Barley Yellow Dwarf Virus Infection in Maize

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Accepted for publication 28 February 1977.

ABSTRACT

STONER, W. N. 1977. Barley yellow dwarf virus infection in maize. Phytopathology 67: 975-981.

Barley yellow dwarf virus (BYDV), isolated from field-infected oats collected near Davis, South Dakota, was transmitted to and recovered from 6 of 18 cultivars of corn (maize) using the bird-cherry oat aphid, Rhopalosiphum padi, as the vector. Systemic infection of BYDV in inoculated corn plants was demonstrated by serial transmission of the virus to barley from leaves that emerged after inoculation. A detailed description of the definitive symptoms of barley yellow dwarf disease in reactive corn cultivars is given. Symptomless carrier cultivars and individual symptomless infected plants were detected by recovery of the virus to

susceptible, reactive, Black Hulless barley (C.I. 666). Symptoms of BYD in corn were slow to develop, appearing first in the lower mature leaves rather than in the younger whorl leaves. Symptoms developed progressively up the stalk in the alternately developing leaves of the bottom one-third to one-half of the plant. Barley yellow dwarf virus was recovered from naturally infected corn plants taken from the field. The importance of corn as a possible virus reservoir in the epidemiology of the barley yellow dwarf disease is discussed.

Additional key words: circulative plant virus, aphid vector, Hordeum vulgare L., Zea mays L.

Barley yellow dwarf has been recognized formally as an infectious disease of various cereal grains and grasses since the virus causative agent was recognized and transmission of it was reported by Oswald and Houston (12) in 1951 and (13) 1953. It is now known from the investigations of Takeshita in 1956 (25) and others that the same virus causes a disease of oats commonly called red leaf or purple leaf. Rademacher and Schwarz (15) used the binomial *Hordeumvirus nanescens* for the virus in their presentation on red leaf of oats to eliminate doubt of the identity of the viral pathogen. The terms "barley yellow dwarf" (BYD) and "barley yellow dwarf virus" (BYDV) will be used in this discussion as they have become most widely accepted in the United States of America to designate the disease and its infectious causative viral agent. Elsewhere the terms "cereal yellows" or "cereal yellow dwarf" and "cereal yellow dwarf virus" frequently are used to denote BYD and BYDV.

The word corn in this discussion will refer to Indian corn or maize, Zea mays L.

Barley yellow dwarf virus has been proven to be a cosmopolitan pathogen (3, 19) existing in several strains that vary in insect vector specificity (2, 8, 16, 17, 18, 26, 28). Periodically BYDV has caused severe economic losses in cereal grains in the United States of America. Murphy et al. (11) reported the extensive epidemic of BYD in 1959 and indicated that losses were very heavy in oats and less so in barleys. The areas of heaviest infection of barley with BYDV in 1959 included significant portions of the best corn-producing areas in Illinois,

Indiana, Iowa, Kansas, Minnesota, Missouri, Nebraska, Ohio, Oklahoma, and South Dakota. Nevertheless, there were no reports of BYDV infections in corn in 1959 or any previous or later indication that any infections of BYDV have occurred naturally in corn.

Host range studies such as those of Oswald and Houston (14), Bruehl and Toko (4), and Watson and Mulligan (27) are conflicting or indicate that corn is susceptible to BYDV only under highly specific experimental conditions.

Allen (1) in 1957 reported suspected experimental infection of Golden Bantam sweet corn with BYDV. He described reddish symptoms that developed in the leaves of inoculated test plants, but indicated that he was unable to recover the virus from corn to corn, corn to barley, or corn to oats in serial transfers. Watson and Mulligan in England (27) reported that transmission of a Kentish strain of BYDV to Natal White Horse Tooth corn produced a stunting in the test plants and that they were able to recover the virus serially. The same type of experiments using Golden Cross Bantam sweet corn as the test host was negative.

