Serological Relationship Between Beet Western Yellows and Beet Mild Yellowing Viruses

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ABSTRACT

A possible relationship between beet western yellows virus (BWYV), the most common virus of sugarbeet in the United States, and beet mild yellowing virus (BMYV), the most prevalent virus of sugarbeet in Europe, has long been suspected. Differences between the viruses in regard to symptomology on beets, epidemiology and host range and the lack of a serological test has hampered studies on their relationships. Twelve BMYV isolates from sugarbeet in England were transferred by *Myzus persicae* to *Capsella bursa-pastoris* and studied in regard to host range, membrane feeding, and serology. The BMYV isolates produced a common reaction on certain key indicator hosts. *Beta vulgaris*, *Capsella bursa-pastoris*, and *Claytonia perfoliata* were all susceptible whereas *Raphanus sativus*, *Lactuca sativa*, Brassica pekinensis, and *Brassica rapa* were all immune. Numerous early trials with membrane feeding of BMYV failed and was thought to be another factor pointing to the differences between BMYV and BWYV. However, early in 1971, by use of highly concentrated preparations, BMYV was transmitted by *M. persicae* which had acquired virus by feeding on purified preparations through artificial membranes. In density-gradient columns, the positions of infectious zones of BMYV corresponded closely with those in gradients containing BWYV. Differences in transmission efficiency through membranes between common BWYV isolates and the BMYV isolates tested seems to be related to virus concentration differences in their hosts. Antisera prepared against 10 strains of BWYV from the United States and England neutralized infectivity of all isolates of BMYV tested. Antisera prepared against the English isolates of BMYV neutralized the infectivity of the American and English BWYV strains, and also the BMYV isolates. The results of these investigations establish a close serological relationship between BWYV from the United States and BMYV from Europe.

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Reports of yellowing of beet fields are recorded from the Netherlands as early as 1912 (2) and from Denmark in 1914 (13). Yellows was described by Quanjer (14) in 1934, who had observed the yellowing disease on sugar and fodder beets since 1910. The implication of a virus as the causal agent was made by Roland (16) and Van Schreven (19), who showed that the yellowing disease agent was transmitted by aphids.

All virus induced yellowing at this stage was termed "virus yellows." Watson (20), in 1940, positively identified the disease in England and termed the disease (sugar) "beet yellows." In 1948, Clinch and Loughnane (1) discussed the occurrence of two mild yellowing viruses in Ireland, but concluded that they were both strains of the beet yellows virus.

Watson (21) in 1951 first pointed out the possibility that "virus yellows" may be induced by a complex of yellowing diseases when she noticed that the mild yellowing virus from Ireland did not precipitate specifically with beet yellows virus antiserum.

Based on lack of a serological response to beet yellows virus antiserum, Russell (17) detailed the widespread distribution and economic significance of a "second" beet yellowing virus (sugar) beet mild yellowing virus (BMYV) in Europe. Duffus (3, 4) characterized a "second" economically significant beet yellowing virus in the United States with his description of (radish yellows virus) beet western yellows virus (BWYV).

Beet western yellows virus subsequently has been shown to be the most common virus of sugarbeet in the United States, and beet mild yellowing virus the most prevalent virus of beet in Europe.

Serological investigations of virus isolates from wild plants and lettuce in Britain have subsequently shown

that BWYV occurs in Europe and is serologically related to a virus of turnip in Europe, turnip yellows virus (10, 11).

Differences in symptoms, host range, membrane feeding, and epidemiology between BWYV and BMYV have hampered studies on their relationships. This paper describes investigations (1970-1974) of the relationships between 12 BMYV isolates from England and BWYV isolates from England and the United States.

