The Range of Symbiosis of Barley and Barley Stripe Mosaic Virus

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ABSTRACT

Barley stripe mosaic virus (BSMV) apparently depends on a single plant species, *Hordeum vulgare* L., for survival in nature. Within that species, only some of the cultivars were able to serve as a host in which the virus could survive indefinitely. Twenty strains of BSMV were tested on four cultivars of barley. The interaction between barley and BSMV fell into three categories: (i) very susceptible, in which little or no seed was produced; (ii) resistant, in which the plants did not become infected with the virus or, if infected, seed transmission was low or absent; and (iii) tolerant, in which some strains of BSMV were apparently able to survive indefinitely in barley. All commercially grown barley cultivars tested fell into the latter category. Some strains of BSMV were unable to survive in any of the barley cultivars, while others were able to survive only in the "tolerant" cultivars.

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The survival of barley stripe mosaic virus (BSMV) in nature apparently depends on a single plant species, *Hordeum vulgare* L. Although BSMV is known to be present in most barley-producing areas of the world, its presence in species other than barley in nature is limited to wheat, *Triticum aestivum* L., and it has been found in this species only two times according to published reports (7).

Seed transmission of BSMV in barley and other crops has been frequently reported (2, 3, 4, 5, 6, 7, 8, 9, 10, 11) when plants were mechanically inoculated. The level of seed transmission of BSMV in barley depends on the age of the plants at the time they become infected (1, 3, 6, 9, 10), the strain of virus (1, 7), and the barley cultivar (10). McKinney and Greeley (7) showed that some strains of the virus are transmitted through the seed at a low level or not at all, and that there are many strains of BSMV, based on host range and symptoms.

The purpose of this study was to determine the effect of several strains of BSMV on four cultivars of barley in relation to survival potential of the virus.

MATERIALS AND METHODS.—Four cultivars of barley (*Hordeum vulgare* L.), ranging from resistant to susceptible to BSMV infection, were tested against 20 BSMV strains over a period of 4 yr. The barley cultivars were 'Black Hulless' (C.I. 666), 'Dickson' (C.I. 10968), 'Modjo 1' (C.I. 14048), and 'Moreval' (C.I. 5724).

The BSMV strains were selected on the basis of their diversity of origin and/or pathogenicity on various host plants, including several barley cultivars.

The 1969 and 1970, field plots consisted of four 3-m-long rows of each barley cultivar, with 30-cm spacing between rows. The two center rows in each plot were inoculated with the virus, and three replications of each barley cultivar-virus strain combination were used. Plants were inoculated in the two-leaf stage with a 1:10 dilution of expressed sap from virus-infected plants and water. Inoculations were made with an artist's paint spray gun at a plant-to-nozzle distance of about 7 cm and a pressure of 3.5 kg/cm^2. Silicon carbide (400-grit) was added to the inoculum at a rate of 10 g/100 ml (w/v). Seven and 13 strains respectively, of BSMV were tested in 1969 and 1970. Check plants were sprayed with a water suspension of abrasive. Three meters of each inoculated row in each plot were harvested. The percent infection in harvested seed was determined by recording the number of infected seedlings grown from about 300 seeds in a greenhouse held at a temperature of 27 ± 2 C and using supplemental lighting of 13,000 lux with a 16-h day. Where there was doubt concerning infection, test plants of Black Hulless barley were inoculated to ascertain the presence or absence of virus in the plants in question. The yield was determined in all plots in 1970, but not in 1969.

Seed harvested from the 1970 plots was used to plant the 1971 plots, which were 3.7 m square, with 15-cm spacing between rows. These plots were not inoculated experimentally, but the percent infection was determined in the field. This was done by determining the number of plants infected in 100 plants at three random locations within each plot, with two replications. A 3-m-square area was harvested from each plot for yield and seed-infection determinations.

In 1972, seed harvested from selected plots in the previous 3 yr was used to plant four 2-m row plots, with 30-cm spacing between rows. The percent infection in the field was determined, and the two center rows of each plot were harvested for seed-transmission determinations. Some seed lots were planted in 3.7-m-square plots, with 15-cm spacing between rows. An area 3 m^2 was harvested for seed-transmission determinations.

