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Characterization of Seedling Infection Types and Adult Plant Infection Responses of Monogenic *Sr* Gene Lines to Race TTKS of *Puccinia graminis* f. sp. *tritici*

Y. Jin, United States Department of Agriculture–Agricultural Research Service, (USDA-ARS) Cereal Disease Laboratory, University of Minnesota, St. Paul; R. P. Singh and R. W. Ward, International Maize and Wheat Improvement Center (CIMMYT), Apdo, Postal 6-641, Mexico D.F., Mexico; R. Wanyera, M. Kinyua, and P. Njau, Kenyan Agricultural Research Institute, National Plant Breeding Research Center, P.O. Njoro, Kenya; T. Fetch, Cereal Research Centre, Agriculture and Agri-Food Canada, Winnipeg, MB, Canada; Z. A. Pretorius, Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa; and A. Yahyaoui, International Center for Agricultural Research in the Dry Areas (ICARDA), Tel Hadya, Aleppo, Syrian Arab Republic

ABSTRACT

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Stem rust, caused by *Puccinia graminis* f. sp. *tritici*, historically was one of the most destructive diseases of wheat and barley. The disease has been under effective control worldwide through the widespread use of host resistance. A number of stem rust resistance genes in wheat have been characterized for their reactions to specific races of *P. graminis* f. sp. *tritici*. Adult plant responses to race TTKS (also known as Ug99) of monogenic lines for *Sr* genes, a direct measurement of the effectiveness for a given gene, have not been investigated to any extent. This report summarizes adult plant infection responses and seedling infection types for monogenic lines of designated *Sr* genes challenged with race TTKS. High infection types at the seedling stage and susceptible infection responses in adult plants were observed on monogenic lines carrying *Sr5*, *6*, *7a*, *7b*, *8a*, *8b*, *9a*, *9b*, *9d*, *9g*, *10*, *11*, *12*, *15*, *16*, *17*, *18*, *19*, *20*, *23*, *30*, *31*, *34*, *38*, and *Wld-1*. Monogenic lines of resistance genes *Sr13*, *22*, *24*, *25*, *26*, *27*, *28*, *32*, *33*, *35*, *36*, *37*, *39*, *40*, *44*, *Tmp*, and *Tr-3* were effective against TTKS both at the seedling and adult plant stages. The low infection types to race TTKS observed for these resistance genes corresponded to the expected low infections of these genes to other incompatible races of *P. graminis* f. sp. *tritici*. The level of resistance conferred by these genes at the adult plant stage varied between highly resistant to moderately susceptible. The results from this study were inconclusive for determining the effectiveness of resistance genes *Sr9e*, *14*, *21*, and *29* against race TTKS. The understanding of the effectiveness of individual *Sr* genes against race TTKS will facilitate the utilization of these genes in breeding for stem rust resistance in wheat.

Historically, stem rust, caused by *Puccinia graminis* f. sp. *tritici*, was one of the most destructive diseases of wheat (*Triticum aestivum* and *T. turgidum* subsp. *durum*) and barley (*Hordeum vulgare*). In recent years, the disease has been under effective control through the widespread

use of host resistance. A number of stem rust resistance genes, designated as *Sr* genes in wheat and its close relatives, were described and cataloged (5,6), and monogenic lines carrying individual *Sr* genes are available in several wheat backgrounds. Most of the *Sr* genes have been characterized for their reactions to specific races of *P. graminis* f. sp. *tritici* (1,6,12), including reactions at the seedling stage to race TTKS (or Ug99), a race which recently emerged in Eastern Africa (8,15,17). In addition to the virulence signified by the TTKS notation, this race is virulent to *Sr31* and, on a global scale, threatens wheat cultivars protected by this resistance gene. Several *Sr* genes present singly or in combination with other *Sr* genes in adapted germplasm (i.e., released cultivars and breeding lines) were found to be effective against race TTKS at the seedling stage (2). The presence of other known or unknown *Sr* genes in the adapted germplasm may confound disease assessment. Host responses to race TTKS in monogenic lines of *Sr* genes at the adult plant stage, a

direct measurement of the effectiveness for a given gene, have not been investigated to any extent. This report summarizes the specific responses to race TTKS of monogenic lines of *Sr* genes, representing the majority of designated *Sr* genes that were available to the senior author during this investigation, based on greenhouse seedling assays and field evaluations in stem rust nurseries planted at Njoro, Kenya in 2005 and 2006.

