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Promising genetic resources for resistance to wheat streak mosaic virus and the wheat curl mite in wheat-*Thinopyrum* partial amphiploids and their derivatives★

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Abstract

Wheat streak mosaic virus (WSMV), vectored by the wheat curl mite (WCM), *Aceria tosichella* Keifer, is one of the most destructive viral diseases of wheat found in many wheat producing areas of the world. Host resistance is the most effective method for controlling this disease and its vector. Symptomatological analysis and enzyme-linked immunosorbent assay (ELISA) were used to characterize WSMV-resistance in wheat-alien partial amphiploid lines and their derivatives. The results showed that most of partial amphiploids derived from *Thinopyrum ponticum* and *Th. intermedium* were free of systemic symptoms with very low ELISA readings that were similar to that of the non-inoculated Chinese Spring control. While the partial amphiploid lines 693 and PWM706 were identified as new genetic resources of resistance to WSMV. The present study demonstrated that both symptomatological and ELISA methods efficiently assessed WSMV-resistance in the wheat-alien hybrids and systemic symptom incidence and ELISA absorbance readings were highly correlated ($r^2 = 0.8658$–0.9323) over time following inoculation. The ELISA results also indicated that the virus did not buildup in the plant tissues of these virus-resistant partial amphiploids. Similar results were observed in chromosome translocation and substitution lines that have the gene *Wsm1* conferring WSMV resistance. However, the lines containing the gene *Wsm1* and all the partial amphiploid lines, except Agrotana, were susceptible to the WCM. One line derived from a cross of wheat and Agrotana, was effective in controlling the spread of WSMV and was highly resistant to the WCM. Another line and an accession of *Triticum dicoccoides* (Koern.) Schweinf. were highly susceptible to WSMV and WCM. Early disease development was delayed in a new hard red winter cultivar McClintock. The partial WSMV-resistance of McClintock was demonstrated by initially low ELISA readings, and a lower percentage of infected plants than other WSMV-susceptible wheat. The use of the identified promising sources of resistance to WSMV and the WCM in wheat breeding is discussed.

Introduction

In the major wheat growing areas of the world, wheat producers have suffered heavy economic losses from periodic epidemics of wheat streak mosaic (WSM) caused by the wheat streak mosaic virus (WSMV) (Weise 1987; Bockus et al. 2001). Studies have demonstrated that WSM not only caused dramatic yield losses in winter wheat (*Triticum aestivum* L.), but also reduced grain end

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use quality (Atkinson and Grant 1967). WSMV is also a viral pathogen of spring wheat (Edwards and McMullen 1988). Genetic control of WSMV epidemics with wheat cultivars resistant to WSMV or its vector the wheat curl mite (WCM), *Aceria tosichella* Keifer, provide the best means for reducing the extent of yield reduction caused by this disease (Martin et al. 1984; Conner et al. 1991; Harvey et al. 1994). However, high levels of WSMV- and WCM-resistance rarely occur within *Triticum* species (Stoddard et al. 1987b; Harvey et al. 1999).

The wild species related to wheat are potential sources of resistance to this devastating viral disease. Among them, *Thinopyrum* species, such as *Th. ponticum* (Podp.) Liu and Wang (syn. *Lophopyrum ponticum* (Podp.) (Löve), and *Th. elongatum* (Host) P. Beauv.) and *Th. intermedium* (Host) Barkworth et D.R. Dewey (syn. *Ag. intermedium* (Host) Beauv.) have been identified as effective sources of resistance to WSMV (Andrews and Slykhuis 1956). A number of wheat-*Thinopyrum* partial amphiploids have been developed in various laboratories throughout the world (Cauderon 1966; Cauderon et al. 1973; Sun 1981; Li et al. 1985; Comeau et al. 1994; Fedak et al. 2000). Compared to comprehensive studies on these partial amphiploids for other diseases, such as the barley yellow dwarf virus (BYDV), only limited information is available on their phenotypic response to WSMV and the WCM (Chen et al. 1998, 1999).

