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UTILIZATION OF WILD AND CULTIVATED EMMER AND OF DIPLOID WHEAT RELATIVES IN BREEDING

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ABSTRACT

Different wheat relatives have contributed greatly towards economic improvement of hexaploid bread wheats. Since its discovery by Aaronsohn in 1906, wild emmer has been widely described and phenotyped for many useful traits such as stripe-rust resistance and high protein. A cultivated emmer landrace, Yaroslav emmer, has contributed durable stem-rust resistance to variety 'Hope', which has become a paramount germplasm for improving resistance to stem rust in bread wheats. Other lines of cultivated emmer, *Triticum dicoccum*, are being used for improved protein percentage. Recently, following the examples of Yaroslav emmer, the International Maize and Wheat Improvement Center, CIMMYT (Centro Internacional De Mejoramiento De Maiz Y Trigo) has embarked on utilization of *Aegilops tauschii* (DD genome) for resistance to *Septoria tritici* leaf blotch and *Fusarium* head scab, drought tolerance, and good bread-making quality traits. Some wild perennial members of the Triticeae genera *Leymus* and *Thinopyrum* are additional promising sources for genes conferring head-scab resistance. Important sources tested in breeding for high protein content and end-use quality traits in bread wheat are wild and cultivated diploid wheats that carry the AA genomes.

INTRODUCTION

The central plant species in the Aaronsohn Lectures is wild emmer, *Triticum dicoccoides* (Körn.) Aarons. The full range of variation in this species as a source for wheat improvement is yet to be realized. One of its applications resides in genes that confer resistance to stripe rust, *Puccinia striiformis* (Gerechter-Amitai et al., 1991). In our presentation, we highlight three issues: (1) the use in breeding of the stem-rust resistance gene *Sr2*, which is responsible for global control of stem rust (*Puccinia graminis* f. sp. *tritici*) epidemics and has been derived from Yaroslav emmer (*T. dicoccum* (Schrank) Schübeler; (2) the use of *Aegilops tauschii* Cosson, the donor of the D genome to modern bread wheat (BW), for transferring disease resistance, drought tolerance, and quality traits; and (3) the use of *T. dicoccum* and *T. dicoccoides* (AABB) for improvement of high protein content and bread-making quality in bread wheat and tests of different diploid wheats that carry the genomes AA for the same purpose.

UTILIZATION OF YAROSLAV EMMER IN CIMMYT WHEAT BREEDING. MCFADDEN'S HOPE: HEXAPLOID WHEAT WITH DURABLE RESISTANCE TO STEM RUST

Yaroslav emmer, grown to some extent as a feed crop in the northern spring wheat area of the United States under the trade name 'Speltz', was observed by McFadden to be almost free of stem rust, leaf rust, loose smut, and bunt in the frequent epidemic years during the early part of this century. He crossed this tetraploid emmer cultivar with the hexaploid wheat cultivar 'Marquis' in 1916. After several generations of mass selection, the hexaploid derivatives 'Hope' (H49-24), H44-24, and H35-24 were released. These wheats showed seedling susceptibility to stem rust races 9 and 30, prevalent in the northwest United States, but expressed a high degree of adult plant resistance in numerous field tests carried out during the early to mid-1930s. Because

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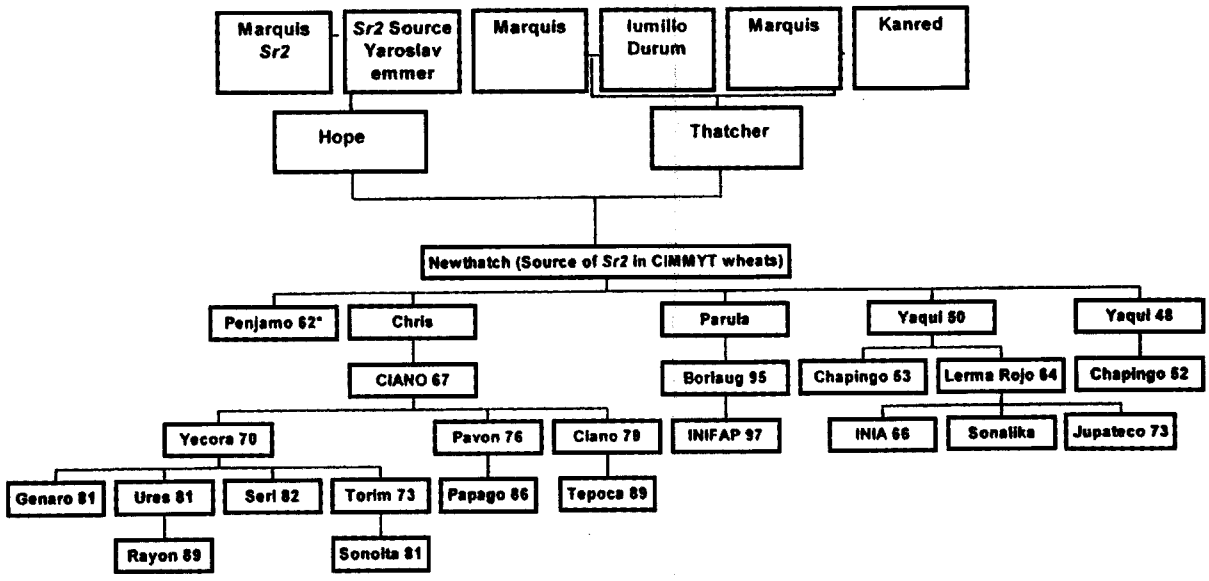

Fig. 1. Contribution of Yaroslav emmer as a source of *Sr2* in CIMMYT wheat varieties.

the infected stems showed no sign of the hypersensitive type of reaction, McFadden (1930) reported that the adult plant resistance in these wheats may involve two mechanisms: "One is the brief opening of the stomata, which largely prevents the entrance of the rust organism, and the other is the inability of the rust organism to reach the exterior of the host and develop a fruiting stage in case it does succeed in gaining entrance into the host." This resistance, now known to be controlled by the gene *Sr2*, located on the short arm of chromosome 3B, is an example of slow rusting (or partial resistance) to stem rust. We also know now that, in certain environments under severe epidemics, wheats carrying only the *Sr2* gene can show intermediate disease levels at maturity. To achieve high degrees of resistance, *Sr2* must be combined with additional minor or major genes. Such gene combinations are commonly known as the *Sr2*-complex.

