

Resistance to stripe rust in *Triticum turgidum*, *T. tauschii* and their synthetic hexaploids

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Abstract

Resistance to stripe rust (caused by *Puccinia striiformis* Westend.) of 34 *Triticum turgidum* L. var. *durum*, 278 *T. tauschii*, and 267 synthetic hexaploid wheats (*T. turgidum* × *T. tauschii*) was evaluated at the seedling stage in the greenhouse and at the adult-plant stage at two field locations. Mexican pathotype 14E14 was used in all studies. Seedling resistance, expressed as low infection type, was present in all three species. One hundred and twenty-eight (46%) accessions of *T. tauschii*, 8 (23%) of *T. turgidum* and 31 (12%) of synthetic hexaploid wheats were highly resistant as seedlings. In the field tests, resistance was evaluated by estimating area under disease progress curve (AUDPC). Synthetic hexaploid wheats showed a wide range of variability for disease responses in both greenhouse and field tests, indicating the presence of a number of genes for resistance. In general, genotypes with seedling resistance were also found to be resistant as adult plants. Genotypes, which were susceptible or intermediate as seedlings but resistant as adult plants, were present in both *T. turgidum* and the synthetic hexaploids. Resistances from either *T. turgidum* or *T. tauschii* or both were identified in the synthetic hexaploids in this study. These new sources of resistance could be incorporated into cultivated hexaploid wheats to increase the existing gene pool of resistance to stripe rust.

Introduction

Stripe rust, or yellow rust, of wheat (caused by *Puccinia striiformis* Westend.), is an important cereal rust in many wheat growing regions of the world, especially in areas with cool and wet environmental conditions (Roelfs et al., 1992). Epidemics have been reported in diverse areas such as China (Saari & Prescott, 1985), Continental Europe, Australia, Ethiopia (Johnson, 1992a) and USA (Line, 1976; Roelfs, 1978). When a severe epidemic occurs, yield losses could reach up to 75% (Roelfs, 1978). Although chemical application and cultural practices have been adopted effectively in controlling an outbreak of this disease (Line, 1982), genetic resistance is the most economical and environmentally safe approach.

Germplasm of various *Triticum* species has been screened for resistance to stripe rust. Resistance

sources have been identified in *T. monococcum*, *T. timopheevii* (Mikhova, 1988), *T. dicoccoides* (van Silfhout et al., 1989; The et al., 1993) and a number of *Aegilops* species (Damanian & Pecetti, 1990). However, examples of successful transfers of the resistance genes to cultivated wheat are limited. To date, only 23 stripe rust resistance genes are characterized (Chen & Line, 1992; Chen et al., 1994; McIntosh, 1988; McIntosh et al., 1992), several of which are race-specific in nature. To sustain resistance to stripe rust, availability of race-specific resistance genes must be increased and genes conferring durable resistance should be identified.

The objective of this study was to evaluate the genetic diversity for stripe rust resistance in *T. turgidum*, *T. tauschii* and synthetic hexaploids (*T. turgidum* × *T. tauschii*).

Materials and methods

Host germplasm

Thirty-four lines of *T. turgidum* L. var. *durum*, 278 accessions of *T. tauschii* (Coss.) Schmal. and 267 synthetic hexaploid wheats (*T. turgidum* × *T. tauschii*) were used. The *T. tauschii* accessions were obtained and maintained by the International Maize and Wheat Improvement Center (CIMMYT) Wheat Wide Crosses Program. The *T. turgidum* lines represent the high-yielding, widely adapted germplasm developed by CIMMYT's durum breeding program. The synthetic hexaploids were produced by the third author through random crossing of the *T. turgidum* lines with the *T. tauschii* accessions. Morocco, a susceptible bread wheat cultivar, was used as the susceptible check in all studies.