Recent problems with corn viruses in the United States have caused many investigators, particularly those taking part in extensive field surveys, to critically examine hundreds of abnormal corn plants individually (24). General symptoms in corn such as yellowing, reddening, stunting, and malformation have been seen frequently. In many cases these symptoms could not be associated with known pathogens or pests, or disorders of climate, or nutrition. Microscopic examination, attempts to culture microorganisms, and mechanical and biological attempts to transmit a virus all failed to indicate the cause of the symptoms. This has led to the question of whether or not corn is a host of BYDV in the United States and the

initiation of these experiments in an attempt to clairify this point.

MATERIALS AND METHODS

Standard greenhouses and laboratory equipment were used throughout the study.

The seeds used were obtained from commercial sources with the exception of the Black Hulless barley (C.I. 666) which was produced in an insect-free isolation greenhouse, and the Horse Tooth corns, which were obtained from the U.S. Dept. Agric. Plant Introduction Center, Ames, IA 50010.

Experimental test plants and food plants used for rearing insects were produced by direct seeding into a standard potting soil mixture in terra-cotta pots. Seeds of the barley plants used for controls and in virus recovery trials were pipped then planted singly in standard potting soil in $5.5 \times 5.5 \times 6$ -cm tapered peat pots and then grown to appropriate size in tin trays.

After manipulation, experimental plants were held in the greenhouse or in controlled temperature growth chambers at 20 C with a 14-hr photoperiod and light intensity of 2,690 to 3,766 lux (2,500 to 3,500 ft-c). These conditions induce maximum symptoms of BYD in wheat (5). The plants were watered daily and fertilized at intervals sufficient to maintain good growth.

Virus free, mixed clone, bird-cherry oat aphids, Rhopalosiphum padi (L.), used in the experiments were produced in seed colonies derived from nymphs taken from field-collected stem mothers isolated in Stender dishes on damp filter paper. Primary colonies of both viruliferous and nonviruliferous aphids were reared in large (36×10 -cm) tubular, ventilated, nitrocellulose plastic cages on healthy greenhouse-grown food plants. Each stock colony used in each test series was checked for infectivity, noninfectivity, preinfectivity, or postinfectivity as the experiments warranted.

Most transfers of aphids were made with a camel's-hair brush. Insects were caged on virus-source plants or test plants in small $(23 \times 4\text{-cm})$, tubular, ventilated, cellulose butyrate plastic cages similar to those used in previous studies or were fed on plant pieces from the source plants placed on damp filter paper in finely screened ventilated plastic containers. Insects were also feed directly on field plants or larger test plants in magnetic leaf cages similar to those described by Kaloostian (9).

The primary virus source for greenhouse studies, designated the Davis isolate, was originally recovered from diseased oat plants taken from a field near Davis, South Dakota. This Davis isolate was similar to the isolate designated PAV-RP by Rochow (20). Characterization and indentity of the virus was determined by aphid vector transmission trials like those conducted by Rochow (20) with the four aphid vector species. Subsequent virus sources were plants subinoculated from the primary source, or were proven infected plants from the experiments in progress.

All positive transmissions of BYD, determined by symptom expression, were confirmed by serial transmissions to Black Hulless (C.I. 666) barley. Symptomless plant carriers of the virus were confirmed in the same manner.

The greenhouses throughout the experiments were

kept free of aphids by fumigation with nicotine and tetraethylpyrophosphate pressure fumigators as evidenced by the fact that all barley control plants in all tests in all series remained healthy and free of BYD symptoms.

RESULTS

Symptoms of barley yellow dwarf in corn.—Experimental infections.—The symptoms of BYD experimentally induced in corn at the Northern Grain Insects Research Laboratory were similar to the brief, generalized, unconfirmed syndrome given by Allen (1) and those briefly indicated by Stoner (23). Three to 6 wk after feeding viruliferous Rhopalosiphum padi(L.) on two- to three-leaved seedlings of susceptible corn cultivars, a dark-red to purple coloration with an irregular advancing margin developed on the tips of the plumule and the oldest leaf or two. The incipient symptom may be easily overlooked since the color change was quite subtle and initially involved only 4-6 mm of the tip or one side of the leaf. The coloration intensified and 2-4 mm more of the leaf laminae were affected in a basipetal direction in succeeding days. The area involved in the reddish-purple coloration progressively developed either as an interveinal striping or as a broad transverse zone with an irregular advancing margin across the veins that was propagated toward the base of the affected leaves. In some cases, coloration developed asymetrically on one border of the lamina without crossing the midrib. Every 2-4 days, after the appearance of initial symptoms in the first leaves, similar symptoms appeared in the next higher alternate younger leaf in a regular sequence until several, generally four to eight, leaves were affected. The total area of the lamina of any given leaf involved in the red-to-purple coloration varied considerably, but it was rare to see more than the terminal two-thirds of a leaf colored, and the area was usually less. Occasionally, however, the entire plumule and/or first small true leaf or two were entirely red.