'Hope' and other resistant derivatives of Yaroslav emmer were extensively used in breeding programs in the United States and Canada in the 1930s and 1940s. The most crucial cross that provided the backbone for stem rust resistance in CIMMYT-derived wheats was 'Hope/Thatcher'. It yielded the wheat cultivar 'Newthatch', developed by Ausemus in Minnesota. Interestingly, 'Thatcher' was itself derived from the tetraploid *durum* cultivar 'Iumillo'. Dr. N.E. Borlaug of CIMMYT used 'Newthatch' in the Mexican Rockefeller Foundation breeding program in the late 1940s and released cultivars such as 'Yaqui 50'. Since then, the *Sr2*-complex has been incorporated into numerous wheat germplasms grown globally in stem-rust-prone areas of America (North, Central, and South), Asia, and Africa. The resistance based on the *Sr2*-complex has remained effective since first identified in the 1920s by McFadden. As far as can be ascertained, the enhanced resistance to stem rust in numerous CIMMYT semi-dwarfs is associated with the *Sr2*-complex (Fig. 1), and time has shown that such resistance to stem rust is durable.

CONTRIBUTION OF *AEGILOPS TAUSCHII* (DD) TO THE IMPROVEMENT OF BREAD WHEAT (*TRITICUM AESTIVUM*, AABBDD) FOR DISEASE RESISTANCE

Of the primary gene pool of Triticeae species, we have given priority to *Aegilops tauschii* (syn. *Ae. squarrosa* L.) for wheat improvement. The species is a recognized source for new variability in several stress responses. *Aegilops tauschii* also contributes to yield components, increased photosynthetic rate, and bread-making quality.

Bridge crosses, utilizing the D genome via synthetic hexaploids (SH), *T. durum* Desf./*Ae. tauschii* (2n = 6x = 42, AABBDD), are potent means for improving bread wheat (BW) performance under biotic and abiotic stresses. Among other results, screening of SH wheats has led to the identification of variable resistance to leaf blotch (*Septoria tritici; Mycosphaerella graminicola* (Fückel) J. Schrot and head scab (*Fusarium graminearum*). Inferences are based upon the disease screening data from three years of testing in locations within Mexico. Resistant SH wheats have also been utilized for BW improvement in response to these biotic stresses. The resulting BW/SH advanced derivatives further express the parental SH-resistance diversity. Some of these results are presented in the following sections.

Table 1
Some synthetic hexaploids (*Triticum turgidum* cultivar/*Ae. tauschii*) resistant to *Septoria tritici* (*Mycosphaerella graminicola*) at Toluca, Mexico, during three years of screening

Durum/*Ae. tauschii*[1]	Cross	Septoria score[2] 1996	1997	1998
Aco89/*Ae. tauschii* (309)	CIGM 90.525	1–1	1–1	2–1
Croc 1/*Ae. tauschii* (879)	CIGM 89.479	1–1	1–1	1–1
Yar//*Ae. tauschii* (518)	CIGM 90.846	1–1	1–1	1–1
68.111/Rgb–u// Ward/3//*Ae. tauschii* (454)	CIGM 92.1723	1–1	1–1	1–1
Sca/*Ae. tauschii* (409)	CIGM 93.237	1–1	1–1	1–1
Cpi/Gediz/3/Goo/Jo69/Cra/4// *Ae. tauschii* (409)	CIGM 93.395	1–1	1–1	1–1
Resistant bread wheat control				
'Bobwhite'		4–1	4–1	4–1
Susceptible bread wheat controls				
'Esmeralda 86'		8–9	8–9	9–9
'Opata 85'		9–9	9–9	9–9

[1]The accession numbers under which *Ae. tauschii* lines are listed in the Wide Crosses working collection are given in parentheses. [2]Double-digit scoring is used. The first digit indicates height of infection with 5 = up to mid-plant and 9 = up to flag leaf; the second digit indicates disease severity on infected leaves, from 1 = low to 9 = total leaf destroyed.

RESISTANCE TO SEPTORIA TRITICI

Wide diversity of resistance in the SH wheats was observed during screening in Toluca, Mexico (Table 1). The durum cultivars involved in these SH combinations were generally susceptible (data not presented). The resistant SH germplasms are all spring types and can be crossed readily to BW cultivars. It is anticipated that this approach will contribute to the availability of additional genetic variation for wheat breeding efforts. The above SH-bridge crosses allow not only for exploitation of *Aegilops tauschii* but also facilitate the incorporation of genetic diversity from the respective durum cultivars. Such SH resistances have been successfully transferred to elite BW cultivars (Table 2). All SH wheats are hulled, but the simple two-gene control of the threshability trait readily yields free-threshing segre-

Table 2
Agronomic characteristics and disease reaction of *Septoria tritici* (*Mycosphaerella graminis*) resistant spring bread wheat/ synthetic hexaploid germplasm grown in Toluca, Mexico. Mean scores for 3 crop cycles, starting in 1996 are given