TABLE 1. Transmission of beet western yellows virus (BWYV) and beet mild yellowing virus (BMYV) by single green peach aphids

Test No.	Number of shepherd's-purse seedlings infected out of 50 inoculated from the indicated source[a]	
	BWYV	BMYV
1	26	9
2	29	12
3	23	7
4	16	6
5	32	14
6	26	10
7	25	8
8	20	7
9	24	11
10	22	9
% transmission	48.6	18.6

[a]BWYV is isolate E-2 from *Capsella* collected from Everton, Bedfordshire, England. BMYV is isolate In from Ingham, England. Nonviruliferous aphids fed on diseased *Capsella* for 24 hours and then on healthy seedlings for 48 hours.

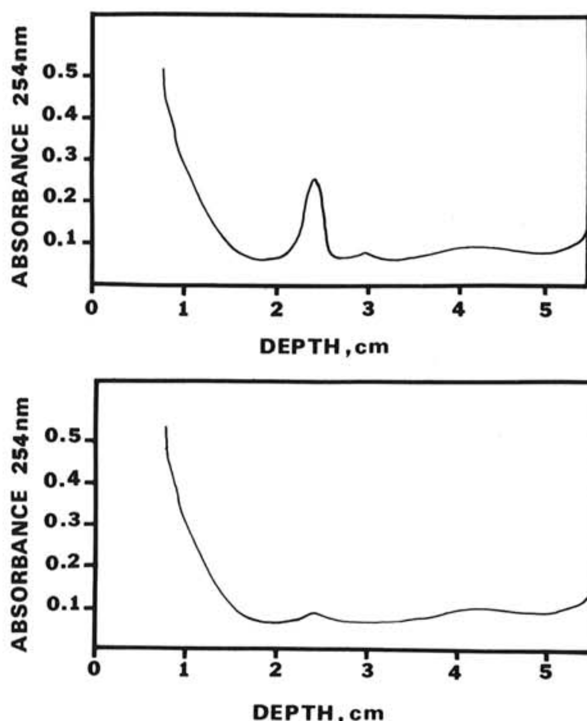

Fig. 1. Scanning patterns of gradient columns after the addition of beet western yellows virus, isolate E-2 (top) and beet mild yellowing virus, isolate In (bottom). Virus samples were obtained from infected shepherd's purse, inoculated, collected, and centrifuged at the same intervals. The samples were concentrated 170X and subjected to density-gradient centrifugation (SW-25 rotor, 4 hours at 55,100 *g*).

MATERIALS AND METHODS.—BMYV isolates tested in these studies came from individual sugarbeet (*Beta vulgaris* L.) plants showing typical BMYV symptoms. During 1970 and 1971, collections of these isolates from various locations in England were selected for laboratory and greenhouse tests.

Nonviruliferous green peach aphids, *Myzus persicae* (Sulzer) reared on chinese cabbage [*Brassica pekinensis* (Lour.) Rupr.], were transferred to detached leaves of the field-collected plants and allowed to feed for 48 hours. The aphids were then transferred to seedlings of sugarbeet, shepherd's purse [*Capsella bursa-pastoris* (L.) Medic.], and groundsel (*Senecio vulgaris* L.). Aphids transferred directly from *B. pekinensis* to indicator plants served as controls, to ensure that the stock aphid colony was free from contaminant viruses.

Host range studies were carried out by inoculation of at least five seedlings, from a number of different species, with 20-30 viruliferous aphids fed on diseased shepherd's purse for 24 hours. The aphids were permitted to feed on the test plants for 48 hours, and were then killed with a nicotine sulfate spray. Recovery attempts from all inoculated plants were carried out to verify susceptibility.

The handling of aphids, strains of BWYV, membrane-feeding technique, and antigen and antiserum preparation were as previously reported (6, 12). Extracts for antigen preparation and infectivity neutralization tests were prepared from shepherd's-purse plants infected with various strains of BWYV and the different isolates of BMYV.

Fresh plant material was ground in a food grinder 1:1 with 0.05 M phosphate buffer, pH 7.0, containing 0.01 M glycine. Crude extracts were clarified by low-speed centrifugation (10 minutes at 4,220 *g*) in a Sorvall SS-1 rotor. Clarified juice was centrifuged for 2 hours at 80,800 *g* in the No. 40 rotor of a Spinco Model L. ultracentrifuge. Pellets were resuspended in 0.05 M phosphate buffer, pH 7.0, containing 0.01 M glycine.