The red coloration never has been noted in the young center growth in the whorl. Neither was there any development of streaking, mottling, or a mosaic pattern such as those seen with other known virus diseases of corn. The center growth remained quite normal in coloration with no indication of etiolation in the whorl or any striping or streaking of the fully expanded leaves as often may be seen in plants with trace element deficiencies.

At about the time the tassel developed in the whorl, just before extension, the lowest leaves showing the red-purple coloration began to dry at the tips and margins. This drying was chronologically progressive in about the same time sequence as the red foliar symptoms and followed the development of the coloration symptom in 6-8 days even though adequate moisture was continuously available. By the time the tassel had completely emerged and extended, the entire range of symptoms occasionally could be seen in a single infected plant, from the bottom leaf or two being completely dried or "fired", to tip reddening in the leaves about one-quarter to one-third up the stalk with the portions of the plant above that appearing normal. The overall aspect of the diseased corn plants with a completely developed

syndrome of BYD was similar to that of corn suffering a phosphorus deficiency as figured in color and described by Hoffer (7).

A small degree of overall stunting was observed in experimentally infected corn. This stunting was proportional in its reduction of size; so, unless check plants are available for comparison, the symptom easily could be overlooked in the field or in lines or cultivars that are otherwise symptomless carriers of the virus. In no case was the stunting alone severe enough to be considered a definitive or diagnostic symptom. The observation of proportional stunting, however, confirms the report of Watson and Mulligan (27) that stunting can be caused by

BYDV infections in corn since the virus was easily and repeatedly recovered both from plants showing clear foliar symptoms and from otherwise symptomless slightly stunted test plants. In the recovery trials the virus was transmitted easily to barley with nonviruliferous aphids placed in magnetic leaf cages and then fed on several locations over the plants.

Field symptoms.—Foliar symptoms of BYD in corn in the field, whether the plants were inoculated from known virus sources or naturally infected, closely resemble those previously described for experimental inoculations in the greenhouse or growth chambers. Some naturally infected field plants were much slower in exhibiting the initial

TABLE 1. Reaction of corn (maize) cultivars to the Davis isolate of barley yellow dwarf virus (BYDV) transmitted by lots of 10 Rhopalosiphum padi

Corn cultivars inoculated	Results	Symptoms	Virus recovery trials	Bulked serial transmissions
Aunt Mary's (Vaughn's)	15/15 ^a	FRD^b	30/30°	5/5°
Bouque	0/15	None	0/30	0/5
Carmel Cross	0/15	None	0/30	0/5
Dixie Blend	0/15	None	0/30	0/5
Early Golden Midget (Hart's)	15/15	FRD	30/30	5/5
Early Sunglow	$0/13^{d}$	None	0/26	0/5
Evergreen Stowell's	0/15	None	0/30	0/5
Golden Beauty	$0/14^{d}$	None	0/28	0/5
Golden Cross Bantam	0/15	None	0/30	0/5
Golden Sunshine (Ferry-Morse)	13/15	FRD	25/26	5/5
Marcross	0/15	None	0/30	0/5
Rainbow (Burpee's)	11/15 ^e	FRD,S	30/30	5/5
Silver Cross Bantam	0/15	None	0/30	0/5
Spancross	0/15	None	0/30	0/5
Sugar King	0/15	None	0/30	0/5
White Horse Tooth	0/ 8 ^f	S	14/16	5/5
White Midget	0/14	None	0/28	0/5
Yellow Horse Tooth	0/11 ^f	S	22/22	5/5

^aIn the indicated fractions, the numerator is the number of plants infected with BYDV; the denominator is the number of plants inoculated.