The symptomatological method is commonly used to evaluate WSMV resistance in wheat breeding programs directed towards improving virus-resistance. Nevertheless, the symptoms caused by WSMV can be indistinguishable from chlorosis arising from nutritional deficiency, other viral pathogens and certain pest infestations (Shahwan and Hill 1984; Montana et al. 1994; Mahmood et al. 1998). Moreover, narrow and dark pigmented leaves often appear in seedlings of wild relatives of wheat as well as their amphiploids, making it difficult to visually assess WSM symptoms (Stoddard et al. 1987b). Recently, WSMV was detected in some samples of a resistant wheat-*Th. ponticum* partial amphiploid, which did not display systematic symptoms (Li et al. 2002). Similarly, WSMV could be purified from inoculated leaves of plants carrying the virus resistance gene *Wsm1* at an early stage following inoculation, and subsequently the virus could be used to infect other WSMV-susceptible wheat (Pfannenstiel and Niblett 1978). Therefore, more research is required to precisely characterize the responses of the wheat-*Thinopyrum* partial amphiploids and *Wsm1* carrying lines to WSMV and monitor the virus build up over time. The enzyme-linked immunosorbent assay (ELISA) is a simple and accurate method to assess WSMV concentration by measuring the viral capsid protein in infected plant tissues (Sherwood 1987; Montana et al. 1996). Symptomatological assessment together with ELISA should allow a more accurate determination of WSMV resistance. The objective of this study was to evaluate the resistance of various sources of wheat-*Th. ponticum* and wheat-*Th. intermedium* amphiploids and their derivatives to WSMV and its vector the WCM, by means of symptomatological assessment and a serological assay. The relationship between ELISA values and systemic symptom development over time was also investigated. This study was also initiated to examine the partial resistance to WSMV in the winter wheat cultivar McClintock.

Materials and methods

Plant materials

The partial amphiploid lines used in this study were derived either from hybrids of wheat-*Th. ponticum* or wheat-*Th. intermedium* (Table 1). The partial amphiploids OK7511542 (Comeau et al. 1994), PWM706 (Fedak et al. 2000), and Agrotana (Chen et al. 1995), derived from wheat × *Th. ponticum*, have all undergone long-term of backcrossing and selection for resistance to various diseases prior to their use in wheat breeding programs. The wheat-*Th. ponticum* amphiploids 693 (Li et al. 1985) and ORRPX (Comeau et al. 1994) were developed in China and Quebec, Canada, respectively. Zhong 4 (Sun 1981) and TAF46 (Cauderon 1966; Cauderon et al. 1973) are partial amphiploids derived from crosses between wheat and *Th. intermedium*.

Several wheat-*Th. ponticum* and wheat-*Th. intermedium* lines were also screened for their resistance to WSMV and the WCM. Lines A29-13-3 (Wang and Zhang 1996), KS93WGRC27 (Gill et al. 1995), and CI 15092 (Wells et al. 1973) were chromosome

Table 1. Percentage of plants with symptoms of wheat streak mosaic following inoculation of wheat-*Thinopyrum* partial amphiploids and their derivatives.

Lines	No. of plants observed	Weeks following inoculation with WSMV					
		1	2	3	4	5	6
693	30	0 c[a]	0 c	0 d	0 d	0 c	0 c
PMW706	36	0 c	0 c	0 d	0 d	0 c	0 c
Agrotana	36	0 c	0 c	0 d	0 d	0 c	0 c
ORRPX	29	0 c	0 c	0 d	0 d	0 c	0 c
OK7211542	36	0 c	0 c	0 d	0 d	0 c	0 c
TAF46	29	0 c	0 c	0 d	0 d	0 c	0 c
Zhong 4	24	0 c	0 c	0 d	0 d	0 c	0 c
54-41-1-4-5-5	35	0 c	0 c	2.8 d	30.6 c	61.1 b	61.1 b
KS93WGRC27	34	0 c	0 c	0 d	0 d	0 c	0 c
A29-13-3	36	0 c	0 c	0 d	0 d	0 c	0 c
CI 15092	31	0 c	0 c	0 d	0 d	0 c	0 c
McClintock	36	5.6 c	56.7 c	75.6 c	79.9 b	88.9 a	88.9 a
7631-3-20	36	91.7 a	97.2 a	100 a	100 a	100 a	100 a
Chinese Spring	34	21.9 b	80.8 b	88.7 b	94.8 a	95.2 a	95.2 a
T. dicoccoides	34	0 c	65.3 c	97.2 ab	97.2 a	97.2 a	97.2 a

