Theor Appl Genet (1995) 90:571–577

T. S. Cox · R. G. Sears · R. K. Bequette

Use of winter wheat × *Triticum tauschii* backcross populations for germplasm evaluation

Received: 20 June 1994 / Accepted: 8 September 1994

Abstract The wild diploid goatgrass, *Triticum tauschii* (Coss.) Schmal., is an important source of genes for resistance to both diseases and insects in common wheat (*Triticum aestivum* L.) We have evaluated grain yield, kernel weight, protein concentration, and kernel hardness of 641 BC_2 F_1-derived families from direct crosses involving four *T. aestivum* cultivars and 13 *T. tauschii* accessions over 2 years and at two Kansas, USA, locations. On average, *T. tauschii* germplasm depressed grain yield and increased protein concentration, whereas kernel weight was affected either positively or negatively, depending on the *T. tauschii* parent. Three *T. tauschii* parents produced a large proportion of families with very soft endosperm. Some variation among progeny of different *T. tauschii* parents resulted from the segregation of genes for resistance to leaf rust (caused by *Puccinia recondita* Rob. ex Desm.). This study confirmed that random BC_2-derived families can be used to evaluate the effects of *T. tauschii* genes in the field. This methodology, although laborious, can provide useful information which is not obtainable by the screening of *T. tauschii* accessions themselves.

Key words *Triticum tauschii* · *Aegilops squarrosa* Wheat · Yield · Protein · Hardness · Leaf rust

Joint contribution of USDA-ARS, the Kansas Agricultural Experiment Station, and the Wheat Genetics Resource Center. Contribution no. 94-242-J. Mention of a proprietary name in the article does not imply approval to the exclusion of other suitable products

Communicated by A. C. Kahler

T. S. Cox ✉
USDA-ARS, Agronomy Department, Throckmorton Hall, Kansas State University, Manhattan, KS, 66506, USA

R. G. Sears
Agronomy Department, Throckmorton Hall, Kansas State University, Manhattan, KS 66506, USA

R. K. Bequette
Grain Science Department, Shellenberger Hall Kansas State University, Manhattan, KS 66506

Introduction

The wild goatgrass, *Triticum tauschii* (Coss.) Schmal. (2n = 14, genome D, syn. *Aegilops squarrosa* L.), is one of the progenitors of common wheat (*Triticum aestivum* L., 2n = 42, genomes ABD). Accessions of *T. tauschii* have been evaluated for a wide range of agronomically important traits, including disease and insect resistance (Pasquini et al. 1980; Gill et al. 1986; Cox et al. 1992a), endosperm proteins affecting end-use quality (Lagudah and Halloran 1988), and physiological traits (Zohary 1969; Limin and Fowler 1981; Le et al. 1986).

Genes with positive effects on complex traits, such as growth rate and grain yield, have been transferred from wild species into oat (*Avena sativa* L.; Lawrence and Frey 1976), sorghum [*Sorghum bicolor* (L.) Moench; Cox et al. 1984], pearl millet (*Pennisetum americanum* L.; Bramel-Cox et al. 1986), potato (*Solanum tuberosum* L.; Peloquin et al. 1989), and soybean [*Glycine max* (L.) Merrill; Carpenter and Fehr 1984]. In wheat, Cantrell and Joppa (1991) have reported that chromosomes from *T. dicoccoides* L. can significantly improve the grain and protein yield of wheat.

Collections of wild *Triticum* species can be evaluated in the field for production and quality characteristics as a first step toward domesticating the species (Waines et al. 1987). However, *T. tauschii* has plant and grain characteristics that differ radically from those of wheat, including thin culms, small leaves, numerous tillers, barrel-shaped, shattering spikes, and large, tough glumes that adhere tightly to the kernels. Consequently, screening *T. tauschii* collections for grain yield or quality is difficult.