TABLE 2. Transmission of barley yellow dwarf virus from corn, by lots of 10 noninfective *Rhopalosiphum padi* using both lower leaf tissues from several plants showing frank symptoms of BYD and symptomless whorl leaf tissues from the same plants as virus sources.

		Red symptom leaf tissue			Symptomless whorl leaf tissue			
	↓ ^a	Test plant	1	1	Test plant	ļ		
BYDV-infected corn cultivar	Corn ^b	Serial virus recovery ^c	↓ Barley ^d	↓ Corn ^b	Serial virus recovery ^c	↓ Barley ^d		
Aunt Mary's	40→	80/80°: 75/76	← 76	18→	36/36 : 32/32	←32		
Golden Midget	18→	36/36 : 34/36	←36	16→	32/32 : 30/32	←32		
Golden Sunshine	39→	76/78 : 78/78	← 78	23→	34/36 : 16/18	←17		
Rainbow	33→	62/66 : 64/66	←33	13→	26/26 : 12/12	←12		
Totals	130	254/260:251/256	223	70	128/130: 90/94	:93		

^aArrows indicate serial (successive) transfers of BYDV.

^bFRD = Foliar reddening followed by drying; S = Slight stunting.

^cTest plants were C.I. 666 (Black Hulless) barley.

dTest plants died in these trials.

Four plants proved to be symptomless carriers of BYDV.

All of the test plants available due to poor seed germination.

^bEarly Golden Midget used as corn test cultivar.

^{&#}x27;Cereal introduction C.I. 666 (Black Hulless) barley used in all "serial virus recovery" tests.

^dCereal introduction C.I. 666 (Black Hulless) used as barley test cultivar.

In all fractional notations the numerator is the number of test plants infected, the denominator the number of plants inoculated.

purpling or reddening symptom in the lower leaves, and not as many of these leaves were necessarily affected before tassel expansion. However, once symptom development was initiated, the sequence of the syndrome progressed at a more accelerated rate in the field than in the experimentally infected plants in the greenhouse or growth chambers. Therefore, drying or "firing" of the reddened lower leaves occurs sooner and may be more severe in field-infected plants, especially if there is moisture stress.

No other abnormalities or distortions such as those described for Wallaby Ear Disease (21) or Maize Rough Dwarf (6) were observed in corn infected with BYDV, and there was no suppression of parenchymal tissue in the laminae of the affected leaves as is often seen in infections of cucumber mosaic virus and certain of its variants (22) in corn.

Cultivar trials.—Sweet corn plants usually are smaller than field corn plants at maturity and are consequently more manageable under pot culture. For this reason it was decided to test a wide spectrum of commercially available sweet corn cultivars for BYVD susceptibility and to include Golden Bantam and White Horse Tooth field corn both of which experimentally had been proven susceptible to the virus. A limited amount of Yellow Horse Tooth seed became available so it was added to the test. Eighteen cultivars were tested three times using five plants per test, three different virus source plants, and 10 viruliferous R. padi per plant. Two recovery tests were made from each test plant to barley with 10 nonviruliferous R. padi 10 wk after inoculation, even though symptoms of BYD were not showing in all of the plants. Finally, serial test transmission tests were made from the recovery barley plants to five more barley plants using nonviruliferous *R. padi* fed on portions of the recovery plants and then transferred in lots of 10 to each of the five bulk serial transmission barley plants. The serial recovery tests was made to satisfy Koch's Postulates (modified for virus studies). The results of the three tests are summarized in Table 1.

Four of the eighteen cultivars tested, Aunt Mary's, Early Golden Midget, Golden Sunshine, and Rainbow (a multicolored, ornamental corn), were susceptible to BYDV infection and produced clear-cut foliar symptoms of the disease. White and Yellow Horse Tooth were susceptible to the virus but manifested only very slight stunting. No symptoms were observed on any other of the cultivars tested nor was BYDV recovered from them. See Table 1.