MATERIALS AND METHODS

Evaluation of seedling infection types.

An isolate (04KEN156) of *P. graminis* f. sp. *tritici*, collected from Kenya in 2004 and identified as race TTKS (17) based on the 16 differentials in the *P. graminis* f. sp. *tritici* differential set of North America (10,11), was used for evaluating the monogenic lines of *Sr* genes. Urediniospores from long-term storage in a -80°C freezer were heat shocked at 40°C for 10 min and placed in a rehydration chamber for 2 to 4 h, where approximately 80% relative humidity was maintained by a KOH solution (14). The urediniospores then were suspended in a light mineral oil (Solrol 170) and inoculated onto the fully expanded primary leaves of 7- to 9-day-old seedlings of wheat lines. Seedlings were incubated in a dew chamber for 14 h at 18°C in the dark, and then for an additional period of 3 to 4 h under fluorescent light. The inoculated plants were placed on a greenhouse bench at $18 \pm 2^{\circ}\text{C}$ with a photoperiod of 16 h. Infection types (ITs), described by Stakman et al. (16), were assessed 14 days post inoculation. A set of the 16 *P. graminis* f. sp. *tritici* differentials and the susceptible checks Chinese Spring and LMPG-6 were used in each inoculation. ITs 0, ;, 1, 2, or combinations thereof were considered low ITs, indicating that the corresponding resistance gene is effective. ITs 3 to 4 were considered high ITs, indicating that the corresponding resistance gene is not effective against the race tested. In each test, 6 to 10 seedling plants were evaluated, and the seedling test was repeated.

Field stem rust evaluations in Njoro, Kenya. The monogenic *Sr* gene lines were

Corresponding author: Y. Jin
E-mail: yuejin@umn.edu

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USDA-ARS Cereal Disease Laboratory maintains seed stocks used in this study and they are available upon request from the corresponding author.

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tested in 2005 and 2006 as part of a larger field stem rust screening nursery in Njoro, Kenya established by the Kenyan Agricultural Research Institute in conjunction with the International Maize and Wheat Improvement Center (CIMMYT) and the Global Rust Initiative. The nursery site was located at 0°20'S, 35°56'E, and 2,185 m in elevation, with an average daily minimum temperature of 9.7°C (night) and an average daily maximum temperature of 23.5°C (noon). Variations of average daily temperatures are approximately ±2°C, occurring mostly during the day hours of the field evaluation period. Dew was formed nearly daily. Entries were planted in single 2-m-row plots on 30 June 2005 and in double 1-m-row plots on 5 May 2006. To facilitate inoculum build-up and uniform dissemination within the nursery, a continuous row of stem rust spreader (a mixture of susceptible cvs. Chozi and Duma carrying *Sr31*) was planted perpendicular to all entries in the 2006 nursery. The spreader rows were inoculated once by dusting them with a mixture of urediniospores and talc powder. The source of inoculum was a bulk of urediniospores collected from experimental plots of Duma in Kenya.

Plant response to rust infection at the adult plant stage was termed "infection response." According primarily to the size of pustules and associated necrosis or chlorosis, infection responses were classified into four discrete categories: R = resistant,

MR = moderately resistant, MS = moderately susceptible, and S = susceptible (13). Infection responses overlapping between any particular two categories were denoted using a dash. For instance, "MR-MS" denoted an infection response class overlapped between the MR and MS categories. Stem rust severity was assessed following the modified Cobb scale (7). Entries were evaluated for infection responses and stem rust severity two to three times between heading and plant maturity. The infection responses and stem rust severity at the soft-dough stage of plant growth were used to represent the final disease scores in this report.

RESULTS AND DISCUSSION

Rust development in Njoro, Kenya.

