

# Stripe Rust Resistance in *Aegilops tauschii* Germplasm

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## ABSTRACT

*Aegilops tauschii* Coss., the D-genome progenitor of hexaploid wheat (*Triticum aestivum* L.), is an important source of useful genes for wheat improvement. We characterized a germplasm collection of 118 *Ae. tauschii* accessions for response to stripe rust, a devastating disease caused by the fungus *Puccinia striiformis* f. sp. *tritici* (*Pst*). We evaluated tillering stage and adult-plant resistance to stripe rust using prevalent *Pst* races from the United States and China. Resistant accessions predominated in *Ae. tauschii* subsp. *strangulata* and *Ae. tauschii* subsp. *tauschii* from the Caspian Sea region. We further analyzed the inheritance of stripe rust resistance by inoculating F<sub>2</sub> plants of 60 crosses with a mixture of Chinese *Pst* races. Crosses between resistant and susceptible lines indicated both dominant and recessive inheritance. Tests of allelism among 14 highly resistant accessions indicated the common presence of *YrAS2388*, previously mapped on chromosome arm 4DS, in all accessions. In conclusion, the study presented valuable data on stripe rust resistance in *Ae. tauschii*, which assist with informed introgression of the D-genome trait for stripe rust resistance in common wheat.

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**Abbreviations:** IT, infection types.

WHEAT STRIPE RUST, caused by the fungus *Puccinia striiformis* f. sp. *tritici* (*Pst*), is one of the most devastating diseases worldwide. It has been reported in more than 60 countries and occurs in many cooler and more humid regions of the world (Chen, 2005). Stripe rust is a regular threat to wheat production in both southwest and northwest China (Wan et al., 2004, 2007).

*Aegilops tauschii* Coss. ( $2n = 2x = 14$ ), the D-genome progenitor of hexaploid wheat (*Triticum aestivum* L.,  $2n = 6x = 42$ ), is a valuable resource for wheat improvement (Warburton et al., 2006; van Ginkle and Ogbonnaya, 2007; Yang et al., 2009; Xu et al., 2010; Reynolds et al., 2011). Based on spike morphology, *Ae. tauschii* is classified into two subspecies, subspecies *tauschii* with elongated cylindrical spikes and subspecies *strangulata* with markedly moniliform spikes (Eig, 1929; van Slageren, 1994). Intermediate or mildly moniliform spike types have also been observed in the two subspecies (Kihara and Tanaka, 1958; Aghaei et al., 2008; Matsuoka et al., 2009), but they are normally assigned to subspecies *tauschii* (Matsuoka et al., 2009). Subspecies *tauschii* has a broad

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geographic distribution extending westwards to Turkey and eastwards to Afghanistan and China, whereas subspecies *strangulata* is distributed only in two disjointed regions, viz. southeastern Caspian Iran and Transcaucasia (Kihara et al., 1965; Tanaka, 1983; Yen et al., 1983; Jakaska, 1995).

Stripe rust resistance in *Ae. tauschii* has been previously correlated with subspecies classification. Almost all analyzed subspecies *strangulata* accessions are resistant, whereas most subspecies *tauschii* accessions are susceptible (Yildirim et al., 1995; Knaggs et al., 2000; Liu et al., 2010). Resistance gene *Yr28* was mapped to *Ae. tauschii* chromosome arm 4DS using a mapping population derived from the synthetic hexaploid wheat W7984 (Singh et al., 2000). The *Yr28* gene donor, *Ae. tauschii* accession WX219 (TA2465), originated from Caspian Iran and belongs to subspecies *strangulata* (Cox et al., 1992; Akhunov et al., 2010; Olson, 2012). Recently, a dominant resistance gene *YrAS2388* was also mapped on chromosome arm 4DS in subspecies *strangulata* accession PI 511384 (AS2388) which originated from the Caspian Sea region of Iran (Huang et al., 2011). However, the allelic relationships among stripe rust resistance genes in different *Ae. tauschii* accessions remain unknown. The objectives of this study were to: (i) investigate the relationship between resistance and subspecies by analyzing tillering stage and adult-plant responses to stripe rust in 118 *Ae. tauschii* accessions; (ii) test allelic relationships among *Pst* resistance genes in different *Ae. tauschii* accessions; and (iii) identify novel genetic factors affecting *Pst* response in *Ae. tauschii*.