RESULTS.—The level of seed transmission varied considerably in the four barley cultivars inoculated with seven strains of BSMV in 1969 (Table 1). In 1969, there was no seed transmission of any of the virus strains in Moreval, the most resistant cultivar inoculated. Seed infection in the other resistant cultivar, Modjo 1, occurred only in those plots inoculated with strains CV 52 (CV refers to Cereal Virus maintained in the USDA-ARS cereal virus collection maintained in the Plant Pathology

Department, North Dakota State University, Fargo, North Dakota 58102) and CV 55, where transmission was only 7 and 2%, respectively. Three strains of the virus were seed-transmitted at a high rate (27%, 62 and 47%) in the seed of Dickson, while three other strains were not transmitted in this cultivar. Although strain CV 65 was 61% seed-transmitted in Black Hulless, little seed was produced on the infected plants. All strains of the virus used in 1969 except CV 67 reduced the vigor of Black Hulless so much that little or no seed was produced. Strain CV 67 was not transmitted through the seed of any of the cultivars.

In 1970, when the same barley cultivars were inoculated with 13 strains of BSMV, the results were somewhat different, reflecting the effect of variable growing conditions on seed transmission (Table 1). Four strains of the virus were transmitted at a relatively high rate in Black Hulless, and seed yield was reduced 93% or more as a result of infection with these strains (Table 2). Seed transmission was more than 10% in Dickson inoculated with nine of the 13 strains (Table 1), and yield was reduced 13 to 88% (Table 2). In Modjo 1, seed transmission was low for all BSMV strains, and yield reduction as a result of virus infection varied from 1 to 31%. In Moreval, seed transmission was low or absent with all but strain CV 29, in which it was 23%. There was no seed transmisison with seven of the BSMV strains in Moreval, while only four were not seed-transmitted in Modjo 1. None of the virus strains reduced the yield significantly in either Moreval or Modjo 1.

In 1971, when all plots were planted with seed harvested from plots inoculated in 1970, the percent infection in harvested seed of all cultivar-strain combinations was lower than the infection in planted seed (Table 3), except Black Hulless infected with CV 32, where the increase was from less than 1 to 2%, in Moreval infected with CV 55, where the increase was from 1 to 2%, and in Dickson infected with CV 12, where the increase was from 11 to 29%.

Seed from plots that had been previously inoculated, either one or two generations, was used to plant the plots in 1972. There was an increase in the amount of infected seed in Dickson infected with strain CV 55 (Table 1), reflecting the fluctuation experienced in other trials.

TABLE 1. The percent seed transmission of 20 strains of barley stripe mosaic virus (BSMV) in four barley cultivars after inoculation and in one or two succeeding generations

Virus strain[a]	Year inoculated	Seed transmission (%) of BSMV in cultivar											
		'Black Hulless'			'Dickson'			'Modjo 1'			'Moreval'		
		generation[b]			generation[b]			generation[b]			generation[b]		
		1	2	3	1	2	3	1	2	3	1	2	3
CV 67	1969	0	[c]		0			0			0		
CV 16	1969	1			0			0			0		
CV 54	1969	2			0			0			0		
CV 40	1970	1	0		1			0			0		
CV 66	1970	tr[d]			7	2	tr	0			0		
CV 41	1969	2			27	7		0			0		
CV 65	1969	61[e]			1			0			0		
CV 17 (PV-130)[f]	1970	3	0		tr	0		0			0		
CV 20	1970	5[e]			32	26	21	0			0		
CV 32	1970	tr	2[e]		tr			tr			0		
CV 21	1970	30[d]			18	4	1	6	tr	0	0		
CV 24	1970	tr			4	1	1	tr			0		
CV 22	1970	tr			19	1		2			1		
CV 29	1970	0			15	0		3	0	0	23	2	tr
CV 31	1970	tr			32	4	tr	3	1	0	1		
CV 12	1970	27[d]			11	29		tr			4	1	1
CV 28	1970	20[d]			44	27	23	2	tr		1		
CV 26	1970	tr			20	5	tr	14	1	tr	8	1	tr
CV 52	1969	no seed			62	52		7	tr		3	tr	
CV 55	1969	no seed			47			2			0		
CV 55	1970	24[d]			42	33	48	4	tr	tr	1	2	0
CK	1969	0			0			0			0		
CK	1970	0			0			0			0		

[a] CV refers to "cereal virus." It is a letter code used for the USDA, ARS cereal virus collection.

[b] Infection in harvested seed from: 1 - inoculated plants; 2 - plants grown from seed harvested in 1; and 3 - plants grown from seed harvested in 2.

[c] There was insufficient seed produced on Black Hulless except when inoculated with strains CV 40, CV 17, CV 32, CV 66, and CV 67, to permit growing to a second generation.

