Resistance to Tan Spot and *Stagonospora nodorum* Blotch in Wheat-Alien Species Derivatives

R. E. Oliver and **X. Cai**, Department of Plant Sciences, North Dakota State University, Fargo 58105; **R.-C. Wang**, United States Department of Agriculture–Agricultural Research Service (USDA-ARS), Forage and Range Research Laboratory, Logan, UT 84322; and **S. S. Xu** and **T. L. Friesen**, USDA-ARS, Northern Crop Science Laboratory, Fargo, ND 58105

ABSTRACT

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Tan spot (caused by *Pyrenophora tritici-repentis*) and *Stagonospora nodorum* blotch (SNB) (caused by *Stagonospora nodorum*) are destructive fungal diseases of wheat (*Triticum aestivum*) throughout the world. Host plant resistance is thought to be an efficient and economical method of control. The objective of the present study was to identify novel sources of tan spot and SNB resistance in wheat genotypes derived from the crosses between wheat and alien species. Evaluations were conducted at the seedling stage in a growth chamber with 100% relative humidity. For each genotype, three replications were used for each disease. Among the 199 wheat-alien species derivatives evaluated, 65 exhibited resistance to tan spot and 30 showed resistance to SNB similar to BR34, a Brazilian wheat line used as the resistant control. Eleven derivatives were resistant to both diseases. Reactions of the derivatives and their respective wheat parents to tan spot and SNB suggest that resistance genes in the derivatives are derived from alien species. These derivatives can serve as desirable bridges for introgression of resistance genes from alien species to cultivated wheat, and could contribute novel and effective tan spot and SNB resistance to wheat breeding.

Tan spot is caused by the fungal pathogen *Pyrenophora tritici-repentis* (Died.) Drechsler, anamorph *Drechslera tritici-repentis* (Died.) Shoemaker. *Stagonospora nodorum* blotch (SNB) is caused by *Stagonospora nodorum* (Berk.) E. Castell. & Germano (syn. *Septoria nodorum* (Berk.) Berk.), teleomorph *Phaeosphaeria nodorum* (E. Müll.) Hedjar. (syn. *Leptosphaeria nodorum* E. Müll.). Both tan spot and SNB are common in many wheat-growing areas throughout the world and can cause substantial losses in yield and quality of grain (12,35). In recent years, tan spot and SNB have become an increasing problem due to soil conservation practices such as no-tillage (34,40), which leaves plant residues on the soil surface, allowing overwintering of the pathogen and a consequent increase in available inoculum. Increased disease severity also could be due to changes in pathogen virulence (17) or use of susceptible wheat cultivars (24,41).

Several studies have characterized the genetics of tan spot and SNB resistance.

Both qualitatively and quantitatively inherited resistance to tan spot and SNB have been identified in wheat (18,19,23,38,41). Resistance genes have been identified on multiple wheat chromosomes (41). *Stagonospora nodorum* and *Pyrenophora tritici-repentis* both are known to produce multiple host-selective toxins (8,17,25–27), with ToxA being produced by both fungi (17). In the tan spot system, at least three host-selective toxins (HSTs) have been identified, with the genes encoding the proteinaceous toxins Ptr ToxA and Ptr ToxB having been cloned (6,29). These HSTs have been shown to be highly important in disease development (8,13,14,22).

SNB also has been shown recently to be an HST system, in which the fungus utilizes multiple proteinaceous toxins to cause disease. Similar to the tan spot system, host sensitivity or susceptibility genes identified to date are all dominant in nature, indicating an inverse gene-for-gene interaction between fungal-produced toxins and host susceptibility genes. Presently, HSTs have been identified, including SnToxA (17), SnTox1 (25), and SnTox2 (15). Each of these HST–host gene interactions has been shown to be highly important in disease development (15,26,27). In addition to race-specific toxin sensitivity genes in the host, tan spot and SNB resistance quantitative trait loci (QTL) also have been identified (7,10,41). For both SNB and tan spot, these QTL have been identified on several of the hexaploid

wheat chromosomes, including 1B, 3B, 3D, and 5B for tan spot and 1B, 4B, 6A, and 7B for SNB (7,27,41).

Although fungicide applications and cultural control practices can reduce disease severity and its detrimental effects (9,37), host resistance is thought to provide the most economically efficient and sustainable method of control for both tan spot and SNB (7,40). Most wheat cultivars, however, are susceptible to these diseases (24,41) and, although sources of resistance have been identified, cultivars with complete resistance are not currently available (1,33). Identification of novel sources of resistance to tan spot and SNB could aid in developing wheat cultivars resistant to these diseases.

Cultivated wheat generally has a narrow genetic base, which minimizes opportunities for developing host resistance to diseases; however, relatives of wheat contain valuable genes for wheat improvement (11,20,21). Genes from alien species have been utilized to enhance genetic resistance to a number of fungal leaf diseases (3,4,21,30). For example, more than 20 genes for resistance to leaf rust (caused by *Puccinia triticina* Erikss.) have been identified from wheat relatives (31). Characterization and introgression of selected genes has allowed reduction of linkage drag and deployment in wheat cultivars, facilitating host resistance to this disease (36). In the past 50 years, many wheat relatives have been hybridized with wheat, resulting in the production of numerous amphiploids, synthetic hexaploid wheat lines, and chromosome addition, substitution, and translocation lines. These genotypes offer excellent resources for identification and utilization of novel resistance genes, because they potentially combine alien resistance genes with a cultivated wheat background (11,20). The objective of the present study was to identify novel sources of resistance to tan spot and SNB in these wheat genotypes. Utilization of these resistance sources in wheat breeding could enhance genetic diversity and aid in developing wheat cultivars with durable resistance to these diseases.