## MATERIALS AND METHODS

### Plant Materials

The 118 *Ae. tauschii* accessions used in the study included 34 accessions of subspecies *strangulata* and 84 accessions of subspecies *tauschii*. One hundred and two accessions were investigated for *Pst* response at both the tillering and adult-plant stages (Table 1). Forty-five accessions, 27 resistant and 18 susceptible, were crossed to generate 60 F<sub>2</sub> populations for genetic analyses and tests of allelism (Tables 2 and 3). Stripe rust susceptible wheat cultivars Huixianhong and SY95-71 were used as disease spreaders.

### Evaluation of the Stripe Rust Resistance Under Field and Greenhouse Conditions

The tillering stage reactions were assessed on 102 accessions at Davis, California, USA. In January 2010, ten seeds of each accession were planted in soil mixes in Ray Leach “cone-tainers” (164ml volume; Stuewe and Sons, OR, USA) and were maintained in greenhouses. At the one leaf stage, four healthy seedlings were chosen for inoculation. By mid-March, seedlings reached 4 to 5 leaf stages and were placed in the field when a stripe rust epidemic was occurring. According to 2010 field survey, seven *Pst* races were detected in Davis, California, including PSTv-12, -14, -30, -33, -35, -36, and -37 (<http://striperust.wsu.edu/>). Most likely, PSTv-37 was the most predominant race in Davis in 2010. After 10 d of natural infection, seedlings were returned to the greenhouse (25°C day,

approximately 15°C night, and a 16-h photoperiod). One week later, infection types (IT) were scored on 6-leaf seedlings (Feekes stages 3 to 4; Large, 1954) using a 0 to 9 scoring scale (Line and Qayoum, 1991). For each accession, four individuals were evaluated and a representative score was called when all individuals developed similar infection types. The *Pst* responses were recorded as resistant (R, 0–3; highly resistant, HR, 0–1; fairly resistant, FR, 2–3), intermediate (M, 4–6; moderate resistance, MR, 4–5; moderate susceptibility, MS, 6), and susceptible (S, 7–9; fairly susceptible, FS, 7; highly susceptible, HS, 8–9).

Field trials to assess adult-plant resistance were conducted at two locations in China. In Sichuan Province, 118 *Ae. tauschii* accessions and 39 F<sub>2</sub> populations were grown at Wenjiang Experimental Station, Sichuan Agricultural University, in the 2011 to 2012 cropping season. Stripe rust epidemics frequently occur at the location of Wenjiang Station. *Ae. tauschii* accessions and the SY95-71 spreader were also inoculated with a Chinese *Pst* mixture including races CYR30, CYR31, CYR32, CYR33, SY11-4, and HY46-8 7 wk after planting. Since the flag leaf stage, response data on the *Aegilops* accessions were recorded three times at 10-d intervals, and the highest score was considered representative for each accession. In Shandong Province, 21 F<sub>2</sub> populations were tested in the Tai'an experimental field of Shandong Agricultural University in the 2011 to 2012 cropping season. To ensure rust infection, seedling plants were inoculated twice with a Chinese *Pst* mixture including races of CYR31, CYR32, and CYR33. Responses were recorded at the flag leaf stage. The *Pst* responses in adult plants were recorded as described in tillering stage assay. In both locations, individual plants were spaced 10 cm apart in 2 m long rows spaced 0.3 m apart. Chi-square statistics ( $\chi^2$ ) were used to validate the proposed inheritance models of stripe rust resistance in F<sub>2</sub> populations and to test the independence between origins and stripe rust resistance of the current *Ae. tauschii* germplasm.

