

# WHEAT GENETICS RESOURCE CENTER: THE FIRST 25 YEARS

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The Wheat Genetics Resource Center, a pioneering center without walls, has served the wheat genetics community for 25 years. The Wheat Genetics Resource Center (WGRC) assembled a working collection of over 11,000 wild wheat relatives and cytogenetic stocks for conservation and use in wheat genome analysis and crop improvement. Over 30,000 samples from the WGRC collection of wheat wild relatives, cytogenetic stocks, and improved germplasm have been distributed to scientists in 45 countries and 39 states in the United States. The WGRC and collaborators have developed standard karyotypes of 26 species of the *Triticum/Aegilops* complex, rye, and some

perennial genera of the Triticeae. They have developed over 800 cytogenetic stocks including addition, substitution, and deletion lines. The anchor karyotypes, technical innovations, and associated cytogenetic stocks are a part of the basic tool kit of every wheat geneticist. They have cytogenetically characterized over six-dozen wheat–alien introgression lines. The WGRC has released 47 improved germplasm lines incorporating over 50 novel genes against pathogens and pests; some genes have been deployed in agriculture. The WGRC hosted over three-dozen scientists especially from developing countries for advanced training. The WGRC was engaged in international agriculture through several collaborating projects. Particularly noteworthy was the collaborative project with Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) on the production of synthetic wheats. It is estimated that “by the year 2003–2004, 26% of all new advanced lines made available through CIMMYT screening nurseries to cooperators for either irrigated or semi-arid conditions were synthetic derivatives.” The WGRC is applying genomics tools to further expedite the use of exotic germplasm in wheat crop improvement.

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## I. INTRODUCTION

“A cytogeneticist is one who curates the genome of an organism, identifies and maintains gene inventories, and delineates a genetic road map. A genetic engineer who constructs exotic stocks for basic and applied research applications. Above all, he is the one person you always get in touch with when you need information and a genetic stock at a moment’s notice!”

Bikram Gill, circa 1982

This is an old-fashioned definition of a cytogeneticist in the tradition of Barbara McClintock, Charley Burnham, and Marcus Rhoades of maize; Ernie Sears of wheat; and Charley Rick of tomato, all tracing their pedigrees to E. M. East at the Bussey Institution of Harvard University. The senior author had the privilege of working as a graduate student with Charley Rick, as a postdoctoral fellow with Ernie Sears, and with Charley Burnham on a collaborative project on developing a chromosomal translocation tester set in tomato (Gill *et al.*, 1980). Rick made frequent trips to South America to collect wild tomato species, ran a gene bank, conducted interspecific hybridization and breeding research, constructed cytogenetic maps, and published the *Tomato Genetic Coop.* Ernie Sears (1954) developed wheat aneuploid stocks to genetically dissect and engineer the polyploid genome of wheat. The senior author also had the fortune of working on wild wheats at the University of California, Riverside, with Giles Waines and Lennert Johnson.

In 1979, on his way to a cytogenetics position at Kansas State University, which is located in one of the largest wheat-growing regions in the world, he stopped to see Ernie Sears in Missouri. His advice, “Kansas has a great breeding program, but they need basic genetics research to complement it.” Of the current research team, coauthor Rollie Sears joined as a wheat breeder in 1980 to be replaced by Allan Fritz in 2000; John Raupp and Duane Wilson joined as research assistants in 1980 and 1984, respectively; Stan Cox as a USDA Research Geneticist in 1984 (to be replaced by Gina Brown-Guedira in 1997); and Bernd Friebe as a research cytogeneticist in 1989.

A two-pronged wheat-research program was initiated. Molecular cytogenetic studies were conducted on “Chinese Spring,” which was used by Ernie Sears to develop aneuploid stocks and accepted as the international model for wheat genetics and polyploidy research. Following the groundbreaking work on the cytogenetic identification of individual chromosomes of “Chinese Spring” wheat (Gill and Kimber, 1974b), a standard karyotype and nomenclature system for wheat chromosomes was developed with the hope that it would “... vastly expand our ability to cytogenetically analyze and manipulate the genome of wheat with unprecedented precision and efficiency” (Gill *et al.*, 1991a). Around the same time, we initiated a collaborative research program with Dr T. R. Endo, then at Nara University, Japan, funded by the Japanese Society for the promotion of Science and the National Science Foundation (NSF) and United States Department of Agriculture National Research Initiative (USDA–NRI) in the United States to develop more than 400 true-breeding deletion stocks in wheat (Endo and Gill, 1996). These deletion stocks were used to develop cytogenetically based, physical maps of molecular markers for the 21 chromosomes of wheat and revealed the nonrandom distribution of genes and recombination along the chromosome length (Delaney *et al.*, 1995b,c; Gill and Gill, 1994; Gill *et al.*, 1993, 1996a,b; Hohmann *et al.*, 1994; Kota *et al.*, 1993; Michelson-Young *et al.*, 1995; Werner *et al.*, 1992a). Sixteen thousand expressed sequence tag (EST) loci were mapped in deletion bins [Qi *et al.*, 2003, 2004; see also *Genetics* (2004), Special Section: Wheat, **168**, 583–712] and compared to the sequenced genome of rice to construct *in silico* wheat maps (<http://www.tigr.org/tdb/e2k1/tael/>) that are driving gene discovery in wheat. The international wheat genetics community is now embarked on a project to sequence the gene space of wheat (Gill *et al.*, 2004). Such a project would have a huge impact on wheat-crop improvement and investigations of polyploidy and its role in genome evolution, speciation, and plant productivity, as most crop plants that feed us are polyploids.

In the second research thrust, we assembled a working collection of wild wheat species for conservation, evaluation, and utilization in germplasm enhancement and broadening the gene pool of wheat. In the beginning, we chose the hard red winter wheat cultivar “Wichita,” released in the 1940s as the recipient wheat parent. This cultivar was a research model in

which Rosalind Morris (University of Nebraska, Lincoln) had developed a complete set of monosomic stocks. We screened a small collection of *Ae. tauschii*, the D-genome donor of bread wheat, and discovered an abundance of resistance to the most virulent races of Hessian fly (Hatchett and Gill, 1981), a highly destructive pest of wheat. Additional screening against leaf rust and other pathogens revealed many single accessions harboring multiple resistance factors against a number of pathogens and pests (Gill *et al.*, 1986b). We used embryo culture to obtain direct hybrids between “Wichita” and *Ae. tauschii*, and recovered highly desirable and homozygous resistant lines in BC<sub>2</sub>F<sub>2</sub> families (Gill and Raupp, 1987), and the first germplasm release was made in 1985 (Gill *et al.*, 1986a). However, it was soon clear that wheat breeders had little interest in “Wichita”-based germplasm. It was not until Stan Cox joined the team and began germplasm-enhancement research with advanced breeding materials in close collaboration with Rollie Sears and the Great Plains wheat breeders that the chasm between basic genetics and breeding work was bridged, and the worldwide impact of the new genetics on wheat varietal improvement programs was achieved as documented here (Cox, 1991, 1998).

In 1984, the Wheat Genetics Resource Center (WGRC) was formally recognized as a center of excellence at Kansas State University with a more secure funding base. The WGRC has been a pioneering center without walls, conducting interdisciplinary and interdepartmental, collaborative, team-oriented research involving K-State and USDA–ARS scientists, locally, and others, nationally and internationally. The hallmarks of the WGRC mission have been full integration of basic and applied research and service to the wheat community as a “one-stop shop” for the free sharing of genetic materials, technical know how, and knowledge through research publications, distribution of germplasm, and training of graduate students, post-doctoral fellows and visiting scientists, especially from developing countries through workshops, hands-on research in WGRC laboratories, and long-term collaborative research projects (for details, see [www.ksu.edu/wgrc](http://www.ksu.edu/wgrc)). The aim of this review is to briefly highlight WGRC research in wheat genetic resources, cytogenetics, genomic breeding, chromosome engineering, and germplasm development, its impact, and the future outlook.

## II. WHEAT GENETIC RESOURCES

### A. TAXONOMIC CONSIDERATIONS

Wheat belongs to the grass tribe Triticeae, which contains approximately 350 species and 13–26 genera. More than 75% of the species are perennial and many are used as forage crops. Annual Triticeae species include wheat,

barley, and rye; all agriculturally important grasses either for human or animal consumption.

Twenty-six classification schemes for wheat and wheat relatives have been proposed since 1917. These early classification systems were based on morphological characteristics. Historically, the genus *Triticum* was treated separately from the genus *Aegilops* although several authors have grouped the two together in one large genus based on cytogenetic evidence. [Kihara \(1954\)](#) was the first to use a genomic treatment and his proposed genome symbols are still in use. Eleven classification systems are accepted, three address only the genus *Triticum* and two only the genus *Aegilops*. Only [Kimber and Sears \(1987\)](#) and [Kimber and Feldman \(1987\)](#) following [Bowden \(1959\)](#) treat all species under the genus *Triticum*. The remaining classification systems support the widely accepted idea of two separate genera, *Triticum* and *Aegilops*. In this publication, we will use the most recent classification proposed by [van Slageren \(1994\)](#). Descriptions of all the historical and current classification systems can be seen at <http://www.ksu.edu/wgrc/Taxonomy/taxintro.html/>.

## B. COLLECTION AND MAINTENANCE

The world collection of *Triticum* and *Aegilops* consists of approximately 17,500 accessions distributed in a dozen or so gene banks worldwide (<http://www.singer.cgiar.org/>). Data previously available only in the literature, through gene bank records or by personal communication can now be accessed via the Internet. The working collection maintained by the WGRC consists of 3119 accessions comprising annual *Triticum* and *Aegilops* species and are listed in [Table I](#). This working collection is a composite, as distinguished from core collections established by pioneering plant explorers. The entries in the germplasm collection are from expeditions by the University of Kyoto (Japan) in 1955, 1959, 1966, and 1970; Johnson and coworkers (University of Riverside, CA, USA) 1966, 1972, and 1973; E. Nevo and colleagues (University of Haifa, Israel); and R. J. Metzger (University of Oregon, Corvallis, USA), J. Hoffman (USDA-ARS), G. Kimber (University of Missouri, Columbia, USA), S. Jena (University of Saskatchewan, Canada), and A. Sencor, M. Kanbertay, and C. Tüten (Aegean Agricultural Research Institute, Menemen, Izmir, Turkey), 1979, 1984, and 1985. Additional accessions from major gene banks of the world include ICARDA (Aleppo, Syria), the USDA Small Grains Collection (Aberdeen, ID, USA), the N.I. Vavilov Institute (St. Petersburg, Russia), and the Institute for Genetics and Crop Plant Research (Gatersleben, Germany).