The pathogen

Pathotype 14E14 (Johnson et al., 1972) of *P. striiformis*, which was used in all studies, occurs predominantly in the Mexican Highlands. It is virulent to stripe rust differential lines Lee, Heines Kolben, Vilmorin 23, Reichersberg 42, Heines Peko, Nord Desprez, Kalyansona, and Arocet R, and avirulent to Chinese 166, Moro, Strubes Dickkopf, Snwon 92/Omar, Hybrid 46, Compair, Carstens V, Spaldings Prolific, and Heines VII.

Greenhouse evaluation

T. tauschii, *T. turgidum* and the synthetic hexaploids were planted following a randomized complete block design with two replicates. Seven- to eight-day-old seedlings (one-leaf stage) of each accession/line were inoculated by spraying urediospores suspended in a light weight mineral oil (Soltrol 170). The inoculated seedlings were placed in a dew chamber overnight at 10–14 °C, and then transferred to a greenhouse maintained with 16 h light/8 h dark photoperiod and 15–20 °C temperature. Infection types were recorded once approximately 3 weeks after inoculation following the 0–9 scale (McNeal et al., 1971). The data were analyzed by analysis of variance (ANOVA) using the general linear model procedure (Steel & Torrie, 1960). Accessions/lines showing low infection type were retested, following the same procedure as described above, to confirm the responses.

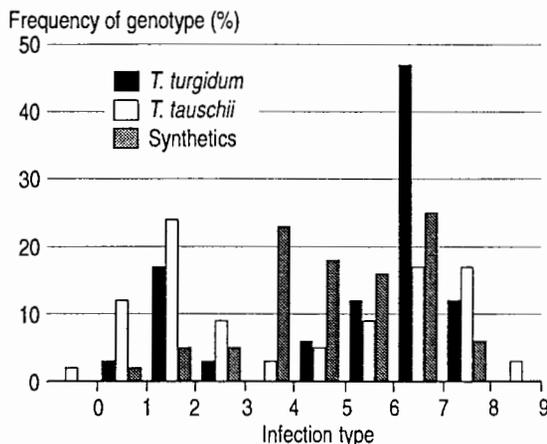


Fig. 1. Frequency distributions for the ITs of *T. turgidum*, *T. tauschii* and synthetic hexaploids.

Field evaluation

T. turgidum and the synthetic hexaploids were evaluated in the field at CIMMYT's experimental stations at Toluca and El Batán during the 1993 crop season. Both sites are located in the Central Highlands of Mexico (near Mexico City) and have a favorable environment for stripe rust development. A randomized complete block design with two replicates was used at Toluca. Seeds were sown in plots of paired rows 0.5 m long with a pathway of 0.5 m between the plots. A stripe rust epidemic was initiated by inoculating spreader rows of cultivar Morocco planted on both sides of the experimental plots. At El Batán, lines were seeded in 2.0 m paired row field plots with a pathway of 0.75 m between plots. Each plot consisted of approximately 40–60 plants. Morocco was again used as spreader rows.

Disease severity estimations were recorded three times at 10-day intervals following the modified Cobb Scale (Peterson et al., 1948). The first disease notes were taken when the susceptible check, Morocco, had reached 100% severity. The disease severity data were used to calculate the area under the disease progress curve (AUDPC) using a computer program developed at CIMMYT. The relative AUDPC (%) of each entry was calculated by using the actual AUDPC of the entry divided by the AUDPC of Morocco. The relative AUDPC data were used for statistical analysis.

Table 1. Mean seedling infection type (IT) of *T. tauschii*, *T. turgidum* and synthetic hexaploids infected by stripe rust under greenhouse conditions

Species	Genome	Mean IT ^a	IT range	Number of lines tested
<i>T. tauschii</i>	D	4.4 ± 0.16 ^b	0–9	278
<i>T. turgidum</i>	AB	5.3 ± 0.38	0–8	34
Synthetics	ABD	5.2 ± 0.21	1–8	267
Morocco (check)	ABD	8.5 ± 0.01	8–9	–

^a ITs follow a scale of 0–9 (McNeal et al., 1971).