## RESULTS

### Stripe Rust Reactions of *Ae. tauschii* Accessions

Tillering stage and adult-plant reactions were successfully evaluated for 97 *Ae. tauschii* accessions. Although the seedling and adult plants were challenged by both U.S. and Chinese *Pst* populations, plants at both growth stages displayed relatively consistent stripe rust reactions (Table 1). Adult plants were easily grouped as resistant (IT 0–3) or susceptible (IT 7–9), but some accessions developed intermediate responses (IT 4–6) at the tillering stage. Plants classified MR as seedlings were resistant as adults whereas those classified MS were rated as susceptible at the adult stage. Tillering stage assay was performed at 4 to 6-leaf stages, indicating that the adult plant resistance in some accessions was already functional at the stage of testing.

All 34 subspecies *strangulata* accessions were resistant (IT 0–3), and 27 of them were from Azerbaijan (2), Iran (23), Transcaucasia (1), and Turkmenistan (1), a number of countries and regions near the Caspian Sea. However,

**Table 1. Stripe rust responses of 118 *Ae. tauschii* accessions<sup>†</sup>**

Acc.	PO	SS	SR	AR	Acc.	PO	SS	SR	AR	Acc.	PO	SS	SR	AR
AS60	IR	T	–	S	Clae 28	IR	T	HS	S	PI 511368	IR	S	HR	R
AS62	–	T	–	S	Clae 30	–	T	MS	S	PI 511370	IR	S	HR	R
AS63	–	T	–	R	Clae 50	–	T	MR	R	PI 511375	–	T	HS	S
AS65	SU	T	–	S	Clae 51	–	T	–	S	PI 511378	IR	T	HR	R
AS66	SC	S	–	R	Clae 68	TR	T	HS	S	PI 511379	IR	T	HR	R
AS87	–	T	–	S	Clae 71	–	T	HS	S	PI 511380	IR	T	HR	R
AS88	–	T	–	S	Clae 72	–	S	MR	R	PI 511382	IR	S	HR	R
AS89	–	T	–	S	PI 210987	AF	T	HS	S	PI 511383	IR	S	HR	R
AS2394	–	S	–	R	PI 220326	AF	T	HS	S	PI 511384	IR	S	–	R
AS2396	IR	S	–	R	PI 220331	AF	T	HS	S	PI 542277	TR	T	HS	S
AS2397	IR	S	–	R	PI 220642	AF	T	HS	S	PI 554310	TR	T	HS	S
AS2399	IR	S	–	R	PI 268210	IR	S	FR	R	PI 554311	TR	T	–	S
AS2402	IL	S	–	R	PI 276975	KZ	T	HS	S	PI 554313	TR	T	HS	S
AS2403	–	S	–	R	PI 276980	SU	T	MS	S	PI 554315	TR	T	HS	S
AS2404	–	S	–	R	PI 276985	IR	T	HR	R	PI 554318	TR	T	FS	S
AS2405	IR	S	–	R	PI 317392	AF	T	HS	S	PI 554319	TR	T	FS	S
Clae 1	PK	T	HS	S	PI 317394	AF	T	HS	S	PI 554320	TR	T	FS	S
Clae 2	PK	T	HS	S	PI 330489	–	S	MR	–	PI 554321	TR	T	HS	S
Clae 3	AF	T	HS	S	PI 369627	–	S	HR	R	PI 554322	TR	T	–	S
Clae 4	AF	T	HS	S	PI 428563	GE	T	FS	S	PI 554323	TR	T	HS	S
Clae 5	AF	T	FS	S	PI 428564	AZ	T	MS	S	PI 560534	TR	T	HS	S
Clae 6	AF	T	HS	S	PI 431598	TM	T	HR	R	PI 560535	TR	T	HS	S
Clae 8	IR	S	HR	R	PI 431599	AZ	S	HR	R	PI 560536	TR	T	HS	S
Clae 9	IR	S	HR	R	PI 431602	TM	S	HR	R	PI 560538	TR	T	HS	S
Clae 10	IR	S	HR	R	PI 431603	AZ	T	FR	R	PI 560754	TR	T	HS	S
Clae 11	IR	S	HR	R	PI 452130	CN	T	HS	S	PI 560755	TR	T	FS	S
Clae 12	IR	S	HR	R	PI 452131	CN	T	HS	S	PI 574465	AZ	S	HR	R
Clae 13	IR	S	HR	R	PI 476874	AF	T	HS	S	PI 574467	RU	T	FS	S
Clae 15	IR	S	HR	R	PI 486265	TR	T	HS	S	PI 574468	AM	T	FS	S
Clae 16	IR	S	HR	R	PI 486266	TR	T	HS	S	PI 603221	WA	T	HS	S
Clae 17	IR	S	MR	R	PI 486267	TR	T	HS	S	PI 603224	RU	T	FS	S
Clae 18	IR	S	HR	R	PI 486271	TR	T	HS	S	PI 603225	TM	T	FS	S
Clae 19	IR	S	HR	R	PI 486274	TR	T	HS	S	PI 603233	AZ	T	FS	S
Clae 20	IR	S	MR	R	PI 499262	CN	T	HS	S	PI 603235	AZ	T	HR	R
Clae 21	IR	T	MR	R	PI 508263	CN	T	HS	S	PI 603246	PT	T	HS	S
Clae 23	IR	T	HS	S	PI 508264	CN	T	HS	S	PI 603249	IR	S	HR	R
Clae 24	IR	T	MR	R	PI 511363	AF	T	HS	S	PI 603252	IR	T	HS	S
Clae 25	IR	T	MR	R	PI 511365	PK	T	HS	S	PI 603255	AM	T	HS	S
Clae 26	IR	T	MR	R	PI 511366	AF	T	HS	S					
Clae 27	IR	T	HS	S	PI 511367	AF	T	HS	S					