[d] tr = <1%.

[e] Very little seed produced, therefore, percent infection may be in error.

[f] This strain of BSMV is stored as PV-130 in the American Type Culture Collection at Rockville, Maryland.

Three of the strains, CV 28, CV 20, and CV 55, were transmitted at a relatively high rate in Dickson. Strains CV 29, CV 66, CV 22, CV 21, CV 24, and CV 26 were unable to survive in this variety because of the low seed-transmission rate. The low seed-transmission rate was correlated with a relatively low rate of spread of the virus from plant to plant under field conditions (R. G. Timian, *unpublished*). Strain CV 31 was seed-transmitted at a relatively high rate in Dickson (32%) when the plants were mechanically inoculated, but the rate of natural spread in the field through leaf contact was low (Table 3) and seed transmission decreased accordingly.

TABLE 2. The yield of seed produced on four barley cultivars inoculated with 13 strains of barley stripe mosaic virus (BSMV), expressed as percent of check. Average of three replications

Virus strain	Seed yield (percent of check)			
	'Black Hulless'	'Dickson'	'Modjo 1'	'Moreval'
CV 12	1**[a]	70*	88	94
CV 32	86**	83	99	100
CV 29	3**	12**	92	78
CV 40	44**	84	87	97
CV 31	5**	43**	89	87
CV 66	85**	87	92	98
CV 28	2**	61**	85	96
CV 20	2**	58**	96	99
CV 22	5**	50**	89	92
CV 21	7**	60**	86	100
CV 24	8**	46**	80	84
CV 26	4**	45**	69	97
CV 55	1**	62**	85	103
CK	100	100	100	100

[a]*, ** Significantly different from the check, based on Duncan's multiple range test at $P = 0.05$ and $P = 0.01$, respectively.

TABLE 3. The percent of virus infection in planted seed, in plants growing in the field, and in harvested seed of four barley cultivars infected with various strains of barley stripe mosaic virus (1971)

Virus strain	Barley cultivar	Percent infection in		
		Planted seed	Plants in field[a]	Harvested seed[b]
CV 12	'Dickson'	11	17	29
	'Moreval'	4	7	1
CV 32	'Black Hulless'	tr[c]	1	2
CV 29	Modjo 1	3	2	0
	Moreval	23	14	2
CV 31	Dickson	32	17	4
	Modjo 1	3	2	1
CV 66	Dickson	7	3	2
CV 28	Dickson	44	35	27
CV 20	Dickson	32	39	26
CV 22	Dickson	19	8	1
CV 21	Dickson	18	10	4
	Modjo 1	6	6	tr[c]
CV 24	Dickson	4	3	1
CV 26	Dickson	20	17	5
	Modjo 1	14	9	1
	Moreval	8	5	1
CV 55	Dickson	42	49	33
	Modjo 1	4	11	tr[c]
	Moreval	1	5	2

[a]Readings made when plants were in the boot stage. Average of 100 plants observed in three locations in two replications.

[b]Based on an average of 300 seed-seedlings from each of two replications.

[c]tr = <1%.

The amount of seed transmission of all 20 strains of BSMV in the four barley cultivars after mechanical inoculation and in two succeeding generations is given in Table 1. There was a relatively high rate of seed transmission of four of the strains in Black Hulless. Three of these were so severely pathogenic that seed production was almost zero. Strain CV 65 was transmitted through 61% of the seed on inoculated plants. The yield of seed in Black Hulless inoculated with this strain of the virus was so low that it could not be tested further. When the virus strains were mildly pathogenic in Black Hulless and seed production was relatively high, seed transmission was very low or absent in inoculated plants.

In Dickson barley, five of the 20 strains of BSMV tested were transmitted through two or three generations at a rate of 21% or more. Two of the strains, CV 41 and CV 31, were transmitted via seed at a high rate (27 and 32%, respectively) in inoculated plants, but the level of transmission declined in the two succeeding generations to near zero. An additional three strains were transmitted at a relatively high rate (15, 19, and 20%, respectively, for strains CV 29, CV 22, and CV 26), but field spread from leaf contact was negligible (R. G. Timian, *unpublished*), and consequently seed transmission declined to only a trace after two generations. Other strains of BSMV were either not transmitted or transmitted at a low rate in Dickson.

In Modjo 1, none of the strains were seed-transmitted at a rate that would assure survival of the virus. Strain CV 26 had the highest seed-transmission rate, 14% in inoculated plants. The transmission rate dropped to a trace or to zero in one or two generations with all strains in which seed infection occurred.