^b Standard error (P = 0.05).

Table 2. Sources of seedling resistance (IT < 3 on a 0–9 scale) to stripe rust identified in *Triticum tauschii* accessions tested under greenhouse conditions

Seedling IT	<i>T. tauschii</i> accession numbers ^a
0	168, 493, 625, 628, 725, 886
0 to 1	175, 180, 196, 210, 234, 235, 236, 273, 301, 305, 306, 350, 408, 429, 431, 498, 510, 511, 633, 646, 658, 895, 700, 781, 783, 872, 890, 891, 895, 904, 939, 948
1 to 2	166, 173, 189, 192, 198, 204, 213, 214, 215, 216, 221, 302, 303, 304, 308, 309, 310, 311, 312, 313, 315, 318, 322, 326, 328, 335, 341, 342, 343, 348, 349, 358, 364, 366, 411, 434, 437, 446, 457, 460, 488, 513, 515, 518, 519, 521, 522, 523, 617, 629, 634, 637, 659, 662, 665, 666, 689, 690, 693, 784, 796, 850, 879, 882, 884, 897
2 to 3	174, 191, 200, 201, 220, 218, 223, 268, 307, 314, 316, 317, 324, 333, 346, 347, 447, 449, 524, 826, 878, 914, 963, 976

^a The accession numbers are based on the working collection being used and maintained by the Wheat Wide Crosses Program at CIMMYT, Mexico. The accessions have a prefix of INTER-VER.

Results and discussion

Greenhouse evaluation

A wide array of infection types (ITs), ranging from low to high, were recorded within each of the species (Fig.

1). The IT variation was statistically significant (P < 0.001) for accessions/lines of each of *T. tauschii* (F = 24.5), *T. turgidum* (F = 21.8) and synthetic hexaploids (F = 10.6). Although *T. tauschii* had the lowest means, differences (P < 0.05) between the species were not significant (Table 1). One hundred and twenty-eight (46%) accessions of *T. tauschii* (Table 2), 8 (24%) *T. turgidum* and 31 (12%) synthetic hexaploids (Table 3) consistently displayed ITs between 0 and 3 in repeated tests. Synthetic hexaploids, which are randomly produced from the crosses of *T. turgidum* × *T. tauschii*, showed the lowest frequency of resistant genotypes compared to their donor species. This indicates that, in certain synthetic hexaploids, the resistances of their donor species either failed to express or only expressed partially.

T. tauschii, the diploid D-genome progenitor of bread wheat, is known to be a rich reservoir of valuable genes for resistance to various diseases and pests of wheat (Knott, 1979; Gill et al., 1986; Cox et al., 1992). In this study, the high frequency of seedling resistant *T. tauschii* accessions (46%) further also confirms the above fact for stripe rust resistance, and could provide diverse sources of resistance to this disease. A high level of seedling resistance to stripe rust was also observed in *T. turgidum*, but the frequency of such genotypes was relatively low. This could be due to a lower frequency of resistance genes in the tested sample, which represented high-yielding durums bred at CIMMYT. Pecetti et al. (1989) found that genotypes of *T. turgidum* from central, southern or southwestern Europe, and South America have a higher frequency of resistant genotypes than those from other locations. The et al. (1993) obtained a similar result in a test of *T. dicoccoides*. Since *T. tauschii* is considered to be the D-genome progenitor of bread wheat and its AB genomes are derived from *T. turgidum*, transferring the seedling

Table 3. Sources of seedling resistance (IT < 3 on a 0–9 scale) to stripe rust identified in *T. turgidum* and synthetic hexaploids tested under greenhouse conditions with their mean relative AUDPC estimated in the field