[a]Mean values followed by the same letter are not significantly different according to Duncan's multiple range test ($p < 0.05$).

translocation or substitution lines, which carry the gene *Wsm1* for resistance to WSMV. Line 54-41-1-4-5-5 was developed from a cross between wheat and Agrotana (Chen et al. 1999). Line 7631-3-20 is a line derived from the wheat-*Th. ponticum* partial amphiploid 7631 (Li et al. 1985), which has 42 chromosomes and stripe rust (*Puccinia striiformis* Westend) resistance (Li H.J. et al. unpublished data). The new hard red winter wheat cultivar McClintock was developed from a cross of GN567 × VT2222 (Brûlé-Babel 2001). An accession of *T. dicoccoides* (Koern.) Schweinf. was also screened for WSMV- and WCM-resistance. The spring wheat cultivars Rescue and Chinese Spring were used as WSMV- and the WCM-susceptible controls.

WSMV inoculation and plant growing condition

Six plants per plot were seeded in 6 × 17 Ferdinand-style rootrainer trays (Spencer-Lemaire, Edmonton, AB), and were arranged in a randomized block design with three replications. WSMV from southern Alberta was increased on the WSMV-susceptible spring wheat cultivar Rescue under greenhouse conditions. WSMV-infected leaves were ground in distilled water and filtered through four layers of cheesecloth, and carborundum (320 grit) was added at a ratio of 1 g per 50 ml of plant extract. Plants at two to three leaf-stage were individually sprayed with the inoculum using an artist's airbrush (Model AF-689, Paasche Airbrush Co., Harwood Heights, IL). The plants were grown at 21 ± 3 °C for the first experiment and at 25 ± 3 °C for the second experiment in a greenhouse with a 16/8 h light/dark photoperiod. The symptoms of WSM were visually rated at weekly intervals following inoculation.

Enzyme-linked immunosorbent assay (ELISA)

An indirect double antibody sandwich (DAS) ELISA (DAS ELISA, PathoScreen Kit, with alkaline phosphatase label, Agdia Inc., Elkhart, IN) was used to detect WSMV in inoculated leaves at 2 weeks, and in newly developing leaves at 4–6 weeks following inoculation. Mock-inoculated Chinese Spring wheat plants were used as the disease-free control. A positive control was provided with the ELISA kit (Agdia Inc., Elkhart, IN). Samples were prepared by bulking equal sized portions of the central parts of a leaf from each plant within a plot. The ELISA was conducted following a published method (Li et al. 2002). Samples, together with the disease-free and positive checks, were arranged in the same ELISA plate. Entries were considered susceptible to the virus when ELISA readings were at least three-fold

greater than the disease-free control. Duncan's multiple range procedure (Steel and Torrie 1960) generated by the general linear model (GLM) procedure of SAS (Version 6, SAS Institute Inc., Cary, NC) was used to compare the percentage of diseased plants and ELISA readings in the entries at each sampling date ($p < 0.5$). Linear regression analysis was used to examine the relationship between visual assessment of WSM incidence and ELISA readings at the three sampling dates.