Germplasm	Days to anthesis	Days to physiolog. maturity	Plant height (cm)	1000-grain weight (g)	Disease damage[1] WS	MS	DS
1. CIGM90.358	83	132	100	39	1-1	1-1	2-1
2. CIGM91.191	83	138	100	38	1-1	2-1	2-1
3. CIGM91.153	83	132	95	37	1-1	1-1	1-1
4. CIGM92.248	88	142	100	33	1-1	1-1	2-1
5. CIGM92.337	83	138	95	35	1-1	1-1	2-1
6. CIGM90.483	80	132	90	25	1-1	2-1	2-1
7. CIGM90.248	83	142	90	29	1-1	1-1	2-1
8. CIGM90.250	83	138	85	41	1-1	1-1	1-1
9. CIGM90.250	83	138	85	41	1-1	1-1	1-1
10. CIGM90.412	83	138	100	39	1-1	1-1	2-1
Resistant bread wheat control							
11. 'Bobwhite' (CM33203)	83	138	90	31	1-1	1-1	4-1
Susceptible bread wheat controls							
12. 'Kauz' (CM67458)	83	135	85	21	6-4	7-4	8-7
13. 'Seri 82' (CM33027)	83	140	90	21	2-1	8-4	8-9

[1]WS = watery stage of grainfill, MS = milky stage, DS = dough stage. Double-digit scoring, as in Table 1.

gates in combinations with bread wheats. A constraint one has to be cognizant of is associated with BW/SH or SH/BW F1 hybrid necrosis.

SH wheats and their SH/BW derivatives possess unique pycnidial characteristics. In general, small quantities of pycnidiospores were produced. In some cases, the lines showed only necrotic areas devoid of pycnidial formation, a reaction type not observed previously in BW germplasm. The SH-derived germplasms with low pycnidiospore production also had an extended latency period of 30 days or more, as compared with the 10–14 day latency period of susceptible BW cultivars.

RESISTANCE TO FUSARIUM GRAMINEARUM

Head scab (*Fusarium graminearum*) of small-grain cereals is a severe disease in warm and humid areas of the world. The disease, which has an adverse effect on grain produced for food and feed, is diagnosed by blemished spike appearance, as well as presence of a toxin. Regions where it was encountered include Africa (Ethiopia), Asia (Iran, China), and South America (Argentina, Brazil, Paraguay, Uruguay). In BW, there is limited identified resistance that has been associated with four genes. Among resistant cultivars are 'Frontana', 'Ning', and 'Sumai'. The potential for identifying additional genes in diverse alien sources ranks high and has been explored in Toluca, Mexico with germplasms derived from annual and perennial Triticeae species of the primary, secondary, and tertiary gene pools.

The SH wheats (*T. durum* × *Ae. tauschii)* most resistant to *Fusarium graminearum* during the three years of field screening at Toluca, Mexico are presented in Table 3. Only those entries with infection scores of less than 20% are shown. Resistant BW controls 'Sumai' and 'Frontana' scored less than 15%, while scores of the susceptible BW control cultivar 'Flycatcher' ranged between 24.6 and 45.5%. The susceptible durum wheat 'Altar 84' scored 48.3 to 53.5%

RESISTANCE IN BW/SH AND PERENNIAL TRITICEAE DERIVATIVES

After two years of testing advanced BW/alien species derivatives, some resistant lines were distributed internationally for multilocational testing. In the third year of the test in Toluca, Mexico (1998), following an excessively high-rainfall crop cycle, disease pressure was severe. This led to higher infection scores for most entries. Altogether, four entries exceeded 20% infection in that year and were discarded from the distributed set. Genetic diversity available in these lines (Table 4) encompasses several *Aegilops tauschii* accessions, *Thinopyrum curvifolium* (Lange) D.R.Dewey, *Th. bessarabicum* (Savul & Rayss) S.R.Loeve, *Th. elongatum* (Host) D.R. Dewey, and *Leymus racemosus* (Lam.) Tselev; the range in scab resistance encountered is promising for BW improvement. The tested germplasms have a Type II resistance. Derivatives of these lines have been identified that also demonstrate Type I and III resistances. The most promising are Mayoor//TKSN1081/*Ae. tauschii* (222) and its sister lines.

CONTRIBUTION OF *AEGILOPS TAUSCHII* TO IMPROVEMENT OF BREAD WHEAT ADAPTED TO LOW MOISTURE CONDITIONS

Results of the yield experiments involving synthetics and advanced lines derived from SH × *Triticum aestivum* crosses are presented. Table 5 shows the ten highest yielders among 61 SH lines that were tested during two years of replicated yield trials. Yields of the synthetics ranged from 638 kg/ha (D67.2/P66.270//*Ae. tauschii* 218) to 4037 kg/ha (Gan/*Ae. tauschii* 897), with an overall mean yield of 2,098 kg/ha. The yields of the two BW controls were 3,276 kg/ha and 3,166 kg/ha for 'Dharwar Dry' and 'Sitta', respectively. Mean biomass yield ranged from 5.53 t/ha (Altar 84/*Ae. tauschii* 219) to 13.8 t/ha (Gan/*Ae. tauschii* 180). Thousand-grain weight was significantly higher in all synthetic genotypes as compared to the control cultivars. Their mean 1000-grain weight ranged from 33.4 g (Botno/*Ae. tauschii* 625) to 51.2 g (Doy 1/*Ae. tauschii* 428) with an overall average of 42.2 g. However, the observed advantages do not imply that these materials should be commercialized directly since other characteristics still need to be improved and stabilized through breeding (tight threshability, susceptibility to lodging, etc.). Different yield responses were presumably due to gametic contributions, as well as to variability of the synthetic's progenitors.