No.	Genotype	Mean disease response		Source of seedling resistance
		Seedling IT ^a range	Relative AUDPC ^b	
<i>T. turgidum</i> L. var. <i>durum</i>				
1	Altar 84 (DW5333) ^c	0–1	5	
2	6973/Ward.7463//74110 (DW5621)	1–2	3	
3	CPT/Gediz/3/Goo//Jo/Cra (DW4876)	1–2	< 1	
4	68111/Rugby//Ward (DW2229)	2	11	
5	Scaup (DW1982)	2	2	
6	Decoy 1 (CW15252)	2	< 1	
7	Sty/Cta//Pal/3/Stn (DW5893)	2	1	
8	Snipe/Yav//Dack/Teal (DW4758)	2–3	2	
Synthetic hexaploid				
1	CPT/Gediz/3/Goo//Jo/Cra/ <i>T. tauschii</i> 215 ^d	1	10	Td ^e & Tt ^e
2	Decoy 1/ <i>T. tauschii</i> 216	1	3	Td & Tt
3	CPT/Gediz/3/Goo//Jo/Cra/ <i>T. tauschii</i> 637	1	6	Td & Tt
4	CPT/Gediz/3/Goo//Jo/Cra/ <i>T. tauschii</i> 358	1	4	Td & Tt
5	Scaup/ <i>T. tauschii</i> 518	1–2	7	Td & Tt
6	CPT/Gediz/3/Goo//Jo/Cra/ <i>T. tauschii</i> 196	1–2	2	Td & Tt
7	CPT/Gediz/3/Goo//Jo/Cra/ <i>T. tauschii</i> 629	1–2	0	Td & Tt
8	68111/Rgb/Ward Resel/Stil/ <i>T. tauschii</i> 783	1–2	2	Tt
9	Scaup/ <i>T. tauschii</i> 523	1–2	2	Td & Tt
10	CPT/Gediz/3/Goo//Jo/Cra/ <i>T. tauschii</i> 208	2	2	Td
11	Decoy 1/ <i>T. tauschii</i> 510	2	1	Td & Tt
12	68111/Rgb/Ward Resel/Stil/ <i>T. tauschii</i> 781	2	5	Tt
13	Snipe/Yav//Dack/Teal/ <i>T. tauschii</i> 904	2	3	Td & Tt
14	Arlequin/ <i>T. tauschii</i> 665	2	5	Tt
15	Decoy 1/ <i>T. tauschii</i> 188	2–3	0	Td
16	CPT/Gediz/3/Goo//Jo/Cra/ <i>T. tauschii</i> 193	2–3	2	Td
17	Decoy 1/ <i>T. tauschii</i> 447	2–3	3	Td & Tt
18	Chen/ <i>T. tauschii</i> 210	2–3	6	Tt
19	Decoy 1/ <i>T. tauschii</i> 515	2–3	2	Td & Tt
20	Sty/Cta//Pal/3/Stn/4/ <i>T. tauschii</i> 431	2–3	2	Td & Tt
21	Yav/ <i>T. tauschii</i> 513	2–3	3	Tt
22	Chen/ <i>T. tauschii</i> 213	2–3	9	Td
23	Altar 84/ <i>T. tauschii</i> 219	3	9	Td
24	GR/Boy/ <i>T. tauschii</i> 311	3	4	Tt
25	68111/Rugby//Ward/ <i>T. tauschii</i> 332	3	8	Td

Table 3. Continued

No.	Genotype	Mean disease response		Source of seedling resistance
		Seedling IT ^a range	Relative AUDPC ^b	
26	Chen/ <i>T. tauschii</i> 429	3	4	Tt
27	Sora/ <i>T. tauschii</i> 192	3	6	Tt
28	Yuk/ <i>T. tauschii</i> 217	3	1	Tt
29	Decoy 1/ <i>T. tauschii</i> 511	3	4	Td & Tt
30	Gan/ <i>T. tauschii</i> 180	3	2	Td
31	Yav/ <i>T. tauschii</i> 493	3	7	Tt

^a ITs follow a scale of 0–9 (McNeal et al., 1971), where Its 0–3 are considered to be resistant.