Evaluation of WCM resistance and its effect on controlling the spread of WSMV

The WCM resistance of the lines in the study of WSMV resistance was determined using a randomized block design with three replications. After seeding, plots usually composed of six seeds each were exposed to an infestation of non-viruliferous WCM by placing the rootrainer trays next to the WCM-colonized plants of the wheat-*Th. intermedium* substitution line T-Ai (Larson and Atkinson 1973), which were grown in a Conviron (Winnipeg, MB) E-7 growth cabinet at 21 °C with a 16/8 h light/dark photoperiod (140 μE m^{-2} s^{-1}). Three weeks after initial exposure, the number of plants with symptoms of rolling and trapping of the leaves caused by the WCM colonization was determined (Thomas and Conner 1986).

Based on the reactions to the WCM colonization, the WCM-resistant lines 54-41-1-4-5-5 and Agrotana, in combination with WCM-susceptible entries, Chinese Spring and Rescue, were selected to test their effectiveness in limiting the transmission of WSMV by viruliferous WCM as previously described (Conner et al. 1991). The number of plants with symptoms of WSMV was determined on a weekly basis for 6 weeks following exposure to the WCM viruliferous for WSMV. All the experiments were conducted twice.

Results

Visual rating of WSM symptoms

The results of the WSMV resistance test from two experiments are given in Table 1. The analysis of variance indicated that the treatment × experiment interactions were not significant for any of the variables, so the results from the two experiments were pooled. Line 7631-3-20 and Chinese Spring were the first lines to show obvious symptoms. Systemic symptoms of WSM appeared in these lines in the first week following manual inoculation. None of the wheat-*Th. ponticum* and wheat-*Th. intermedium* partial amphiploids tested showed any WSM symptoms (Table 1). The chromosome translocation and substitution lines A29-13-3, KS93WGRC27, and CI 15092 also were free of symptoms. Line 54-41-1-4-5-5 remained symptomless for the first 3 weeks after inoculation. Although 30% of plants in 54-41-1-5-5 expressed WSM symptoms at 4 weeks after inoculation, subsequent development of symptoms in this line was much slower than the WSMV susceptible Chinese Spring check (Table 1). Throughout the investigation, the symptoms developed more slowly in the winter wheat cultivar McClintock than in the WSMV-susceptible control Chinese Spring or the line 7631-3-20. After the first 4 weeks, the percentage of plants showing symptoms in McClintock was significantly lower than in Chinese Spring (Table 1). In the last 2 weeks, 11% healthy plants of McClintock remained symptomless. The symptoms intensified quickly in the accession of *T. dicoccoides*, although it did not show any mosaic symptoms a week after inoculation (Table 1).

Detection of WSMV in wheat × Thinopyrum hybrids by ELISA

The ELISA absorbance readings ranged from 0.081 to 0.099 for the disease-free plants of Chinese Spring, which was similar to 0.078–0.093 for the extraction buffer. At 2 weeks after inoculation, the ELISA values of line 693 were comparable to those of the non-inoculated check Chinese Spring (Table 2). The virus was not detected in line 693 at the two subsequent sampling dates. This indicated that WSMV did not build up in leaves of line 693. Similar results were obtained in other wheat-*Th. ponticum* amphiploid lines, such as PWM706, ORRPX, OK7211542 and Agrotana (Table 2). However, WSMV built up quickly in line 7631-3-20. This line showed high absorbance readings, which corresponded with its early development of visual symptoms. There was no significant difference in ELISA values among the lines 7631-3-20, *T. dicoccoides*, and Chinese Spring.

Table 2. Wheat curl mite (WCM) reactions and ELISA values for wheat streak mosaic virus (WSMV) in wheat-*Thinopyrum* partial amphiploids and their derivatives.