Furthermore, the expression of genes affecting such traits may be very different when the genes are introgressed into common wheat. In several grain crops, parental performance has proven to be a poor predictor of progeny performance in wide crosses (Bramel-Cox and Cox 1989). In wheat, even the expression of some simply inherited disease-resistance genes was altered when

these genes were transferred to a higher ploidy level (Knott 1978; Kerber and Green 1980).

Large-scale, random introgression of wild or unadapted germplasm into adapted populations, although quite labor-intensive, can provide useful information on the potential value of wild accessions (Bramel-Cox and Cox 1989). In the present study, we have evaluated the agronomic and quality traits of random, backcross-derived lines from crosses between elite winter wheat cultivars and 13 accessions of *T. tauschii*. Our objectives were to determine (1) the value of these *T. tauschii* parents for improvement of hard red winter wheat and (2) the degree to which genes from *T. tauschii* parents affect the yield and quality of wheat, either positively or negatively.

Materials and methods

Twenty-two accessions of *T. tauschii*, collected in southwest Asia by Kyoto University scientists (Kihara et al. 1965) and maintained in the United States by the Wheat Genetics Resource Center at Kansas State University, were chosen for crossing. Accessions were selected to represent the geographical range of the collection. Pollen from *T. tauschii* plants was used to fertilize emasculated spikes of four hard red winter wheat cultivars: Karl, TAM 107, TAM 200, and Century. F_1 embryos were rescued on an artifical medium (Gill and Raupp 1987), and the F_1 plants were backcrossed as females to their respective common wheat parents by the approach method (Curtis and Croy 1958). The development of BC_1 populations is described in detail by Cox et al. (1991). Root tips from all germinating BC_1F_1 seeds were fixed, and chromosome numbers were determined by the method of Endo and Gill (1984). All male-fertile BC_1F_1 plants were backcrossed as males to their respective wheat parents, and root tips from all germinating BC_2F_1 seeds were fixed to determine chromosome numbers. Plants were grown in the greenhouse to produce BC_2F_1-derived F_2 families ($BC_2F_{1:2}$ families). All $BC_2F_{1:2}$ families for which at least 2 g of seed were available were sown, in bulk, in 1 m^2 plots at Manhattan, Kan. in October, 1988, and $BC_2F_{1:3}$ families were bulk-harvested in June, 1989.

Sufficient seed of $BC_2F_{1:3}$ families for field testing was produced by 21 crosses derived from 13 accessions of *T. tauschii*. Bulk $BC_2F_{1:3}$ families were evaluated in harvest year 1990 at Manhattan and Hutchinson, Kansas; $BC_2F_{1:4}$ families were evaluated in 1991 at the same locations. Each of the four experiments was sown in a randomized complete-block design with two replicates. Within each replicate, families were randomized within each of four blocks, with all families in a block having a common recurrent parent. Plots within blocks were divided into contiguous groups of ten, and one random plot in each group contained the recurrent parent of the families in that block. Plots at Manhattan comprised three rows, each 3.5 m long, with 18 cm between rows within plots and 26 cm between plots. Plots at Hutchinson were 1.5 m long, but otherwise identical to those at Manhattan.

All experiments were sown in early to mid-October and harvested in late June. Sowing rates were approximately 6 g m^{-2}. At Manhattan, 100 kg ha^{-1} N and 30 kg ha^{-1} P were applied to the soil before sowing, and 80 kg ha^{-1} N and 30 kg ha^{-1}P were applied at Hutchinson.

Both experiments at Manhattan and the 1991 experiment at Hutchinson were harvested with a small-plot combine. At Hutchinson in 1990, plots were harvested with a cutter-binder and threshed using a stationary thresher; grain from the latter plots was used as seed for both 1991 experiments. Grain yield was recorded for each plot in grams per square meter, and 200 kernels were counted and weighed to provide an estimate of weight per kernel in milligrams (herein, kernel weight) for each plot. Fifteen-gram bulk samples of grain from each plot were ground in a Udy mill (Udy Corp., Ft. Collins, Colo., USA), and grain protein concentration and hardness were estimated using a Percon Inframatic 8620 near-infrared spectrometer (Perten Instruments NA, Inc., Reno, Nev., USA) calibrated according to AACC (1983). The hardness calibration was based on Federal Grain Inspection Service results for a set of samples ranging from very soft wheats to durum wheat (*T. turgidum* L.). The protein calibration was based on Kjeldahl results (N × 5.6; AACC 1983) for samples exhibiting a wide range of protein concentrations. Calibration was checked by determining Kjeldahl protein concentration of every 20th sample.