**Table I**  
**Composition of the WGRC Gene Bank, 2005 (Genome Symbols in Parentheses)**

Species	Number of accessions
Diploid ( $2n = 14$ ) species	
<i>T. monococcum</i> L. (A <sup>m</sup> )	600
<i>T. urartu</i> Tumanian ex Gandilyan (A <sup>u</sup> )	173
<i>Ae. bicornis</i> (Forssk.) Jaub. & Spach (S <sup>b</sup> )	12
<i>Ae. caudata</i> L. (C)	18
<i>Ae. comosa</i> Sm. In Sibth. & Sm. (M)	20
<i>Ae. longissima</i> Schweinf. & Muschl. (S <sup>l</sup> )	9
<i>Ae. mutica</i> Boiss. (T)	10
<i>Ae. searsii</i> Feldman & Kislev ex Hammer (S <sup>s</sup> )	18
<i>Ae. sharonensis</i> Eig (S <sup>sp</sup> )	9
<i>Ae. speltooides</i> Tausch (S)	92
<i>Ae. tauschii</i> Coss. (D)	528
<i>Ae. umbellulata</i> Zhuk. (U)	46
<i>Ae. uniaristata</i> Vis. (N)	20
<i>H. villosa</i> (L.) Schur (V)	94
Polyloid tetraploid ( $2n = 28$ ) and hexaploid ( $2n = 42$ ) <i>Triticum</i> and <i>Aegilops</i> species.	
<i>T. timopheevii</i> Zhuk. (A <sup>1</sup> G)	295
<i>T. turgidum</i> L. (AB)	488
<i>T. aestivum</i> L. (ABD)	301
<i>Ae. biuncialis</i> Vis. (U <sup>bi</sup> M <sup>bi</sup> )	36
<i>Ae. columnaris</i> Zhuk. (U <sup>co</sup> X <sup>co</sup> )	11
<i>Ae. crassa</i> Boiss (4x (X <sup>cr</sup> D <sup>cr1</sup> ), 6x (X <sup>cr</sup> D <sup>cr1</sup> D <sup>cr2</sup> ))	27
<i>Ae. cylindrica</i> Host (C <sup>c</sup> D <sup>c</sup> )	42
<i>Ae. geniculata</i> Roth (U <sup>g</sup> M <sup>g</sup> )	139
<i>Ae. juvenalis</i> (Thell.) Host (X <sup>j</sup> D <sup>j</sup> U <sup>j</sup> )	9
<i>Ae. kotschy</i> Boiss. (U <sup>k</sup> S <sup>k</sup> )	18
<i>Ae. neglecta</i> Req. ex Bertol (U <sup>n</sup> X <sup>n</sup> and U <sup>n</sup> X <sup>n</sup> N <sup>n</sup> )	66
<i>Ae. peregrina</i> (Hack. in J. Fraser) Marie & Weiller (U <sup>p</sup> S <sup>p</sup> )	29
<i>Ae. triuncialis</i> L. (U <sup>t</sup> C <sup>t</sup> )	183
<i>Ae. vavilovii</i> (X <sup>va</sup> S <sup>va</sup> S <sup>va</sup> )	8
<i>Ae. ventricosa</i> Tausch (N <sup>v</sup> D <sup>v</sup> )	16
<i>T. zhukovskiy</i> Menabde & Ericz (A <sup>1</sup> AG)	1
Genetic stocks	
<i>Ae. tauschii</i> synthetic and parental lines	311
Alien addition	371
Alien substitution	251
Alloplasmic	8
Amphiploid/partial amphiploid	121
Aneuploid	299
Deletion/duplication/deficiency	421
Germplasm	75

(continued)

Table I (continued)

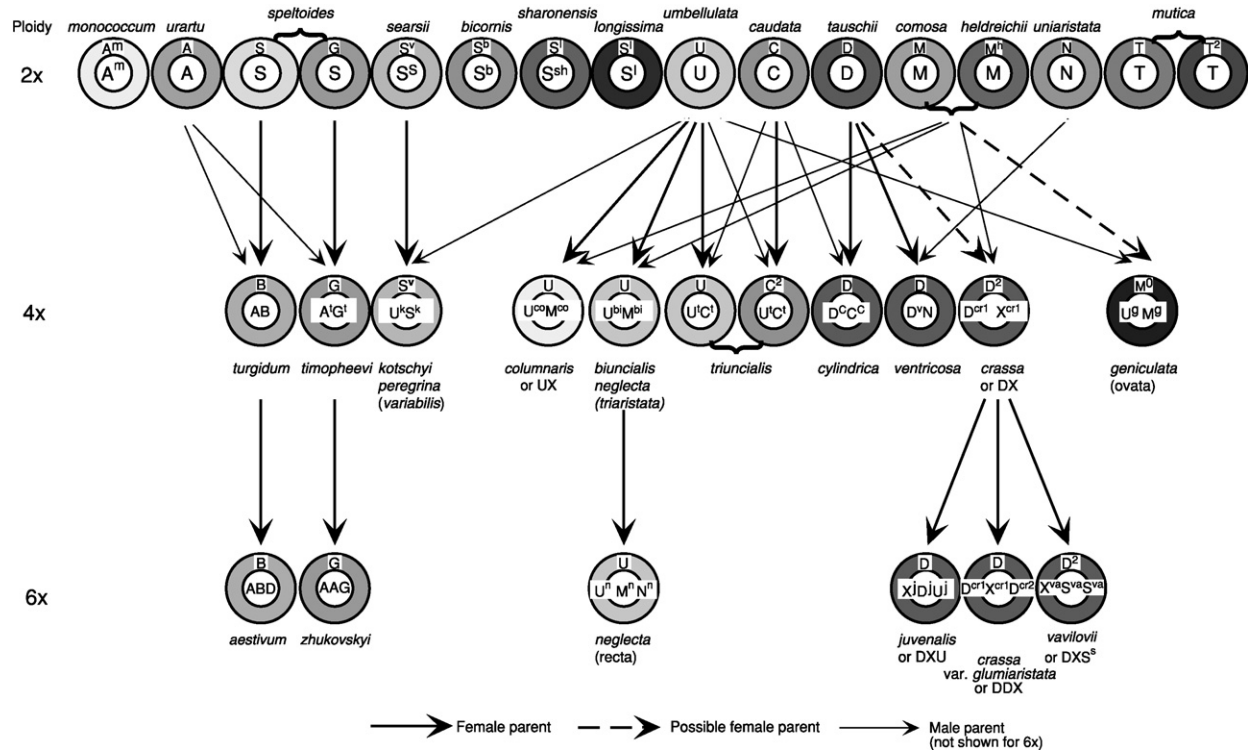
Species	Number of accessions
Mutant/Marker	401
Mapping and RIL populations (44 populations)	5,551
Substitution	149
Translocation	143
Transgenic	33
TOTAL	11,497

For evolutionary relationships between the *Triticum* and *Aegilops* species, see Fig. 1.

Samples in the working collection are maintained at 40 °F (4 °C) and 25% RH. Seed is stored in moisture-proof, heat-sealable pouches from the Kapac Corporation (Minneapolis, MN). These pouches are trilaminar (50 GA PET/0.00035 foil/3 mil LLDPE) and form a nearly impervious barrier against humidity. In addition, a 5-g packet of silica gel is included in the pouch as a desiccant. Whenever seed is removed from a pouch, the silica gel packet is checked and replaced if necessary. When the number of seed in a line drops below 100, five plants are grown to ensure an adequate supply. At that time, additional pest resistance screening may be done and/or the lines checked for proper species identification.

Long-term storage of seed in a freezer is maintained at -20°C. Seed samples are stored in the same moisture-proof, heat-sealable pouches as the samples in the working collection. Under these conditions, seed viability should approach 50 years. This permanent collection was started in 1991 and is housed off-site at the Kansas Crop Improvement Association in Manhattan, KS.

Detecting duplicate accessions and identifying geographical areas where the germplasm collections are lacking is a foremost priority. We have completed a search of available databases via the Internet and using a world collection database established by ICARDA, Aleppo, Syria. Database development and coordination among gene banks will reduce duplication of research and promote the utilization of germplasm resources (Raupp *et al.*, 1997). When we detect a potential duplication, storage protein profiles are used for genetic confirmation. We are making a concerted effort to obtain complete and accurate passport data on the accessions with the help of other researchers and gene bank coordinators. Database searches also helped with missing collection data. The policy of the WGRC now is to provide this valuable passport data when seed is requested.



**Figure 1** The *Triticum* and *Aegilops* genera contain 13 diploid, 14 tetraploid, and 6 hexaploid species and are a classic example of speciation by allopolyploidy. The polyploids constitute the A-genome cluster, which includes wild and cultivated wheat, the U-genome cluster, and the D-genome cluster. The knowledge of evolutionary relationships is important for their use in wheat crop improvement. This figure is modified with permission from the author [Tsunewaki, K. (1996). Plasmon analysis as a counterpart of genome analysis. In "Methods of Genome Analysis in Plants" (P. P. Jauhar, Ed.). Reprinted with permission of CRC Press, Boca Raton, FL].



Several researchers (Chapman, 1985; Croston and Williams, 1981; Holubec *et al.*, 1992) have identified priority areas for wheat germplasm collection. Researchers near the priority areas hopefully can, or have, filled these gaps, permitting germplasm exchange with cooperating gene banks. We have completed such surveys for *Ae. speltooides*, *Ae. tauschii*, and *Haynaldia villosa* (L.) Schur and hope to complete the same for other species in the WGRC gene bank.

The WGRC has established contacts with curators in Japan, Germany, the Russian Federation, Syria, and elsewhere to promote joint studies and sharing of germplasm. Under our visiting scientist program, we invite scientists from these and other countries for joint research. Our aim is to establish the world's most comprehensive "working collection" of wild wheats and promote basic and applied research on this collection, and on conservation and utilization of the world's germplasm of wheat.

### C. EVALUATION AND GENETIC DIVERSITY ANALYSIS OF THE WGRC COLLECTION

The species collection, hybrid derivatives, amphiploids, and addition and translocation lines are intensely evaluated for useful genetic variation by national and international research collaborators. A large number of accessions from the germplasm collection have been evaluated for host plant resistance to leaf rust (*Puccinia triticina* Eriks.), stem rust (*Puccinia graminis* Pers. f. sp. *tritici* Eriks. & Henn.), yellow rust (*Puccinia striiformis* West.), Karnal bunt (*Tilletia indica* Mit.) [= *Neovossia indica* (Mit.) Mund.], leaf blotch [*Stagonospora nodorum* (Berk.) Castellani & E. G. Germano] [= *Septoria nodorum* (Berk.) Berk. in Berk. & Broome], scab or head blight (*Fusarium graminearum* Schwabe), tan spot [*Dreschlera tritici-repentis* (Died.) Shoem.], powdery mildew [*Blumeria graminis* (DC.) E. O. Speer] (= *Erysiphe graminis* DC. ex Merat), wheat streak mosaic virus, barley yellow dwarf virus, Hessian fly (*Mayetiola destructor* Say), greenbug (*Schizaphis gramineum* Rondani), Russian wheat aphid (*Diuraphis noxia* Mordvilko), and wheat curl mite (*Eriophyes tulipae* Kiefer). The screening of wild wheat germplasm is ongoing and continuously documented (Brown-Guedira *et al.* 1996b, 2002; Cox *et al.*, 1992a; Deol *et al.*, 1995; Gill *et al.* 1983, 1985, 1986b; Lubbers *et al.*, 1991; Malik *et al.*, 2003b; Raupp *et al.* 1988, 1995; Smith *et al.*, 2004; Stoddard *et al.*, 1987).