	ELISA absorbance values following inoculation of WSMV				
Lines	No of plants observed	2 weeks	4 weeks	6 weeks	WCM[b]
693	30	0.092 c[a]	0.094 b	0.080 c	0 b
PWM706	36	0.083 c	0.102 b	0.167 c	0 b
Agrotana	36	0.103 c	0.098 b	0.097 c	100 a
ORRPX	29	0.089 c	0.104 b	0.077 c	0 b
OK7211542	36	0.082 c	0.079 b	0.080 c	0 b
TAF46	29	0.077 c	0.082 b	0.079 c	0 b
Zhong 4	24	0.080 c	0.085 b	0.075 c	0 b
54-41-1-4-5-5	35	0.093 c	0.101 b	0.427 b	100 a
KS93WGRC27	34	0.082 c	0.109 b	0.081 c	0 b
A29-13-3	36	0.081 c	0.099 b	0.077 c	0 b
CI 15092	31	0.095 c	0.087 b	0.076 c	0 b
McClintock	36	0.318 b	0.374 a	0.691 a	0 b
7631-3-20	36	0.496 a	0.452 a	0.560 ab	0 b
Chinese Spring	34	0.462 ab	0.455 a	0.538 ab	0 b
T. dicoccoides	34	0.485 ab	0.495 a	0.563 ab	0 b
Non-inoculated Chinese Spring		0.094	0.099	0.081	

[a]Mean values followed by the same letter are not significantly different according to Duncan's multiple range test ($p < 0.05$).
[b]Percentage of plants resistant to WCM colonization at 3 weeks after exposure to the WCM.

WSMV was not detected with the ELISA in the line 54-41-1-4-5-5 until 6 weeks after inoculation. The ELISA readings in line 54-41-1-4-5-5 remained lower than those of the WSMV-susceptible entries Chinese Spring and 7631-3-20 for the first 4 weeks (Table 2). The ELISA results did not show any evidence of WSMV in the two *Th. intermedium* amphiploid lines TAF46 or Zhong 4, nor in the translocation or substitution lines KS93WGRC27, A29-13-3, and CI 15092 at any of the sampling dates.

At the first sampling date, the ELISA value for the winter wheat cultivar McClintock was lower than those of the susceptible Chinese Spring and the line 7631-3-20. Over time, the ELISA readings increased in McClintock as more infected plants appeared. ELISA also detected a rapid buildup of the WSMV in *T. dicoccoides*, which agrees the visual evaluation of the symptoms (Table 2).

A linear regression analysis was carried out to examine the relationship between ELISA absorbance readings and WSMV incidence in all the lines. Regression analysis demonstrated that ELISA absorbance readings vs. the percentage of infected plants at 2, 4 and 6 weeks, were highly correlated ($r^2 = 0.9251$, 0.9323, and 0.8658, respectively).

WCM resistance and its effect on the spread of WSMV

Out of the seven partial amphiploid lines tested, only Agrotana was resistant to the WCM. All of the plants of lines 693, PWM706, PRRPX, OK7211542, TAF46 and Zhong 4, showed symptoms of rolling or trapping of the leaves caused by the WCM colonization (Table 2). The lines A29-13-3, KS93WGRC27, and CI 15092 were all highly susceptible to the WCM. Neither 7631-3-20 nor McClintock escaped colonization by the WCM. The accession of *T. dicoccoides* was as susceptible to the WCM as Chinese Spring (Table 2). Line 54-41-1-4-5-5, a derivative of wheat × Agrotana, was as resistant to the WCM as its parent, Agrotana. There were no symptoms of WCM colonization in 54-41-1-4-5-5 or in Agrotana (Table 2).

Chinese Spring exhibited severe mosaic symptoms within a week after exposure to the viruliferous WCM (Figure 1). The symptoms of WSM also developed quickly in the WCM-susceptible wheat cultivar Rescue. When exposed to viruliferous WCM, no systemic symptoms of WSM were visible in Agrotana due to its excellent WCM- and WSMV-resistance. The WCM-resistance of 54-41-1-4-5-5 was effective in controlling the spread of