Density-gradient centrifugation was done in a SW-39 rotor for 2 hours at 73,450 *g*. Gradient columns were prepared by layering 0.9 ml each of 20, 30, 40, 50, and 60% sucrose dissolved in 0.05 M phosphate buffer, pH 7.0, containing 0.01 M glycine. Samples were removed from the zone 18-26 mm from the top of the tubes by means of a j-shaped hypodermic needle.

Gradient columns for scanning patterns were made by layering 4, 7, 7, and 7 ml respectively of 10, 20, 30, and 40% sucrose dissolved in 0.05 M phosphate buffer, pH 7.0, containing 0.01 M glycine. Centrifugation was done in a SW-25 rotor for 4 hours at 55,100 *g*. The gradient columns were photometrically scanned with an ISCO Density-Gradient Fractionator by use of the sensitive (0.5 O.D.) scale.

All density-gradient fractions used in feeding extracts were adjusted to 20% sucrose (by dilution with buffer) before they were placed on the membranes. This dilution prepared the samples for membrane feeding and resulted in preparations concentrated about 50 times the concentration of the original sap.

Aphids which had fed through membranes were tested

for transmissibility on shepherd's purse. Control aphids from the same colony, but which did not have access to the virus, were also tested on this host to ensure that no viruliferous aphids were in the stock colony.

RESULTS.—*Host range*.—Numerous host range tests with isolates of BMYV from sugarbeet in Britain have indicated a narrow host range for these isolates (18). Further studies (10) of 58 different BMYV isolates from sugarbeet fields throughout eastern England indicated that none of these infected lettuce, *Lactuca sativa*, whereas isolates of BWYV from lettuce in Britain did not infect sugarbeet.

Since September, 1970, inoculation of more than 8,900 plants representing 42 species in 12 families in these studies has confirmed the limited host range of the 12 BMYV isolates selected for these tests.

The known host range of BMYV has been extended by eight new species: six in the Cruciferae [*Arabidopsis thaliana* (L.) Heynh., *Brassica kaber* (DC.) L. C. Wheeler, *Crambe abyssinica* Hochst. ex R. E. Fries, *Lepidium nitidum* Nutt., *L. sativum* L., *Thlaspi arvense* L.]; one in the Chenopodiaceae [*Beta macrocarpa* Guss.]; and one in the Boraginaceae [*Amsinckia douglasiana* DC.].

The BMYV isolates tested produced a common reaction on certain key indicator hosts. *Beta vulgaris*, *Capsella bursa-pastoris*, and *Claytonia perfoliata* Donn. ex Willd. were susceptible to all 12 isolates, and produced diagnostic symptoms when infected. On the other hand, radish (*Raphanus sativus* L.), lettuce (*Lactuca sativa* L.), chinese cabbage (*Brassica pekinensis*), and turnip (*Brassica rapa* L.) were immune.

Symptoms.—In Europe, BMYV produces a bright orange coloration on the tips of affected sugarbeet leaves. Such leaves are often attacked by fungi such as *Alternaria*. The yellowing induced by most isolates of BWYV in the United States is more evenly distributed over the lamina, but is still more prominent on the tips. The yellowing, in most instances, in the U. S. is of a pale-yellow type. Secondary infection by *Alternaria* is also common. Infected plants in California sometimes have an orange coloration contrasted to the more typical pale yellow plants. In studies of 86 virus isolates from various locations in California, some differences in host range and host response between orange and pale yellow isolates were noticed, but the entities tested serologically did not differ serologically (Russell and Duffus, *unpublished*).