<sup>†</sup>Table head abbreviations: Acc. (accession No.), PO (place of origin), SS (subspecies), SR (seedling reaction at tillering stage), and AR (adult plant reaction, field test data from Sichuan). Accessions with AS codes are from the Triticeae Research Institute, Sichuan Agricultural University, China; accessions with codes PI or Clae were from USDA-ARS, USA. Some AS lines were originally from the Weizmann Institute of Science, Israel, and original IDs were TQ-11 (AS2394), TQ-13 (AS2396), TQ-17-1 (AS2397), TQ-22/2 (AS2399), TQ-27 (AS2402), TQ-28 (AS2403), TQ-294 (AS240), and TQ-38 (AS2405). Places of origin include AF (Afghanistan), AM (Armenia), AZ (Azerbaijan), CN (China), GE (Georgia), IL (Israel), IR (Iran), KZ (Kazakhstan), PK (Pakistan), PT (Portugal), RU (Russian Federation), SC (Transcaucasia), SU (Former Soviet Union), TM (Turkmenistan), TR (Turkey), and WA (Western Asia). Morphologically intermediate forms between the two typical ssp. *tauschii* (T) and *stragulata* (S) were included in ssp. *tauschii*. Seedling and adult plant reactions to *Pst* were previously described in materials and methods. A dash (-) denotes unknown or not available.

the subspecies *tauschii* accessions reacted differentially; 13 accessions were resistant and 71 were susceptible (IT 7–9). All resistant subspecies *tauschii* accessions originated from countries near the Caspian Sea. In contrast, 45 subspecies *tauschii* accessions collected in Afghanistan, China, Pakistan, and Turkey were susceptible. Although susceptible subspecies *tauschii* accessions were described from Azerbaijan, Iran, and Turkmenistan where resistant accessions were also found, it seems that areas near the Caspian Sea

may be hotspots for the presence of stripe rust resistance in *Ae. tauschii*. A Chi-square test indicated a significant association between accessions collected in the Caspian Sea area and stripe rust resistance ( $P < 0.01$ )

### Genetic Analysis of Stripe Rust Resistance in *Ae. tauschii*

We generated F<sub>2</sub> populations from 60 crosses to examine the nature of stripe rust resistance at the adult plant