MATERIALS AND METHODS

Plant materials. In all, 199 wheat-alien species derivatives were evaluated for resistance to tan spot and SNB. These de-

Corresponding author: T. L. Friesen
E-mail: timothy.friesen@ars.usda.gov

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rivatives resulted from crosses between various wheat genotypes and 10 species of wheat relatives (Table 1). These wheat-alien species derivatives were provided mainly by Dr. Stephen Jones, Department of Crop and Soil Sciences, Washington State University, Pullman; Dr. Peidu Chen, Department of Agronomy, Nanjing Agricultural University, China; and Dr. Yue Jin, United States Department of Agriculture–Agricultural Research Service, University of Minnesota, St. Paul. Pedigrees, plant identification (PI) numbers, accession numbers, and chromosome constitutions of these derivatives, if known, are provided in Table 2. A Brazilian wheat line, BR34, and a North Dakota hard red spring wheat cultivar, Grandin, were used as resistant and susceptible controls, respectively, for evaluation of reaction to tan spot and SNB.

Evaluation for tan spot resistance. Evaluation for tan spot resistance followed the methods of Xu et al. (42) using the *P. tritici-repentis* isolate Pti2. Isolate Pti2 is a South Dakota race 1 field isolate which has been used in several previous studies (10,16,42). Briefly, plants were grown in SC10 164-ml cone-containers (Stuewe and Sons, Inc. Corvallis OR), with three plants per cone and each genotype represented by three cones in each of three replicates, with each replicate being separated by time. Cones were arranged in racks of 98, bordered by the susceptible control. Plants at the two- to three-leaf stage were sprayed with the spore suspension of isolate Pti2 of *P. tritici-repentis* race 1 at a concentration of 3,000 conidia ml⁻¹ until run-off. Following inoculation, plants were kept in a growth chamber at 100% relative humidity at 21°C for 24 h with a 12-h photoperiod, then transferred to a growth chamber at 21°C with a 12-h photoperiod.

Disease evaluations were conducted 7 days after inoculation. Disease lesions were scored on a 1-to-5 scale, according to the rating system developed by Lamari and Bernier (22), where 1 is resistant (small dark-brown to black spots without surrounding chlorosis or tan necrosis), 2 is moderately resistant (small dark-brown to black spots with very little chlorosis or tan necrosis), 3 is moderately susceptible (small dark-brown to black spots com-

pletely surrounded by a distinct chlorotic or tan necrotic ring, with lesions generally not coalescent), 4 is susceptible (small dark-brown or black spots completely surrounded with chlorotic or tan necrotic zones, with some lesions coalescent), and 5 is highly susceptible (dark-brown or black centers that may or may not be distinguishable, and most lesions consisting of coalescing chlorotic or tan necrotic zones). Genotypes with an equal amount of two lesion types were assigned an intermediate score.

Evaluation for SNB resistance. Evaluation for seedling SNB resistance was conducted using the same conditions and experimental design as described for tan spot. Inoculation with *S. nodorum* followed the methods of Liu et al. (27) and was performed at the two- to three-leaf stage, using isolate Sn2000. Sn2000 is a North Dakota field isolate used previously in disease evaluation, which is known to produce SnToxA and SnTox1 (17,25–27,42). The spore suspension was adjusted to a concentration of 1 × 10⁶ conidia ml⁻¹, and disease evaluation was conducted 7 days after inoculation. Disease reaction was scored on a 0-to-5 scale according to Liu et al. (27), where 0 is highly resistant (absence of visible lesions), 1 is resistant (few penetration points, with lesions consisting of flecking or small dark spots), 2 is moderately resistant (lesions consisting of dark spots with little surrounding necrosis or chlorosis), 3 is moderately susceptible (dark lesions completely, 2 to 3 mm, surrounded by necrosis or chlorosis), 4 is susceptible (larger or chlorotic lesions, 4 mm or greater, with little coalescence), and 5 is highly susceptible (large coalescent lesions with very little green tissue remaining). Genotypes with equal numbers of two lesion types were assigned an intermediate score.

Statistical analysis. Analysis of variance (ANOVA) was conducted using the Statistical Analysis System (SAS, version 9.1; SAS Inc., Cary, NC) with Fisher's protected least significant difference used for mean separation between genotypes. To evaluate the effect of alien chromatin on a wheat background, derivatives with a common wheat parent were grouped and each pedigree group was analyzed sepa-

ately. Susceptible and resistant controls were included in each ANOVA.

RESULTS

A large proportion of derivatives exhibited moderate to high levels of resistance to tan spot, SNB, or both. Of the 199 derivatives, more than half exhibited at least moderate SNB resistance and 150 had an SNB reaction significantly lower than Grandin, the susceptible control (Table 2). Among the 132 derivatives grouped according to a single wheat parent, 46 showed a significantly lower reaction than the respective wheat parental lines and 30 derivatives exhibited SNB reactions statistically similar to BR34, the resistant control. For tan spot, 111 derivatives had disease scores lower than Grandin and 65 derivatives showed resistance similar to BR34. In all, 44 derivatives showed a tan spot reaction significantly lower than their respective wheat parents and 37 derivatives were classified as resistant or moderately resistant. Of these 37 derivatives, however, 21 were also at least moderately resistant to SNB. A number of these derivatives have been shown to also contain genes for Fusarium head blight resistance (32). Thus, these genotypes represent a source of resistance to multiple diseases.