The nursery location was highly conducive for stem rust development due to daily formation of dew during the crop season, presence of stem rust inoculum on a geographically limited "green bridge" of wheat and barley crops maturing year round, and a relatively long grain-filling period (45 to 50 days) after heading. Although the planting date of the 2005 field nursery was later than normal planting dates (early to mid-May), plants and rust developed normally. Some drought stress was experienced in the nurseries at planting in 2005 and during early plant development in 2006. Supplemental water was provided to ensure normal development of

plants. During the crop seasons in both years, fungal diseases other than stem rust and stripe rust (caused by *P. striiformis* f. sp. *tritici*) were minimal. Stripe rust was predominant from plant emergence to heading, and stem rust predominated thereafter. Wheat with a strong photoperiod sensitivity matured 2 to 3 weeks later compared with materials that were not sensitive. Based on responses of the stem rust race differential lines, infections in the nursery were due primarily to race TTKS in both years.

Stem rust resistance genes not effective against TTKS. Monogenic lines that exhibited high ITs (IT 3 or higher) at the seedling stage and stem rust severity and infection responses comparable with the susceptible checks at the adult plant stage are listed in Table 1. The infection responses, primarily of a susceptible type and with high disease severity, indicated that *Sr5*, *6*, *7a*, *7b*, *8a*, *8b*, *9a*, *9b*, *9d*, *9g*, *10*, *11*, *12*, *15*, *16*, *17*, *18*, *19*, *20*, *23*, *30*, *31*, *34*, *38*, and *Wld-1* were not effective against race TTKS. The results from the field evaluations corroborated the high ITs to TTKS observed at the seedling stage as well as previous observations based on seedling tests (8,17). A number of these genes, namely *Sr6*, *7a*, *7b*, *9a*, *9b*, *10*, *11*, *12*, *16*, *17*, and *Wld-1*, are present, often in combinations, in wheat cultivars in North America and other regions and have played a role in stabilizing stem rust resistance. The ineffectiveness of these genes at Njoro may

Table 1. Infection types (ITs) on seedling and infection responses (IRs) on adult plants of monogenic stem rust resistance gene lines that are ineffective against race TTKS of *Puccinia graminis* f. sp. *tritici*

Line	Sr gene	IT ^b	Stem rust severity and IR ^a		Material type	Background in
			2005 Kenya	2006 Kenya		
LMPG-6	...	3	60 MS-S	60 S	Susceptible check	...
Chinese Spring	...	4	80 S	80 S	Susceptible check	...
ISr5-Ra	5	4	70 S	70 S	Single gene stock	Chinese Spring
ISr6-Ra	6	4	80 S	70 S	Single gene stock	Chinese Spring
Kenya Governor/10*MQ//8*LMPG	7a	3+	70 S	80 S	Single gene stock	LMPG-6
ISr7b-Ra	7b	4	60 S	80 S	Single gene stock	Chinese Spring
ISr8-Ra	8a	4	80 S	80 S	Single gene stock	Chinese Spring
Barletta 77	8b	4	100 S	70 S	Cultivar	...
ISr9a-Ra	9a	4	80 S	80 S	Single gene stock	Chinese Spring
W2691Sr9b	9b	4	100 S	70 S	Single gene stock	W2691
ISr9d-Ra	9d	3+	80 S	80 S	Single gene stock	Chinese Spring
CnsSr9g	9g	4	80 S	80 S	Single gene stock	Chinese Spring
W2691Sr10	10	3+	100 S	70 S	Single gene stock	W2691
ISr11-Ra	11	4	80 S	70 S	Single gene stock	Chinese Spring
Bt/TcSr12	12	3+	80 S	60 S	Single gene stock	Baart
Prelude*2/Sr15	15	4	70 S	...	Single gene stock	Prelude
ISr16-Ra	16	4	70 S	60 MS-S	Single gene stock	Chinese Spring
Prelude/8*Mq/2*/Esp 5/8/9	17	4	60 MS	80 S	Single gene stock	LMPG-6
LcSr18R1	18	4	70 S	...	Single gene stock	Little Club
LcSr19Mq	19	4	80 S	...	Single gene stock	Little Club
LcSr20Mq	20	3+	80 S	...	Single gene stock	Little Club
Exchange selection	23	4	80 S	...	Cultivar	...
BtSr30Wst	30	3+	60 S	60 MS-S	Single gene stock	Baart
Line E/Kavkaz	31	4	80 S	80 S	Single gene stock	Line E
Sr31 (Benno)/6*LMPG	31	3	100 S	80 S	Single gene stock	LMPG-6
Compair	34	4	80 S	60 MS-S	Cultivar	...
RL 6081	38	;23	50 S	40 S	Single gene stock	Thatcher
Bt/Wld	Wld-1	3+	80 S	60 S	Single gene stock	Baart

^a IRs at the adult plant stage following the descriptions of Roelfs et al. (13), where R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible.