The 21 synthetic × BW derivatives included in the experiment were best yielders under optimum moisture and management conditions. This was the first time that these materials were subjected to drought stress tests. Grain yield, yield components, and other agronomic characteristics of the eight highest-yielding advanced BW derivatives during the two years of replicated trials are shown in Table 6. One line, Croc 1/*Ae.tauschii* 205//Weaver (4,449 kg/ha), yielded significantly more than the highest-yielding BW control cultivar 'Nesser' (3,732 kg/ha). The lowest-yielding derivative was Croc 1/*Ae. tauschii* 205//Kauz (3,287 kg/ha). The overall mean grain yield for all derivatives tested was 3,741 kg/ha. Improved 1000-kernel weight of 86% of the synthetic derivatives was significantly higher than that of the control cultivars. Their mean 1000-grain weight ranged from 28.8 g (Croc 1/*Ae. tauschii* 205//Kauz) to

Table 3

Fusarium head scab infection percentages of some D genome synthetic hexaploids. Means for 3 cycles of testing are given. Disease scores were taken 35 days after a one-time artificial inoculation in field plantings at Toluca (MV), Mexico

Pedigree of synthetic hexaploid[1]	Mean percent infection scores		
	MV1996	MV1997	MV1998
68112/Ward//*Ae. tauschii* (369)	5.0	10.6	13.8
Dverd2/*Ae. tauschii* (1026)	7.5	2.0	13.8
Ceta/*Ae. tauschii* (1029)	7.6	10.0	13.8
Ceta/*Ae. tauschii* (1043)	4.0	1.7	16.5
Lck59.611/*Ae. tauschii* (313)	9.4	11.6	–
Rabi//Gs/Cra/3/*Ae. tauschii* (190)	14.7	16.8	Late
Gan/*Ae. tauschii* (437)	–	10.3	13.8
CPI/Gediz/3/Goo//Jo69/Cra/4/*Ae. tauschii* (633)	–	17.2	14.7
Gan/*Ae. tauschii* (408)	–	18.1	13.8
'Flycatcher' (susceptible bread wheat)	24.6	40.5	45.5
'Altar 84' (susceptible durum wheat)	53.5	48.3	50.3
'Sumai' (resistant bread wheat)	12.4	11.3	17.4
'Frontana' (resistant bread wheat)	8.7	6.1	6.8

[1]*Ae. tauschii* accession numbers as in Table 1.

Table 4

Mean *Fusarium* head scab infection percentages of some conventional and wide crosses. Disease scores were taken 35 days after a one-time artificial inoculation in field plantings at Toluca (MV), Mexico

Pedigree of germplasm[1]	Cross	MV1996[2]	MV1997[3]	MV1998[3]
Mayoor//TKSN1081/*Ae. tauschii* (222)	CASS 94Y00009S-9PR-2M	5.9	5.2	13.4
Mayoor//TKSN1081/*Ae. tauschii* (222)	CASS 94Y00009S-13PR-1M	4.5	8.3	12.2
Mayoor//TKSN1081/*Ae. tauschii* (222)	CASS 94Y00009S-50PR-2B	0.8	4.5	9.8
Mayoor//TKSN1081/*Ae. tauschii* (222)	CASS 94Y00009S-51PR-2B	6.3	7.6	9.7
Mayoor//TKSN1081/*Ae. tauschii* (222)	CASS 94Y00009S-51PR-4B	7.0	4.1	9.4
Mayoor	CIGM 84.295	6.6	6.3	15.4
Turaco/5/Chirya3/4/Siren//Altar84/*Ae. tauschii* (205) /3/ 3*Buc	CASS 94Y00034S	5.2	5.5	9.2
Sabuf /5/Bcn/4/Rabi//Gs/Cra/3/ *Ae. tauschii.*(190)	CASS 94Y00042S	8.4	4.1	17.0
Chinese Spring (CS)/*L. racemosus*//CS/3/Pvn	CIGM 81.1282-15B-2B	9.9	9.0	6.7
CS/ *L. racemosus* //CS/3/Pvn	CIGM 81.1282-15B-3B	9.3	5.7	5.1
CS/*Th. curvifolium*//Glenn/3/Ald/Pvn/4/CS/*L. racemosus* //2*CS/3/Cno79	CIGM 88.750-4PR	5.3	10.6	7.0
Altar 84/*Ae. tauschii*(224)//Yaco/6/Croc1/ *Ae. tauschii*(205)/5/Br12*3/4/…..	CIGM 93.581	3.9	10.0	6.3
Turaco/5/Chir3/4/Siren//Altar84/ *Ae. tauschii*(205)/3/3* Buc	CASS 94Y00034S	8.3	10.6	18.3
Sabuf/3/Bcn//Ceta/ *Ae. tauschii* (895)	CASS 94Y00043S	10.1	2.3	12.4
Chir3/5/CS/*Th. curvifolium*//Glenn/3/Ald/Pvn/4/CS/ *L. racemosus*//2*CS/3/Cno 79	CIGM 93.612	9.4	6.1	7.5
Amphidiploids				
CS/*Th. elongatum* (2n = 8x = 56)		5.5	5.1	12.3
CS/*Th. bessarabicum* (2n = 8x = 56)		6.0	5.2	11.4
Resistant bread wheat controls				
'Sumai'		12.4	11.3	17.4
'Frontana'		8.7	6.1	6.8
Susceptible controls				
'Flycatcher' (bread wheat)		24.6	40.5	45.5
'Altar 84' (durum)		53.5	48.3	50.3

[1] *Ae. tauschii* accession numbers as in Table 1. [2] Based on inoculation of 5 spikes. [3] Based on inoculation of 10 spikes.