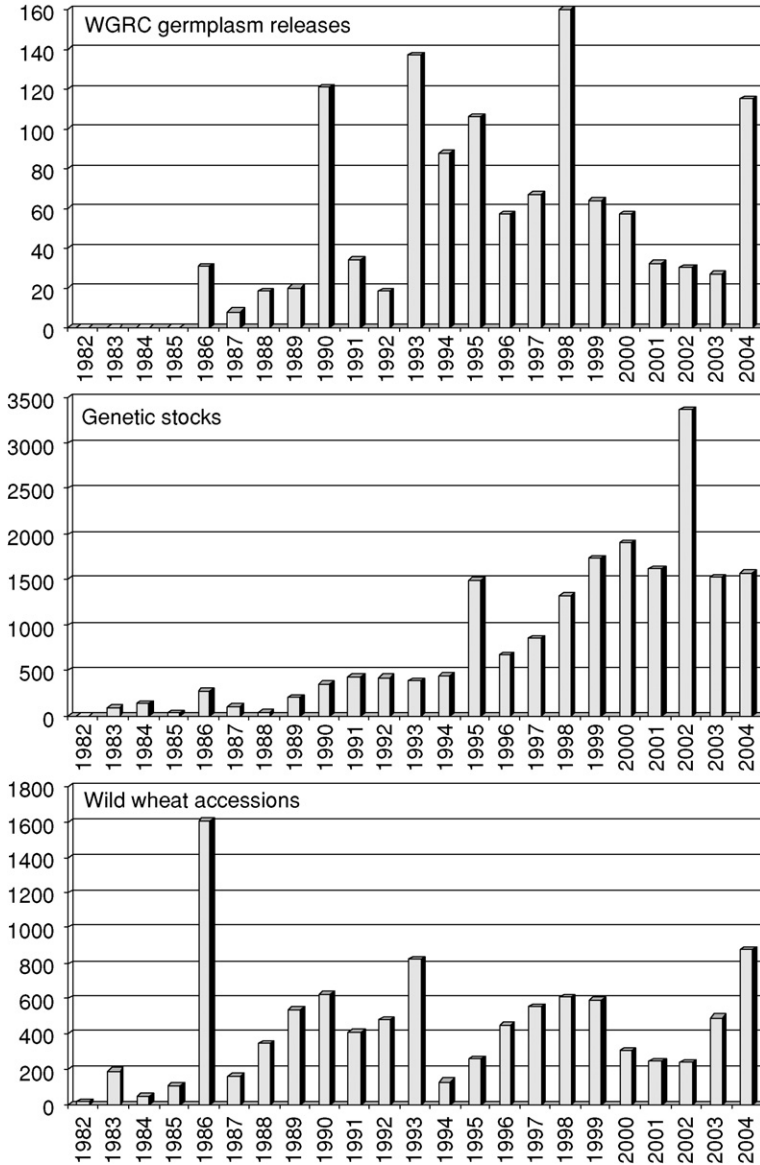
### D. DISTRIBUTION OF THE COLLECTION

Even though there were already extensive collections of wild relatives in the United States and elsewhere by the 1950s, there were only a few sporadic instances of their use in breeding programs. From its very inception, the

WGRC has actively sought to promote the use of wild wheat relatives (the diploid and tetraploid donor species) in broadening the genetic base of cultivated wheat by free sharing of germplasm at no charge and free of Intellectual Property Rights (IPR) (Fig. 2). The WGRC even played a more critical role in increasing use of wild species germplasm by documenting tremendous genetic diversity in the collection and by demonstrating its rapid transfer to wheat by using routine embryo rescue and cytogenetic methods. This naturally created a lot of excitement and as can be seen in Fig. 2, by 1986 there was a large increase in the number of requests for wild species germplasm. That year, the senior author was on a sabbatic leave in Australia, and, as a result of these contacts, the Commonwealth Scientific and Research Organization (CSIRO) began a large project on the use of *Ae. tauschii* in wheat improvement. We also worked with Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) to focus on wheat progenitor species in their wide-crossing program rather than perennial grasses as had been the case until then. Another category of germplasm, cytogenetic stocks, also have seen steady increase in demand, especially the deletion stocks spurred by their use in genome-mapping projects. By 2004, we had distributed 30,222 samples (1461 requests) of seed to scientists in 45 countries and 39 states in the United States. Of these, 18,952 were for cytogenetic stocks, 10,080 for wild wheats, and 1461 for improved germplasm. The number of requests for improved germplasm is an underestimate as it does not include data from the USDA who also distributed samples of seed. Whereas the WGRC has distributed germplasm free of cost until now, with tight budgets and increased demands for germplasm, cost recovery may be an option that needs to be explored in the near future.

### III. ADVANCES IN MOLECULAR CYTOGENETICS OF WHEAT AND TRITICEAE SPECIES

“Molecular cytogenetics may be defined as instant cytological, genetic, phylogenetic, and molecular mapping of chromosomes *in situ*” (Gill, 1995). Molecular cytogenetic identification of individual chromosomes is essential for analyzing the biological aspects of chromosome structure, function, evolution, and engineering the genome for crop improvement. Wheat has served as a model system for plant molecular cytogenetics research beginning in the 1970s (see reviews by Faris *et al.*, 2002; Friebe and Gill, 1995; Gill, 1993, 1995; Gill and Friebe, 1998, 2002; Gill and Sears, 1988; Jiang and Gill, 1994b). Each wheat chromosome is divisible into biologically meaningful heterochromatic and euchromatic regions (Gill *et al.*, 1991a). Many DNA sequences when used as probes in conjunction with *in situ*



**Figure 2** Requests for wheat genetic materials from 1982 through 2004.

hybridization provide further opportunities for molecular karyotyping (Rayburn and Gill, 1985, 1987) and genome painting (Lapitan *et al.*, 1986; Zhang *et al.*, 2004b). Molecular descriptors have been developed for

cytogenetic landmarks such as heterochromatin (Badaeva *et al.*, 1996a; Rayburn and Gill, 1986), nucleolus organizer regions (Badaeva *et al.*, 1996b; Jiang and Gill, 1994a; Mukai *et al.*, 1990, 1991), centromeres (Jiang *et al.*, 1996; Zhang *et al.*, 2001, 2004a), subtelomeric regions (Li *et al.*, 2004; Zhang *et al.*, 2004a), and telomeres (Friebe *et al.*, 2001; Werner *et al.*, 1992b).

Initially, telocentric chromosomes were C-banded to cytogenetically identify the 21 chromosomes belonging to the A, B, and D genomes of hexaploid wheat “Chinese Spring” (Gill and Kimber, 1974b; Gill *et al.*, 1991a). The chromosomes of AB-genome tetraploids, and the A- and D-genome diploids were constructed based on comparative banding analysis with the ABD genome of wheat (Friebe and Gill, 1995). The A<sup>1</sup>G-genome chromosomes of *T. timopheevii* subsp. *timopheevii* were cytogenetically identified based on their pairing affinities with wheat telocentrics and the C-banding analysis of paired chromosomes (Badaeva *et al.*, 1994; Chen and Gill, 1983; Gill and Chen, 1987). The chromosomes of related Triticeae species with different genomes were cytogenetically identified by C-banding analysis of alien chromosome additions to “Chinese Spring” wheat as first demonstrated in rye (Gill and Kimber, 1974b; Mukai *et al.*, 1992).

The knowledge and biological resources of the model wheat genome and other characterized basic Triticeae genomes can in turn be used to determine the cytogenetic and phylogenetic affinity of individual chromosomes of the other alien taxa. This was demonstrated in the analysis of the genome structure of *Ae. cylindrica* (Linc *et al.*, 1999). The C- and D-genome chromosomes of *Ae. cylindrica* were identified by comparative C-banding and fluorescent *in situ* hybridization (FISH) with D-genome specific DNA sequences. The karyotypes of other D-genome and U-genome cluster diploid and polyploid species have been similarly analyzed (Badaeva *et al.*, 2002, 2004). Standard karyotypes have been developed for all the species of *Triticum* and *Aegilops*, and certain species of *Secale*, *Haynaldia*, *Agropyron*, *Elymus*, and *Hordeum* (Table II). The standard karyotypes allow cytogenetical monitoring of the transfer of alien chromosome segments during wide hybridization (Friebe *et al.*, 1996b; Jiang and Gill, 1994a).

## IV. GENOMIC BREEDING AND INTERGENOMIC TRANSFERS BY CHROMOSOME ENGINEERING

### A. THE JOURNEY FROM GENOME SHARING TO GENE DONORS

Between 1918 and 1925, Sakamura (1918) and his student Kihara (1919) at Hokkaido University, Japan, and Sax (1922) at Harvard University reported their classic studies on the genetic architecture of the various

**Table II**  
**Standard Karyotypes and Cytogenetic Identification of Individual Chromosomes, Deletion, Addition, or Substitution Lines of *Triticum*, *Aegilops*, and other Triticeae Species in Wheat Characterized and Maintained by the WGRC**

Species	Ploidy level (2n)	Genome formula	Chromosome addition lines	Telosomic addition lines	Substitution lines	Reference
<i>Ae. bicornis</i>	2x	S <sup>b</sup>				Badaeva <i>et al.</i> , 1996a,b; Friebe and Gill, 1995
<i>Ae. biuncialis</i>	4x	U <sup>bi</sup> M <sup>bi</sup>				Badaeva <i>et al.</i> , 2004
<i>Ae. caudata</i>	2x	C	6		1	Badaeva <i>et al.</i> , 1996a,b; Friebe <i>et al.</i> , 1992c
<i>Ae. columnaris</i>	2x	U <sup>co</sup> X <sup>co</sup>				Badaeva <i>et al.</i> , 2004
<i>Ae. comosa</i>	4x	M	1			Badaeva <i>et al.</i> , 1996a,b; Friebe <i>et al.</i> , 1996a; Nasuda <i>et al.</i> , 1998
<i>Ae. crassa</i>	4x	X <sup>cr</sup> D <sup>cr1</sup>				Badaeva <i>et al.</i> , 1998, 2002
<i>Ae. crassa</i>	6x	X <sup>cr</sup> D <sup>cr1</sup> D <sup>cr2</sup>				Badaeva <i>et al.</i> , 1998, 2002
<i>Ae. cylindrica</i>	4x	C <sup>c</sup> D <sup>c</sup>	1	1		Endo and Gill, 1996, Linc <i>et al.</i> , 1999
<i>Ae. geniculata</i>	4x	U <sup>g</sup> M <sup>g</sup>	14		11	Friebe <i>et al.</i> , 1999a
<i>Ae. juvenalis</i>	6x	X <sup>j</sup> D <sup>j</sup> U <sup>j</sup>				Badaeva <i>et al.</i> , 2002
<i>Ae. kotschyi</i>	4x	U <sup>k</sup> S <sup>k</sup>				Badaeva <i>et al.</i> , 2004
<i>Ae. longissima</i>	2x	S <sup>l</sup>	7 + 7 + 1	14	43	Badaeva <i>et al.</i> , 1996a,b; Friebe <i>et al.</i> , 1993c
<i>Ae. mutica</i>	2x	T	B			Badaeva <i>et al.</i> , 1996a,b; Friebe <i>et al.</i> , 1995b, 1996a
<i>Ae. neglecta</i>	4x	U <sup>n</sup> X <sup>n</sup>				Badaeva <i>et al.</i> , 2004
<i>Ae. neglecta</i>	6x	U <sup>n</sup> X <sup>n</sup> N <sup>n</sup>				Badaeva <i>et al.</i> , 2004
<i>Ae. peregrina</i>	4x	U <sup>p</sup> S <sup>p</sup>	14	26		Friebe <i>et al.</i> , 1996c