Systemic infection of barley yellow dwarf virus in corn.—Once the symptoms of BYD in corn were known to be relatively localized in the lower leaves of the plant with no apparent symptoms in the young center growth of the whorl, the question of whether or not there was entire systemic invasion by the virus arose. Therefore, virus recovery tests were made from the plants showing clear foliar symptoms in subsequent experiments. Nonviruliferous R. padi were fed on red-purple tip pieces of leaves taken from the fourth leaf upward of each plant (to avoid the plumule and first two true leaves which had been subjected to inoculative feeding of vectors) and on tip pieces from the three or four unfurling whorl leaves (when they were available). After 48 hr of feeding, these aphids were then transferred in lots of 10 to a single healthy corn test seedling (cultivar Early Golden Midget) and to two barley test seedlings where they fed for another

TABLE 3. Alternating serial transfers of barley yellow dwarf virus (BYDV) to different host plants using *Rhopalosiphum padi* as the vector. Positive transmission readings are based on frank symptom expression in the test plants confirmed by recovery of the virus to barley indicator plants

Experiment no. and BYDV source plants		Serial virus transfers (left to right)						
Experiment 1		Barley	-	Corn ^b	-	Corn	-	Barley
Aunt Mary's	-	10/10 ^c		16 ^d		24/29		38/38
Early Golden Midget		10/10		9		16/18		23/26
Golden Sunshine		10/10		23		40/46		65/65
Rainbow		10/10		15		18/36		45/46
Experiment 2		Barley	-	Corn	-	Barley	→	Barley
Aunt Mary's	•	10/10		16		59/64		58/60
Early Golden Midget		5/5		5		20/20		$13/14^{f}$
Golden Sunshine		10/10		24		85/96		87/96
Rainbow		10/10		12		43/48		37/48
Experiment 3		Barley	-	Corn		Oatse		Barley
Aunt Mary's	•	10/10		16		61/64		56/60
Early Golden Midget		10/10		5		20/20		$13/14^{\rm f}$
Golden Sunshine		10/10		24		89/96		91/96
Rainbow		10/10		12		43/48		$37/48^{8}$

^aCereal introduction C.I. 666 (Black Hulless) barley used as test host throughout the experiments.

^bCultivar Early Golden Midget corn was used as test host throughout the experiments.

^{&#}x27;In fractional representations numerators equal the number of plants infected, the denominators the number of plants inoculated.

Infected corn plants with frank foliage symptoms.

^{&#}x27;Test cultivar was Clintland #60 oats.

One test barley plant died in this series.

^gTwo test barley plants died in this series.

48 hr. When symptoms appeared in these test plants (about 2 wk for the barley and 8-10 wk for the corn) serial transfers were made again with nonviruliferous *R. padi* in lots of 10 to a pair of test barley plants from each corn plant and as a bulked trial from each pair of the first transfer barley plants.

Transmissions from corn to corn to barley and from corn to barley to barley occurred in a range of 90-100% in both the symptom and no symptom leaf tests. The data of these tests are summarized in Table 2. One-hundred and thirty individual plants of four cultivars used in the test were carrying BYDV in the tissues of symptomatic leaves. and seventy of the plants that afforded symptomless whorl leaves were also carrying the virus in these tissues. The virus was universally transmitted to both corn and barley and then to serial recovery barley plants. The differential numbers of tests indicated in Table 2 resulted from differences in available numbers of virus source plants, leaves available from the source plants, and the number of aphid vectors surviving the feeding periods. Occasionally, there was a skip on a single plant of the paired barleys, but the remaining plant always was positive. Two test corn plants and four test barleys died during the experiments.

Alternation of host plants of barley yellow dwarf virus.—Since Allen (1) was not able to serially transfer or recover BYDV from corn test plants and Watson and Mulligan (27) had experienced both positive and negative results in BYDV recovery from different corn cultivars, there was ambiguity in relation to BYDV transmission to corn.