Table 5

Agronomic traits of synthetic hexaploids (*Triticum durum* × *Aegilops tauschii*) and two bread wheat control cultivars 'Dharwar Dry' and 'Sitta'. Combined data from two years of field tests under reduced moisture conditions at Cd. Obregon, Mexico

Cross[1]	Grain yield (kg/ha)	Biomass (t/ha)	1000-kernel weight (g)	Flowering day	Physiological maturity day	Plant height (cm)
Gan/*Ae. tauschii* (897)	4037	11.9	38.7	82	120	99
D67.2/P66.270//*Ae. tauschii*(257)	3277	12.4	46.2	99	136	109
Doy1/*Ae. tauschii* (458)	3225	12.4	50.1	93	133	109
Yav3/Sco//Jo69/Cra/3/Yav79/4/ *Ae. tauschii*(498)	3181	12.4	46.5	94	133	91
Croc 1/*Ae. tauschii* (518)	3153	9.4	46.1	85	126	90
Doy1/*Ae. tauschii* (428)	3150	11.0	51.2	94	130	111
Doy1/*Ae. tauschii* (188)	3072	12.5	47.5	94	127	106
Cpi/Gediz/3/Goo//Jo69/Cra/4/ *Ae. tauschii* (208)	3053	12.2	47.0	94	129	109
Lck59.61/*Ae. tauschii*(324)	3025	11.9	40.0	106	137	101
Gan/*Ae. tauschii*(180)	3022	13.8	43.6	94	130	100
Bread wheat controls						
'Dharwar Dry'	3276	9.2	29.1	80	114	94
'Sitta'	3166	9.4	26.6	80	114	79
Least significant difference (5%)	209	0.5	1.2	1	1	3
Coefficient of variation (%)	9	10	6	2	2	5

[1] *Ae. tauschii* accession numbers as in Table 1.

Table 6

Agronomic traits of synthetic hexaploid × bread wheat derivatives and two bread wheat control cultivars 'Nesser' and 'Dharwar Dry'. Combined data from two years of field trials under reduced moisture conditions at Cd. Obregon, Mexico

Cross[1]	Grain yield (kg/ha)	Biomass (t/ha)	1000-kernel weight (g)	Flowering day	Physiological maturity day	Plant height (cm)
Croc 1/*Ae. tauschii* (205)//Weaver	4449	10.2	39.1	77	114	78.6
Croc 1/*Ae. tauschii* (224)//Opata	4100	11.4	34.0	80	117	82.2
Altar 84/*Ae. tauschii*//Ocoroni	4095	10.8	31.7	83	119	78.8
Croc 1/*Ae. tauschii* (224)//Opata	4060	10.2	38.6	80	117	86.2
Croc 1/*Ae. tauschii* (205)//Weaver	4045	9.6	36.5	76	114	76.6
Altar 84/*Ae. tauschii*//Opata	4035	10.6	38.5	80	115	87.6
Croc 1/*Ae. tauschii* (205)//Kauz	4022	10.5	28.8	88	122	72.6
Croc 1/*Ae. tauschii* (205)//Weaver	3872	10.1	36.9	77	116	72.2
Bread wheat controls						
'Nesser'	3732	10.9	23.9	79	115	72.6
'Dharwar Dry'	3224	9.2	28.8	79	115	96.8
Least significant difference (5%)	333	1.1	2.9	1	2	5.4
Coefficient of variation (%)	10	10	4.0	1	1	4

[1] *Ae. tauschii* accession numbers as in Table 1.

39.1 g (Croc 1/*Ae. tauschii* 205//Weaver). The best-yielding entries are being seed propagated as candidates for the 17th Semi-arid Wheat Screening Nursery that is to be distributed internationally and tested under drought.

The yield performance of the best AABBDD synthetics and their derivatives was similar to or better than that of the highest-yielding BW controls. Large seed size and high 1000-grain weight are traits which can be capitalized on in a BW yield enhancement program. To date, more than 650 synthetic hexaploids have been developed by the Wheat Wide Crosses Program at CIMMYT, the majority involving a unique *Ae. tauschii* accession. This germplasm consists of spring types that are highly crossable to advanced bread wheats, hence offering an easier route for their practical utilization and global distribution.

CONTRIBUTIONS OF *TRITICUM MONOCOCCUM* (AA), *TRITICUM URARTU* (AA), *AEGILOPS TAUSCHII* (DD), *TRITICUM BOEOTICUM* (AA), AND *TRITICUM DICOCCUM* (AABB) TO BREAD WHEAT END-USE QUALITY

Gluten, which is composed of gliadins and glutenins, confers cohesiveness and visco-elastic properties to bread and pasta doughs (Lafiandra et al., 1993; Shewry and Tatham, 1994; Gupta et al., 1995). However, the rather limited number of allelic variants controlling glutenin subunits is becoming smaller as a consequence of selection for specific glutenin proteins associated with improved quality (Morgounov et al., 1993).

Several studies reveal that wild diploid species carrying A- and D-genomes have greater allelic variations than cultivated wheat for gene loci controlling glutenin subunits (Waines and Payne, 1987; Lagudah and Halloran, 1988; Ciaffi et al., 1992; Lafiandra et al., 1993; William et al., 1993). These alien genes are a potential means of expanding the number of allelic variants controlling proteins with desirable quality effects in cultivated wheat.

Several amphiploids (hexaploid synthetics) involving accessions of diploid Triticeae species (*Aegilops tauschii, Triticum boeoticum* Boiss. emend. Schiem., *T. monococcum* L., and *T. urartu* Tuman.) and durum wheat have been produced at CIMMYT, as a means of improving the resistance/tolerance of bread and durum wheats to biotic and abiotic stresses. These synthetic amphiploids have also been examined in relation to grain characteristics associated with end-use quality of bread and durum wheats. A brief discussion of their evaluation related to gluten (dough)-quality properties is presented in this paper.