(continued)

Table II (continued)

Species	Ploidy level (2n)	Genome formula	Chromosome addition lines	Telosomic addition lines	Substitution lines	Reference
<i>Ae. searsii</i>	2x	S <sup>s</sup>	7	14	50	Badaeva <i>et al.</i> , 1996a,b; Friebe <i>et al.</i> , 1995d
<i>Ae. sharonensis</i>	2x	S <sup>sh</sup>	10 × 1			Badaeva <i>et al.</i> , 1996a,b; Friebe and Gill, 1995; Friebe <i>et al.</i> , unpublished
<i>Ae. speltoides</i>	2x	S	7 + B	7	6	Badaeva <i>et al.</i> , 1996a,b; Friebe and Gill, 1995; Friebe <i>et al.</i> , 2000b, unpublished
<i>Ae. tauschii</i>	2x	D	7 (in durum wheat)	7		Badaeva <i>et al.</i> , 1996a,b, 2002; Dhaliwal <i>et al.</i> , 1990; Friebe <i>et al.</i> , 1992a
<i>Ae. triuncialis</i>	4x	U <sup>1</sup> C <sup>t</sup>				Badaeva <i>et al.</i> , 2004
<i>Ae. umbellulata</i>	2x	U	6	9		Badaeva <i>et al.</i> , 1996a,b, 2004; Friebe <i>et al.</i> , 1995c
<i>Ae. uniaristata</i>	2x	N				Badaeva <i>et al.</i> , 1996a,b; Friebe <i>et al.</i> , 1996a
<i>Ae. vavilovii</i>	6x	X <sup>va</sup> S <sup>va</sup> S <sup>va</sup>				Badaeva <i>et al.</i> , 2002
<i>Ae. ventricosa</i>	4x	N <sup>v</sup> D <sup>v</sup>				Badaeva <i>et al.</i> , 2002
<i>T. aestivum</i> deletion lines	6x	ABD	416 (deletion)			Endo and Gill, 1996; Gill and Kimber, 1974b; Gill <i>et al.</i> , 1991a

<i>T. timopheevii</i> subsp. <i>timopheevii</i>	4x	A <sup>1</sup> G			6	Badaeva <i>et al.</i> , 1995; Brown-Guedira <i>et al.</i> , 1996a Gill and Chen, 1987
<i>T. timopheevii</i> subsp. <i>dicoccoides</i>	4x	AB				
<i>T. monococcum</i> subsp. <i>monococcum</i>	2x	A <sup>m</sup>	6 (trisomics)			Friebe <i>et al.</i> , 1990b
<i>Haynaldia villosa</i>	2x	V	10			Lukaszewski, unpublished; Qi <i>et al.</i> , 1999
<i>Secale cereale</i>	2x	R	7	11		Gill and Kimber, 1974a; Mukai <i>et al.</i> , 1992 Friebe <i>et al.</i> , 2000a
<i>S. cereale</i> deletion lines	2x	R	33 (deletion)			Friebe <i>et al.</i> , 2000a
<i>Agropyron</i> <i>intermedium</i>	6x	E <sub>1</sub> E <sub>2</sub> X	6			Friebe <i>et al.</i> , 1992b
<i>Elymus ciliaris</i>	4x	S <sup>c</sup> Y <sup>c</sup>	11	1		Jiang <i>et al.</i> , 1993a; Wang <i>et al.</i> , 1999
<i>E. trachycaulus</i>	4x	S <sup>t</sup> H <sup>t</sup>	7	11		Jiang <i>et al.</i> , 1993a; Morris <i>et al.</i> , 1990
<i>E. tsukushiense</i>	6x	S <sup>ts</sup> H <sup>ts</sup> Y <sup>ts</sup>	3	1	1	Wang <i>et al.</i> , 1999
<i>Hordeum chilense</i>	2x	H <sup>ch</sup>	5	1		Cabrera <i>et al.</i> , 1995
<i>Leymus racemosus</i>	4x	JN	7		2	Qi <i>et al.</i> , 1997

For chromosome addition lines, a B indicates a B chromosome addition line; for *Ae. sharonensis*, 10 different accessions were used for producing addition lines of one chromosome.

wheat species. They analyzed chromosome numbers and meiosis in wheat species and hybrids, and were the first to establish the basic chromosome number of seven and document polyploidy (2x, 4x, 6x) in the wheat group. The chromosome pairing data established that 2x and 4x wheats had one genome (AA) in common, and 4x and 6x wheat had two genomes (AABB) in common. These were exciting observations and established polyploidy as a major macrospeciation process and wheat as a great polyploidy genetic model. This method of delineating species evolutionary relationships based on chromosome pairing affinities in interspecific hybrids came to be called the genome-analyzer method (Kihara, 1954). These hybrids, of course, also could be exploited in plant breeding for interspecific gene transfers and numerous species hybrids have since been produced (Cox, 1998; Friebe *et al.*, 1996b; Jiang *et al.*, 1994a; Sharma and Gill, 1983).

Armed with the genome analyzer method, the hunt was on for the B-genome donor of 4x and 6x wheats and the extra genome (termed D-genome donor) of 6x wheat. In the 1940s, *Ae. tauschii* (syn. *Ae. squarrosa*) was simultaneously discovered in Japan and the United States as the donor of the D genome of hexaploid wheat (Kihara, 1944; McFadden and Sears, 1944, 1946). McFadden and Sears (1944, 1946) reported artificial synthesis of bread wheat by crossing tetraploid wheat with *Ae. tauschii* and chromosome doubling of the F<sub>1</sub> hybrid by colchicine (often the F<sub>1</sub> hybrids are self-fertile due to the functioning of restitution gametes). The so-called synthetic wheat, upon crossing with bread wheat, showed 21 bivalents at meiosis indicating complete chromosome homology and produced fully fertile progeny. Presumably, one or a few gametes of primitive tetraploid wheat and *Ae. tauschii* were sampled in the origin of 6x wheat from rare hybridization event that occurred in some farmer's field (as no wild 6x wheats are known in the Middle East) in the west Caspian region of Iran about 7000 years ago. Therefore, bread wheat has a very narrow genetic base, and the wheat crop was often decimated by many diseases, especially rusts. Unfortunately, the particular accession of *Ae. tauschii* used to produce the synthetic wheat was susceptible to rust (Sears, personal communication) and, hence, the notion that *Ae. tauschii* contributed little of value to bread wheat (discussed in more detail in Gill, 1993). It would take another 50 years for the full exploitation of synthetic wheats for wheat breeding (see later section).

Kihara and his colleagues undertook extensive collections of *Ae. tauschii* from its area of geographical distribution and documented extensive genetic diversity in natural populations of *Ae. tauschii* including rust resistance (reviewed in Kihara *et al.*, 1965). Kihara and coworkers also produced a large number of synthetic wheats but that remained of academic interest. In North America, Kerber and Dyck (1969), and Joppa *et al.* (1980) transferred rust and greenbug resistance to wheat from *Ae. tauschii*.



As briefly mentioned earlier, in the 1980s the WGRC launched a large-scale, sustained, and systematic effort on documenting genetic variation in *Ae. tauschii* and its rapid transfer to bread wheat by direct hybridization. We began with a small collection of *Ae. tauschii* maintained at UC–Riverside (Waines) based on the original collections of Vavilov (St. Petersburg, Russian Federation). In 1983, on the eve of the 7th International Wheat Genetics Symposium in Kyoto, Japan, Ernie Sears obtained Kihara’s collection of *Ae. tauschii* for the WGRC. Our current collection of *Ae. tauschii* stands at 556 (24 duplicate) accessions. Eighteen of the 47 improved hard red winter wheat germplasm releases from the WGRC trace their pedigree to *Ae. tauschii* (Table III provides details of genes transferred).

In 1986, we began a collaborative project with CIMMYT (with Drs Byrd Curtis and Mujeeb Kazi) for the production of synthetic wheats derived from high-yielding durum and 216 accessions of *Ae. tauschii* that were shipped to CIMMYT that year. Another 40 accessions were shipped later. The synthetic wheats have played a huge role in broadening the gene pool of bread wheat. According to Maarten van Ginkel (personal communication) “by the year 2003–2004, 26% of all new advanced lines made available through CIMMYT screening nurseries to cooperators for either irrigated or semi-arid conditions were synthetic derivatives.”

Another sample of 313 accessions was sent to Australia where Rudi Appels and Evans Lagudah began a large-scale program to exploit *Ae. tauschii* for wheat improvement program in that country.

Serendipitously, *Ae. tauschii* has proved to be a genetic workhorse for molecular genetic analysis of wheat and provided a window on the composition of a basic Triticeae genome (Li *et al.*, 2004). In the late 1980s, we began wheat genome mapping using restriction fragment length polymorphism (RFLP) markers and discovered that it was impractical due to the low level of polymorphism among wheat cultivars and, instead, observed a high level of polymorphism (>80% using four restriction enzymes) in a sample of *Ae. tauschii* accessions (Kam-Morgan *et al.*, 1989). Gill, *et al.* (1991) constructed the first genetic linkage map of *Ae. tauschii* and the current map consists of 730 loci incorporating placement of 160 defense-related genes (Boyko *et al.*, 2002). A high rate of recombination is the hallmark of this wild mapping population of 56 F<sub>2</sub> plants, where cosegregating markers have rarely been observed. In a pioneering paper, Lubbers *et al.* (1991) used RFLP markers to analyze the structure of the gene pool and define centers of genetic diversity in *Ae. tauschii* as a guide for its exploitation in wheat-improvement programs. There also were first reports of RFLP-linked markers to pest-resistance genes (Gill *et al.*, 1991; Ma *et al.*, 1993) and quantitative trait loci (QTLs) and insights into patterns of genetic introgression in wheat/*Ae. tauschii* populations (Fritz *et al.*, 1995a,b). Incidentally, the *Pst*I library genomic clone KSUD14, reported to be linked to a rust resistance gene at the distal end of 1DS arm (Gill *et al.*, 1991),