**Table 2. Genetic analysis of adult plant stripe rust responses in *Aegilops tauschii*.<sup>†</sup>**

Female parent		Male parent		No. of F <sub>2</sub> plants in each class					Statistical tests		
Acc. <sup>‡</sup>	AR <sup>‡</sup>	Acc.	AR	R	MR	M	MS	S	Seg.	χ <sup>2</sup>	P
PI 511382	R	AS62	S	82	–	–	–	21	3:1 <sup>¶</sup>	1.17	0.28
PI 511382	R	AS87	S	78	–	–	–	29	3:1 <sup>¶</sup>	0.25	0.62
PI 511382	R	AS88	S	104	–	–	–	33	3:1 <sup>¶</sup>	0.06	0.81
PI 511382	R	PI 508263	S	63	–	7	–	24	3:1 <sup>¶</sup>	0.31	0.58
PI 486266	S	PI 511382	R	73	–	3	–	25	3:1 <sup>¶</sup>	0.01	0.91
PI 511383	R	AS62	S	125	–	–	–	34	3:1 <sup>¶</sup>	1.11	0.29
PI 511383	R	AS89	S	155	–	–	–	41	3:1 <sup>¶</sup>	1.74	0.19
PI 511383	R	PI 486274	S	42	–	29	–	20	3:1 <sup>¶</sup>	1.74	0.19
Clae 9	R	PI 560536	S	42	–	42	–	20	3:1 <sup>¶</sup>	1.74	0.19
PI 511384	R	AS62	S	79	–	–	–	26	3:1 <sup>¶</sup>	0.003	0.96
PI 511384	R	AS87	S	115	–	–	–	35	3:1 <sup>¶</sup>	0.22	0.64
AS66	R	AS62	S	81	–	–	–	37	3:1 <sup>¶</sup>	2.54	0.11
AS66	R	AS89	S	76	–	–	–	32	3:1 <sup>¶</sup>	1.23	0.27
PI 330489	R	Clae 1	S	29	–	42	–	28	1:2:1 <sup>#</sup>	2.29	0.32
PI 554323	S	PI 431602	R	68	–	6	–	21	3:1 <sup>¶</sup>	0.09	0.76
PI 560754	S	PI 431602	R	43	–	19	–	18	3:1 <sup>¶</sup>	0.66	0.42
Clae 5	S	PI 369627	R	20	37	–	16	15	1:2:1 <sup>#</sup>	4.25	0.12
Clae 10	R	PI 560536	S	21	50	–	21	19	MG <sup>††</sup>		
Clae 16	R	Clae 5	S	59	–	14	–	14	3:1 <sup>¶</sup>	1.32	0.25
Clae 1	S	Clae 11	R	13	23	–	26	61	1:3 <sup>¶</sup>	1.20	0.27
Clae 11	R	Clae 68	S	6	21	–	40	25	1:3 <sup>¶</sup>	0.93	0.34
Clae 12	R	Clae 27	S	8	48	–	44	21+2 <sup>§</sup>	MG <sup>††</sup>		
Clae 50	R	Clae 27	S	4	–	12	–	60	MG <sup>††</sup>		
Clae 19	R	PI 554323	S	17	8	–	6	79+4 <sup>§</sup>	1:3 <sup>¶</sup>	0.57	0.45
Clae 26	R	PI 554323	S	8	–	14	–	79	MG <sup>††</sup>		
Clae 24	R	Clae 2	S	3	27	–	25	64+6 <sup>§</sup>	1:3 <sup>¶</sup>	0.07	0.80
Clae 6	S	Clae 8	R	3	13	–	35	40+1 <sup>§</sup>	1:3 <sup>¶</sup>	2.84	0.09
Clae 8	R	Clae 6	S	10	21	–	53	15	1:3 <sup>¶</sup>	2.10	0.15
Clae 27	S	Clae 72	R	54	–	20	–	23	3:1 <sup>¶</sup>	0.97	0.32
Clae 72	R	Clae 6	S	19	–	31	–	39	1:3 <sup>¶</sup>	1.86	0.17

<sup>†</sup> In this table, these populations having only two IT groups (resistant/R and susceptible/S) were evaluated in Sichuan, China, and the other populations having additional IT groups (MR, M, and MS) were evaluated in Shandong, China.