Transmission of the Davis isolate of BYDV with R. padi had become relatively easy and consistent in the four indicator cultivars (Aunt Mary's, Early Golden Midget, Golden Sunshine, and Rainbow) that were used in these studies. Moreover, transfers of the virus from barley to corn and back to barley had confirmed the positive results of Watson and Mulligan (27) and firmly established the fact that at least these cultivars, under experimental conditions at Brookings, were susceptible to BYDV infection.

A question, however, still remained. Could passage of the virus through corn have an attenuating effect on the virus? If so, this could at least partially explain eariler failures to recover the virus from known experimentally inoculated corn plants and corn plants from the field suspected of being infected with BYDV.

In an attempt to clarify the question of virus attenuation, three experiments were conducted in which cereal host plants of the virus in different genera were alternated in serial transfers. A summary of these tests is given in Table 3. In each of the three separate experiments, BYDV consistently was transmitted with *R. padi* from all four of the test corn cultivars. Transmission was effected serially in three sequences: (i) corn to barley to corn to barley to barley, and (iii) corn to barley to corn to oats (cultivar Clinton #60) to barley. Symptoms were just as pronounced and severe in the final barley test plants as they were in the initial infectivity barley check plants.

Natural infection of corn with barley yellow dwarf virus.—Results with corn in the foregoing experiments tend to agree with earlier observations made by Watson

and Mulligan (28) in small (cereal) grains; i.e., symptom expression "depends upon the age of the plant at the time of infection, the time of observation (after inoculation), and, probably, on the strain or isolate of the virus used." They also suggested that cultivars of small grains differ in resistance to infection, symptom expression, and to the degree of injury caused by the virus. Such was also the case with the corn cultivars used in the foregoing experiments, at least in terms of differences that could be observed in resistance to infection and symptom expression.

It was decided, therefore, to determine whether natural infections of BYDV did occur in the field at Brookings. Four, 24-plant rows of the cultivars Aunt Mary's, Early Golden Midget, Golden Sunshine, and Rainbow (known to develop definitive foliar symptoms of BYD) were planted in a repeated sequence one after the other in random skips and blank rows in the breeding line corn nursery after the breeding corns were well started. Four seeds per hill were planted and, after sprouting, all but the best seedling in each hill were rogued. This left six plants of each cultivar replicated four times in four rows, or a total of 24 plants of each cultivar randomly dispersed over the experimental block. These plants were observed weekly and received the same care as that given to the entire nursery.

Foliar symptoms of BYD began to appear in a few of these plants when the tassels were beginning to emerge. As symptoms developed in the individual plants, nonviruliferous *R. padi*, in small magnetic leaf cages, were put on each plant on five different leaves. After these insects had fed for 48 hr they were brought into the laboratory and transferred in lots of 10 to barley recovery seedlings for a 48-hr feeding period. In most cases there were sufficient aphids alive to set up five recovery barley plants, but in two trials only enough aphids survived for four and in another trial there were only enough for three. All of the barley recovery seedlings were infected with BYDV, and bulked serial transfers from each group of barley recovery plants to a successive pair of barley seedlings were positive.

Natural field infections of BYDV had occurred in two of 24 Aunt Mary's, three of 24 Early Golden Midget, two of 24 Golden Sunshine, and two of 24 Rainbow. Barley yellow dwarf virus also was recovered in a similar manner from a single plant each of Golden Hybrid Blend and Breeding Line #3505 (a field corn) from the same nursery after they were observed to have typical BYD symptoms. Natural infections of BYDV in corn occurred in the tests in nine of 96 experimental field plants and in two other field plants scattered randomly in the nursery plot.

DISCUSSION

The data obtained in the experiments reported herein indicate that the Davis isolate of BYDV can easily and consistently be transmitted to, and recovered from, several commercially available corn cultivars by the bird-cherry oat aphid, $R.\ padi.$ "Wild" BYVD, with an unknown vector or vectors, in the field at Brookings, South Dakota, was found to infect corn at a low level[natural BYDV infection of $\pm 2\%$ has been demonstrated in cereal grains in eastern South Dakota in nonepiphytotic years (10)] and could be transmitted

easily to barley using R. padi as the vector.