**Table III**  
**Germplasm Releases from the WGRC, Salient Traits, and Genetic Basis of Traits were Known**

Germplasm	NPGS accession number	Pedigree	Resistance(s) and other traits	Gene(s)	Chromosome location(s) and/or linked markers	Reference
KS85WGRC01	PI499691	TA1644 ( <i>Aegilops tauschii</i> )/Newton//Wichita	Hessian fly, soilborne mosaic virus	<i>H22</i>	1DL	Gill <i>et al.</i> , 1986a; Raupp <i>et al.</i> , 1993
KS86WGRC02	PI504517	TA1649 ( <i>Ae. tauschii</i> )/2*Wichita	Leaf rust	<i>Lr39</i>	2DSGWM210	Raupp <i>et al.</i> , 2001; Singh <i>et al.</i> , 2003
KS87UP9	PI535771	Random-mated population	Segregating for male sterility	<i>Ms3</i>	5AWG341	Cox <i>et al.</i> , 1991b; Qi and Gill, 2001
KS89WGRC03	PI535766	TA1642 ( <i>Ae. tauschii</i> )/2*Wichita	Hessian fly	<i>H23</i>	6DSKSUH4	Gill <i>et al.</i> , 1991d; Ma <i>et al.</i> , 1993; Raupp <i>et al.</i> , 1993
KS89WGRC04	PI535767	TA1695 ( <i>Ae. tauschii</i> )/3*Wichita	Hessian fly, greenbug, soilborne mosaic virus	<i>Gbx</i>	7DLGDM150WMC157	Gill <i>et al.</i> , 1991c; Zhu and Smith, unpublished
KS89WGRC06	PI535796	TA2452 ( <i>Ae. tauschii</i> )/TA1642 ( <i>Ae. tauschii</i> )//2*Wichita/3/Newton	Hessian fly	<i>H24</i>	3DLBCD451	Gill <i>et al.</i> , 1991d; Ma <i>et al.</i> , 1993; Raupp <i>et al.</i> , 1993
KS89WGRC07	PI535770	Wichita//TA1649 ( <i>Ae. tauschii</i> )/2*Wichita	Leaf rust	<i>Lr40(Lr21)</i>	1DS (gene cloned)	Gill <i>et al.</i> , 1991b; Huang and Gill, 2001; Huang <i>et al.</i> , 2003

KS89WGRC08	PI549276	ND7532/Chaupon ( <i>Secale cereale</i> )// 4*ND7532	Hessian fly resistance; cell-culture-derived; germplasm named “Hamlet” (2B or not 2B)	<i>H21</i>	T2BS-2RL	Friebe <i>et al.</i> , 1990a; Sears <i>et al.</i> , 1992a
KS89WGRC09	PI536992	Cell-culture derived line of ND7532	Stress tolerance; from <i>in vitro</i> selection for resistance to abscisic acid	—	—	Sears <i>et al.</i> , 1992b
KS90WGRC10	PI549278	TAM107*3/TA2460 ( <i>Ae. tauschii</i> )	Leaf rust	<i>Lr41</i> (may be allelic to <i>Lr39</i> )	2DSGDM35	Cox <i>et al.</i> , 1992b; Singh <i>et al.</i> , 2003
KS91WGRC11	PI566668	Century*3/TA2450 ( <i>Ae. tauschii</i> )	Leaf rust	<i>Lr42</i>	1DS	Cox <i>et al.</i> , 1994b,c
KS91WGRC12	—	Century*3/TA2541 ( <i>Ae. tauschii</i> )	Leaf rust (adult-plant); segregating for resistance to wheat soilborne mosaic and wheat spindle streak mosaic viruses	—	—	
KS91WGRC14	PI560335	Cando ( <i>Triticum</i> <i>turgidum</i> )/Veery	Greenbug, leaf rust, and powdery mildew; first transfer of T1BL 1 RS to durum wheat	<i>Pm8</i> , <i>Lr26</i> , <i>Sr31</i> , <i>Yr9</i>	T1BL-1RS	Friebe <i>et al.</i> , 1993a
KS92WGRC15	PI566669	TAM200/ KS86WGRC02// Karl	Leaf rust	<i>Lr40</i>	—	Cox <i>et al.</i> , 1994c
KS92WGRC16	PI592728	Triumph 64/3/ KS8010-71/ TA2470 ( <i>Ae.</i> <i>tauschii</i> )/TAM200	Leaf rust	<i>Lr43</i> (may be allelic to <i>Lr21</i> , <i>Lr39</i> )	7D	Brown-Guedira, unpublished; Cox <i>et al.</i> , 1997; Hussein <i>et al.</i> , 1997

(continued)

Table III (continued)

Germplasm	NPGS accession number	Pedigree	Resistance(s) and other traits	Gene(s)	Chromosome location(s) and/or linked markers	Reference
KS92WGRC17	PI592729	Vona/4/Suwon 92/ Balbo ( <i>S. cereale</i> )// TAM106/3/Amigo	Hessian fly	<i>H25</i>	T6BS-6BL-6RL	Friebe <i>et al.</i> , 1991a; Mukai <i>et al.</i> , 1993; Sebesta <i>et al.</i> , 1997
KS92WGRC18	PI592730	TAM106/4/Suwon 92/Balbo// TAM106/3/Amigo	Hessian fly	<i>H25</i>	T4BS-4BL-6RL	Friebe <i>et al.</i> , 1991a; Mukai <i>et al.</i> , 1993; Sebesta <i>et al.</i> , 1997
KS92WGRC19	PI592731	Vona/4/Suwon 92/ Balbo//TAM106/ 3/Amigo	Hessian fly	<i>H25</i>	T4BS-4BL-6RL	Friebe <i>et al.</i> , 1991a; Mukai <i>et al.</i> , 1993; Sebesta <i>et al.</i> , 1997
KS92WGRC20	PI592732	TAM101/4/Suwon 92/Balbo// TAM106/3/Amigo	Hessian fly	<i>H25</i>	Ti4AS-4AL 6RL-4AL	Friebe <i>et al.</i> , 1991a; Mukai <i>et al.</i> , 1993; Delaney <i>et al.</i> , 1995a; Sebesta <i>et al.</i> , 1997
KS92WGRC21	PI566670	TAM200*3/TA2570 ( <i>Ae. tauschii</i> )	Powdery mildew, wheat soilborne mosaic virus, wheat spindle streak mosaic virus	—	—	Cox <i>et al.</i> , 1994d
KS92WGRC22	PI566671	Century*3/TA2567 ( <i>Ae. tauschii</i> )	Powdery mildew, wheat soilborne virus, wheat spindle streak mosaic virus	—	—	Cox <i>et al.</i> , 1994d
KS92WGRC23	PI566672	Karl*3//PI 266844/PI 355520 ( <i>Triticum monococcum</i> subsp. <i>monococcum</i> )	Leaf rust	—	—	Cox <i>et al.</i> , 1994c

KS92WGRC24	PI574489	Yilmaz-4/ 2*KS84HW196	Russian wheat aphid	—	—	Martin and Harvey, 1991
KS92WGRC25	PI574490	Yilmaz-4/ KS84HW196/2/ Dodge	Russian wheat aphid	—	—	Martin and Harvey, 1991
KS93WGRC26	PI572542	Karl*3/TA2473 ( <i>Ae. tauschii</i> )	Hessian fly	<i>H26</i>	4DL	Cox and Hatchett, 1994; Cox <i>et al.</i> , 1994a
KS93WGRC27	PI1583794	Karl*4/CI17884	Wheat streak mosaic virus	<i>Wsm1</i>	T4DL-4Ai#2S	Friebe <i>et al.</i> , 1991b; Gill <i>et al.</i> , 1995; Wells <i>et al.</i> , 1982 Friebe <i>et al.</i> , 1995a
KS93WGRC28	PI1583795	MS6RL(6D)/ TAM104	Powdery mildew	<i>Pm20</i>	T6BS-6RL	Friebe <i>et al.</i> , 1995a
KS94WGRC29	PI986954	PI 220127//TAM200/ KS87H66	Russian wheat aphid, stem rust, leaf rust, white kernel	—	—	Martin and Harvey, 1994
KS94WGRC30	PI986955	PI 220127//TAM200/ KS87H66	Russian wheat aphid, stem rust, leaf rust	—	—	Martin and Harvey, 1994
KS94WGRC31	PI1586956	PI 220350/ KS87H57// TAM200/ KS87H66/3/ KS87H325	Russian wheat aphid, stem rust, leaf rust; segregating for resistance to Hessian fly	—	—	Martin and Harvey, 1994
KS94WGRC32	PI1586957	TAM107*2// KS8010-4-1/ TA359 ( <i>T. monococcum</i> subsp. <i>aegilopoides</i> )	Leaf rust	—	—	

(continued)

Table III (continued)

Germplasm	NPGS accession number	Pedigree	Resistance(s) and other traits	Gene(s)	Chromosome location(s) and/or linked markers	Reference
KS95WGRC33	PI595379	KS93U69*3/TA2397 ( <i>Ae. tauschii</i> )	Septoria leaf blotch, leaf rust	<i>Lr41</i>	—	
KS96WGRC34	PI604219	TAM107/TA749 ( <i>T. monococcum</i> subsp. <i>aegilopoides</i> )/ Wrangler	Leaf rust	—	—	Cox <i>et al.</i> , 1999b
KS96WGRC35	PI604220	Wrangler*3/TA28 ( <i>Triticum timopheevii</i> subsp. <i>armeniacum</i> )	Leaf rust	—	—	Brown-Guedira <i>et al.</i> , 1999b
KS96WGRC36	PI604221	TAM107*3/TA870 ( <i>T. timopheevii</i> subsp. <i>armeniacum</i> )	Leaf rust	<i>Lr50</i>	2BL,GWM382	Brown-Guedira <i>et al.</i> , 1999b, 2003
KS96WGRC37	PI604222	Arlin*3/TA895 ( <i>T. timopheevii</i> subsp. <i>armeniacum</i> )	Powdery mildew; white kernel	—	—	Brown-Guedira <i>et al.</i> , 1999c
KS96WGRC38	PI604223	KS90WGRC10*3/ TA895 ( <i>T. timopheevii</i> subsp. <i>armeniacum</i> )	Tan spot	—	—	Brown-Guedira <i>et al.</i> , 1999a
KS96WGRC39	PI604224	Wrangler*3/TA2460 ( <i>Ae. tauschii</i> )	Tan spot	—	—	Brown-Guedira <i>et al.</i> , 1999a
KS96WGRC40	PI604225	KS95WGRC33 reselection	Septoria glume blotch, wheat curl mite, leaf rust	<i>Cmc3,Cmc4</i>	T1AL·1RS,6DS,GDM141	Cox <i>et al.</i> , 1999a; Malik <i>et al.</i> , 2003a