^b Relative AUDPC is % of the AUDPC of the susceptible check Morocco.

^c The DW number is the accession number of *T. turgidum* that is maintained by the Gene Bank of CIMMYT, Mexico.

^d The accession number of *T. tauschii* that is used and maintained by the Wheat Wide Cross Program at CIMMYT, Mexico. The accessions have a prefix of INTER-VER.

^e Td = *T. turgidum*; Tt = *T. tauschii*.

resistance to hexaploid bread wheats can be achieved either by direct hybridization, or by bridge crosses following the production of the synthetic hexaploids. Several genes from *T. tauschii* for resistance to leaf rust (Gill & Raupp, 1987), stem rust (Kerber & Dyck, 1979) and Hessian fly (Gill et al., 1988) have been transferred directly to bread wheat germplasm. However, if synthetic hexaploid wheats are used, then genes from *T. turgidum* and *T. tauschii* can be transferred to the high-yielding wheats simultaneously. In general, this would not require cytological follow-up and, therefore, can be handled in any breeding program. We have identified a number of synthetic hexaploid wheats with a high level of seedling resistance to stripe rust (Table 3). Their resistances originated from either the corresponding resistant *T. turgidum* parent, or the resistant *T. tauschii* parent, or from their combinations. This indicates that the resistance genes present in either parental species do express in at least some synthetic hexaploid backgrounds. Synthetic hexaploid wheats, which derive resistance from both parental species, should be superior to those that derive resistance from a single parent because of the accumulation of genes from both of the parents.

Since all *T. tauschii* accessions tested have a strong winter type growth habit, evaluation of their resistance was limited to greenhouse tests. However, this may underestimate their potential for contributing adult plant resistance genes like the example of the leaf rust resistance gene *Lr22a*, which is derived from *T. tauschii*.

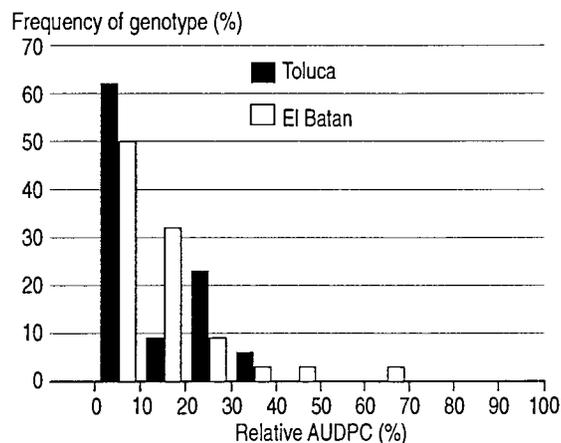


Fig. 2. Frequency distribution for relative AUDPC (%) of *T. turgidum*, at Toluca and El Batan.

Field evaluation

Among the lines tested at Toluca, significant differences ($P < 0.001$) in relative AUDPC was found for both *T. turgidum* ($F = 14.2$) and the synthetic hexaploids ($F = 14.6$). The relative AUDPC of the *T. turgidum* lines ranged between 0.1 to 49.4%, and 21 (62%) lines showed 10% or less relative AUDPC compared to the susceptible check Morocco (Fig. 2). Although the range of relative AUDPC was higher at El Batan (0 to 70%), 17 of the 21 lines remained highly resistant (10% or less) at both locations. In contrast, the synthetic hexaploids had a wide range of relative

Table 4. Mean relative AUDPC of *T. turgidum* and synthetic hexaploids infected by stripe rust under field conditions

Species	Location	Mean relative AUDPC ^a	Relative AUDPC range	Number of lines tested
<i>T. turgidum</i>	Toluca	13.3 ± 2.0 ^b	0– 50	34
	El Batan	12.3 ± 2.4	0– 70	34
Synthetic	Toluca	27.2 ± 1.5	0–100	267
	El Batan	40.9 ± 1.7	0–100	267

^a Relative AUDPC is % of the AUDPC of the susceptible check Morocco.