<sup>‡</sup>Table headings: Acc, accession; AR, adult plant response.

<sup>§</sup>Numbers after the plus symbol (+) denote F<sub>2</sub> individuals highly susceptible (HS) to *Pst*.

<sup>¶</sup>The segregation model was based on comparisons between resistant (R and MR types) and susceptible (MS, S, and HS types) individuals.

<sup>#</sup>The segregation model was based on comparisons among resistant (R type), intermediate (M, MR, and MS types), and susceptible (S and HS types) individuals.

<sup>††</sup>MG, multigenic. Observed phenotypes could not be fitted to a simple Mendelian model.

stage in *Ae. tauschii* (Tables 2 and 3). Thirty populations segregated for stripe rust response, 29 were homogenous resistant, and one control population derived from a cross between susceptible parents was homogenous susceptible.

The 30 segregating populations were derived from 18 resistant accessions paired with susceptible parents. Resistance in 10 crosses involving resistant subspecies *strangulata* accessions, viz. AS66, Clae 9, Clae 10, Clae 16, PI 330489, PI 369627, PI 431602, PI 511382, PI 511383, and PI 511384 and susceptible lines, was in each case likely conferred by a single dominant or semidominant gene (Table 2). In most cases, when a resistant accession was crossed to different susceptible genotypes the inheritance pattern was the same. For example, the resistance of PI 511382 was dominant when crossed with AS62, AS87, AS88, PI 486266, and PI 508263. We then focused on a

large F<sub>2</sub> population of PI 511384 and AS87 that was earlier used to map the *YrAS2388* allele. Of 1910 individuals, 1432 plants were resistant and 478 were susceptible, confirming dominant inheritance of the *YrAS2388* gene ( $\chi^2 = 0.001$ ,  $P = 0.98$ ).

Resistance was recessive in crosses involving Clae 8, Clae 11, Clae 12, Clae 19, Clae 24, Clae 26, and Clae 50, among which the last three accessions were subspecies *tauschii*. Occasionally, dominant and recessive inheritance of resistance was determined by the susceptible parent used. For example, resistance in subspecies *strangulata* Clae 72 was dominant when it was crossed with Clae 27, but was recessive when the cross was with Clae 6. Recessive inheritance occurred in reciprocal crosses between Clae 6 and Clae 8. Likely, the susceptible genotype Clae 6 tends to mask resistance in heterozygous plants. In contrast, the same

**Table 3. Tests of Allelism with YrAS2388 in *Aegilops tauschii*.<sup>†</sup>**

Female parent			Male parent			No. of F <sub>2</sub> plants	
Acc.	SS	AR	Acc.	SS	AR	R	S
AS66	S	R	AS63	T	R	138	0
AS66	S	R	Clae 8	S	R	115	0
AS66	S	R	PI 511382	S	R	126	0
AS66	S	R	PI 511383	S	R	131	0
AS66	S	R	PI 511384	S	R	137	0
AS2404	S	R	Clae 8	S	R	108	0
AS2404	S	R	PI 511382	S	R	139	0
PI 511382	S	R	AS63	T	R	155	0
PI 511382	S	R	AS2394	S	R	140	0
PI 511382	S	R	AS2396	S	R	173	0
PI 511382	S	R	AS2397	S	R	90	0
PI 511382	S	R	AS2402	S	R	151	0
PI 511382	S	R	AS2403	S	R	78	0
PI 511382	S	R	Clae 8	S	R	153	0
PI 511382	S	R	PI 511383	S	R	131	0
PI 511382	S	R	PI 511384	S	R	130	0
PI 511383	S	R	AS63	T	R	197	0
PI 511383	S	R	AS2396	S	R	156	0
PI 511383	S	R	AS2397	S	R	140	0
PI 511383	S	R	AS2399	S	R	125	0
PI 511383	S	R	AS2405	S	R	110	0
PI 511383	S	R	Clae 8	S	R	61	0
PI 511384	S	R	AS63	T	R	124	0
PI 511384	S	R	AS2394	S	R	159	0
PI 511384	S	R	AS2396	S	R	189	0
PI 511384	S	R	AS2399	S	R	193	0
PI 511384	S	R	AS2405	S	R	143	0
PI 511384	S	R	Clae 8	S	R	92	0
PI 511384	S	R	PI 511383	S	R	149	0
AS60	T	S	AS65	T	S	0	120