KS98WGRC41	—	Cando ( <i>T. turgidum</i> )/ KS92WGRC20// 2* Cando	Hessian fly; first transfer of <i>H25</i> to durum wheat	<i>H25</i>	Ti4AS-4AL-6RL-4AL	Friebe <i>et al.</i> , 1999b
KS99WGRC42	—	Karl 92/PI94641( <i>T.</i> <i>turgidum</i> subsp. <i>dicoccum</i> )// 2* Jagger	Hessian fly	<i>H<sup>T.dic</sup></i>	1AS,CFA22153,BARC253	Brown-Guedira <i>et al.</i> , 2005e; Liu <i>et al.</i> , 2006
KS99WGRC43	—	Karl 92/PI94641// 2* Jagger	Hessian fly	—	1A	
KS00WGRC44	—	TAM 107*3/TA1715 ( <i>Ae. tauschii</i> )	Leaf rust	—	2DS	
KS04WGRC45	—	Heyne*2//Chinese Spring*2/TA12052 ( <i>Elymus</i> <i>trachycaulus</i> )	Leaf rust	—	T1H'S:1BL	Friebe <i>et al.</i> , 2005
KS04WGRC46	—	Wrangler*3/TA960 ( <i>T. timopheevii</i> subsp. <i>armeniicum</i> )	FHB	—	—	Brown-Guedira <i>et al.</i> , 2005a
KS04WGRC47	—	Karl 92*4/TA1836 ( <i>Ae. speltooides</i> )	Leaf rust	—	—	Brown-Guedira <i>et al.</i> , 2005c
KS04WGRC48	—	KS94U216*2/ 92R149	Powdery mildew, leaf rust; the powdery mildew gene is from <i>Haynaldia villosa</i>	<i>Pm21, Lr21</i>	T6AL-6VS,1DS	Brown-Guedira <i>et al.</i> , 2005b
KS04WGRC49	—	Karl 92**3/TA2473 ( <i>Ae. tauschii</i> )	Unique high-molecular- weight glutenin and gliadin subunits from <i>Ae. tauschii</i> ; increased loaf volume	<i>Glu-D1-1j, Glu-D1-2i</i>	1DS	Brown-Guedira <i>et al.</i> , 2005d; Knacksted, 1995

KS89WGRC5 and KS91WGRC13 were found to duplicate previously released germplasm and were withdrawn.

was sequenced as a PCR-based marker by Talbert *et al.* (1994), and proved to be the *Lr21* gene cloned 12 years later by Huang *et al.* (2003).

The *Ae. tauschii* genome, at 4000 Mb, is smaller than the A and B genomes, and essentially collinear to the D genome of bread wheat. The D genome consists of 92% repetitive DNA and 8% low-copy DNA of which 3% may be genes (Li *et al.*, 2004). However, genes are organized in clusters (Gill *et al.*, 1996a,b), and the sequencing of one such cluster revealed a 46-kb retroelement-free gene island containing seven coding sequences (Brooks *et al.*, 2002). Li *et al.* (2004) have shown that gene-rich regions can be filtered from the repetitive DNA using several approaches, especially the cot based cloning and sequencing (CBCS) method (Peterson *et al.*, 2002). A BAC-contig map of *Ae. tauschii* anchored to the genetic map is under construction (<http://wheat.pw.usda.gov/PhysicalMapping/>).

As mentioned above, the leaf rust-resistance gene *Lr21* introgressed from *Ae. tauschii* into wheat was among the first wheat genes to be isolated by map-based cloning (Huang *et al.*, 2003). Because most *Ae. tauschii*-introgressed agronomic genes lie in cotransferred, polymorphic chromosomal segments of high-gene density and recombination (Boyko *et al.*, 2002; Qi *et al.*, 2004), and most have been tagged with molecular markers, the above-mentioned genomic resources will greatly facilitate molecular cloning of these genes and open novel avenues for wheat crop improvement.

Whereas the D genome of *Ae. tauschii* and the D genome of 6x wheat recombine freely, such is not the case with transfers from A- and B-genome diploid donors to the AB genome of polyploid wheats, which share ca. 0.5 million years of coevolutionary history (Huang *et al.*, 2002). The 4A chromosome in polyploid wheats is highly rearranged and no longer pairs with 4A of diploid wheats (Chen and Gill, 1983; Naranjo *et al.*, 1987, 1988). The B-genome diploid donor has not been identified with certainty, and *Ae. speltoides* is the closest living relative (Huang *et al.*, 2002). As a result, fewer genetic transfers have been attempted from A- and B-genome diploid donors and far fewer have been agronomically desirable.

The A-genome, diploid wheat *T. monococcum* was one of the first crops to be domesticated (subsp. *monococcum*) from its wild form (subsp. *aegilopoides*) (Heun *et al.*, 1997) and is still cultivated in isolated areas. With a genome size of 5500 Mb, resources such as molecular genetic linkage map and large insert library are available (Dubcovsky *et al.*, 1996; Lijavetsky *et al.*, 1999). Because of diploidy and ease of cultivation, it is particularly suitable for mutagenesis. Vernalization genes *VRN1* and *VRN2* were recently cloned in diploid wheat (Yan *et al.*, 2003, 2004). Another sibling, A-genome, wild diploid wheat species *T. urartu* actually is now recognized as the A-genome donor of polyploid wheats (Dvorak *et al.*, 1993). The diploid wheats, both cultivated and wild forms, have good resistance to most of the common diseases of higher ploidy wheats (Gill *et al.*, 1993). New genes for leaf rust resistance were introgressed from diploid



wheat by direct hybridization in WGRC germplasm lines WGRC23, WGRC32, and WGRC34 (Table III). There is variation for crossability of different diploid wheats with common wheat. *Triticum urartu* is a poor pollen producer, and direct hybrids with common wheat have been difficult to produce. The F<sub>1</sub> hybrids between 6x wheat and subsp. *aegilopoides* were female fertile, and WGRC32 and WGRC34 were developed from these crosses. However, most wheat/subsp. *monococcum* hybrids were female sterile, except those with accession PI355520. The hybrid-fertility gene in PI355520 is controlled by a single dominant gene. The WGRC23 was developed by crossing the leaf rust-resistant donor accession PI266844 with PI355520, and then crossing the F<sub>1</sub> hybrid to a recipient wheat cultivar. Even then, there is poor pairing between putative homologous A-genome chromosomes and even some homologous pairing occurs in some hybrids (Cox *et al.*, 1991a). Upon cytological examination, WGRC23 was found to contain 40 complete chromosomes and one pair each of 6BL telocentrics and 6BS acrocentrics (Cox *et al.*, 1994c).

The putative B-genome donor, *Aegilops speltoides*, also has excellent resistance to most common diseases of wheat (Gill *et al.*, 1985). However, the degree of difficulty of genetic transfers from *Ae. speltoides* to wheat is an order of magnitude higher than from the A-genome diploids discussed above. Although hybrids are easier to produce than those involving A- or D-genome diploids, such hybrids suffer from poor homologous pairing, enhanced homoeologous pairing, and chromosome breakage. Quite a few genes for resistance to leaf rust (*Lr28*, *Lr35*, *Lr36*, and *Lr47*), stem rust (*Sr32* and *Sr39*), and one each for powdery mildew (*Pm12*) and greenbug (*Gb5*) have been transferred from *Ae. speltoides* into wheat, but none of them have as yet made any impact in agriculture (Table IV). The T7S–7A translocation involving chromosome 7S of *Ae. speltoides* and 7A of wheat in CI17884 with genes *Gb5/Lr47* was identified by Friebe *et al.* (1991b, 1996b), and further recombinants with genes *Gb5* and *Lr47* were isolated by Dubcovsky *et al.* (1998, see Table III). We have released only one line, WGRC47, containing a new, as yet unnamed, leaf rust-resistance gene extracted from *Ae. speltoides* (Table III).

Genetic transfers from diploid donors to 4x and 6x wheats probably happened rarely in nature (except the hybridization event that produced 6x wheat as discussed earlier), because the F<sub>1</sub> hybrid seed is normally highly shriveled and embryo rescue is routinely employed in experimental introgression research. However, hybrids between 4x and 6x wheats produce plump seed and are partially fertile. Fully fertile 4x or 6x derivatives are easily recovered upon backcrossing 5x hybrids to either parent (4x or 6x). Such enrichment of the A and B genomes of diverse land races of 6x wheats undoubtedly occurred during the 6000–7000 years of cultivation, as these genomes are relatively more polymorphic, whereas the D genome remained monomorphic (see Cox, 1998, for more details). The gene *Sr2*, which has

**Table IV**  
**Alien Transfers Derived From *Triticum* and *Aegilops* Species**

Alien species	Germplasm	Alien target gene(s)	Description	Size of alien translocation	Size of missing segment	FL of break point	Mode of transfer <sup>a</sup>	Type <sup>b</sup>	Agricultural contribution <sup>c</sup>	Reference
<i>T. timopheevii</i> subsp. <i>timopheevii</i>	C747	<i>Sr36/Pm6</i>	T2B/2G#1				HR	C	++	Allard and Shands, 1954; Friebe <i>et al.</i> , 1996b; Jorgensen and Jensen, 1973; McIntosh and Gyrafas, 1971; McIntosh and Luig, 1973; Nyquist, 1957, 1962
	Line W	<i>Sr37</i>	T4B/4G#1				HR	C	-	Friebe <i>et al.</i> , 1996b; Gyrafas, 1968; McIntosh, 1991; McIntosh and Luig, 1973
	Thatcher/ <i>Lr18</i>	<i>Lr18</i>	T5BS-5BL-5G#1L				HR	C	-	Friebe <i>et al.</i> , 1996b; McIntosh, 1983; Yamamori, 1994
	146-155-T	<i>Pm27</i>	T6BS-6G#1S-6G#1L-6BL				MNU	C	-	Järve <i>et al.</i> , 2000
	RL6087	<i>Sr40</i>	T2BL/2G#2S				HR	C	-	Dyck, 1992; Friebe <i>et al.</i> , 1996b
<i>Ae. comosa</i>	Compair		T2DS-2M#1L-2M#1S			0.84	HR	N	-	McIntosh <i>et al.</i> , 1982; Nasuda <i>et al.</i> , 1998; Riley <i>et al.</i> , 1968a,b
	2A-2M#4/2	<i>Yr8/Sr34</i>	T2AS-2M#1L-2M#1S			0.84	HR	N	-	
	2D-2M#3/8 R1A, R1B, R4A, R6A	<i>Pm13</i>	T2DS-2M#1L-2M#1S T3BL-3BS-3S <sup>1</sup> #1S	20-27% of 3S <sup>1</sup> #1S		0.84	HR HR	C C	- -	Biagetti <i>et al.</i> , 1998; Cemi <i>et al.</i> , 1999; Ceoloni <i>et al.</i> , 1988, 1992, 1996; Donini <i>et al.</i> , 1995
<i>Ae. longissima</i>	R1D, R2A, R2B		T3DL-3DS-3S <sup>1</sup> #1S	27% of 3S <sup>1</sup> #1S		HR	C	-		
<i>Ae. speltoides</i>	2A/2M#4/2	<i>Lr28</i>	T4AS-4AL-7S#2S				HR	C	-	Friebe <i>et al.</i> , 1996b; McIntosh <i>et al.</i> , 1982; Naik <i>et al.</i> , 1998
	2D/2M#3/8		T4AS-4AL-7S#2S				HR	C	-	