^b ITs at the seedling stage following the descriptions of Stakman et al. (16), where IT 0, 1, 2, or combinations thereof were considered low infection types, and IT 3 to 4 were considered high infection types.

Table 2. Infection types (ITs) on seedling and infection responses (IRs) on adult plants of monogenic stem rust resistance gene lines that are effective against race TTKS of *Puccinia graminis* f. sp. *tritici*

Line	Sr gene	IT ^b	Stem rust severity and IR ^a		Material type	Background in
			2005 Kenya	2006 Kenya		
LMPG-6	...	3	60 MS-S	60 S	Susceptible check	...
Chinese Spring	...	4	80 S	80 S	Susceptible check	...
St464	13	2+	40 MR-MS	40 MS	Cultivar (durum)	...
Combination VII	13 (+17)	2+	40 MR-MS	40 MS	Two gene stock	W2691
Khapstein/9*LMPG	13	2+	...	30 MS	Single gene stock	LMPG-6
Sr22TB	22	1;	10 R	20 R-MR	Single gene stock	...
T. momoc.Deriv./9*LMPG	22	1	...	20 R-MR	Single gene stock	LMPG-6
LcSr24Ag	24	2	10 MR	20 R-MR, 5 S	Single gene stock	Little Club
Agent/9*LMPG	24	2-	...	10 R-MR, 5 S	Single gene stock	LMPG-6
LcSr25Ars	25	2+	60 MR-MS	20 MR-MS	Single gene stock	Little Club
Agatha/9*LMPG	25	2	...	20 MR-MS	Single gene stock	LMPG-6
Eagle (Australia)	26	1	40 MR-MS	5 R	Cultivar	...
PW327/4*Tc/9*LMPG	26	1	...	10 R	Single gene stock	LMPG-6
73,214,3-1/9*LMPG	27	;	20 MR	10 R	Single gene stock	LMPG-6
W2691/Sr28Kt	28	;13	40 MS-S	30 MR-MS	Single gene stock	W2691
CnsSr32 A.s.	32	1+	30 R	10 R	Single gene stock	Chinese Spring
C82,1CS+Sr32/6*LMPG	32	1	10 R	10 R	Single gene stock	LMPG-6
RL 5405	33	2,3	30 MR	30 MR-MS	Single gene stock	Tetra Canthatch
Tetra Canthatch/7*LMPG	33	2+	...	40 MR-MS	Single gene stock	LMPG-6
Mq(2)5*G2919	35	;	10 MR-MS	1 R	Single gene stock	Marquis
W2691SrTt-1	36	0	0	0	Single gene stock	W2691
CI12632/8*LMPG	36	0;	5 MR	0	Single gene stock	LMPG-6
W3563	37	;1-	...	5 R/60 S	Single gene stock	W2691
RL 6082	39	1	5 R/70 S	5 R/10 MS	Single gene stock	Thatcher
RL 6088	40	1	5 R	10 R	Single gene stock	RL 6071
Taf-2	44	1+	10 R-MR	10 R	Single gene stock	...
CnsSrTmp	Tmp	2+	40 MS	30 MR-MS	Single gene stock	Chinese Spring
W199/Tt113*W199	Tt-3	2+	...	10 R	Single gene stock	...
Federation SrTt-3/6*LMPG	Tt-3	3-	...	5 RMR	Single gene stock	LMPG-6

^a IRs at the adult plant stage following the descriptions of Roelfs et al. (13), where R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible; “/” indicates a mixture of plants, predominant type given first.

^b ITs at the seedling stage following the descriptions of Stakman et al. (16), where IT 0, ;, 1, 2, or combinations thereof were considered low infection types, and IT 3 to 4 were considered high infection types.

partially explain the susceptibility of U.S. spring wheat cultivars to race TTKS (2). This also may explain the widespread susceptibility to race TTKS in CIMMYT-released cultivars (Y. Jin and R. Singh, unpublished) regardless of whether *Sr31* was present.

