017-T, W64A-N, and W64A-T.

Cultivars that developed only chlorotic spots or flecks were Commander (Del Monte), Jubilee (Rogers Bros.), and PI183783.

Four cultivars, Gold Tag 2080 (Ferry Morse [F-M]), Stylepak (F-M), SX201 (Pioneer), and XL45A (Ramsey) exhibited red leaf tips and chlorotic spots.

The following cultivars were symptomless, but systemically infected: Cochiti (PI218131), DeKalb 640 (Ramsey), Drought Proof (PI217415), Earliking (L.M.), Early Sunglow Hybrid (Burpee), F-G 4315 (Funks), 4085 (Funks), Gold Tag 770 (F-M), Mandan Red Flour (PI213808), Morning Sweet Sun (L.M.), Natal Yellow Horsetooth (PI221846), Navajo (PI218160), N.K. 19 Dent (PI214198), Pioneer 40452, PI183766, PI201842, PI185664, PI262491, Pouyastruc (PI120023), PX-20 (N.K.), RX-35A (Asgrow), San Xavier (PI218184), Spancross (L.M.), Sugar King (N.K.), Texas Native Dent (PI414182), White Midget (0560), Yellow Horsetooth (75985), and Yukovarski Zulan (PI184278).

Virus was not recovered from 23 plants of cultivar Zorat corn (PI227398).

TABLE 2. ELISA test of Washington barley yellow dwarf virus (BYDV) isolates from corn with New York strain-specific antiserum[a]

Sample[b]	ELISA reading (A_{405}) with PAV-specific antiserum[c]
Fresh leaves	
BYDV-inoculated corn XL45A[d]	0.270
Corn field isolate C-1 in barley[e]	0.230
Corn field isolate Pride 110 in barley[e]	0.168
Corn field isolate Jubilee in barley[e]	0.190
Acetone powders	
BYDV-inoculated corn IXL4[d]	0.000
Corn field isolate 15-S[f]	0.000
BYDV-inoculated barley[d]	0.690
Uninoculated barley[g]	0.004
ELISA controls	
Healthy barley	0.000
NY PAV-inoculated	0.680
Buffer	0.000

[a] Tested by W. F. Rochow, Cornell University, Ithaca, NY.
[b] Tissue (3 g) ground in liquid N_2, then in phosphate-buffered saline plus Tween-20, and finally chloroform clarification.
[c] PAV (*padi-avenae*) is the vector-nonspecific strain of BYDV.
[d] Greenhouse-grown and experimentally inoculated with Washington BYDV isolates by transmission with *R. padi*.
[e] BYDV field isolates transferred to cultivar Luther barley by *R. padi*.
[f] Frozen leaves of BYDV-infected field-grown corn.
[g] Frozen leaves of greenhouse-grown cultivar Luther barley.

DISCUSSION

Natural weed and cultivated grass hosts of BYDV and its vectors have been implicated as major virus-vector sources in certain grain growing areas (4,14). Such hosts are scarce in eastern Washington during July and August due to the arid nature of the region. Although many known weed hosts resume growth after fall rains, aphid infestations of fall-planted grains have already occurred; therefore, these weeds do not appear important in BYDV disease epidemiology in the Columbia Basin. The results of this study, however, indicate that corn grown throughout the summer in the vicinity of potential winter wheat and other small grain fields is an important oversummering reservoir of both the BYDV and an important virus vector, *R. padi*.

Corn has been experimentally infected with BYDV in greenhouse studies but is immune to most isolates (1,9,14,15,21,23). Field-grown, but experimentally inoculated corn showed decreases in height, stalk diameter, and number of ears (15). Though Kieckhefer et al (11) reported a 2% residual virus level in aphids collected from midwest corn fields, the source from which aphids actually acquired the virus was undetermined. Therefore, we believe this is the first report of BYDV recovery directly from naturally infected, but symptomless field corn. However, the source(s) of BYDV inoculum for virus-infested field corn remains unidentified.

The Washington BYDV corn isolates are designated PAV-like, vector-nonspecific isolates since they react homologously with NY-PAV-sera (vector-nonspecific) in the ELISA test (Table 2) and heterologously with antisera to three distinct NY-vector-specific BYDV strains (RPV, MAV, and RMV) (2). Additionally, the isolates are designated as vector-nonspecific because all three Washington-derived grain aphid species were able to experimentally transmit the corn isolates to barley in greenhouse tests. Similar patterns of both aphid transmission and/or serological reactivity occurred previously with PAV-like vector-nonspecific Washington wheat isolates (5,19).

Based on inoculations using aphid vectors, Washington PAV-like isolates systemically infected many corn cultivars previously cited as immune or resistant (9,14,16,21,23). The lack of symptoms under field conditions suggests that corn is generally a symptomless host of BYDV in the Columbia Basin. However, symptom development may be temperature related. In greenhouse tests using corn cultivars commonly grown in the Columbia Basin (and known to be symptomless under field conditions), the development of foliar symptoms seemed to be favored by low (18–25 C vs 25–30 C) temperatures. Additionally, foliar symptoms appeared sooner and were more prominent in plants maintained at cooler temperatures (18–25 C) (2). Further, comparably inoculated corn plants, transplanted to field plots during the summer of 1980, did not develop distinct foliar symptoms like those observed in greenhouse-maintained plants (2).

In the 1980–1981 studies, *M. avenae* was the only aphid initially associated with BYDV-infected corn fields. By midsummer, only *R. padi* could be found in corn fields, and extremely high populations were observed (1,000 per plant) (2). Likewise, *R. padi* was the aphid initially associated with BYDV-infected winter wheat seedlings planted adjacent to virus-infected corn fields. The relative importance of corn as a BYDV reservoir in eastern Washington with respect to winter grains is difficult to assess since virus infection of small grains occurs statewide, though irrigated corn is grown predominantly in the Columbia Basin. Though disease incidence in small grains has increased, a direct correlation with increased corn acreages remains speculative. We suspect, however, that the virus moves directly from infected corn to fall-planted wheat seedlings, since *R. padi* and the BYDV were recovered simultaneously from wheat fields planted adjacent to *R. padi* infested, BYDV-infected corn. Though aphid migration studies were not undertaken, the potential exists for the migration of viruliferous *R. padi* from virus-infected, Columbia Basin-grown wheat to surrounding dryland wheat fields. Whether the BYDV and/or vectors were capable of utilizing corn as a host previously, or if recent adaptations in host range have occurred, remains unknown. Examination of long-distance and intrafield migration patterns are needed statewide to determine virus sources and flight routes of viruliferous aphids.

The discovery of the role of corn in the epidemiology of BYDV was hindered by three major factors which may affect the assessment of corn as a BYDV reservoir in other regions. First, foliar symptoms were not associated with naturally infected corn and appear to be low-temperature-dependent (2). Second, analyses by ELISA testing are unreliable due to high background readings when field-grown corn tissue is the virus source. Therefore, time-consuming aphid transmission tests are still the most reliable assay for BYDV. Third, unlike field situations, some grain aphid species did not survive well on corn in the greenhouse. Therefore, the efficient assessment of BYDV incidence in corn and the elucidation of its significance as a symptomless virus host will be hampered until a more rapid and sensitive assay method is developed.

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