Of the 65 derivatives with tan spot resistance similar to BR34, 24 had the wheat cv. Chinese Spring as a parent. Chinese Spring is moderately susceptible to tan spot (Table 2). Within this set of derivatives, three had significantly higher resistance than Chinese Spring, including two disomic addition lines containing chromosomes K and L from *Leymous racemosus* (Table 2, no. 6 and 7), and a disomic substitution line containing chromosome 1E from *Thinopyrum ponticum* (Table 2, no. 22). Therefore, these alien chromosomes are likely to harbor genes for tan spot resistance. Interestingly, one line within this set of derivatives (Table 2, no. 31) was significantly more susceptible to tan spot than Chinese Spring. Of the 30 derivatives with SNB reactions similar to BR34, none were in the Chinese Spring group, although five derivatives (Table 2, no. 26, 28, 31, 32, and 35) were more resistant to SNB than Chinese Spring.

Table 1. Wheat relatives used in the development of wheat-alien species derivatives

Species	Chromosome number	Genomes
<i>Aegilops tauschii</i> (Coss.) Schmal.	2n = 2x = 14	DD
<i>Leymus racemosus</i> Lam.	2n = 4x = 28	NsNsXmXm
<i>Elymus rectisetus</i> (Nees) Á. Löve & Connor	2n = 6x = 42	StStYYWW
<i>Thinopyrum junceum</i> (L.) Love	2n = 6x = 42	EEEEEE or JJJJEE
<i>Th. ponticum</i> (Podp.) Z-W. Liu & R.-C. Wang [syn. <i>Agropyron elongatum</i> (Host) Beauv., <i>Elytrigia pontica</i> (Podp.) Holub., <i>Lophopyrum ponticum</i> (Podp.) Á. Löve]	2n = 10x = 70	EEEEEEEEEE
<i>Th. intermedium</i> (Host) Barkworth & D.R. Dewey	2n = 6x = 42	EEEEStSt or JJEESTSt
<i>Th. elongatum</i> (Host) D.R. Dewey	2n = 2x = 14	EE
<i>Dasypyrum villosa</i> L.	2n = 2x = 14	VV
<i>Avena sativa</i> L.	2n = 6x = 42	AACCDD (differing from Triticeae)
<i>Secale cereale</i> L.	2n = 2x = 14	RR

Table 2. Mean seedling reactions of wheat-alien species derivatives to *Stagonospora nodorum* and *Pyrenophora tritici-repentis*^a