	C95.24	<i>Sr32</i>	T2AL·2S#1L-2S#1S					HR	C	-	Friebe <i>et al.</i> , 1996b; McIntosh, 1991
	C82.1		T2BL/2S#1S					HR	C	-	
	C82.2		T2DL-2S#1L-2S#1S					HR	C	-	
	RL5711	<i>Lr35/Sr39</i>	T2B/2S#2					HR	C	-	Friebe <i>et al.</i> , 1996b; Kerber and Dyck, 1990; Seyfarth <i>et al.</i> , 1999
		<i>Pm12</i>	T6BS-6S#1S-6S#1L					HR	C	-	Jia <i>et al.</i> , 1996; Miller <i>et al.</i> , 1987
	2-9-2	<i>Lr36</i>	T6S#2S-6BS-6BL					HR	C	-	Dvorak, 1977; Dvorak and Knott, 1990
	CI17884	<i>Gb5/ Lr47</i>	T7AS-7S#1S-7S#1L	8.54 μm	0.63 μm of 7AS (size of wheat segment present)	0.85	I		C	-	Dubcovsky <i>et al.</i> , 1998; Friebe <i>et al.</i> , 1991b, 1996b; Tyler <i>et al.</i> , 1987; Wells <i>et al.</i> , 1973, 1982
		<i>Gb5</i>	Ti7AS-7AL-7S#1L-7AL	40-50 cM				HR	C	-	Dubcovsky <i>et al.</i> , 1998
		<i>Lr47</i>	Ti7AS-7S#1S-7AS-7AL	20-30 cM				HR	C	-	Dubcovsky <i>et al.</i> , 1998
	Transfer (T47)	<i>Lr9</i>	T6BS-6BL-6U#1L	0.41 μm	0.51 μm of 6BL	0.92	I		C	+	Autrique <i>et al.</i> , 1995; Friebe <i>et al.</i> , 1995c; Schachermayer <i>et al.</i> , 1994; Sears, 1956, 1972; Zhang <i>et al.</i> , 1998
<i>Ae. umbellulata</i>	T40		T6BL-6BS-6U#1L	4.65 μm	3.29 μm of 6BS	0.23	I		N	-	
	T41		T4BL-4BS-6U#1L	5.08 μm	2.90 μm of 4BS	0.23	I		N	-	
	T44		T2DS-2DL-6U#1L	1.66 μm	0.19 μm of 2DL	0.71	I		N	-	
	T52		T7BL-7BS-6U#1L	2.84 μm	1.13 μm of 7BS	0.48	I		N	-	
<i>Ae. ventricosa</i>	Roazon	<i>Pch1</i>	T7DS-7D <sup>v</sup> #1L					HR	C	+	Doussinault <i>et al.</i> , 1983; Jahier <i>et al.</i> , 1979, 1989, 1996
	VPM1	<i>Lr37/ Sr38/ Yr17</i>	T2AL·2AS-2M <sup>v</sup> #1					HR	C	+	Bariana and McIntosh, 1993, 1994; Bonhomme <i>et al.</i> , 1995; Helguera <i>et al.</i> , 2003; Seah <i>et al.</i> , 2001
	H-93-33	<i>H27</i>	DS4D(4M <sup>v</sup> )	N/A		N/A	N/A		N/A	-	Delibes <i>et al.</i> , 1997

<sup>a</sup>Mode of transfer is I, irradiation; or HR, homologous recombination.

<sup>b</sup>Type includes C, compensating; N, noncompensating; TC, tissue culture; S, spontaneous; EMS, EMS-induced; or NMS, *N*-methyl-*N*-nitrosourea-induced translocations.

<sup>c</sup>Agricultural contribution listed as ++, significant; +, some; and —, none; N/A, not applicable; and FL, fraction length.

provided durable resistance to stem rust for the last 50 years, was transferred to 6x wheat from a 4x wheat land race, “Yaroslav emmer,” in the 1930s (McFadden, 1930). A QTL for high protein has been transferred to 6x wheat from wild 4x *T. turgidum* subsp. *dicoccoides* (Khan *et al.*, 2000).

As a part of a US–AID project in Morocco in the 1980s, we transferred Hessian fly resistance gene *H25* from WGRC20 (6x) to develop WGRC41 (4x) for durum wheat breeding in Morocco where Hessian fly infestations are endemic (Friebe *et al.*, 1999b). We also transferred the wheat–rye translocation chromosome T1BL-1RS, which carries a battery of resistance genes (*Pm8*, *Lr26*, *Sr31*, and *Yr9*) deployed in the world’s highest yielding wheats (6x) to 4x wheat released as WGRC14, for use in durum wheat breeding (Friebe *et al.*, 1993a). A land race accession of 4x wheat (*T. turgidum* subsp. *dicoccum*) proved to be highly resistant to US biotypes of Hessian fly, and one of the genes was transferred to 6x wheat to develop WGRC42 (Brown-Guedira *et al.*, 2005e). Molecular mapping revealed that this gene is located in a gene-rich region of chromosome 1A short arm (1AS) and closely linked with flanking markers GWM33 and CFA2153 (Liu *et al.*, 2006). The same markers also were linked with Hessian fly-resistance genes, which were, until now, erroneously mapped on chromosome 5A (Liu *et al.*, 2005b). It appears that 1AS is a hotspot of Hessian fly-resistance genes and merits further molecular analysis.

Another 4x wheat, *T. timopheevii* is a sibling species of *T. turgidum*. Its subspecies *timopheevii* is a minor crop in Transcaucasia, especially Georgia, and the wild subsp. *armeniacum* is distributed in Transcaucasia with a center of genetic diversity in northeast Iraq (Badaeva *et al.*, 1994). Pridham (1939) and Shands (1941) recognized the high level of disease resistance in *T. timopheevii* (see also Brown-Guedira *et al.*, 1996b) and attempted direct introgression of alien genes into wheat in the 1930s and transferred gene complex of *Sr36/Pm6*, which had a major impact in production agriculture (Table IV). Other transfers from *T. timopheevii* include genes for resistance to rusts and powdery mildew (*Lr18*, *Sr37*, *Sr40*, and *Pm27*). We have transferred new genes for resistance to leaf rust, powdery mildew, tan spot, and Fusarium head blight (FHB) from subsp. *armeniacum* to 6x wheat in the WGRC lines 35–38 and WGRC46. The novel resistance to FHB is noteworthy as it is the most devastating disease of wheat crop in recent years and caused over \$1.3 billion crop loss in 1993 (McMullen *et al.*, 1997).

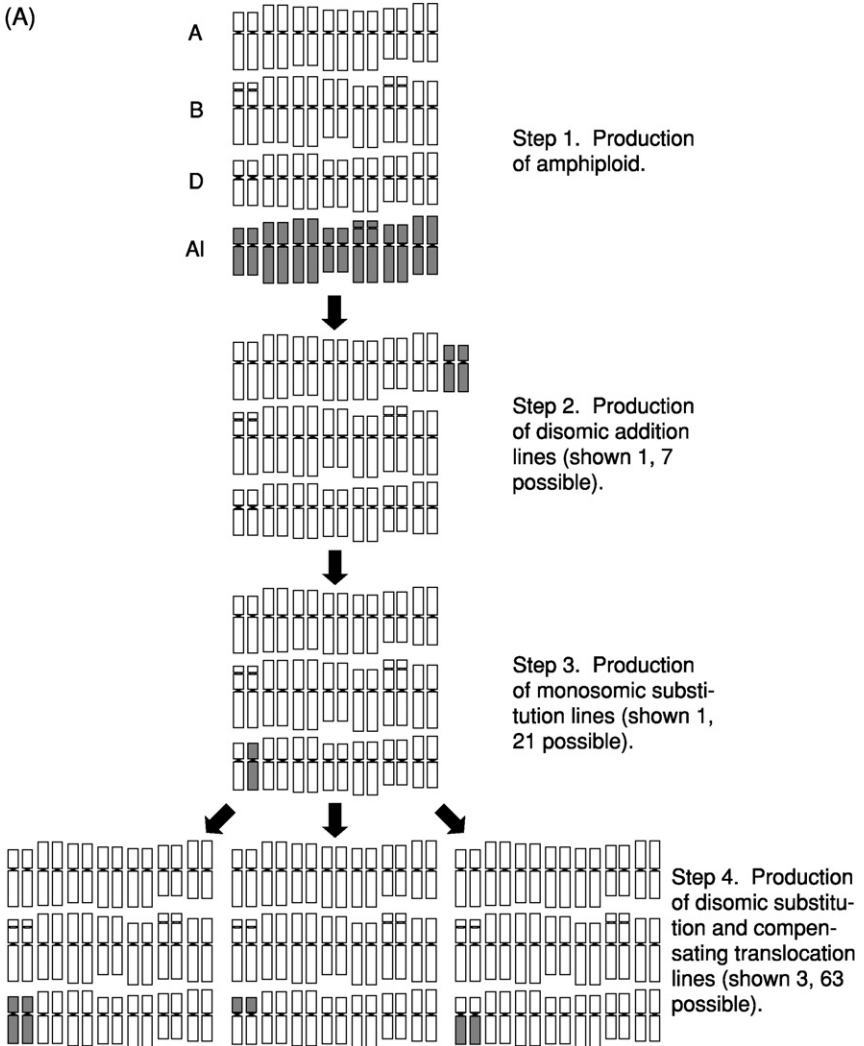
## B. INTERGENOMIC TRANSFERS BY CHROMOSOME ENGINEERING

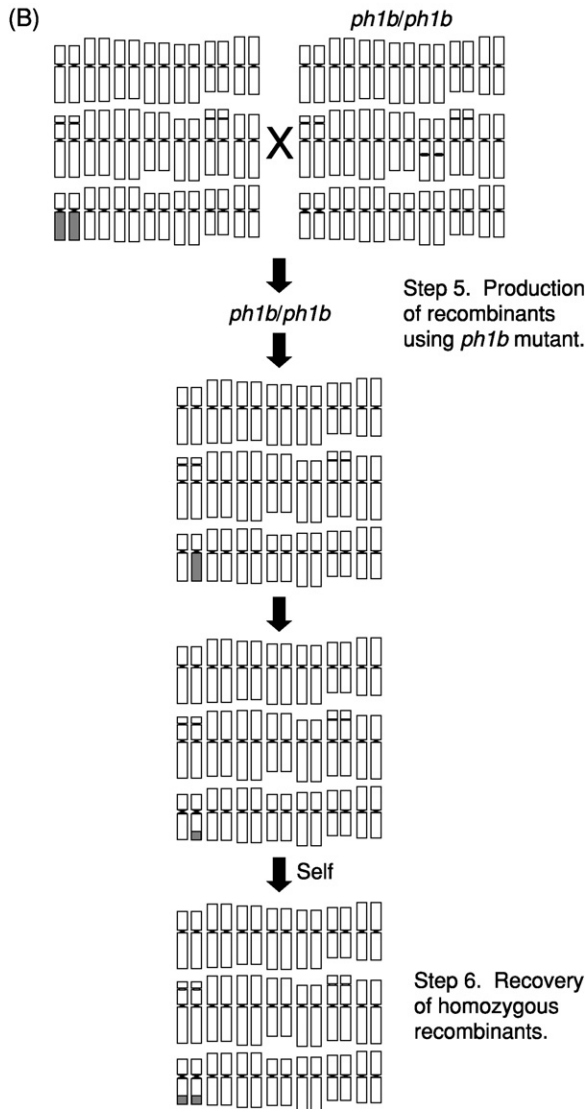
Whereas genes from genome-donor species into wheat can be transferred by homologous recombination, special techniques, such as irradiation (Sears, 1956) or induced homologous recombination (Riley *et al.*, 1968a,b),