D-GENOME SYNTHETIC HEXAPLOIDS (2N = 6X = 42; AABBDD)

Interspecific hybridization using D-genome *Ae. tauschii* accessions (2n = 2x = 14; DD) is preferred because of their genetic proximity to the D-genome of BW. Sixty-one elite SH wheat lines (D-genome synthetics) were examined in relation to their high molecular weight (HMW) and *Glu-B3*-controlled low molecular weight (LMW) glutenin subunit composition, using sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE). The SH wheat lines had 11 *Glu-D1* glutenin subunits composed of two bands (Table 7). Some of these showed mobilities corresponding to those

Table 7
Mean values for gluten strength parameters of hexaploid synthetic (*T. durum* × *Ae. tauschii*) wheats, grouped according to glutenin subunit composition group

Glutenin-subunit group	n	Flour protein (%)	SDS sediment. val.[1] (ml)	Alveograph W × 10^{-4}J	Mixograph mixing time (min)
Glu-D1 (Ae. tauschii					
2+12 (also in BW)	4	13.3	17.0	234	1.7
2+T2	3	12.5	15.5	187	1.6
1.5+12	11	12.6	15.6	185	1.4
1.5+T2	2	12.6	14.5	180	1.7
2.1+12	7	12.1	14.5	179	1.5
5+10 (also in BW)	11	11.9	12.2	158	1.4
5+10.5	4	12.2	14.8	156	1.4
2.1+10	6	13.5	14.4	147	1.1
3+10.5	3	11.9	13.7	136	1.4
2+12/T2	2	12.9	16.0	124	1.4
1.5+10	8	13.0	14.0	118	1.2
Glu-B1[2]					
6+8	25	12.6A	15.3A	176A	1.5A
7+8	21	12.3A	15.4A	193A	1.6A
20	20	12.7A	12.2B	127B	1.1B
Glu-B3[2]					
LMW-1	17	12.8A	12.3A	111A	1.1A
LMW-2	49	12.4A	15.2B	185B	1.6B

[1] 1.0 g flour sample. [2] Values within each group followed by the same letter are not significantly different ($p < 0.05$).

of subunits 2+12 and 5+10 found in BW. The considerably larger *Glu-D1* allelic variation in *Ae. tauschii* compared to BW observed among these germplasms has been reported elsewhere (Lagudah and Halloran, 1988; Ciaffi et al., 1992; William et al., 1993). The ranges in the values obtained for flour protein, SDS-sedimentation (SDSS) volume, alveographic dough strength value (W), and mixograph dough-mixing time (Table 7) indicate that the SH wheat population is comprised of lines with weak to medium-strong gluten types. The differences in quality characteristics observed were not assigned to individual *Glu-D1* HMW glutenin subunits because the SH amphiploids (Table 7) were produced using durum wheat lines having different *Glu-B1* and *Glu-B3* controlled glutenin alleles which also contributed differentially to the quality characteristics of the SH wheats. In order to elucidate the quality effects of individual *Glu-DI* subunits of *Ae. tauschii* more stringently, further studies are required for which a common durum wheat background may be crucial.

Hybridization of SH wheats to BW cultivars susceptible to *Helminthosporium sativum*, followed by selection, has generated 18 elite advanced derivatives with superior plant type, disease resistance, and diversity in gluten quality characteristics. Table 8 shows seven of these hybrids possessing intermediate gluten strength (alveograph W values between 201–335 $\times 10^4$ J), suitable for the production of both flat and leavened breads and biscuits.

The study revealed that *Ae. tauschii* could be utilized to substantially increase the number of HMW glutenin subunits present in BW. However, it will be necessary to first identify the new glutenin subunits that can contribute positively to gluten strength. This information will be advantageous for combining pertinent accessions by direct hybridization with desirable bread wheats, and for more detailed studies of the *Glu-D1* and *Glu-B3* glutenins with significant quality effects.

A-GENOME SYNTHETIC HEXAPLOIDS (2N = 6X = 42)

Crossing *Triticum durum* with A-genome diploid accessions of *Triticum. boeoticum, T. monococcum*, and *T. urartu* resulted in AAB-genome F1 hybrids that produced AAAABB hexaploids following colchicine treatment of the F1 hybrids. One hundred fifty-five A-genome hexaploids (AAAABB) were included in this study. Durum wheat varieties, accessions of the diploid species, and derivatives of crosses between them were analyzed for their HMW glutenin subunit composition, using SDS-PAGE. All durum wheat lines contained the *Glu-A1* null allele. The diploid species showed greater *Glu-A1* allelic variation than is commonly found in durum and bread wheats (3 alleles). *Triticum boeoticum, T. urartu*, and *T. monococcum* possessed 6, 5, and 3 HMW glutenin alleles, respectively. Most of the diploid species accessions had subunits that could be characterized electrophoretically by a strong, slow-moving x-type band and a fainter fast-moving y-type band. The bread and durum wheats commonly possess a null allele or subunits 1 or 2* and are composed of only one band (x-type). One *T. urartu* subunit was composed of only the x-type component, with a mobility similar to that of subunit 2*. A larger number of *Glu-A1* allelic variations in *T. urartu* and *T. boeoticum* compared to cultivated wheat has been reported previously (Waines and Payne, 1987; Ciaffi et al., 1992; Lafiandra et al., 1993). The A-genome SH lines combined the gluten-forming proteins present in their parents. In two cases, the y-type subunit of the diploid species (*T. boeoticum* or *T. urartu*) was not expressed in the derivatives (data not shown).