^b Standard error ($P = 0.05$).

AUDPC (0 to 100%) at both of the locations (Table 3). A total of 81 (30%) lines had 10% or less relative AUDPC at Toluca, however, the frequency (18%) was lower at El Batan. Comparison of the mean for relative AUDPC for the two species indicated that *T. turgidum* was significantly more resistant ($P < 0.05$) than the synthetic hexaploids at both field locations (Table 4). Significant location effect ($P < 0.01$) was observed for the synthetic hexaploids, but not for the *T. turgidum* lines. However, the correlation of relative AUDPC of genotypes between the two locations was significantly high for both *T. turgidum* ($r = 0.793$, $P < 0.01$) and the synthetic hexaploids ($r = 0.739$, $P < 0.01$). This indicates that the performances of most genotypes at the two locations were related. The synthetic hexaploids showed a higher mean relative AUDPC at El Batan. This was possibly due to a natural epidemic of stripe rust that occurred at El Batan earlier than the artificially created epidemic at Toluca. The early epidemic could cause high initial disease ratings for some genotypes, especially for those that are intermediate for disease responses, resulting in high overall AUDPC estimates. The typing of the *P. striiformis* cultures from El Batan indicated that the natural epidemic was also caused by the pathotype 14E14.

Generally, genotypes with seedling resistance gave a good level of field resistance. Of 8 *T. turgidum* lines identified to be resistant at the seedling stage, 7 had a mean relative AUDPC of less than 10%. A similar result was also found in the synthetic hexaploids (Table 3). It is well recognized that most genes, which confer rust resistance at the seedling growth stage, also confer adequate levels of resistance at the adult plant stage. Stripe rust resistance genes in *T. turgidum* and synthetic hexaploids showed no exception to it. Ten genotypes of *T. turgidum* and 17 synthetic hexaploids could possess genes for adult plant resistance as they displayed

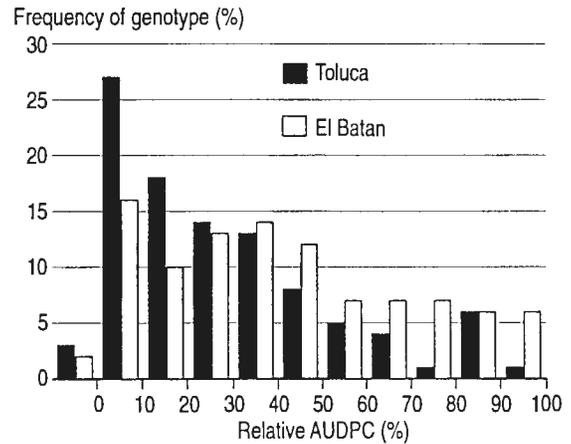


Fig. 3. Frequency distribution for relative AUDPC (%) of Synthetic hexaploid wheats at Toluca and El Batan.

moderate to high infection types in seedlings and low relative AUDPC (Table 5). Some synthetic hexaploids, such as Cerceta/*T. tauschii* 783 (no. 1 in Table 5), must carry genes for adult plant resistance derived from the *T. turgidum* parent because Cerceta was identified to be resistant at the adult plant stage only. Some other synthetic hexaploids with similar results are nos. 2, 5, 9, 10 and 14 in Table 5.