A mixture of ITs (or mesothetic with IT ranging from ; to 3-) was observed on line RL 6081, a Thatcher near-isogenic line carrying *Sr38* (6). The terminal stem rust severity was moderately low, although infection response was of a susceptible type. The low ITs at the seedling stage and relatively low disease severity in the Kenyan field nursery likely were due to the background genotype because cv. Thatcher exhibited low ITs to race TTKS at the seedling stage (2) and MR to MS infection responses in the Kenyan field nurseries (Y. Jin, unpublished).

Stem rust resistance genes effective against TTKS. Monogenic lines that exhibited low ITs at the seedling stage and R or MR to MS responses at the adult plant stage are listed in Table 2. When a gene was found to be effective against TTKS in the 2005 field nursery, a different monogenic line of the same gene was evaluated in the 2006 field nursery for confirmation purposes. With the exception of *Sr39*, most of the *Sr* genes with low ITs to race TTKS observed in this study appeared to match the expected low infections of these genes

to other incompatible races of *P. graminis* f. sp. *tritici* (6,12). Line RL 6082, the monogenic line carrying *Sr39*, produced an IT of ;1 instead of the expected low IT of 1 to 2. Resistance genes *Sr22*, *24*, *26*, *27*, *32*, *33*, *35*, *36*, *37*, *39*, *40*, *44*, and *Tt-3* exhibited mostly R to MR infection responses with relatively low disease severity in the field nurseries in both years, indicating that these genes are highly effective against race TTKS. Off-type (or S) plants were observed on monogenic lines for *Sr37* and *Sr39*. Monogenic lines for *Sr37* and *SrTt-3* were not tested in the 2005 field nursery. Among these effective resistance genes, resistance gene *Sr24* occurs in a high frequency in various wheat germplasms (2,15). The utilization and effectiveness of resistance genes *Sr26* and *36*, present in certain adapted germplasms, were reviewed by Roelfs (9).

In 2005, resistance gene *Sr24* was highly effective in the Kenyan field nursery based on stem rust ratings on the monogenic line LcSr24Ag (Table 2) as well as observations on breeding lines and cultivars known to carry this gene (R. Singh and Y. Jin 2005, unpublished). Infection responses were R to MR, with terminal stem rust severity up to 20%. However, infection responses of MS to S types were observed on the two monogenic lines for *Sr24*, LcSr24Ag, and Agent/9*LMPG (Table 2), and many breeding lines carry-

ing *Sr24* in the 2006 Kenyan field nursery. The proportion of the S stem rust pustules was low ($\leq 5\%$) in comparison with the R- and MR-type pustules on *Sr24* lines. The identity of the stem rust race producing these MS to S infection responses on *Sr24* lines is being investigated.

Monogenic lines with resistance genes *Sr13*, *25*, and *Tmp* exhibited MR to MS infection responses and moderate levels of stem rust severity in the Kenyan field stem rust nurseries in 2005 and 2006. The levels of rust severity and infection responses were similar on cultivars and breeding lines carrying *Sr25* (R. Singh, unpublished) and *SrTmp* (Y. Jin, unpublished). Although *Sr13* has not been used to any extent in common wheat according to Knott (4), this gene is likely to be present in combinations with *Sr9e* and *14* in many of the durum cultivars developed in North Dakota because the durum cv. Langdon, which derives *Sr13* from Khapli, appears commonly in the pedigrees (3). Many of these durum cultivars have been highly resistant to stem rust in North America, and a number of them were resistant to race TTKS at the seedling and adult plant stages (Y. Jin, unpublished).