Code ^b	Pedigree	<i>S. nodorum</i>		<i>P. tritici-repentis</i>	
		Score ^c	Reaction	Score ^d	Reaction
BR34	<i>Triticum aestivum</i> cultivar	0.16	HR	1.35	R
Grandin	<i>T. aestivum</i> cultivar	3.62	MS	3.88	MS
Chinese Spring (CS)	<i>T. aestivum</i> cultivar	2.83	MR	2.67*	MR
1	CS- <i>Leymous racemosus</i> disomic addition line (DAL) 21"+1"[A]	3.67	MS	2.33*	MR
2	CS- <i>L. racemosus</i> DAL 21"+1"[F]	3.33	MS	2.67*	MR
3	CS- <i>L. racemosus</i> DAL 21"+1"[H]	3.50	MS	3.33	MS
4	CS- <i>L. racemosus</i> DAL 21"+1"[I]	3.00	MS	2.50*	MR
5	CS- <i>L. racemosus</i> DAL 21"+1"[J]	3.67	MS	2.33*	MR
6	CS- <i>L. racemosus</i> DAL 21"+1"[K]	2.50*	MR	1.50*	R
7	CS- <i>L. racemosus</i> DAL 21"+1"[L]	2.67	MR	1.17*	R
8	CS- <i>L. racemosus</i> DAL 21"+1"[N]	2.00*	MR	3.67	MS
9	CS/ <i>Thinopyrum junceum</i> DAL AJDAj1	2.50*	MR	2.83	MR
10	CS/ <i>Th. junceum</i> DAL AJDAj2	2.50*	MR	1.67*	R
11	CS/ <i>Th. junceum</i> DAL AJDAj3	2.67	MR	2.00*	MR
12	CS/ <i>Th. junceum</i> DAL AJDAj4	2.33*	MR	1.83*	R
13	CS/ <i>Th. junceum</i> DAL AJDAj5	3.17	MS	2.33*	MR
14	CS/ <i>Th. junceum</i> DAL AJDAj6	3.00	MS	1.83*	R
15	CS/ <i>Th. junceum</i> DAL AJDAj7	3.00	MS	2.00*	MR
16	CS/ <i>Th. junceum</i> DAL AJDAj8	3.17	MS	2.50*	MR
17	CS/ <i>Th. junceum</i> DAL AJDAj9	3.00	MS	2.17*	MR
18	CS/ <i>Th. junceum</i> DAL AJDAj11	3.17	MS	2.00*	MR
19	CS/ <i>Th. junceum</i> DAL HD3505	3.83	MS	3.00	MS
20	CS/ <i>Th. junceum</i> DAL HD3508	5.00	HS	2.00*	MR
21	CS/ <i>Th. junceum</i> DAL HD3515	3.50	MS	1.83*	R
22	Disomic CS- <i>Th. ponticum</i> substitution 1E/1D (2n = 42)	2.17*	MR	1.50*	R
23	Disomic CS- <i>Th. ponticum</i> substitution 7E/7A (2n = 42)	2.67	MR	2.17*	MR
24	Disomic CS- <i>Th. ponticum</i> substitution 7E/7B (2n = 42)	2.00*	MR	1.83*	R
25	Disomic CS- <i>Th. ponticum</i> substitution 7E/7D (2n = 42)	2.17*	MR	2.17*	MR
26	CS/ <i>Th. ponticum</i> (PI206624)//CS	1.83*	R	2.17*	MR
27	CS/ <i>Th. ponticum</i> (PI206624)//CS	2.67	MR	2.33*	MR
28	CS/ <i>Th. ponticum</i> (PI206624)//CS	1.33*	R	2.67*	MR
29	CS/ <i>Th. intermedium</i> (PI264770)//CS	2.50*	MR	2.17*	MR
30	CS/ <i>Th. intermedium</i> (PI264770)//CS	2.50*	MR	2.83	MR
31	CS/ <i>Th. intermedium</i> (PI264770)//CS	1.50*	R	4.33	S
32	CS/ <i>Th. intermedium</i> (PI264770)//CS	1.67*	R	3.33	MS
33	CS/ <i>Th. intermedium</i> (PI264770)//CS	2.33*	MR	2.50*	MR
34	CS/ <i>Th. intermedium</i> (PI264770)//CS	3.00	MS	2.17*	MR
35	CS <i>ph1</i> mutant/ <i>Th. intermedium</i> (PI264770)//CS	1.83*	R	1.83*	R
36	CS <i>ph1</i> mutant/ <i>Th. intermedium</i> (PI264770)//CS	2.33*	MR	2.17*	MR
LSD	...	0.98	...	1.11	...
Madsen	<i>Triticum aestivum</i> cultivar	2.17*	MR	3.83	MS
37	Madsen/Spitzer (wheat- <i>Thinopyrum ponticum</i> amphiploid)	1.67*	R	2.67*	MR
38	Madsen/Spitzer	2.33*	MR	2.83*	MR
39	Madsen/Spitzer	1.50*	R	2.00*	MR
40	Madsen/Spitzer	2.00*	MR	3.17	MS
41	Madsen/Spitzer	1.50*	R	3.67	MS
42	Madsen/Spitzer	1.67*	R	2.17*	MR
43	Madsen/Spitzer	1.50*	R	2.83*	MR
44	Madsen/Spitzer	1.67*	R	3.00	MS
45	Madsen/Spitzer	2.50*	MR	3.33	MS
46	Madsen/Spitzer	0.50*	HR	3.33	MS
47	Madsen/Spitzer	1.17*	R	4.33	S
48	Madsen/Spitzer	2.83*	MR	3.83	MS
49	Madsen/Spitzer	1.83*	R	3.50	MS
50	Madsen/Spitzer	1.33*	R	2.83*	MR
51	Madsen/Spitzer	2.33*	MR	3.00	MS
52	Madsen/Spitzer	1.50*	R	2.83*	MR
53	Madsen/Spitzer	2.50*	MR	2.50*	MR
54	Madsen/Spitzer	2.17*	MR	3.67	MS
55	Madsen/Spitzer	1.83*	R	4.17	S
56	Madsen/Spitzer	1.50*	R	3.00	MS
57	Madsen/Spitzer	3.67	MS	3.83	MS

(continued on next page)

^a HR = highly resistant, R = resistant, MR = moderately resistant, S = susceptible, HS = highly susceptible, and * = significantly different from susceptible control (Grandin) at $P = 0.05$.

^b BR34 = resistant control, Grandin = susceptible control, LSD = least significant difference, and TCWL 178704 = Turkish common wheat line 178704.

^c *Stagonospora nodorum* blotch evaluation: 0 = highly resistant, 1 = resistant, 2 = moderately resistant, 3 = moderately susceptible, 4 = susceptible, and 5 = highly susceptible.

^d Tan spot evaluation: 1 = resistant, 2 = moderately resistant, 3 = moderately susceptible, 4 = susceptible, and 5 = highly susceptible.

^e *Thinopyrum turgidum* cultivar.

^f *Triticum aestivum* cultivar.

^g Wheat-*Thinopyrum intermedium* derivative.

Table 2. (continued from preceding page)