Table 8
Quality characteristics and HMW-glutenin subunit composition of medium-strong gluten type lines derived from crosses between synthetic hexaploids and bread wheat lines

Name of wheat line	Flour protein (%)	SDS-PAGE sediment. val.[1] (ml)	Alveograph W × 10^{-4} J	Mixograph mixing time, (min)	HMW glutenin subunits 1A[2]	1B[2]	1D[2]
Altar 84/*Ae. tauschii* (191)//Opata	12.3	19.0	335	2.4	2*	13 + 16	2.1 + T2.5
Altar 84/*Ae. tauschii* (224)//2*Opata	11.6	18.0	201	2.2	2*	13 + 16	2 + 12
Altar 84/*Ae. tauschii*(224)//Yaco	12.8	18.5	248	1.5	0	7 + 8	2 + T2
Altar 84/*Ae.tauschii* (224)//2*Yaco	12.1	20.0	280	1.5	2*	7 + 8	2 + 12/T2
Altar 84/*Ae. tauschii* (224)//2*Yaco	12.1	18.5	259	1.5	2*	13 + 16	2 + 12/T2
Altar 84/*Ae. tauschii*(224)//Seri	12.8	17.0	243	1.7	1	7 + 9	5 + 10
Altar 84/*Ae.auschii* (221)//Siren	10.3	13.5	255	–	0	7 + 8	5 + 10
Opata (BW)[3]	11.7	19.5	262	1.8	2*	13 + 16	2 + 12
Yaco (BW)[3]	9.6	14.5	183	1.4	0	13 + 16	2 + 12

[1]1.0 g flour sample. [2]Chromosome control. [3]Bread wheat parental line.

Grain protein and SDS sedimentation (gluten-strength parameter) values of the A-genome hexaploids and their parents are shown in Table 9. All three diploid species groups have a higher protein content (up to 30.2% in *T. boeoticum*) than durum wheat. The protein content of the A-genome hexaploid groups was intermediate between that of their parents. The diploid species groups had higher mean SDS sedimentation (SDSS) values than their durum wheat parents. The A-genome hexaploids of *T. boeoticum* had slightly higher mean SDSS values than durum wheats. The opposite was observed for the hexaploid derivatives of *T. urartu* and *T. monococcum.*

The generally low SDSS values of the hexaploid derivatives suggest that the large SDSS volumes of the diploid species may have been due to higher protein content and not due to high protein (gluten) quality. In spite of this, some *T. boeoticum*-based hexaploid wheat lines possessed larger SDSS volumes than durum wheat, suggesting that some diploid accessions may carry *Glu-A1* glutenin alleles with a positive gluten quality effect.

VARIATIONS IN END-USE QUALITY TRAITS AND GLUTENIN SUBUNIT COMPOSITION IN TRITICUM DICOCCUM

High molecular weight glutenin-subunit composition is implicated in the definition of gluten strength in both BW and durum wheat (Payne et al., 1981; Pogna et al., 1990). In addition, variations in LMW glutenin subunit composition, under the control of the *Glu-B3* locus, have been found associated with variations in gluten strength in durum wheat (Pogna et al., 1990; Peña et al., 1994). The number of *Glu-A1*- and *Glu-B1*-encoded HMW glutenin subunits in *T. dicoccum* is larger than that in durum and BW (Vallega and Waines, 1987; Vallega, 1988; Branlard et al., 1989).

Peña et al. (1995) examined both variation in quality (grain hardness, protein content, and SDSS volume) and the relationship between quality and HMW and LMW glutenin subunit composition (SDS-PAGE) in 137 accessions of *T. dicoccum.* These accessions were grown at the El Batan experiment station, State of Mexico, Mexico in 1990 and 1991. A high variation in *Glu-A1*- and *Glu-B1*-encoded HMW glutenin subunit composition was observed in this population, with 6 and 14 allelic variants for *Glu-A1* and *Glu-B1*, respectively (Table 10). Seven of the subunits observed were different from those described by Payne and Lawrence (1983), but may be the same as the ones designated with Roman numerals by Vallega and Waines (1987). One sample showed very faint bands or absence of bands in the electrophoretic zone of *Glu-B1*. It was tentatively designated as "undefined" and may correspond to the allelic variant described by Vallega and Waines (1987) as *Glu-B1-I* or "null B" allele. Both *Glu-B3*-encoded LMW glutenin subunits 1 (LMW-1) and 2 (LMW-2), commonly found in durum wheat, were present in this population.

Population means and range values for grain hardness as determined by the pearling index test, grain protein, and SDSS volumes are shown in Table 11. All but two accessions had pearling index values corresponding to hard grain. The soft-grain character observed in two lines was unexpected since tetraploid wheat is generally characterized as being hard-grained, in part due to the lack of D-genome chromosomes, specifically 5D, which carries genes associated with grain softness. The grain hardness mean value did not vary with harvest year or with the type of LMW glutenin subunit present in the population.

The grain protein percentage varied widely, with some accessions having values above 20%. The population means were slightly higher in 1990 than in 1991.

Table 9

Mean grain protein and SDS-PAGE sed. val.[1] of *Triticum durum*, diploid species, and the synthetic hexaploid durum × diploid wheat derivatives. The genomes of the latter are shown in bold

	Grain protein (%)			Grain SDS-PAGE sed. val.[1] (ml)	
Genomic group	n	mean	range	mean	range
T. durum	10	13.6	11.9–15.0	8.0	7.5–9.5
T. boeoticum	38	23.9	11.9–30.2	19.5	7.5–24.0
A^b AB	42	17.7	14.6–19.5	8.7	5.0–12.0
T. urartu	11	23.2	21.0–27.3	16.0	7.0–23.0
A^u AB	11	17.0	14.4–19.1	6.1	4.0–8.0
T. monococcum	5	18.5	17.4–20.4	15.0	11.0–21.0
A^m AB	7	15.7	15.2–16.5	5.7	4.5–7.5

[1]1.0 g flour sample.

Table 10
HMW (*Glu-A1* and *Glu-B1*) and LMW (*Glu-B3*) glutenin subunit distribution in a *Triticum dicoccum* population[a]

Glu-A1		*Glu-B1*		*Glu-B3*	
HMW subunits	percent distrib.	HMW subunits	percent distrib.	LMW subunits	percent distrib.
1	45.2	13+18	14.6	LMW-1	34.3
null	24.8	14+15	13.8	LMW-2	65.7
2*	18.2	6+8	13.1		
1.1	6.6	20	11.5		
1.5*	3.6	7+8*	11.5		
2.5*	1.4	17+18	11.5		
		22	7.7		
		7+8	4.6		
		"undef."	3.1		
		7	2.3		
		17/8	2.3		
		18	1.5		
		13+19	1.5		
		7*+8	0.8		

[a]Source: Peña et al. (1995).