In each block of each experiment, adjusted means for the recurrent parent and all BC_2-derived families, as well as error mean squares, were obtained for grain yield, kernel weight, protein concentration, and hardness, using the NEIGHBOR nearest-neighbor procedure of the AGROBASE 4.1 computer package (Agronomix, Portage la Prairie, Manitoba, Canada). The least significant difference (lsd) for comparing the adjusted mean of a BC_2-derived family and that of its recurrent parent in a single experiment was computed as $\text{lsd} = t*[s_e^2*(0.5+0.5r^{-1})]^{1/2}$, where s_e^2 was the error mean square, r was the number of recurrent-parent plots in a replicate, and t was the t-value at the $P = 0.05$ probability level, for the number of degrees of freedom associated with s_e^2.

For comparison of families with different recurrent parents and/or in different experiments, 'scores' were computed for all traits as $\text{score} = (\bar{x}_{BC2} - \bar{x}_R)*\text{lsd}^{-1}$, where $\bar{x}_{BC2}$ was the adjusted BC_2-derived family mean and $\bar{x}_R$ the recurrent parent mean in an experiment. Therefore, a family with a score greater than 1 or less than −1 had a mean that differed significantly from that of its recurrent parent in that experiment.

Analyses of variance across experiments were computed using scores for the four traits. A different analysis was done for each recurrent parent and its progeny. Because scores were computed by dividing mean differences by lsds (which consisted of error standard deviations multiplied by a constant for each recurrent parent), the pooled error mean square for scores was a constant for each recurrent parent and equal to $t^{-2}*(0.5+0.5*r^{-1})^{-1}$. Mean scores across experiments were interpreted as follows. A family having a mean score with absolute value greater than 1.0 or less than −1.0 did not necessarily differ significantly from its parent in every experiment, but conversely, a family that was always significantly higher or always significantly lower than its recurrent parent in every experiment would have a score greater than 1.0 or less than −1.0, respectively. Families with such scores were considered to be consistently different from their recurrent parent.

Results

Chromosome numbers

Somatic chromosome numbers were obtained for 88 BC_1F_1 plants and their 859 BC_2F_1 progeny, of which 503 produced sufficient seed for field testing (Table 1). The BC_1F_1 plants had chromosome numbers distributed from 36 to 49, with peaks at 42 and 49 (Table 1, Cox et al. 1991). These plants were backcrossed as males to select against aneuploid pollen but, even so, only 65% of BC_2F_1 plants were euploid. With the exception of one 58-chromosome plant, numbers ranged from 38 to 49. Of those plants producing enough seed for field testing, 76% were euploid, and numbers ranged from 41 to 47.

The chromosome numbers of BC_2F_1 plants depended only to a limited extent on the chromosome numbers of their BC_1F_1 parents. Euploid BC_2F_1 plants comprised 73% of the progeny from 42-chromosome BC_1F_1s, 57% of those from 36- to 39-chromosome BC_1F_1s, and 66% of those from 49-chromosome BC_1F_1s. The progeny of 42-, 36- to 39-, and 49-chromo-

Table 1 Distributions of somatic chromosome numbers among BC_1F_1 plants and BC_2F_1 plants within BC_1F_1-derived families from crosses between winter wheat cultivars and *Triticum tauschii*