Code ^b	Pedigree	<i>S. nodorum</i>		<i>P. tritici-repentis</i>	
		Score ^c	Reaction	Score ^d	Reaction
58	Madsen/Spitzer	4.17	S	3.17	MS
59	Madsen/Spitzer	3.33	MS	3.17	MS
60	Madsen/Spitzer	0.33*	HR	4.00	S
61	Madsen/Spitzer	0.33*	HR	2.50*	MR
62	Madsen/Spitzer	1.50*	R	3.33	MS
63	Madsen/Spitzer	0.33*	HR	2.83*	MR
64	Madsen/Spitzer	0.17*	HR	1.50*	R
65	Spitzer/Madsen	2.33*	MR	2.67*	MR
66	Spitzer/Madsen	0.33*	HR	3.67	MS
67	Spitzer/Madsen	1.83*	R	2.83*	MR
68	Spitzer/Madsen	1.50*	R	3.33	MS
69	Spitzer/Madsen	1.67*	R	3.17	MS
70	Spitzer/Madsen	1.83*	R	4.17	S
71	Spitzer/Madsen	1.67*	R	3.50	MS
72	Spitzer/Madsen	2.50*	MR	3.67	MS
73	Spitzer/Madsen	2.17*	MR	4.00	S
74	Spitzer/Madsen	1.00*	R	3.00	MS
75	Spitzer/Madsen	1.17*	R	3.33	MS
76	Spitzer/Madsen	1.50*	R	2.83*	MR
77	Spitzer/Madsen	2.33*	MR	4.67	S
78	Spitzer/Madsen	0.33*	HR	4.00	S
79	Spitzer/Madsen	2.00*	MR	2.83*	MR
80	Spitzer/Madsen	0.17*	HR	3.50	MS
81	Spitzer/Madsen	0.83*	R	4.33	S
82	Spitzer/Madsen	0.83*	R	3.83	MS
83	Spitzer/Madsen	2.00*	MR	3.33	MS
84	Spitzer/Madsen	1.67*	R	3.67	MS
85	Spitzer/Madsen	1.83*	R	3.83	MS
86	Spitzer/Madsen	0.33*	HR	2.50*	MR
87	Spitzer/Madsen	1.33*	R	4.00	S
88	Spitzer/Madsen	1.33*	R	3.83	MS
89	Spitzer/Madsen	1.50*	R	3.83	MS
90	Spitzer/Madsen	1.17*	R	2.33*	MR
91	Spitzer/Madsen	1.00*	R	2.00*	MR
92	Spitzer/Madsen	1.17*	R	2.67*	MR
93	Spitzer/Madsen	1.00*	R	2.50*	MR
94	Spitzer/Madsen	1.83*	R	3.83	MS
95	Spitzer/Madsen	1.17*	R	2.67*	MR
96	Spitzer/Madsen	0.50*	HR	3.00	MS
97	Spitzer/Madsen	2.00*	MR	2.33*	MR
98	Spitzer/Madsen	2.00*	MR	4.17	S
99	Spitzer/Madsen	1.67*	R	4.33	S
100	Spitzer/Madsen	2.17*	MR	4.17	S
101	Spitzer/Madsen	0.67*	R	2.50*	MR
102	Spitzer/Madsen	1.00*	R	2.50*	MR
LSD	...	0.69	...	1.04	...
TCWL 178704	<i>Triticum aestivum</i> cultivar	1.33*	R	3.33	MS
103	TCWL 178704- <i>Thinopyrum ponticum</i> derivative	2.00*	MR	4.00	S
104	TCWL 178704- <i>Th. ponticum</i> derivative	0.83*	R	1.67*	R
105	TCWL 178704- <i>Th. ponticum</i> derivative	1.83*	R	2.83*	MR
106	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 46)	0.17*	HR	1.83*	R
107	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 46)	0.67*	R	1.83*	R
108	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 47)	0.33*	HR	1.67*	R
109	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 47)	0.00*	HR	1.67*	R
110	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 47)	0.17*	HR	1.83*	R
111	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 47)	0.50*	HR	2.17*	MR
112	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 47)	0.33*	HR	1.83*	R
113	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 47)	1.67*	R	2.67*	MR
114	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 47)	0.67*	R	1.50*	R
115	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 48)	0.17*	HR	1.83*	R
116	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 48)	1.17*	R	1.83*	R
117	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 48)	0.50*	HR	2.17*	MR
118	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 57)	0.50*	HR	2.00*	MR
119	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 68)	1.17*	MR	2.50*	MR
120	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 70)	1.33*	R	2.00*	MR
121	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 70)	2.50*	MR	1.67*	R
122	TCWL 178704- <i>Th. ponticum</i> derivative (2n = 70)	3.00*	MS	2.67*	MR
LSD	...	0.47	...	0.98	...
Langdon	<i>Triticum turgidum</i> cultivar	3.50	MS	4.17	S
123	Langdon/ <i>Aegilops tauschii</i> (RL5560)	3.67	MS	1.83*	R
124	Langdon/ <i>Ae. tauschii</i> (PI268210)	0.67*	R	2.17*	MR

(continued on next page)

Table 2. (continued from preceding page)