Table 11
Mean and range values for quality characteristics of a *Triticum dicoccum* population[a]

	Lines with LMW-1 (n = 47)		Lines with LMW-2 (n = 90)	
Quality parameter	mean ± SD	range	mean ± SD	range
Pearling index (%)				
1990	41 ± 4	39–60	40 ± 1	39–43
1991	40 ± 4	36–61	39 ± 1	36–46
Grain protein (%)				
1990	17.1 ± 2.3	13.3–23.9	17.4 ± 1.8	12.7–24.4
1991	15.9 ± 2.3	10.9–22.4	15.9 ± 1.7	12.5–21.6
SDS-PAGE sediment. (ml)				
1990	6.2 ± 2.3	3.0–13.5	5.7 ± 2.5	2.0–12.0
1991	4.8 ± 1.6	2.5–10.5	4.7 ± 1.8	2.0–9.0

[a]Source: Peña et al. (1995).

Variations in grain protein content were not associated with LMW glutenin subunit composition. SDSS volume varied widely, indicating high variability in gluten strength in this species. The SDSS population means varied with harvest year in the same manner as grain protein. Variations in SDSS volume could not be related to variations in LMW glutenin subunit composition. This latter result was unexpected, considering the correlation between SDSS volume and LMW glutenin subunit composition in durum wheat (Pogna et al., 1990; Peña et al., 1994). *Glu-A1* subunits null and 2*, *Glu-B1* subunit 6+8 and subunits with single components were associated with inferior gluten strength. *Glu-A1* subunit 1.1 and *Glu-B1* subunits 14+15 and 13+18 were associated with superior gluten strength.

These results confirm previous findings that *T. dicoccum* accessions possess more diverse alleles for synthesis of gluten-type proteins than modern cultivated wheats. Therefore, *T. dicoccum* could be considered as a potential source for gluten strength improvement in both BW and durum wheat.

TRANSFERRING A HIGH-PROTEIN GENE (HPG) FROM *TRITICUM DICOCCOIDES* INTO BREAD AND DURUM WHEATS

Protein quantity and quality are both important grain factors defining end-use quality in both BW and durum wheat. Once protein quality of a genotype is fixed through breeding, its expression (as gluten strength)

Table 12
Quality characteristics of Canadian wheat lines carrying a high-protein gene

Sample ID	Grain protein[1] (%)	Flour protein (%)	SDS sediment. val. (ml)	Alveograph W × 10^{-4}	Alveograph P/L	Bread loaf vol.	HMW glutenin subunits
90B01-F3$a	17.6	15.7	19.0	325	0.9	970	2*,7+9,5+10
90B01-F3$b	17.3	15.6	20.0	349	0.8	950	2*,7+9,5+10

[1] 14% moisture basis.

depends largely on the protein content of the grain. Protein content is a very important quality factor determining the commercial value of a wheat crop. When agricultural practices and environmental conditions favor increases in yield, this is accompanied by a reduction in grain protein content. This generally occurring negative relationship between yield and protein content results from both competition for available nitrogen between protein and starch synthesis pathways and a dilution effect due to increased starch content in the grain of high-yielding wheat crops.

Recently, Humphreys et al. (1997) achieved the incorporation of a high-protein gene (HPG, originating from *T. dicoccoides* germplasm derived from Israel and carried by 'ND-643') in semi-dwarf wheat lines that are high-yielding by Canadian standards. Rapid advances were achieved by combining the use of marker-assisted selection (PCR-based) with double haploid production to fix new genomic constitutions (Humphreys et al., 1998). The spring wheat 'Glupro' (ND-643) carries a segment of the *T. dicoccoides* 6BS chromosome arm, including a region coded by the *Gli-B2* and *Nor-2* genes (Humphreys et al., 1998).

In 1995, crosses were made between CIMMYT's high-yielding lines ('Pikus', 'Bacanora', 'Tia') and two Canadian BW lines (and ND-643) carrying the HPG gene from *T. dicoccoides*. Enough grain samples were produced during the 1995–1996 crop cycle at Cd. Obregon, Mexico to allow for determination of characteristics related to bread-making quality. These quality data are shown in Table 12. High protein, strong gluten, and excellent bread-making quality characterized both Canadian lines. At present, accessions originating from crosses between CIMMYT germplasm and HPG lines are in the F5 generation. Selection for high protein will be performed this year.

CONCLUSIONS

Wild and Yaroslav emmer and diploid wheat relatives have contributed greatly to the economic improvement of hexaploid bread wheats. Wild emmer has been characterized as possesing stripe-rust resistance and high protein grain. CIMMYT's wheat breeding effort using the cultivar 'Hope', a derivative of Yaroslav emmer, as the principal source of durable resistance to stem rust, was a success story worldwide. Following the examples of Yaroslav emmer, CIMMYT has utilized *Aegilops tauschii* for resistances to *Septoria tritici* and *Fusarium graminearum*, drought tolerance, and good bread-making quality. Synthetics derived from hybridizing *Triticum durum* with A-genome diploid accessions of *T. boeoticum, T. monococcum,* and *T. urartu* have emerged as potential sources of breeding for high protein content and end-use quality traits in bread wheat. Similarly, *T. dicoccum* and *T. dicoccoides* offer novel genes readily deployable for the improvement of gluten strength and gluten protein content, respectively. The information on desirable traits obtained with the A- and D-genome germplasms will be advantageous in combining pertinent accessions of alien diploid species with durum and bread wheats. Therefore emphasis in alien-trait introgression will be on the integration of stable disease resistance and quality attributes from the A- and D-genomes. The germplasm so derived should provide genetic stocks for global wheat research.

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