BC_1F_1 chromosome #	# BC_1 families examined	Chromosome numbers of BC_2F_1 plants													
		38	39	40	41	42	43	44	45	46	47	48	49	58	All
36	2	1	0	0	0	10	7	1							19
37	3	1	0	0	2	7	1	1	1						13
38	3			2	5	9									16
39	5			1	11	27	4	1	0	1					45
40	7				7	40	7	2							56
41	11		1	1	16	99	9								126
42	15				22	114	6	8	3	1	0	1	0	1	156
43	1														13
44	5				1	37	13	7	4	1	1				64
45	1					2									2
46	6				3	23	8	7	3	8	2				54
47	8					54	23	19	7	4	3	1			111
48	4					16	6	4	1	2	2	1			32
49	17			1	3	105	18	16	7	2	5	1	1		159
All (total)[a]	88	2	1	5	70	556	102	59	26	19	13	4	1	1	859
All (evaluated)[b]					31	382	38	24	20	7	1				503

[a] Sums for all progeny for which chromosome numbers were available (Chromosome numbers were not determined for 138 progeny that were field-tested)

[b] Sums for all progeny producing sufficient seed for field testing.

some BC_1F_1s had similar mean chromosome numbers of 42.2, 42.7, and 41.9, respectively.

T. tauschii accessions producing progeny

Families with enough seed to field-test were derived from only 13 of 22 *T. tauschii* accessions that had been crossed originally, and of the 52 possible cross combinations (13 accessions × 4 recurrent parents) only 21 were represented in the field (Table 2). This attrition occurred for several reasons. A few crosses could not be made because of asynchrony of heading; some produced inviable embryos or seedlings; others produced F_1 plants that set no BC_1 seed even after repeated pollination; and still others produced partially or wholly male-sterile BC_1 and BC_2 plants that set insufficient seed for testing. However, no sterility was observed among those families that did reach the field, in either seed-increase or experimental plots.

T. tauschii accessions that produced progeny for field-testing had collection sites spanning four countries

Table 2 Accession numbers and collection sites of 13 *T. tauschii* accessions; numbers of BC_2F_1-derived families produced with each recurrent parent; and mean scores by *T. tauschii* parent over all progeny and environments for grain yield, kernel weight, protein concentration, and hardness

Triticum tauchii accession	Collection site	Number of lines from crosses with				Mean score[a]			
		Karl	TAM 107	TAM 200	Century	Grain yield	Kernel weight	Protein conc.	Hardness
TA 2402	Doski, Afghanistan	6			8	−0.48*	−0.72*	0.32*	−0.80*
TA 2448	Tehran suburbs, Iran				37	−0.47*	0.09*	0.25*	0.09
TA 2450	Behshahr, Iran				40	−0.68*	0.40	0.90*	−2.04*
TA 2460	Khoshyailagh, Iran		37	35	43	−0.09*	0.68*	0.87*	−0.87*
TA 2504	46 Km N of Van, Turkey			33		−0.19*	−0.24*	0.17*	0.75*
TA 2507	77 Km N of Van, Turkey			41	48	−0.90*	−0.21*	0.73*	0.36*
TA 2524	Avej, Iran			18		−0.26*	0.50*	0.00	−0.10
TA 2541	Formrok, Afghanistan			5	46	−0.58*	−0.23*	0.69*	−0.67*
TA 2542	Barak, Afghanistan		16		21	−0.51*	−0.52*	1.92*	−1.31*
TA 2547	Jurm, Afghanistan				20	−0.66*	−0.32*	−0.06	−2.19*
TA 2552	37 Km E. of Barak, Af.			31	4	−0.65*	0.44	0.52*	−0.06
TA 2567+ TA 2570	Yerevan, Armenia	3		51	72	−0.54*	−0.43*	0.53*	0.33*

[a] Mean difference between single-environment means of all families and means of their recurrent parents, expressed in single-environment lsd units

(Table 2). In all experiments, some families derived from accessions TA 2450, TA 2460, and TA 2541 segregated for resistance to leaf rust (caused by *Puccinia recondita* f. sp. *tritici* Rob. ex Desm.). TA 2450 and TA 2460 carry genes designated *Lr42* and *Lr41*, respectively (Cox et al. 1994a), which are effective in the seedling stage. Families derived from TA 2541 that segregated for resistance were detectable only at the adult plant stage in the field.