Code ^b	Pedigree	<i>S. nodorum</i>		<i>P. tritici-repentis</i>	
		Score ^c	Reaction	Score ^d	Reaction
125	KAD1 (Langdon- <i>Thinopyrum ponticum</i> amphiploid, 2n = 42)	2.83*	MR	2.67*	MR
126	KAD7 (Langdon- <i>Th. ponticum</i> amphiploid, 2n = 42)	2.33*	MR	2.83*	MR
127	KAD8 (Langdon- <i>Th. ponticum</i> amphiploid, 2n = 42)	2.50*	MR	2.17*	MR
128	KAD9 (Langdon- <i>Th. ponticum</i> amphiploid, 2n = 42)	2.17*	MR	2.83*	MR
LSD	...	0.50	...	0.96	...
Fukuhokomugi	<i>Triticum aestivum</i> cultivar	4.17	S	3.83	MS
129	Fukuhokomugi/ <i>Elymus rectisetus</i> DAL A1026	4.17	S	3.17*	MS
130	Fukuhokomugi/ <i>E. rectisetus</i> DAL A1034	4.17	S	3.17*	MS
131	Fukuhokomugi/ <i>E. rectisetus</i> DAL A1048	4.50	S	3.17*	MS
132	Fukuhokomugi/ <i>E. rectisetus</i> DAL A1057	2.17*	MR	2.50*	MR
LSD	...	0.52	...	0.62	...
Other					
133	Botno ^e / <i>Ae. tauschii</i> (625)	3.17	MS	2.33*	MR
134	CS/ <i>Thinopyrum ponticum</i> (PI206624)//Madsen	2.17*	MR	2.17*	MR
135	CS/ <i>Th. ponticum</i> (PI206624)//Madsen	2.50*	MR	1.67*	R
136	CS/ <i>Th. ponticum</i> (PI206624)//CS//Madsen	2.17*	MR	3.17	MS
137	CS/ <i>Th. ponticum</i> (PI206624)//CS//Madsen	2.00*	MR	2.50*	MR
138	CS/ <i>Th. ponticum</i> (PI206624)//CS//Madsen	2.00*	MR	4.17	S
139	CS <i>ph1</i> mutant/ <i>Th. ponticum</i> (PI206624)//Madsen	1.33*	R	2.33*	MR
140	CS/ <i>Th. intermedium</i> (PI264770)//Madsen	1.33*	R	3.83	MS
141	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	2.33*	MR	3.50	MS
142	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	1.50*	R	4.00	S
143	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	3.00	MS	2.33*	MR
144	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	1.50*	R	3.00	MS
145	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	2.33*	MR	2.67*	MR
146	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	2.00*	MR	3.33	MS
147	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	2.17*	MR	2.17*	MR
148	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	2.17*	MR	2.83	MR
149	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	2.00*	MR	3.50	MS
150	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	1.67*	R	2.67*	MR
151	CS/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	2.67*	MR	3.67	MS
152	CS <i>ph1</i> mutant/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	3.17	MS	3.83	MS
153	CS <i>ph1</i> mutant/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	1.50*	R	3.00	MS
154	CS <i>ph1</i> mutant/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	1.50*	R	2.17*	MR
155	CS <i>ph1</i> mutant/ <i>Th. intermedium</i> (PI264770)//CS//Madsen	2.50*	MR	2.50*	MR
156	TA3392 (Wheat- <i>Th. intermedium</i> amphiploid)	0.33*	HR	2.50*	MR
157	TA3409 (Wheat- <i>Agropyron distichum</i> amphiploid)	3.00	MS	3.33	MS
158	TA3425 (CS/ <i>Ag. elongatum</i>)	1.33*	R	1.50*	R
159	TA3426 (CS/ <i>Ag. scripeum</i> amphiploid)	2.33*	MR	1.83*	R
160	TA4014 (Agent 3DL Lr24)	3.67	MS	3.33	MS
161	TA5033 (TAM101 Ti4AS-4AL-6RL-4AL H25)	1.83*	R	3.33	MS
162	TA5041 (TAM104 T6B-6RL Pm20)	2.83	MR	2.50*	MR
163	TA5501 (Heine IV T1DS-1DL-7Ai#2L Lr38)	0.67*	R	3.50	MS
164	TA5502 (Heine IV T7Ai#2L-5AS-5AL Lr38)	1.67*	R	3.67	MS
165	TA5503 (Heine IV T6DS-6DL-7Ai#2L Lr38)	1.33*	R	3.50	MS
166	TA5504 (Wheat- <i>Ag. intermedium</i> translocation T3DL-3DS-7Ai#2L)	1.83*	R	2.00*	MR
167	TA5505 (Heine IV T2AS-2AL-3DS-3DL Lr38)	0.67*	R	3.00	MS
168	TA8023 (wheat- <i>Th. juncea</i> amphiploid, AABBDDJJ) (2n = 56)	1.50*	R	1.33*	R
169	AgCs (CS- <i>Th. elongatum</i> amphiploid, 2n = 56)	1.50*	R	1.33*	R
170	PI550711 (wheat- <i>Thinopyrum</i> amphiploid)	3.17	MS	3.50	MS
171	XC97-1-55 (wheat- <i>Thinopyrum</i> amphiploid)	1.00*	R	2.00*	MR
172	Eltan/ <i>Th. ponticum</i> (PI206624)	1.67*	R	2.17*	MR
173	PI550715 (wheat- <i>Th. ponticum</i> amphiploid, 2n = 56)	0.50*	HR	3.00	MS
174	PI550715/Eltan	0.83*	R	2.17*	MR
175	PI550715/Spitzer (blue seeds)	0.17*	HR	2.50*	MR
176	6VS-6AL translocation/Yang158 ^f	4.00	S	3.00	MS
177	Yang158/6VS-6AL translocation/Yang158	4.00	S	2.83	MR
178	Wheat- <i>Dasyphyrum villosa</i> 6VS/6AL translocation	2.67*	MR	3.00	MS
179	6VS/6AL trans./Yangmai5 ^f *3/Sheng32109 ^f	3.83	MS	3.17	MS
180	(CS/3/Xiangmai1 ¹ /D. villosa//Xiangmai1)/(6VS-6AL translocation/Yang158)	3.67	MS	3.00	MS
181	CS/ <i>L. racemosus</i> //CS/3/Wangshuibai ^f	0.67*	R	2.67*	MR
182	Sumai3 ¹ //CS/ <i>L. racemosus</i> /3/Yang158	0.17*	HR	2.50*	MR
183	Sumai3//CS/ <i>L. racemosus</i> /3/Yang158	3.00	MS	4.50	S
184	CS/ <i>L. racemosus</i> /3/Xiangmai1/ Haynaldia villosa//Xiangmai1	1.67*	R	3.83	MS
185	3D- <i>Agropyron</i> transfer #11	1.83*	R	2.67*	MR
186	3D- <i>Agropyron</i> transfer #16	1.67*	R	2.83	MR
187	GN775 (<i>Triticum durum</i> // <i>Aegilops tauschii</i> // <i>Ae. ventricosa</i> /3/oat)	1.33*	R	2.33*	MR
188	Amigo (wheat-rye and <i>Thinopyrum ponticum</i> translocation)	1.17*	R	3.00	MS
189	MT-2 ^g /Stephens ^f	3.17	MS	2.83	MR
190	MT-2/Stephens	1.83*	R	4.50	S
191	MT-2/Stephens	2.83	MR	2.50*	MR