TABLE 2. Transmission of beet western yellows virus (BWYV) and beet mild yellowing virus (BMYV) by green peach aphids fed on concentrated preparations

Test No.	Transmission of the indicated virus isolate by the indicated number of aphids after feeding through membranes[a]			
	BWYV		BMYV	
	5	25	5	25
1	4[b]	20	0	3
2	4	20	1	4
3	6	20	1	6
4	5	20	0	3
5	4	20	0	2
% transmission	23	100	2	18

[a]BWYV is isolate E-2 from *Capsella* collected from Everton, Bedfordshire, England. BMYV is isolate In from Ingham, England. The virus samples were obtained from infected shepherd's purse, inoculated, collected and centrifuged at the same intervals. The samples were concentrated 170X and subjected to density-gradient centrifugation. The samples for infectivity assays were removed from the virus peak obtained in scanning patterns.

[b]Number of plants infected out of 20 inoculated.

TABLE 3. Serological interactions of United States and English beet western yellows virus (BWYV) antiserum and English beet mild yellowing virus (BMYV) isolates

Sample tested	Infectivity of virus zone after incubation with the indicated sera											
	A1[a]	In	F-6	G-8	G-9	GB-2	GB-3	GB-4	GB-5	GB-6	GB-7	GB-8
ASST 1-3[b] + virus[c]	0[d]	0	0	0	0	0	0	0	0	0	0	0
ASST 3-1 + virus	0	0	0	0	0	0	0	0	0	0	0	0
ASST 7-2 + virus	1	0	0	0	0	0	0	0	0	0	0	0
ASST 8-1 + virus	0	0	0	0	0	0	0	0	0	0	0	0
ASST 9-1 + virus	0	0	0	0	0	0	0	0	0	0	0	0
ASST 10-1 + virus	0	0	0	0	0	0	0	1	0	0	0	0
ASST 11-1 + virus	0	0	0	0	0	0	0	0	0	0	0	0
ASE-1 + virus	0	0	0	0	0	0	0	0	0	0	0	0
ASE-3 + virus	0	0	0	0	0	0	0	0	0	0	0	0
ASTuYV-1 + virus	0	0	0	0	0	0	0	0	0	0	0	0
ASBYV + virus	17	14	7	6	14	10	11	17	11	16	12	11
ASHSP 4 + virus	10	12	11	13	10	7	14	15	8	16	9	15
ASHSP 5 + virus	9	13	10	16	15	8	11	14	13	14	14	13
Buffer + virus	8	13	8	15	13	14	7	16	12	17	10	12

[a]English isolates of BMYV.

[b]Antisera to different strains of BWYV and controls. Antiserum to United States isolates of BWYV (ASST); antiserum to English isolates of BMYV (ASE); antiserum to turnip yellows isolate of BWYV (ASTuYV); antiserum to beet yellows virus (ASBYV); antiserum to healthy shepherd's purse (ASHSP).

[c]The virus samples were obtained from infected shepherd's purse, cleared by low-speed cenrifugation, and pelleted by ultracentrifugation. Pellets were resuspended in buffer to approximately 1/250 of the original volume of sap. The virus sample was mixed with an equal volume of serum and incubated for 2 hours at 37 C. Incubated mixtures were subjected to density-gradient centrifugation, and samples for infectivity assays were removed from the zone 18-26 mm from the top of SW-39 tubes.

[d]The number of plants infected of 20 inoculated with groups of 25 green peach aphids fed through membranes on each sample.

TABLE 4. Serological interactions of antiserum to English beet mild yellowing virus (BMYV) isolates with United States and English beet western yellows virus (BWYV)

Sample tested	Infectivity of virus zone after incubation with the indicated sera							
	BWYV[a] ST-1	BWYV ST-3	BWYV ST-7	BWYV ST-8	BWYV E-1	BWYV E-3	BMYV In	BMYV GB-5
ASBMYV-IN[b] + virus[c]	0[d]	0	0	0	0	0	0	0
ASBMYV-GB-5 + virus	0	0	0	0	0	0	0	0
ASST-1-3 + virus	0	0	0	0	0	0	0	0
ASHSP-4 + virus	20	20	20	20	20	20	15	12

[a]United States strains of BWYV; (ST-1), (ST-3), (ST-7), (ST-8); English isolates of BWYV; (E-1), (E-3); English isolates of BMYV; (In), (GB-5).