Data for crosses involving the accessions TA 2567 and TA 2570 were combined. These two accessions were collected in Yerevan, Armenia; they had identical genotypes at 25 molecular-marker loci (Lubbers et al. 1991); they had identical gliadin electrophoregrams (unpublished); and progeny of both accessions segregated for a high level of resistance to spindle-streak mosaic virus in nurseries at other locations (Cox et al. 1994c).

Analyses of variance

A total of 641 BC_2F_1-derived families (including 138 families for which the chromosome numbers of their parent plants were not known) was evaluated in field experiments. In the analyses of variance (data not shown), mean squares for variation among genotypes were significant more often than were interaction mean squares. Mean squares for "crosses", "BC_1 families", and "BC_2 within BC_1" were significant for 10, 11, and 12 of the 16 possible trait-recurrent parent combinations, respectively. In contrast, the "crosses × experiments" and "(BC_2 within BC_1) × experiment" were significant for only four each. Alternative analyses of variance (data not shown) using either (1) the chromosome number of the BC_2F_1 parent plant as a class variable or (2) deviations from the euploid number 42 as a linear variable showed no effect of the chromosome numbers of BC_2F_1 plants on any trait in BC_2F_1-derived families.

Mean scores

Genes from *T. tauschii* had a consistently negative effect on grain yield scores averaged over recurrent parents (Table 2). Mean scores over the four environments ranged from − 0.09 for TA 2460 to − 0.90 for TA 2507, and all scores were significantly less than zero (i.e., signficantly lower than that of the recurrent parent). Mean kernel weight scores were positive for progeny of five accessions and negative for six. Leaf-rust resistance within some segregating families derived from TA 2450 and TA 2460 undoubtedly helped increase kernel weight by delaying senescence of the flag leaf.

Mean scores for protein concentration were either positive or not different from zero, depending on the parent (Table 2). The positive mean protein scores were generally of a magnitude similar to that of the negative grain yield scores, except in progeny of TA 2460 (which segregated for *Lr41*) and TA 2542. Progeny of TA 2542 had protein scores that were disproportionately large compared with their smaller, negative yield scores. Mean hardness scores were also variable, with TA 2450, TA 2542, and TA 2547 having very large negative effects.

Trait means and lsds across the four environments (Table 3) provide an indication of productivity and quality levels associated with the scores reported in Tables 2, 4, and 5; however, statistical comparisons among the means of different recurrent parents or the progeny of different parents in Table 3 are not valid. All trait means and lsds were within a range typical of yield levels in Kansas.

Distribution of scores

Distributions of grain-yield scores for individual BC_2F_1-derived families were negatively skewed for most accessions (Table 4). Seventy-six percent of families had mean scores between − 1.0 and 1.0, and 23% had mean scores less than − 1.0. Only eight families, all derived from TA 2460 and all segregating for *Lr41*, had mean scores greater than 1.0. Kernel-weight scores were distributed more symmetrically. Five accessions produced progeny with mean scores exceeding 2.0, which translate into kernel weights approximately 3 to 4 mg greater than that of the respective recurrent parent.

Protein-score distributions (Table 4) were skewed positively, in almost a mirror-image of grain-yield scores. A total of 43 families derived from eight accessions had scores of 2.0 or greater, generally exceeding their recurrent parents' protein concentration by one

Table 3 Mean grain yield, kernel weight, protein concentration, and hardness of four recurrent parents, and 641 BC_2F_1-derived families from crosses between four wheat cultivars and accessions of *T. tauschii*