(continued on next page)

Table 2. (continued from preceding page)

Code ^b	Pedigree	<i>S. nodorum</i>		<i>P. tritici-repentis</i>	
		Score ^c	Reaction	Score ^d	Reaction
192	Stephens//Harlan JR35 ^c /Maroccos ^c ///Stephens	1.17*	R	2.83	MR
193	Yangmai5	1.33*	R	2.50*	MR
194	Yangmai158	3.83	MS	2.83	MR
195	Yangmai10 ^f	3.83	MS	3.17	MS
196	Sumai 3 (purple anthers)	3.33	MS	3.67	MS
197	C04-13 (CS/ <i>Ae. speltooides</i>)	0.67*	R	2.50*	MR
198	C08-4 (CS/ <i>Ae. speltooides</i>)	3.17	MS	2.83	MR
199	C11-5 (CS/ <i>Ae. speltooides</i>)	3.17	MS	2.33*	MR
LSD	...	0.83	R	1.08	R

Sixty-six lines were derived from the cross between 'Madsen' and 'Spitzer' (X. Cai and S. S. Jones, *unpublished*). Madsen, a common soft white winter wheat cultivar, had a lower SNB reaction than the susceptible check, Grandin. Spitzer, a partial wheat-*T. ponticum* amphiploid, was not tested in this study. Of the 66 Madsen-Spitzer lines evaluated, 16 were more resistant to SNB than Madsen and 6 (Table 2, no. 39, 42, 64, 90, 91, and 97) exhibited tan spot reactions similar to BR34. For SNB, of 23 Madsen-Spitzer derivatives that were more resistant than Madsen, 13 (Table 2, no. 46, 60, 61, 63, 64, 66, 78, 80-82, 86, 96, and 101) had reactions comparable to BR34. Derivative no. 64 exhibited excellent resistance to both SNB and tan spot, whereas lines 57, 58, and 59 showed significantly higher SNB disease reactions than the Madsen parental line. The disease reactions of Spitzer are unknown; however, the high level of resistance observed in several derivatives suggests that Spitzer, or gene interaction in the progeny lines, may contribute to this resistance. None of the lines in this subset of material had a significantly more susceptible tan spot disease reaction than Madsen.

The Turkish common wheat line 178704, a parent to 20 derivatives evaluated in this study, was moderately susceptible to tan spot (Table 2). Fifteen of the derivatives (Table 2, no. 104, 106-112, 114-118, 120, and 121) were significantly more resistant than the Turkish wheat parent and exhibited tan spot reactions comparable to BR34. These derivatives contain various amounts of *T. ponticum* chromatin, again suggesting that this species is a valuable source of resistance to tan spot. No derivatives in this subset had a significantly higher tan spot disease reaction than the parental Turkish common wheat line. More than half of the Turkish common wheat line derivatives exhibited SNB resistance significantly greater than the wheat parent, including one derivative with apparent immunity (Table 2, no. 109). Nine derivatives had SNB resistance similar to BR34 (Table 2, no. 108-112, 115, 117, and 118). These nine derivatives also exhibited comparably high levels of resistance to tan spot. Although four of the Turkish com-

mon wheat line derivatives had significantly higher SNB disease reactions, none were highly susceptible, with the highest average disease reaction among these lines being 3.0 on the 0-to-5 scale.

Langdon, a durum wheat cultivar, was susceptible to tan spot (Table 2). The six Langdon-alien species derivatives contained chromatin from either *Aegilops tauschii* or *T. ponticum* and were all significantly more resistant than Langdon. In addition, three lines (Table 2, no. 123, 124, and 127) were not significantly different from BR34, showing a high level of tan spot resistance. Five of the six Langdon derivatives exhibited an SNB reaction significantly lower than Langdon, with no. 124 having the highest level of resistance in this group.

Fukuhokomuji, a Japanese common wheat cultivar, has been used to develop disomic addition lines containing chromosomes from the alien species *Elymus rectisetus*. Although all four lines evaluated in this study were significantly more resistant than the wheat parent for tan spot, none were comparable to BR34 (Table 2). For both SNB and tan spot, one derivative (Table 2, no. 132) was significantly more resistant than the wheat parent.

Derivatives with complex pedigrees or unavailable wheat parents were grouped together. Of these 67 derivatives, 17 exhibited tan spot reactions similar to BR34, with no. 135, 158, 159, 168, and 169 having the highest levels of tan spot resistance in this group (Table 2). Nine derivatives had SNB resistance similar to BR34 (Table 2, no. 156, 163, 167, 173-175, 181, 182, and 197). These derivatives were highly resistant, with SNB reactions approaching immunity. Although these pedigrees complicate identification of the resistance sources, all highly resistant derivatives include a parental *Thinopyrum* sp. It seems likely, therefore, that resistance genes are carried by several species within this genus.

