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Resistance to *Wheat streak mosaic virus* and *Triticum mosaic virus* in wheat lines carrying *Wsm1* and *Wsm3*

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Abstract *Wheat streak mosaic virus* (WSMV) *and Triticum mosaic virus* (TriMV) are important viruses of wheat (*Triticum aestivum* L.) in the Great Plains of United States. In addition to agronomic practices to prevent damage from these viruses, temperature sensitive resistance genes *Wsm1*, *Wsm2* and *Wsm3*, have been identified. However, threshold temperatures for *Wsm1* and *Wsm3* have not been clearly defined. To better understand these two resistance genes, wheat lines C.I.15092 (*Wsm1*), KS96HW10–3 (*Wsm1*), and KS12WGGRC59 (*Wsm3*) were evaluated for WSMV resistance at 27, 30, 33 and 35 °C and for TriMV resistance at 18, 21, 24, 27, 30, 33 and 35 °C. The results showed that only C.I.15092 remained resistant at 30 °C for both viruses. This line also tolerated TriMV at 33 and 35 °C with less sever symptom and lower infection rates. Wheat lines KS96HW10–3 and KS12WGGRC59 hold resistance to TriMV up to 21 °C. Molecular marker results suggested that the resistance in C.I.15092 is most probably conditioned by the resistance gene *Wsm1* and additional gene(s) other than *Wsm2* and *Wsm3*.

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Wheat (*Triticum aestivum* L.) production is constrained by pests and diseases. In the Great Plains of the United States especially, wheat streak mosaic (WSM) caused by *Wheat streak mosaic virus* (WSMV) is economically important because of significant yield reduction (French and Stenger 2003; Burrows et al. 2009; Velandia et al. 2010; Price et al. 2010). In 2006, *Triticum mosaic virus* (TriMV) was first identified in Hays, KS (Seifers et al. 2006). Since then TriMV has been found throughout the Great Plains (Burrows et al. 2009; Fuentes-Bueno et al. 2011). TriMV infection also can cause significant yield losses in wheat (Seifers et al. 2011). WSMV and TriMV are assigned to the genera *Tritimovirus* and *Poacevirus*, respectively, in the family *Potyviridae* (Stenger et al. 1998; Tatineni et al. 2009). Both viruses are transmitted by the wheat curl mite (*Aceria tosichella* Keifer) (Slykhuis 1955; McMechan et al. 2014) and induce similar symptoms in wheat (Seifers et al. 2008). TriMV is usually found in double infections with WSMV; WSMV often occurs alone (Byamukama et al. 2013). WSMV and TriMV are synergistic, with double infections causing more yield loss than single infections (Byamukama et al. 2014).

The use of genetic resistance for plant viruses is considered advantageous as control due to effectiveness and durability with no additional management inputs required (Gómez et al. 2009). Damage from co-infection of the two viruses is high and limited

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Table 1 Resistance of wheat lines to *Triticum* mosaic and wheat streak mosaic viruses 21 days after inoculation

Wheat line	Systemic infection of plants (%)[x] maintained at different temperature										
	Triticum mosaic virus (TriMV)							Wheat streak mosaic virus (WSMV)			
	18 °C	21 °C	24 °C	27 °C	30 °C	33 °C	35 °C	27 °C	30 °C	33 °C	35 °C
KS96HW10–3	0	0	100	100	100	93.8	95	100	100	100	100
RonL	100	100	100	100	100	100	100	100	100	100	100
KS12WGGRC59	10	10	100	100	100	100	100	95	100	100	100
C.I.15092	0	5	0	0	0	17	44.5	0	0	82	100
Non-inoculated	0	0	0	0	0	0	0	0	0	0	0

[x] (Number of infected plants/total number of plants) ×100

availability of known resistant germplasm adds extra challenges to breeding against these viruses. All of known resistance to WSMV and TriMV being effective only up to 18 °C (Seifers et al. 2013b). So far, three known resistance genes (*Wsm1*, *Wsm2*, and *Wsm3*) have been identified. Both *Wsm1* and *Wsm3* originated from *Agropyron intermedium*; *Wsm2* was discovered in wheat. C.I.15092, substituted with a whole *Agropyron* chromosome (4Ai-2), was the first wheat line carrying *Wsm1* (Martin et al. 1976). It showed resistance to WSMV at 27 °C, but this resistance broke at 35 °C (Pfannenstiel and Niblett 1978). However, there are no reports about the response of C.I. 15092 to TriMV infection. Later on, several translocated wheat lines carrying only the short arm (or partial short arm) of the *Agropyron* chromosome 4Ai-2 (4Ai-2S or 4Ai-1S), which harbors *Wsm1*, were derived from C.I.15092 (Friebe et al. 1991; Gill et al. 1995; Gill et al. 2008). These translocation wheat lines can hold WSMV resistance up to 20 °C and TriMV resistance at 18 °C but resistance to both breaks at 24 °C (Seifers et al. 1995, 2013a; Gill et al. 2008). *Wsm2* resistance was only effective against WSMV at or below 18 °C (Seifers et al. 2006), was not resistant to TriMV (Friebe et al. 2009). Resistance gene *Wsm3* was located on the long arm of *Agropyron* chromosome 3 and was translocated into wheat line KS12WGGRC59 (Friebe et al. 2011). *Wsm3* was effective for control of WSMV at 24 °C and TriMV at 18 °C but TriMV resistance broke at 24 °C (Friebe et al. 2011; Liu et al. 2011). It is not clear if *Wsm1* and *Wsm3* can hold resistance to TriMV at a temperature between 18 and 24 °C, or if *Wsm3* can hold WSMV resistance at a temperature higher than 24 °C. Our objective was to examine the WSMV and TriMV resistance of *Wsm1* and *Wsm3* at various temperature levels (WSMV at 27, 30, 33, 35 °C and TriMV at 18, 21, 24, 27, 30, 33, 35 °C) to gain a better understanding of these two resistance genes.