Recurrent parent	# of lines	Grain yield ($g\ m^2$)	Kernel weight (mg)	Protein concentration (%)	Hardness (NIR value)
Karl		361	30.0	15.5	56.1
Karl/*T. tauschii*	43	330	28.6	15.5	54.9
TAM 107		322	29.7	13.7	70.6
TAM 107/*T. tauschii*	60	320	30.1	14.2	67.5
TAM 200		325	21.6	13.9	50.1
TAM 200/*T. tauschii*	207	292	21.7	14.2	53.3
Century		308	22.5	13.8	50.6
Century/*T. tauschii*	331	279	22.5	14.1	47.5

Table 4 Distributions of mean scores for grain yield, kernel weight, and protein concentration among BC_2F_1-derived familes from *T. tauschii* parent

Trait	*Triticum tauschii* accession	Number of progeny with mean score[a]				
		Less than −1.99	−1.99 to −1.00	−0.99 to 0.99	1.00 to 1.99	Greater than 1.99
Grain yield	TA 2448		6	31		
	TA 2450		10	30		
	TA 2460	1	6	93	8	
	TA 2504		2	31		
	TA 2507	5	33	51		
	TA 2524		4	14		
	TA 2541		16	35		
	TA 2542	1	5	35		
	TA 2547	1	7	12		
	TA 2552		6	29		
	TA 2467+ TA 2570	1	23	135		
Kernel weight	TA 2448		4	26	7	
	TA 2450		2	29	7	2
	TA 2460		2	58	33	15
	TA 2504		3	29	0	1
	TA 2507	1	10	75	3	
	TA 2524			13	5	
	TA 2541		10	29	5	2
	TA 2542	2	8	17		
	TA 2547		1	19		
	TA 2552		2	24	5	4
	TA 2567+ TA 2570	3	29	123	4	
Protein concentration	TA 2448		1	31	5	
	TA 2450			21	17	1
	TA 2460	1	1	71	26	9
	TA 2504		1	25	3	1
	TA 2507		1	61	18	9
	TA 2524			1	17	
	TA 2541		1	32	11	7
	TA 2542		1	19	7	10
	TA 2547		2	16	2	
	TA 2552		1	25	8	1
	TA 2567+ TA 2570		7	106	41	5

[a] Mean difference between single-environment family means and means of their respective recurrent parents, expressed in single-environment lsd units

percentage point or more. Variability for hardness was much greater than that for other traits (Table 5). Distributions for TA 2450, TA 2460, and TA 2547 were bimodal, with secondary peaks at the soft end of the scale. Fully 44% of families derived from TA 2450 and 40% of those from TA 2547 had hardness scores lower than −3.0.

Discussion

Evaluation of these interspecific BC_2-derived populations illustrates one method by which the effects of genes from *T. tauschii* can be evaluated in the field. This method has advantages and disadvantages relative to the alternative, which consists of producing amphiploids between *T. tauschii* accessions and various tetraploid wheats. Synthetic hexaploids, as these amphiploids are commonly known, have the same genomic content as common wheat, are true-breeding, and can be evaluated for traits that cannot be evaluated easily using diploid accessions (Kerber and Tipples 1969; May and Lagudah 1992). However, no tetraploid stocks are available that are well adapted to the southern Great Plains of the United States, and field-testing of their synthetic hexaploid progeny here would be difficult.

Direct *T. aestivum* × *T. tauschii* backcrosses, although not true-breeding, do permit evaluation of the effects of *T. tauschii* genes in a well-adapted genetic background. With two backcrosses, 87.5% of the D genome, and over 96% of the total hexaploid genotype of the recurrent parent, are expected to be restored on average. In this study, chromosome numbers were not completely stabilized in the BC_2F_1, but aneuploid genotypes were gradually eliminated through attrition. Synthetic hexaploids, although originally euploid, can also exhibit chromosomal instability (Gill et al. 1987).