The reported BYDV infections in corn were systemic and caused definitive foliar symptoms in some cultivars but were symptomless in others. The majority of the cultivars tested, however, were immune to BYDV. When symptoms of BYD are expressed in a susceptible corn cultivar they occur in the older leaves rather than in the younger whorl leaves. This is the reverse of the usual situation in which systemic symptom expressions are most severe in the younger, more rapidly growing tissues. Several factors, alone or in combination, could account for this reversal: (i) the unusually long time lapse after inoculation before symptoms are expressed could indicate a slow or sparing buildup of virus titre; (ii) late symptom expression could be caused by an inherent characteristic of the particular (Davis) isolate of BYDV; (iii) anatomically, the so-called older leaves of the test corn plants were chronologically the ones in the most rapid state of growth at the time of infection and therefore may be the first to have tissues developing a capability for symptom expression; (iv) plant culture conditions during the developmental period after inoculation may not have optimal (relatively cool temperatures favor symptom expression of BYD in wheat (5), but are not necessarily optimal for corn growth); and (v) genetic factors in different corn cultivars may vary for susceptibility and/or symptom expression resulting in a range of reactions from susceptible to immune. Particular corn cultivars could exhibit only partial or differential resistance and be susceptible to BYDV infection only in the earlier seedling stages of growth.

Since we now know that certain cultivars of corn are susceptible to BYDV, and natural infections of the virus in corn can occur in the field, why hasn't BYD been found and reported previously in commercial corn plantings? Several factors could account for this, especially if BYDV infections were at a very low level. Some of these are: (i) corn cultivars (hybrids) currently in use may be symptomless tolerant carriers of the virus or may even be immune; (ii) a proper combination of virus, vector, and corn cultivar may not occur commonly, so infection is either rare or does not take place; (iii) the long time interval necessary for BYD symptoms to develop in corn, plus the similarity of the symptoms to others caused by well known factors, have caused BYDV infections to be ignored or overlooked; (iv) the timing of the movement of BYDV in a proper vector for successful inoculation may be out of phase with normal corn culture, so infection does not occur or may be relatively rare; and (v) relatively high summertime temperatures may result in masking of the symptoms of BYD in corn.

Whatever the reason that natural infection of BYDV in corn has not been reported previously, extensive, more critical, surveys of commercial corn plantings may yield information, not only for a better understanding of the relationship of BYDV to corn, but may also give a clearer picture of what is happening in the field to initiate epidemics in the cereal grains. A positive determination of infection in field plants must be coupled with the survey to confirm the indexing method used in the survey. Another line of investigation that should be pursued is testing of currently planted field corn cultivars and inbred lines now used for hybridization, for susceptibility to BYDV.

A massive reservoir of BYDV, postulated by some investigators as necessary to account for epidemics of BYD in cereal grains, has never been found either in migrating aphid vectors, native grasses, or forbs in the epidemic areas. Is it possible that such a reservoir has been concealed in symptomless carriers in commercial row crops? If so, corn may be a part of such a reservoir or, at least, play a part in summer carry over of BYDV and subsequent fall infection of winter small grains.