[b]Antiserum to BMYV isolate In (ASBMYV-In); antiserum to BMYV isolate GB-5 (ASBMYV-GB-5); antiserum to BWYV strain 1 (ASST-1-3); antiserum to healthy shepherd's purse (ASHSP-4).

[c]The virus samples were obtained from infected shepherd's purse, cleared by low-speed centrifugation, and pelleted by ultracentrifugation. Pellets were resuspended in buffer to approximately 1/50 of the original volume of sap in the case of the BWYV isolates and to approximately 1/250 in the BMYV isolates. The virus sample was mixed with an equal volume of serum and incubated for 2 hours at 37 C. Incubated mixtures were subjected to density-gradient centrifugation, and samples for infectivity assays were removed from the zone 18-26 mm from the top of SW-39 tubes.

[d]The number of plants infected of 20 inoculated with groups of 25 green peach aphids fed through membranes on each sample.

Membrane feeding.—The possible relationships of BWYV and BMYV prompted membrane-feeding studies with techniques shown to be successful for BWYV (6). The application of this technique was necessary to facilitate further characterization of the virus by serum neutralization of infectivity (7, 12). Membrane feeding attempts with BMYV during the period from 1967 through 1970 were unsuccessful. These attempts were conducted at the same time and in the same manner that English isolates of BWYV from lettuce and weeds were successfully transmitted through membranes. Early in 1971, more highly concentrated virus preparations (200X) from shepherd's purse were used as the virus source. Green peach aphids successfully transmitted these isolates of BMYV through Parafilm (Marathon Products, Neenah, Wisconsin) membranes to healthy shepherd's-purse seedlings. The infectious fractions in the density-gradient columns were in one zone 18-26 mm from the top of SW-39 tubes. This is the same location in the density-gradient columns from which BWYV has been repeatedly recovered.

Transmission rate through membranes.—Early failures to transmit BMYV isolates through membranes enhanced the evidence of host range, symptomology, and epidemiology that BMYV and BWYV were indeed separate virus entities. Following the discovery in 1970 (10) that BWYV occurred in Europe, renewed interest in the possible relationships of these entities prompted further testing on membrane feeding of BMYV isolates. These studies resulted in transmission of BMYV in small amounts through Parafilm membranes.

—1).—*Transmission efficiency.*—Tests to determine if individual green peach aphids were more efficient vectors of the common BWYV isolates that the BMYV isolates were conducted to determine if this was a factor in the low transmission of BMYV through membranes. Nonviruliferous green peach aphids were fed for 24 hours on shepherd's-purse plants infected for the same period of time (3 to 4 weeks) with isolates of BWYV (E-2 from *Capsella*, Everton, England) and BMYV (In from sugarbeet, Ingham, England). Single aphids were given a 48-hour infection feeding period on shepherd's-purse test plants. The results of 10 separate tests (Table 1) indicated a marked difference in the efficiency of individual green peach aphids in transmitting these two virus isolates. BWYV was transmitted to 48.6% of the shepherd's-purse test plants, whereas BMYV was transmitted to only 18.6%.

—2).—*Relative virus concentration.*—Symptoms induced by most isolates of BWYV were in general slightly more severe on shepherd's-purse test plants than those induced by BMYV. Tests to determine if the milder symptoms were the result of lower virus concentrations and if this played a role in the inefficient transmission of the BMYV isolates from shepherd's purse were carried out with the E-2 isolate of BWYV and the In isolate of BMYV. Preparations of the two isolates from shepherd's purse plants infected three to four weeks were concentrated 170X in the ultracentrifuge. Relative concentration was determined after analytical density gradient centrifugation (SW-25 rotor, 4 hours, 23,000 rpm) by measuring the area under the curve corresponding to each virus; the area under the peak of the BWYV isolate was about seven times that of the BMYV isolate (Fig. 1).