<sup>†</sup>Table head abbreviations: Acc. (accession No.), SS (subspecies), and AR (adult plant reaction). PI 511384 is a carrier of YrAS2388. A control population from two susceptible parents AS60 and AS65 was included showing homogenous susceptibility to *Pst*. The field test was performed in Sichuan, China.

susceptible accession was associated with both dominant and recessive inheritance when crossed with different resistant accessions. For example, resistance of PI 330489, Clae 72, and PI 431602 was dominant in combinations with the susceptible genotypes Clae 1, Clae 27, and PI 554323. However, when the same susceptible parents were crossed with the resistant genotypes Clae 11, Clae 12, Clae 19, Clae 26, or Clae 50, the *Pst* resistance was inherited recessively.

In subspecies *strangulata* accession PI 511384, the single dominant allele YrAS2388 was mapped on chromosome arm 4DS (Huang et al., 2011). To determine allelic relationships, we inoculated 29 F<sub>2</sub> populations involving intercrosses of 14 resistant accessions, including one subspecies *tauschii* accession (AS63) and 13 subspecies *strangulata* accessions (AS66, AS2394, AS2396, AS2397, AS2399, AS2402, AS2403, AS2404, AS2405, Clae 8, PI 511382, PI 511383, and PI 511384) (Table 3). All F<sub>1</sub> and F<sub>2</sub> individuals of the 29 combinations were resistant (IT 0–3), indicating that YrAS2388 could be present in all 14 resistant lines. The allelism test

also indicated the presence of YrAS2388 in Clae 8, which contradicted recessive *Pst* resistance in crosses between Clae 6 and Clae 8. Such a phenomenon documents a reversal of dominance possibly caused by epistatic interaction among different genetic factors. Of the 14 resistant accessions, 8 were collected in Iran, 5 had unknown origins, and one originated from Transcaucasia. It seems likely that the YrAS2388 allele on chromosome arm 4DS represents a common resistance gene in *Ae. tauschii* germplasm, especially in accessions collected from the Caspian Sea region.

## DISCUSSION

Stripe rust resistance in *Ae. tauschii* appears to be associated with the geographical origin of accessions and taxonomic subspecies. *Ae. tauschii* subsp. *tauschii* is dispersed throughout the species range, whereas the subspecies *strangulata* is limited to the southeastern Caspian coastal region and the Caucasus (Eig, 1929). The wheat-growing region along the Caspian Sea has mild and moist summers that favor stripe rust epidemics once every 3 to 4 yr (Niemann et al., 1968; Khazra and Bamdadian, 1974; Reviewed in Ziyaev et al., 2011). Accessions resistant to stripe rust predominate in the Caspian Sea region, with the majority belonging to *Ae. tauschii* subsp. *strangulata* (Yildirim et al., 1995; Knaggs et al., 2000; Liu et al., 2010). Interestingly, regions near the Caspian Sea also possess a higher frequency of resistance to leaf rust and stem rust in *Ae. tauschii* (Cox et al., 1992; Rouse et al., 2011).