LITERATURE CITED

- ALLEN, T. C. 1957. Symptoms of golden bantam corn inoculated with barley yellow dwarf virus. Phytopathology 47:1 (Abstr.).
- ALLEN, T. C. 1957. Strains of the barley yellow-dwarf virus. Phytopathology 47:481-490.
- BRUEHL, G. W. 1961. Barley yellow dwarf, a virus disease of cereals and grasses. Am. Phytopathol. Soc. Phytopathol. Monogr. 1:5-52.
- BRUEHL, G. W., and H. V. TOKO. 1957. Host range of two strains of the cereal yellow-dwarf virus. Plant Dis. Rep. 41:730-734.
- FITZGERALD, P. J., and W. N. STONER. 1965. Effect of temperatures, light intensities and photoperiods on yellow dwarf symptoms in wheat. Crop Sci. 5:201-203.
- HARPAZ, I. 1972. Maize rough dwarf: a planthopper virus disease affecting maize, rice, small grains, and grasses. Published by Israel Universities Press (Keter Publishing House, Ltd., Jerusalem). 251 p., 63 fig.
- HOFFER, G. N. 1941. Deficiency symptoms of corn and small grains. Pages 55-98 in G. Hambidge, ed. Hunger signs in crops. The American Society of Agronomy and the National Fertilizer Association, Washington, D.C. 327 p.
- JEDLINSKI, H., and C. M. BROWN. 1965. Cross protection and mutual exclusion by three strains of barley yellow dwarf virus in Avena sativa L. Virology 26:613-621.
- KALOOSTIAN, G. H. 1955. A magnetically suspended insect cage. J. Econ. Entomol. 48:756-757.
- KIECKHEFER, R. W., and W. N. STONER. 1967. Field infectivities of some aphid vectors of barley yellow dwarf virus. Plant Dis. Rep. 51:981-985.
- MURPHY, H. C., et al. 1959. The epidemic of barley yellow dwarf on oats in 1959. Page 316 in Plant Dis. Rep. Suppl. 262. 377 p.
- OSWALD, J. W., and B. R. HOUSTON. 1951. A new virus disease of cereals transmissible by aphids. Plant Dis. Rep. 35:471-475.
- OSWALD, J. W., and B. R. HOUSTON. 1953. The yellowdwarf virus disease of cereal crops. Phytopathology 43:128-136.
- OSWALD, J. W., and B. R. HOUSTON. 1953. Host range and epiphytology of the cereal yellow dwarf disease. Phytopathology 43:309-313.
- RADEMACHER, B. VON, and R. SCHWARZ. 1958. Die Rotblattrigkeit oder Blattrote des Hafers - eine Viruskrankheit (Hordeumvirus nanescens). Z. Pflanzenkrankh. (Pflanzenpathol.) Planzenschutz 65:641-650.
- ROCHOW, W. F. 1959. Differential transmission of barley yellow dwarf virus from field samples by four aphid species. Pages 356-360 in Plant Dis. Rep. Suppl. 262. 377 p.
- ROCHOW, W. F. 1959. Transmission of strains of barley yellow dwarf virus by two aphid species. Phytopathology 49:744-748.
- 18. ROCHOW, W. F. 1960. Specialization among greenbugs in the transmission of barley yellow dwarf virus.

- Phytopathology 50:881-884.
 19. ROCHOW, W. F. 1961. The barley yellow dwarf virus disease of small grains. Adv. Agron. 13:217-248.
- 20. ROCHOW, W. F. 1969. Biological properties of four isolates of barley yellow dwarf virus. Phytopathology 59:1580-
- 21. SCHINDLER, A. J. 1942. Insect transmission of wallaby ear disease of maize. J. Austr. Inst. Agric. Sci. 8:35-37.
- 22. STONER, W. N., et al. 1965. A review of corn stunt disease (Achaparramiento) and its insect vectors, with resumes of other virus diseases of maize. U.S. Dep. Agric. Spec. Rep. ARS 33-99, 35 p.
- 23. STONER, W. N. 1965. Studies of transmission of barley yellow dwarf virus to corn (Zea mays). Phytopathology 55:1078 (Abstr.).

- 24. STONER, W. N., et al. 1968. Corn (maize) viruses in the continental United States and Canada. U.S. Dep. Agric. Spec. Rep. ARS 33-118, 95 p.
- 25. TAKESHITA, R. M. 1956. Identity of the oat red-leaf virus with the barley yellow-dwarf virus. Phytopathology 46:436-440.
- 26. TOKO, H. V., and G. W. BRUEHL. 1959. Some host and vector relationships of strains of the barley yellow dwarf virus. Phytopathology 49:343-347.
- 27. WATSON, M. A., and T. MULLIGAN. 1957. Cereal yellow dwarf virus in Great Britain. Plant Pathol. 6:12-14.
- 28. WATSON, M. A., and T. E. MULLIGAN. 1960. Comparison of two barley yellow-dwarf viruses in glasshouse and field experiments. Ann. Appl. Biol. 48:559-574.