Adult-plant resistance to stripe rust has been reported to be present in many bread wheat cultivars (Johnson, 1992b; Milus & Line, 1986; Schultz & Line, 1992; Singh & Rajaram, 1994). Some of these adult plant resistances to stripe rust have remained durable. However, some known adult-plant resistance genes (such as *Yr11* to *Yr14*) are race-specific (Johnson, 1992b). Undoubtedly, identification of adult plant resistance in both *T. turgidum* and their synthetic hexaploids provides an opportunity to search for new sources of

Table 5. *T. turgidum* and synthetic hexaploids that showed intermediate to high seedling infection types and good adult-plant resistance to stripe rust in field tests

Line no.	Genotype	Mean disease response	
		Seedling IT ^a range	Relative AUDPC ^b
<i>T. turgidum</i> L. var. <i>durum</i>			
1	Chen (DW2192) ^c	6–7	1
2	Garza/Boy (DW5141)	6–7	3
3	68111/Rgb//Ward Resel/3/Stil (DW5047)	6–7	3
4	Aos (DW5807)	5–6	4
5	Agami (DW5086)	4–5	4
6	Yar (DW5324)	6–7	5
7	Alg86/4/Fg/Pales//Mexi/3/Ruff /Fg/5/Ente (DW4851)	6–7	5
8	Cerceta (DW4829)	6–7	6
9	Yav/Scot//Jo/Cr/3/Yav79 (DW5907)	5	6
10	D67.2/P66.270	7–8	7
Synthetic hexaploid			
1	Cerceta/ <i>T. tauschii</i> 783 ^d	3–4	< 1
2	Yar/ <i>T. tauschii</i> 783	4–5	1
3	Altar84/ <i>T. tauschii</i> 211	3–4	2
4	Altar84/ <i>T. tauschii</i> 198	6	2
5	Cerceta/ <i>T. tauschii</i> 665	5	2
6	Scooper/ <i>T. tauschii</i> 407	3–4	3
7	Gan/ <i>T. tauschii</i> 408	4–5	3
8	Sora/ <i>T. tauschii</i> 884	4–5	4
9	Garza/Boy/ <i>T. tauschii</i> 307	5–6	4
10	Chen/ <i>T. tauschii</i> 215	4	5
11	Agami/ <i>T. tauschii</i> 457	4	5
12	Yuk/ <i>T. tauschii</i> 864	5–6	6
13	TkSn1081/ <i>T. tauschii</i> 700	4–5	6
14	D67.2/P66.270/ <i>T. tauschii</i> 211	5–6	7
15	Sora/ <i>T. tauschii</i> 211	4	7
16	Altar84/ <i>T. tauschii</i> 188	4–5	8
17	Cabecinegra/ <i>T. tauschii</i> 457	4	10

^a ITs follow a scale of 0–9 (McNeal et al., 1971), where ITs > 3 are considered to be intermediate, or susceptible.

^b Relative AUDPC is % of AUDPC of the susceptible check Morocco.

^c The DW number is the accession number of *T. turgidum* that is maintained by the Gene Bank of CIMMYT, Mexico.

^d The accession number of *T. tauschii* that is used and maintained by the Wheat Wide Cross Program at CIMMYT, Mexico. The accessions have a prefix of INTER-VER.

resistance, some of which could be durable. Synthetic hexaploids, which combine seedling resistance genes from *T. tauschii* and adult plant resistance genes from *T. turgidum*, for example, Chen/*T. tauschii* 210 (no. 18

in Table 3), may be more attractive for wheat breeding.

In the present study, we did not attempt to study the allelic relationship of seedling, or the adult plant

resistance genes identified in *T. tauschii*, *T. turgidum* or in the synthetic hexaploids with already characterized genes. However, it is likely that some genes might be different from the known genes, because only *Yr8*, *16*, *18*, *20*, *22* and *23* are known to be present in the D genome of wheat, and none of them are derived from *T. tauschii* directly. Moreover, except for *Yr8*, which is derived from *T. comosa*, *Yr16* and *18* are not effective in the seedlings against the pathotype, and the cultivar Lee, which carries *Yr7*, *22*, *23*, is susceptible to the pathotype used in our study. Further studies with a wider array of pathotypes may reveal additional variability of resistance.

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