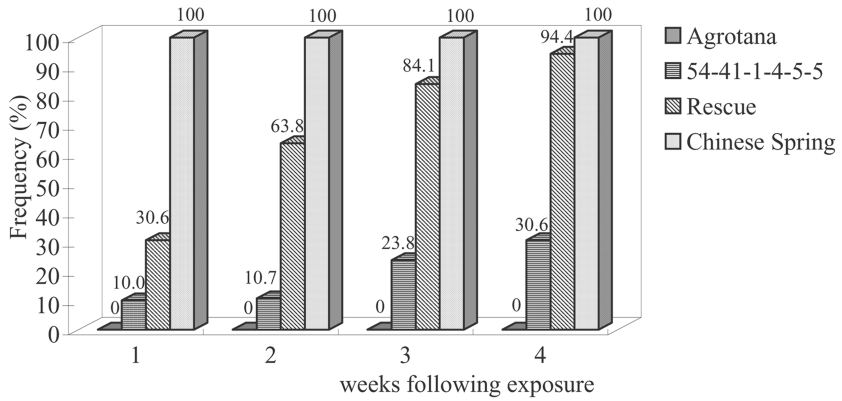

Figure 1. The percentage of plants showing WSM symptoms following exposure to viruliferous WCM.

WSMV. Only a small percentage of the plants in line 54-41-1-4-5-5 had WSM symptoms a week following exposure. The WSM symptoms developed in 28.9% of the plants of 54-41-1-4-5-5 at 4 weeks after exposure to viruliferous WCM, compared to 100 and 94.4% infected plants in Chinese Spring and Rescue, respectively.

Discussion

The wheat grass species, *Th. ponticum* and *Th. intermedium* are perennial species that are often highly resistant to WSMV and its vector the WCM (Andrews and Slykhuis 1956). In this study, WSMV resistance was well expressed in partial amphiploid lines derived from crosses of wheat-*Th. ponticum* and wheat-*Th. intermedium*, although none of them were originally selected for WSMV resistance. No systemic symptoms developed in these amphiploid lines throughout the duration of this study (Table 1). ELISA absorbance readings at each sampling date in these partial amphiploids were comparable to those of the non-inoculated control of Chinese Spring, indicating that WSMV did not build up in their plant tissues. The partial amphiploid lines 693 and PWM706, which are both derived from wheat-*Th. ponticum* crosses, were identified as new sources of WSMV-resistance. The WSMV resistance of other partial amphiploid lines, such as Agrotana, ORRPX, OK7211542, TAF46, and Zhong 4 was confirmed by their low ELISA values *versus* the high values for Chinese Spring. The lines KS93WGRC27, A29-13-3, and CI 15092, which possess the gene *Wsm1* that confers WSMV resistance (Wells et al. 1973; Gill et al. 1995; Wang and Zhang 1996), did not show systemic WSM symptoms at any time during the investigation. ELISA values in these lines were as low as that in the non-inoculated Chinese Spring check. The expression of WSMV-resistance conferred by the gene *Wsm1* is temperature sensitive (Pfannenstiel and Niblett 1978; Seifers et al. 1995). The growing temperatures in this study were not high enough to interfere with the expression of WSMV-resistance in these lines. The results of ELISA also indicated that WSMV did not buildup in lines carrying the gene *Wsm1* under mild temperatures, which indicated the WSMV-resistance of the gene *Wsm1* remained effective. However, these lines were not resistant to WCM colonization. All of the partial amphiploids, except Agrotana, were susceptible to the WCM. The stripe rust resistant line 7631-3-20, derived from a wheat-*Th. ponticum* cross, had no WSMV- or WCM-resistance. The accession of *T. dicoccoides* was also susceptible to both WSMV and the WCM.

The partial amphiploid line Agrotana has been used in developing germplasm with resistance to WSMV and the WCM. Line 54-41-1-4-5-5 was derived from a cross of wheat × Agrotana and has resistance to WSMV and the WCM. The WSMV resistance in line 54-41-1-4-5-5 appears to delay the buildup of WSMV for the first few weeks following inoculation, based on ELISA values. This suggests that an undetermined mechanism might exist in line 54-41-1-4-5-5, which inhibits either the multiplication or movement of WSMV in the plant tissues.