Disease reactions of the wheat parents ranged from susceptible to moderately resistant, with the majority exhibiting moderate susceptibility to both diseases. Therefore, it appears that the alien species in these derivatives harbor both tan spot

and SNB resistance genes, and that these genes have been transferred to the wheat-alien species derivatives.

DISCUSSION

We identified genotypes with resistance to tan spot and SNB from 199 wheat-alien species derivatives, in which *A. tauschii*, *L. racemosus*, *E. rectisetus*, *T. ponticum*, *T. junceum*, *T. intermedium*, *T. elongatum*, *Dasypyrum villosa*, *Avena sativa*, and *Secale cereale* were involved. Resistance in these derivatives could result from the alien species and, thus, be derived from genomes different from those in wheat. These derivatives, therefore, may represent novel sources of resistance to both diseases. Introgression and pyramiding of alien resistance genes and currently identified resistance genes in the primary gene pool will broaden the genetic variability of wheat and strengthen resistance of wheat to these diseases.

Ten different alien species were involved in the development of the derivatives evaluated in this study. A number of derivatives exhibited significantly higher levels of resistance to tan spot, SNB, or both than their respective wheat parents, suggesting that alien chromatin confers resistance in these derivatives. Alien chromatin present in these derivatives has not been characterized; therefore, little information can be extrapolated from the present data as to what alien chromosomes harbor resistance genes. Further cytogenetic and molecular characterization will be needed for these derivatives to be efficiently utilized in wheat breeding.

The genome differences, however, have been a major challenge for gene introgression from these alien species into wheat in terms of hybridization between wheat and the wild species and recombination between wheat and alien chromosomes. The resistant wheat-alien species derivatives identified in this study include amphiploids and alien chromosome addition, substitution, and translocation lines. Many of these derivatives contain large amounts of alien chromatin, which harbor genes conditioning undesirable traits such as late maturity and low yield potential in addition to resistance genes. Therefore, they

may not be utilized directly in breeding for tan spot and SNB resistance. They are, however, ideal "bridge" materials for introgression of resistance genes into wheat genomes and development of elite breeder-friendly germplasm with resistance to both diseases. On the other hand, some of the resistant alien chromosome translocation lines may contain small amounts of alien chromatin without obvious linkage drag. These lines could be used directly in cultivar development without prebreeding efforts.

Resistant derivatives with large amounts of alien chromatin may be engineered to eliminate unwanted alien chromatin and genes using the *ph1b* mutant and homologous pairing promoters such as the *Ph1* gene (5). This will enhance recombination between wheat and alien chromatin and lead to production of wheat-alien chromosome translocation lines. Gene transfer is further enhanced by molecular cytogenetic techniques such as fluorescent in situ hybridization (FISH), which reveals the amount and location of alien chromatin (39). Introgression of the identified resistance genes to a cultivated wheat background is underway. This prebreeding phase could minimize linkage drag and improve the agronomic characteristics and adaptation of the progeny, producing breeder-friendly, disease-resistant germplasm. Eventually, this research will allow wheat breeders access to the alien gene pool and facilitate development of broad-spectrum resistance to these diseases.

Both the tan spot and SNB systems are known to involve host-selective toxins, which correspond to dominant host sensitivity genes in an inverse gene-for-gene manner (15,28). Each of these toxin-host gene interactions have been shown to be highly important in disease development (7,15,26,27). Several other resistance factors that have not been connected with HST production in the pathogen also have been identified. Faris and Friesen (10) identified several QTL that were effective across several races, including races producing Ptr ToxA, Ptr ToxB, and Ptr ToxC. This study showed that a high level of resistance can be obtained even in the presence of toxin sensitivity. This is also the case in the SNB system, where qualitative or quantitative resistance genes have been identified on at least 19 of the 21 hexaploid wheat chromosomes (41).

In addition to identifying a major toxin sensitivity gene on chromosome 1B, Liu et al. (27) identified several resistance QTL that were not associated with toxin sensitivity. The presence of non-toxin-associated resistance loci likely indicates various forms of active resistance that, if pyramided, could potentially lead to high levels of resistance. Friesen et al. (15) showed that some lines sensitive to SnToxA were still highly resistant to a SnToxA-producing *Stagonospora nodorum*

isolate if other nontoxin-associated resistance QTL were present in the lines. This would also indicate, similar to the tan spot system, that nontoxin-associated resistance can be highly effective even in the presence of toxin sensitivity genes.

Collectively, these studies show the importance of identifying and utilizing different sources of resistance for effective control of both tan spot and SNB. In the present study, several of the derivatives acquired higher levels of resistance by gaining chromosomes from other species. This would indicate that nontoxin-associated forms of resistance are being added. This would be the assumption because all known toxin sensitivities in these two systems are known to be inherited in a dominant fashion. Therefore, if additional toxin sensitivity were added, resistance would be decreased rather than increased. However, an increase in susceptibility compared with the parent from which the line was derived was identified in several derivatives for SNB and one derivative for tan spot (line no. 31). For SNB, these lines with increased susceptibility (line no. 19, 20, 57, 58, 59, 103, 105, 121, and 122) occurred in the Chinese Spring, Madsen/Spitzer, and Turkish common wheat groups. Due to the toxin-producing ability of *P. tritici-repentis* and *S. nodorum*, it is highly likely that alien chromatin in the derivatives contains toxin sensitivity genes not present in the wheat parental lines. It also is possible that suppressors of resistance could be present in the alien chromatin, which shut down an active host resistance mechanism (2). More analysis of these derivatives, including population development, is needed to identify the mechanism of increased susceptibility.

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