Green peach aphids fed on samples from the peaks indicated a five- to ten-fold higher transmission rate with the BWYV samples (Table 2).

Serological relationships.—After the application of the membrane feeding technique to BMYV isolates, attempts were made to study the serological relationships of these isolates to English and American BWYV isolates. The virus:antiserum mixtures were subjected to density-gradient centrifugation prior to the feeding of insects (12). In this case, evidence of serological reaction was based on the failure to encounter infectivity in the normal virus zone. It has been demonstrated in other studies (8) that where neutralization has occurred, infectious virus can not be obtained from any zone in the density-gradient centrifugation tubes.

Ten antisera prepared against different isolates of BWYV from previous studies (7, 10, 11, 12) were tested against 12 English isolates of BMYV collected from sugarbeet from various locations in England. Buffer (0.05 M phosphate, pH 7.0, containing 0.01 M glycine), two antisera prepared against healthy shepherd's purse, and

antiserum prepared against the beet yellows virus were tested against the same isolates and served as controls (Table 3). Antisera prepared against two of the English isolates of BMYV were tested against six BWYV strains from the U. S. and England and two English BMYV isolates. Antiserum prepared against healthy shepherd's purse and against ST-1 BWYV were tested against the same isolates and served as controls (Table 4).

Antisera against all of the BWYV strains tested effectively neutralized the infectivity of the 12 English BMYV isolates. In two instances, one infected plant occurred from samples incubated with certain sera. These isolates that survived incubation were subsequently tested with the same and other sera and were found to have escaped neutralization because of a low titer of the sera.

Antisera against the English isolates of BMYV neutralized the infectivity of the U. S. and English BWYV strains tested and also the BMYV isolates tested.

DISCUSSION.—Previous serological studies of BWYV-like yellowing viruses have established a serological relationship between BWYV in the United States and yellowing virus isolates from weeds and lettuce in England (10). They have also established a close serological relationship between BWYV from the United States and England and turnip yellows virus (11) from turnips in England and Germany.

The results of these experiments show a close serological relationship between BWYV from the United States and England and BMYV from England. They show for the first time a relationship between the most common beet virus in the United States and the most prevalent virus of beet in Europe. The serological relationship of these 12 BMYV isolates studied, however, does not preclude the possibility that other unknown yellowing entities may also occur in beet fields of the United States or Europe, and may be confused with the diseases called beet western yellows and beet mild yellows. BMYV and BWYV induce similar symptoms in certain key indicator hosts and are transmitted in a similar way be vectors, but differ in symptomology on sugarbeet and differ greatly in epidemiology and host range. All isolates of BMYV thus far collected from sugarbeet fields in England have failed to infect lettuce, radish, or chinese cabbage and the BWYV isolates from lettuce have failed to infect sugarbeet. According to the available evidence, therefore, BMYV isolates from sugarbeet do not constitute a threat to the lettuce crop and BWYV isolates from lettuce do not constitute a threat to the sugarbeet crop in England at the present time.

The differences in transmission efficiency between the common BWYV isolates in shepherd's purse and the isolates of BMYV tested seems to be related to virus concentration in this Cruciferous host. The virus concentration differences noted in these studies probably are the result of long time affinities with distinct host species. Different variants of BWYV seem to predominate in different plant species (5), and in Europe for a number of years, at least three virus strain types have occurred, BMYV, TuYV and BWYV.

The reasons for, and the mechanisms involved in, the distinct groups of BWYV strains in Europe (BMYV, BWYV and TuYV) and the possible role of other viruses in the complex such as barley yellow dwarf virus (BYDV) are not yet known. Preliminary serological evidence indicates a relationship between BWYV and barley yellow dwarf virus (9). Perhaps a mechanism such as heterologous encapsidation, as suggested by Rochow (15) for BYDV may have resulted in "new" diseases, transmitted by different insects and with different epidemiological patterns.

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