Stem rust resistance genes for which effectiveness against TTKS is uncertain. Stem rust resistance genes that exhibited inconsistency between seedling and adult plant stages or discrepancies in the as-

Table 3. Infection types (ITs) on seedling and infection responses (IRs) on adult plants of monogenic stem rust resistance gene lines their effectiveness against race TTKS of *Puccinia graminis* f. sp. *tritici* is uncertain

Line	Sr gene	IT ^b	Stem rust severity and IR ^a		Material type	Background in
			2005 Kenya	2006 Kenya		
LMPG-6	...	3	60 MS-S	60 S	Susceptible check	...
Chinese Spring	...	4	80 S	80 S	Susceptible check	...
Vernstein	9e	4	60 MR-MS	50 MS	Single gene stock	Chinese Spring
K253/3*Steinw./8*LMPG	9e	3+	...	40 MS	Single gene stock	LMPG-6
Line A sel	14	4	50 S	30 MR-MS	Single gene stock	W2691
CS_T_mono_deriv	21	3	70 S	80 S	Single gene stock	Chinese Spring
T. mono. deriv./8*LMPG	21	3	...	30 MS-S	Single gene stock	LMPG-6
Pusa/Etoile de Choisy	29	23	80 S	50 MS	Single gene stock	...
Pld*8/Et. de Ch//6*LMPG	29	3-	...	30 MR-MS	Single gene stock	LMPG-6

^a IRs at the adult plant stage following the descriptions of Roelfs et al. (13), where R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible.

^b ITs at the seedling stage following the descriptions of Stakman et al. (16), where IT 0, 1, 2, or combinations thereof were considered low infection types, and IT 3 to 4 were considered high infection types.

assessments of infection responses between the years are listed in Table 3. The expected low IT for resistance gene *Sr9e* was ; to 2 (6,12). This gene was reported to be ineffective against TTKS (8,17) based on seedling tests. The two tester lines for *Sr9e* were unambiguously high to race TTKS at the seedling stage (Table 3), but exhibited infection responses of MR to MS types in the field nurseries. This may suggest that *Sr9e* is not completely ineffective to race TTKS at the adult plant stage or, alternatively, that these lines may possess adult plant resistance not previously known. The effectiveness of *Sr9e* in a tetraploid background is unknown and needs to be investigated. This gene may have played a partial role in conferring the aforementioned resistance to stem rust in durum cultivars.

Resistance gene *Sr21* was thought to be effective against TTKS based on the intermediate ITs at the seedling stage observed on Einkorn (8). A high IT (IT 3) was observed on CS_T_mono_deriv., a monogenic line of *Sr21* in the Chinese Spring background (Table 3). This line also exhibited an S infection response with stem rust severity comparable to the S checks in the Kenyan field nurseries. However, the monogenic line for *Sr21* in the LMPG-6 background, T. mono. deriv./8*LMPG, was MS to S, with a moderately low stem rust severity in the 2006 field nursery, indicating that *Sr21* might be partially effective. Additional studies are needed to resolve the effectiveness of *Sr21* to race TTKS.

A high seedling IT (IT 4) and an S infection response in the 2005 field nursery were observed on Line A sel, monogenic for *Sr14*. The same line, however, exhibited MR to MS infection responses in the 2006 field nursery. Seedling IT of monogenic lines for *Sr29* appeared to be in the range of the expected low ITs for this gene (Table 3). An S infection response with high disease severity was observed on Pusa/Etoile de Choisy. The monogenic line for *Sr29* in the LMPG-6 background, however, exhibited MR to MS infection responses with relatively low disease sever-

ity. Thus, the effectiveness of *Sr14* and *Sr29* to race TTKS could not be ascertained based on the available data.

Conclusion. Based on field studies in Njoro, Kenya, this report confirmed the broad virulence that race TTKS possesses, especially virulence to genes commonly used in combinations for stem rust resistance in wheat cultivars. A number of designated stem rust resistance genes in monogenic backgrounds were found to be effective against race TTKS at the adult plant stage. With a few exceptions, most of these genes appeared to be detectable for their effectiveness against race TTKS at the seedling stage, permitting the selection of resistance based on seedling tests. The low ITs to race TTKS observed for these resistance genes in this study corresponded to the expected low ITs of these genes to other incompatible races of *P. graminis* f. sp. *tritici*. Several of the *Sr* genes effective against race TTKS are present in unadapted germplasm. A concerted effort should be made to incorporate these effective genes into adapted backgrounds and to develop gene combinations that can provide broad-based durable resistance to race TTKS. In view of anticipated pathogenic adaptation of race TTKS, single deployment of *Sr* genes is strongly discouraged because it will erode the limited number of resistance genes remaining effective to this potentially devastating variant of the stem rust pathogen.

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