In Moreval, most strains were not transmitted through the seed of inoculated plants. One strain, CV 29, was transmitted through 23% of the seed of inoculated plants, but in the two succeeding generations the transmission rate dropped to a trace.

DISCUSSION.—Survival of BSMV in nature depends on several factors and results from these and other studies (5, 6, 9, 11) support this hypothesis. These factors include a tolerant reaction in the host that is infected with the virus, so that virus will spread from infected to healthy plants in the field through leaf contact; a relatively high transmission rate of the virus in barley seed; a relatively small reduction in kernel plumpness; a yield reduction of not more than about 50%; and infection of the host plant several days before anthesis, in order to infect the seed.

In the present study, the above criteria were met by relatively few of the host-virus combinations. Black Hulless was very susceptible to most strains of the virus, but little or no seed was produced in plants inoculated with any of the virus strains tested. Transmission through the seed was high in plants inoculated with strains CV 12, CV 28, CV 21, and CV 55, but the amount and size of seeds produced were very small. Consequently, these

strains could not survive in this cultivar. CV 32 did not severely affect the Black Hulless plants, but this strain of the virus was seed-transmitted at a very low rate. There was a slight increase in seed infection (2%) in the second-generation plants, but further testing would be necessary to see whether this represents a real increase in seed transmission. CV 65 was transmitted at a high rate in Black Hulless plants but seed production from this cultivar-virus combination was so low that further testing was not possible. The results from inoculation of Black Hulless with the 20 virus strains strongly indicate that BSMV cannot survive in this cultivar.

Several factors are against survival of any of the BSMV strains in the resistant cultivars Moreval and Modjo 1. The most important factor is the resistance to infection of these cultivars. Only two strains (CV 29 and CV 26) infected a majority of the inoculated Moreval plants. The level of seed transmission in Moreval was substantially reduced in the second generation after inoculation with strain CV 29. This reduction strongly indicates that CV 29 would not be able to survive in this cultivar. Strain CV 26 infected almost all plants of inoculated Moreval, but seed transmission was low and dropped to 1% when seed was grown the following year. These results provide evidence that BSMV cannot survive in Moreval, either because of its resistance to infection or because of the lack of seed transmission.

In Modjo 1 barley, a number of strains infected a moderate percentage of the inoculated plants. There was relatively little spread from plant to plant in the field in this cultivar, which would work against this cultivar serving as a continuing host for the virus. Symptoms in this cultivar were relatively mild, which should favor survival of the virus; however, seed transmission was low, amounting to one percent or less in the second generation after inoculation. Therefore, none of the virus strains tested appears to be able to survive in this cultivar.

In Dickson barley, a number of the virus-host relationships affecting survival are involved. This cultivar is resistant to strain CV 66 of the virus; consequently, seed transmission was low and decreased to 2% in the second generation. All other strains of the virus tested infected more than 50% of the plants inoculated. Seed transmission was low (20% or less) in plants inoculated with nine of the strains, even though the infection rate was high in inoculated plants. Some strains of the virus are inherently weak in ability to infect the embryo or are inactivated as the seed matures (1). Where seed transmission was low in inoculated plants, it decreased to a much lower level in the second generation, and these strains will probably not survive in this cultivar. Four of the strains, CV 31, CV 28, CV 20, and CV 55, infected almost all inoculated plants, and seed transmission was high. In the second generation after inoculation, the infection dropped to a low level with strain CV 31. This resulted, in part at least, from the loss of vigor in infected plants. The level of seed transmission in Dickson infected with strains CV 28, CV 20, and CV 55 remained at a high level through the third generation, and apparently the virus-host relationship is such that survival of the virus is assured.

Dickson, a 6-row commercially grown Manchurian-type barley, gives a moderate reaction to BSMV. This cultivar thus provides a vehicle of survival for BSMV. Plants that are infected grow vigorously enough to provide a means of virus spread. Seed transmission is sufficiently high to provide for the survival of some virus strains at a relatively high level in seed. All of the commercially grown barley cultivars that have been tested for reaction to BSMV respond in a manner similar to that of Dickson. Therefore, one may conclude that any one of them may provide a vehicle of survival for BSMV.

Black Hulless represents a reaction type in which the plant is so susceptible that little or no seed is produced on infected plants, precluding virus survival in such cultivars. Moreval and Modjo 1 are either too resistant to infection or have a low enough level of seed transmission to prevent the survival of BSMV.

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