Gill and Raupp (1987) recommended using BC_1F_1 plants as males to select for 21-chromosome male gametes, which presumably would have a competitive advantage. However, over one-third of the BC_2F_1 plants we developed in this way were aneuploid. Large

Table 5 Distribution of mean scores for hardness among BC_2F_1-derived lines from *T. tauschii* parents

Triticum tauschii accession	Number of lines with mean score[a]								
	Less than −4.99	−4.99 to −4.00	−3.99 to −3.00	−2.99 to −2.00	−1.99 to 1.00	−0.99 to 0.99	1.00 to 1.99	2.00 to 2.99	Greater than 2.99
TA 2448			2	0	2	27	0	2	1
TA 2450	8	6	4	3	1	17	2		
TA 2460	11	5	3	3	9	51	21	5	
TA 2504					1	19	13		
TA 2507		1	2	4	12	48	18	4	
TA 2524				2	3	8	5		
TA 2441	2	1	3	2	8	25	10		
TA 2442	1	1	1	5	13	15	1		
TA 2447	5	2	1	1	2	8	1		
TA 2567+ TA 2570		2	1	0	7	15	10		
					12	105	16		

[a] Mean score = mean difference between single-environment family means and the mean of their respective recurrent parent, expressed in single-environments lsd units. Total numbers of families may not be equal for each trait because of missing data

numbers of aneuploid pollen grains may have been produced by BC_1F_1 plants, so that their competitive disadvantage, if present, was circumvented. However, the lack of visible or measurable effects of chromosome numbers of BC_2F_1 plants on the fertility or performance of their progeny suggests that seed increase via selfing eliminated most aneuploid individuals.

We failed to obtain viable, fertile families from many of the parental combinations, and a much larger number of families were derived from crosses with Century than from crosses with other hexaploid parents. In addition to mere chance, this probably reflects interactions among genes from specific parents; however, a controlled experiment would be required to demonstrate this.

Considerable genetic variability for productivity and quality traits occurred in the populations we studied, both among and within crosses derived from different *T. tauschii* accessions. Variation for yield, kernel weight, and protein concentration extended beyond the boundaries delineated by physiological relationships among these three traits. By far the greatest variability was for kernel hardness. The strongly bimodal nature of hardness distributions in some crosses suggests that some *T. tauschii* accessions carry major gene(s) conditioning soft endosperm. The one gene known to confer soft endosperm in hexaploid wheat, *Ha*, is located on the short arm of chromosome 5D (Law et al. 1978) and presumably is derived originally from the *T. tauschii* parent of common wheat.

Except in families segregating for *Lr41*, *T. tauschii* genes had no large effects on grain yield analagous to those reported, for example, in introgressed populations of oat (Lawrence and Frey 1976) and pearl millet (Bramel-Cox et al. 1986). However, the families we evaluated were derived from BC_2F_1 plants, and any segregation within families was not detectable. Many of these BC_2-derived families did give yields similar to those of their elite recurrent parents; therefore, deleterious genes were at a low frequency.

Evaluation of the populations described herein has led to the selection and release of five germplasms. Two of them – KS90WGRC10 (TAM 107*3/TA 2460; Cox et al. 1992b) and KS91WGRC11 (Century*3/TA 2450; Cox et al. 1994b) – carry *Lr41* and *Lr42*, respectively, which are detected easily by screening seedlings of the *T. tauschii* accessions and their progeny. But three other germplasms have disease resistances that were detectable only through screening of backcross progeny in the field: KS91WGRC12 (Century*3/TA 2541; resistant to leaf rust as adult plants; unpublished) and KS92WGRC21 and KS92WGRC22 [TAM 200*3/TA 2570 and Century*3/TA 2567, respectively; both carrying genes from *T. tauschii* for resistance to soilborne mosaic virus, spindle streak mosaic virus, and powdery mildew (caused by *Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici*); Cox et al. 1994c].

In summary, random BC_2-derived families can be used to evaluate effects of *T. tauschii* genes on quantitative and qualitative traits in the field. This methodology, although laborious, can provide useful information which is not obtainable by the screening of *T. tauschii* accessions themselves.

Acknowledgements The authors are grateful to Leann Harrell, Elburn Parker, and Larry Patton for essential technical assistance and to Richard Fels for making the chromosome counts.

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