The YrAS2388 allele on chromosome arm 4DS of subspecies *strangulata* PI 511384 was previously shown to exhibit dominant inheritance (Liu et al., 2010; Huang et al., 2011; current study). Test of allelism was performed among intercrosses of 14 resistant accessions which included the YrAS2388 carrier PI 511384. Assuming the largest recombination value of 50%, minimum family sizes required to distinguish dominant genes in repulsion are 13, 58, and 235 for one, two, and three genes, respectively, at the 5% significance level (Hanson, 1959). In current tests of allelism, family sizes ranged from 61 to 197, which were large enough to distinguish one to two dominant genes. In addition, common parents were used in different intercrosses. For example, PI 511384 was paired with AS63, AS2394, AS2396, AS2399, AS2405, Clae 8, and PI 511383. According to the current study, many *Ae. tauschii* accessions, such as Clae 8, PI 511382, PI 511383, and PI 511384 and especially those of subspecies *strangulata*, carry YrAS2388. In addition, Clae 9 and PI 511383 are likely the same genotype as disclosed by whole genome SNP analysis (unpublished data), suggesting the presence of YrAS2388 in Clae 9. The test of allelism also indicated that YrAS2388 is in subspecies *tauschii* accession AS63, suggesting that YrAS2388 predates the differentiation of subspecies *tauschii* and *strangulata*. Considering their geographical origins, 9 of 15 likely YrAS2388 carriers were

from Caspian Iran, one was from Transcaucasia and the other five had unknown origins. Therefore, the *YrAS2388* allele is a common source of stripe rust resistance in *Ae. tauschii* accessions from the Caspian Sea region (Yildirim et al., 1995; Knaggs et al., 2000; Liu et al., 2010).

Dominant or semidominant resistance was discovered in another five subspecies *strangulata* accessions, including CIAe 10, CIAe 16, PI 330489, PI 431602, and PI 369627. However, the relationships among resistance of these accessions and *YrAS2388* remain unknown. Recessive resistance was identified in CIAe 11, CIAe 12, CIAe 19, CIAe 26, CIAe 50 and other *Ae. tauschii* accessions. The study further documented a possible reversal of dominance in CIAe 8 and CIAe 72. Reversals of dominance of disease resistance may occur with use of different pathogen races or different contrasting parents (Hooker and Saxena, 1971; Chen and Lane, 1993). For example, the *Yr3a* allele in wheat cultivars Cappelle Desprez, Druchamp, and Nord Desprez was dominant in crosses with Yamhill, but was recessive in crosses with Chinese 166 (Chen and Lane, 1993). Sometimes, rust resistance can be masked by inhibitor or suppresser genes. Resistances to leaf rust and stem rust resistance from diploid or tetraploid wheat backgrounds were not effective in synthetic hexaploid wheat (Kerber, 1983; Bai and Knott, 1992). How reversals of dominance occur and whether suppresser genes have a role in the current study remain to be addressed.

In 'native' common wheat, no *Pst* resistance gene has been identified on chromosome arm 4DS. However, genes on 4DS from *Ae. tauschii* confer stripe rust resistance in synthetic hexaploid wheat (Singh et al., 2000; Huang et al., 2011). The synthetic hexaploid wheats, "Syn-SAU-86" and "Syn-SAU-88", were developed from *T. turgidum* subsp. *turgidum* and *Ae. tauschii* AS2388 (PI 511384). The synthetic hexaploids are more resistant (IT 2–4) than their durum parents (IT 6–8) at the adult plant stage (Huang et al., 2011). The *YrAS2388* gene from PI 511384 probably confers partial resistance at the hexaploid level. Coincidentally, stripe rust resistance gene *Yr28* from *Ae. tauschii* WX219 was also mapped on chromosome arm 4DS (Singh et al., 2000). We hypothesize that *YrAS2388* and *Yr28* are the same gene since both genes were actually mapped to the distal region of chromosome arm 4DS. At the hexaploid level in synthetic wheat derivatives, although *YrAS2388* is not as effective as in its original diploid background, it is still an important source for stripe rust resistance, and its performance in polyploidy wheat relies on genetic backgrounds and environmental conditions (Singh et al., 2000; Huang et al., 2011).

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