The percentage of plants showing symptoms in line 54-41-1-4-5-5 were significantly lower than those of Chinese Spring at the final observation (Table 1). The WSMV resistance gene(s) in *Th. ponticum* is located on a group 6 chromosome (Larson and Atkinson 1973). The level of WSMV resistance of the *Th. ponticum* group 6 chromosome addition line was not comparable to that of its partial amphiploid parent. It has been speculated that an interaction between group 5 and 6 chromosomes of *Th. ponticum* might be required for the expression of a high level resistance to WSMV (Stoddard et al. 1987a). ELISA values higher than that of the disease-free control were also observed in individual samples of the wheat-*Thinopyrum* partial amphiploid PWM706 at late stage after inoculation, although overall the ELISA readings were not significantly different from the other resistant lines (data not shown). Unstable resistance to WSMV has been observed in other wheat-*Th. ponticum* substitution and translocation lines under greenhouse conditions, but not in the field (Pfannenstiel and Niblett 1978). The inhibition of a buildup of the virus and the late expression of systemic symptoms following inoculation, together with WCM resistance, make line 54-41-1-4-5-5 useful in the genetic improvement of wheat.

Visual assessment of symptoms is the most widely used method for the evaluation of resistance to WSMV. It is attractive to breeders because it is relatively easy to detect symptoms, requires less labor and expense than other methods. It permits the evaluation of large population with reasonable accuracy. The results presented here further confirmed the ease of following the development of WSM symptoms in wheat-*Thinopyrum* amphiploids as well as their derivatives. Studies have demonstrated that symptom development was associated with a build up of the virus, in terms of ELISA color intensity as a measure of the serological quantification of viral protein (Jedlinski et al. 1977; Skaria et al. 1985; Ranieri et al. 1993). However, a similar association could not be clearly drawn in a study involving wild wheat species ($r^2 = 0.262$) (Stoddard et al. 1987b). The authors attributed the low correlation to the fact that disease incidence rather than symptom severity was recorded. In the present study, ELISA intensities were highly correlated with the incidence of plants displaying systemic symptoms among the lines tested ($r^2 = 0.8658$–0.9323). This might be partly due to the easier detection of the symptoms caused by WSMV in this study. Symptoms caused by WSMV infection can be confused with chlorotic symptoms caused by nutritional deficiencies and certain pest infestations (Shahwan and Hill 1984). Moreover, WSMV infection may occur in combination with other wheat viruses such as BYDV, the High Plains virus, or Agropyron mosaic virus (Montana et al. 1994; Mahmood et al. 1998). This might confuse the detection of WSM symptoms both in the greenhouse and the field. Therefore, ELISA is needed to further characterize WSMV in plants that show mosaic symptoms. In general, the symptomatology assay is an adequate method for assessing WSMV infection in wheat breeding programs, while ELISA technique provides precise quantification of WSMV capsid protein in infected plant tissues.

The precise serological approach for detection of WSMV in combination with symptomatology provides an effective means for selecting partial resistance to WSMV in wheat breeding programs. The new hard red winter wheat cultivar McClintock initially had a lower ELISA value and slower development of mosaic symptoms than Chinese Spring (Tables 1 and 2). The symptoms in diseased plants of McClintock were not as severe as those in Chinese Spring and other susceptible lines such as 7631-3-20 and *T. dicoccoides*. This suggests that partial resistance to WSMV may exist in McClintock. Reductions in virus accumulation and lower incidences of WSM have been associated with reduced yield losses in wheat (Seifers and Martin 1988). Field experiments are needed to determine the effectiveness of the late expression of WSM symptom in McClintock in preventing yield reductions. Since McClintock is highly resistant to stem rust (*Puccinia graminis tritici* Eriks. et Henn.) and leaf rust (*P. recondita* Rob. ex Desm. F. sp. *tritici* Eriks. et Henn.) and has a high yield potential (Brûlé-Babel 2001), McClintock could serve as valuable germplasm in a wheat breeding program to improve WSMV-resistance. Work is under way to use its partial resistance to WSMV in the development of winter wheat cultivars.

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