In this study, isolate 06–123 of TriMV (Seifers et al. 2006) and Sidney 81 isolate of WSMV (Seifers et al. 1995) were used for inoculation. Three wheat lines carrying *Wsm1* or *Wsm3* were tested, including

Table 2 Enzyme linked immunosorbent assay (ELISA) of wheat lines inoculated with *Triticum* mosaic and wheat streak mosaic viruses

Wheat line	ELISA absorbance value[z] at different temperatures										
	Triticum mosaic virus (TriMV)							Wheat streak mosaic virus (WSMV)			
	18 °C	21 °C	24 °C	27 °C	30 °C	33 °C	35 °C	27 °C	30 °C	33 °C	35 °C
KS96HW10–3	0.01	0.01	0.32	0.44	0.50	0.18	0.13	0.12	0.12	0.20	0.23
RonL	0.15	0.19	0.31	0.33	0.31	0.15	0.13	0.20	0.11	0.29	0.25
KS12WGGRC59	0.01	0.03	0.38	0.33	0.28	0.12	0.12	0.12	0.14	0.23	0.21
C.I.15092	0.04	0.03	0.02	0.02	0.02	0.03	0.02	0.04	0.04	0.12	0.14
Non-inoculated	0.03	0.04	0.03	0.02	0.03	0.05	0.03	0.03	0.03	0.03	0.04

[z] Average value of all the plants in each line

KS96HW10–3 (*Wsm1* with the short arm - Seifers et al. 2013a), KS12WGGRC59 and C.I.15092. RonL (*Wsm2* - Lu et al. 2011) also was included as a susceptible check. This study was conducted in growth chambers (Percival Model PGC-15 WC) and each test (a certain virus at a certain temperature) had two replications with a randomized complete block design. At the one-leaf stage, plants were inoculated by spraying sap extracts from WSMV or TriMV infected leaves. The plants were scored for symptoms at 21 days after inoculation (DAI) as described in Lu (Lu et al. 2011). Indirect ELISA procedures were performed for virus detection and molecular markers were used to detect the existence of any of the three known WSMV resistance genes (*Wsm1*, *Wsm2* and *Wsm3*). Details about planting, inoculum preparation, inoculation technique, and indirect ELISA procedure can be found in the Supplemental Material.

The results showed that the check line RonL was susceptible in all the tests and the other three lines carrying *Wsm1* or *Wsm3* maintained TriMV resistance at 18 and 21 °C (Table 1). However, KS96HW10–3 and KS12WGGRC59 developed mosaic symptoms for TriMV at 24 °C and above, and for WSMV at 27 °C or above (Table 1). The observed resistance to WSMV and TriMV in C.I.15092 was sustained at both 27 and 30 °C (Table 1). Symptoms of systemic infection of both viruses was noted on C.I.15092 after two weeks of inoculation at 33 °C and 35 °C. WSMV symptoms on C.I.15092 were severe and the percentage of infected plants was higher with 82 % at 33 °C and 100 % at 35 °C. However, this germplasm was still tolerant to TriMV at 33 °C and 35 °C showing less severe symptoms with lower percentages of plants infected (17 % at 33 °C and 44.5 % at 35 °C) (Table 1).

ELISA test results further confirmed the observations (Table 2). Temperature sensitivity of WSMV resistance in lines KS96HW10–3, RonL, and KS12WGGRC59 agrees with previous reports stating that 1) *Wsm2* carrier lines such as RonL are not resistant at temperatures higher than 18 °C, 2) resistance can be observed up to 20 °C in KS96HW10–3 and, 3) up to 24 °C in KS12WGGRC59 (*Wsm3*) (Seifers et al. 1995, 2006, 2013a, b). Previous studies showed that *Wsm1* and *Wsm3* were TriMV-resistant at 18 °C but not at 24 °C (Friebe et al. 2009; Liu et al. 2011), while C.I.15092 was resistant to WSMV at 27 °C but not at 35 °C (Pfannenstiel and Niblett 1978). Through testing at more defined temperature levels, we found that *Wsm1* and *Wsm3* held TriMV resistance up to 21 °C, and that C.I.15092 held TriMV and WSMV resistance up to 30 °C.

Using molecular markers, we verified the presence of *Wsm1* in KS96HW10–3 and C.I.15092; *Wsm2* in RonL and *Wsm3* in KS12WGGRC59. These results suggest that the high temperature resistance observed in C.I.15092 is not exclusively from *Wsm1* and that *Wsm2* or *Wsm3*do not contribute to resistance in this wheat line. Therefore, other unknown gene/s most likely attributed to high temperature resistance in addition to *Wsm1* in C.I.15092.

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