are required for intergenomic transfers, as an example, from the R genome of rye to the A or B genomes of wheat. A flow diagram of such manipulation is presented in [Fig. 3A and B](#). All Triticeae taxa have a basic chromosome number of  $1n = 1x = 7$ . Speciation in the Triticeae seems to have proceeded in two steps. First, there is a reproductive isolation by virtue of hybrid sterility or ecological preference even though the genomes are still relatively undifferentiated and capable of meiotic pairing and recombination. As an example, A-genome species hybrids between *T. monococcum* and *T. urartu* have seven ring bivalents at MI of meiosis but are sterile. Interspecific hybrids between *Ae. sharonensis* and *Ae. longissima* form 5II and 1IV (the genomes are differentiated by one reciprocal translocation) and are partially fertile. Over longer evolutionary periods of time, genomes become highly differentiated and are no longer capable of pairing, often designated by assigning different alphabetic symbols to their genomes. The genome differentiation may be nonstructural, as is the case between wheat and barley, where almost complete gene synteny and chromosome-level homology is maintained even after 12 millions of coevolution ([Li and Gill, 2002](#)). Alternatively, the genome differentiation may be structural as is the case between rye and wheat [they diverged from each other more recently, that is, 6 million years ago ([Huang et al., 2002](#))], and most rye chromosomes are highly rearranged compared to wheat and barley ([Devos et al., 1993](#)). The information on the mode of genome differentiation is necessary for the choice of strategy to be used for intergenomic transfers. The method of choice for intergenomic transfer for highly rearranged alien chromosomes is irradiation and it is induced homologous pairing for syntenic alien chromosomes.

In intergenomic transfers, the production of amphiploids between wheat and alien species is the first step, followed by the isolation of alien addition, substitution, and translocation lines ([Fig. 3A](#)). Although the production of an amphiploid is highly desirable, certain combinations are resistant to doubling. In these cases, the  $F_1$  hybrid can be directly backcrossed to produce alien addition lines. Cytological techniques, such as C-banding and genomic *in situ* hybridization and molecular marker analysis, are critical for the monitoring of alien introgression (for reviews, see [Friebe et al., 1996b](#); [Jiang and Gill, 1994b](#); [Jiang et al., 1994a](#)) as spontaneous translocations and other more complex chromosomal translocations are often encountered in backcross derivatives ([Jiang and Gill, 1993](#); [Jiang et al., 1993a, 1994c](#)). Two papers are particularly noteworthy ([Friebe et al., 1991b](#); [Mukai et al., 1993](#)) as the first applications of modern chromosome analysis to complex germplasm that eventually led to the release of germplasm lines WGRC17–20 and WGRC27 ([Table III](#)). Overall, 11 of the 49 WGRC germplasm lines trace their origin to intergenomic transfers from rye (R genome), *H. villosa* (V genome), *Agropyron intermedium* (Host) Beauvois (E and X genomes), and *Elymus trachycaulus* (Link) Gould ex Shinnors (S and H genomes).

Actually, 8 of the 11 intergenomic transfers are of rye origin. As discussed earlier, WGRC14 and WGRC41 represent redeployment of rye genes from 6x to 4x wheat. WGRC8 contains the Robertsonian translocation chromosome T2BS·2RL with the 2RL of rye carrying Hessian fly resistance gene *H21* (Table III). This germplasm is late flowering and attempts have been made to reduce the size of the rye segment by homologous recombination (Ferrahi, 2001). WGRC17–20 trace their origin to breeding material





**Figure 3** (A) Genetic scheme for intergenomic transfers from alien species into wheat. Production of disomic substitution and compensating translocation lines involves producing an amphiploid containing wheat (ABD) and alien (A1) genomes (Step 1), followed by production of alien chromosome disomic addition lines (Step 2), monosomic substitution lines (Step 3), and the production of disomic alien chromosome substitution or Robertsonian translocation lines (Step 4). (B) Robertsonian compensating translocation lines are the starting material for the production of wheat–alien chromosome recombinant lines by using *ph1* gene-induced homologous recombination.

developed by Emil Sebesta of USDA–ARS, Oklahoma State University. He irradiated a 6x wheat line with a pair of added 6RL telocentric chromosomes of rye carrying Hessian fly resistant gene *H25*. In retrospect, this was a good strategy, as we know now that 6R is a rearranged chromosome and contains segments derived from homologous chromosomes 6, 3, and 7 (Devos *et al.*, 1993). Sebesta, and his collaborator J. Hatchett, subjected the irradiated progenies to further breeding and agronomic selection under field conditions to isolate a number of Hessian fly-resistant lines. We analyzed these lines by molecular cytogenetic analysis to identify three different wheat–rye translocations (Friebe *et al.*, 1991a; Mukai *et al.*, 1993). One line (deployed in 6x WGRC20 and 4x WGRC41) contained a tiny rye segment inserted into wheat chromosome 4A, the first documented case of an intercalary alien transfer (Friebe *et al.*, 1991a). Postdoctoral fellow Donna Delaney identified a group-7 specific molecular marker tightly linked to *H25* at the tip of 6R that is orthologous to group 7 of the Triticeae (Delaney *et al.*, 1995a). *H25* is located in a high recombination region at the distal end and should be amenable to molecular cloning.

The development of a germplasm containing *Pm20* (WGRC28) is an example of the use of a homologous recombination between two wheat–rye addition lines derived from different rye accessions for gene transfer (Friebe *et al.*, 1994a). The original germplasm had the T6BS·6RL wheat–rye translocation chromosome carrying a fertility-restoration gene specific to *T. timopheevii* cytoplasm on 6RL. The recombinant T6BS·6RL chromosome present in WGRC28 now carries both genes. This is proof of the concept experiment of a proposal (see Friebe *et al.*, 1994a) where each basic alien Triticeae genome (seven chromosomes) should be incorporated into wheat in the form of 14 different, compensating, wheat–alien translocation chromosomes. These stocks in turn can be used as probes to extract additional genes from the donor gene pool by homologous recombination. In this way, we can cytogenetically access all the basic genomes and the vast Triticeae gene pool for wheat improvement.

We have selected *H. villosa* because its genome is already introduced into wheat as seven wheat–alien chromosome addition lines (Lukaszewski, unpublished) as the first candidate taxa for genome manipulation as proposed above. One (short arm of 6V called 6VS) of its 14 arms is already incorporated into wheat in the form of a wheat–*H. villosa* translocation chromosome T6AL·6VS and carries genes for powdery mildew and wheat curl mite resistance (Qi *et al.*, 1996). This translocation has been transferred into hard red wheat germplasm WGRC48 (Table III). For producing additional translocations, Jamie Wilson (M.S. student) crossed wheat monosomic 4D (20'' + 4D') with DA4V (21'' + 4V''), selected double monosomic F<sub>1</sub> plants (20'' + 4D' + 4V''), and allowed them to self. The univalent chromosomes at meiosis are prone to misdivision at the



centromeres and frequently form Robertsonian translocation chromosomes (Friebe *et al.*, 2005). In a sample of 200 plants, we identified two Robertsonian translocations for both arms and another translocation with a noncentromeric breakpoint (J. J. Wilson, unpublished). A similar strategy will be used to produce additional Robertsonian translocations for the remaining arms. These materials will be released as germplasm for extensive evaluation by the breeding community for a variety of stress resistance, physiological, quality, and agronomic traits. Those germplasm lines where *H. villosa* chromatin-controlled traits are identified will be candidates for further genomic manipulation by induced homologous recombination.

Resistance to devastating virus diseases, such as wheat streak mosaic virus (WSMV) and barley yellow dwarf virus (BYDV), is among a few traits that to a large extent are lacking in wheat. The perennial Triticeae grasses, such as *Agropyron* (in the old sense), have excellent resistance to both diseases, and breeders have been working with these sources of resistance since the 1940s. Wells at South Dakota State University developed wheat germplasm resistant to WSMV from wheat/*A. intermedium* hybrid derivatives using high pairing *Ae. speltoides* (Wells *et al.*, 1982). We analyzed this germplasm using molecular cytogenetic techniques (Friebe *et al.*, 1991b) and have identified one line containing a compensating translocation T4DL-4Ai#2S where the short arm of chromosome 4Ai of *A. intermedium* with resistance to WSMV (designated *Wsm1*) was translocated to the long arm of chromosome 4D of wheat. Obviously, this line arose from a breakage-fusion mechanism involved in the origin of Robertsonian translocations and not through recombination. It also contained an almost complete chromosome 7S from *Ae. speltoides* substituting for chromosome 7A of wheat and specified resistance to greenbug (*Gb5*). This chromosome was fixed in wheat because of its meiotic drive and, eventually, we were able to develop the WSMV-resistant line WGRC27 containing T4DL-4Ai#2S but lacking 7S (Table III). WGRC27 has been extensively used in wheat breeding, but no wheat cultivars have been released due to a yield penalty. We are now actively pursuing chromosome engineering to reduce the size of this alien segment through homologous recombination. We analyzed another WSMV-resistant germplasm line derived from wheat/*A. elongatum* derivatives, but this material was more complex and not suitable for improved germplasm development (Jiang *et al.*, 1993b). We also have been developing alien addition and translocation lines from wheat/*E. ciliaris* (SY) (Jiang *et al.*, 1993a) and wheat/*E. trachycaulus* derivatives (Jiang *et al.*, 1994c; Morris *et al.*, 1990), but no resistant germplasm to any of the viruses was developed except the recent release of a rust-resistant line WGRC45 carrying the T1BL-1H'S translocation chromosome (Table III).

Besides developing improved germplasm, we have carried out cytogenetic analysis of intergenomic transfers from many sources with a view to more

clearly define the germplasm, the mechanism of its origin, and promote further manipulation in those cases where such transfers are agronomically undesirable (Tables IV–VI). Cytogenetic analysis was used to determine if the translocations occurred between homoeologous chromosomes (called compensating translocation) or nonhomoeologous chromosomes (called non-compensating), and the compensations indices calculated based on the size of the exchanged wheat and alien segments replaced. Other aspects of these alien transfers have been discussed in detail elsewhere (Friebe *et al.*, 1996b; Jiang *et al.*, 1994a).

## V. DOCUMENTATION OF GENETIC NOVELTY

Before any new gene in a germplasm for potential release can be designated and entered in the wheat gene catalog, its genetic novelty must be established by a number of criteria including recording of specific infection type to standard races of the pathogen or the insect, genetic allelism studies, and its map position on a chromosome or a genetic linkage map. A single criterion, such as a unique infection type, is not sufficient because it may be influenced by genetic background. In fact, in cases where a number of accessions of donor germplasm are resistant to all known races of the pathogen or pest, genetic analysis may be the only choice to establish the novelty of a gene in each resistant accession before resources are invested in its genetic transfer to a crop plant. In their first report, Hatchett and Gill (1981) found 5 out of 20 accessions of *Ae. tauschii* were resistant to Hessian fly biotype D, the most virulent biotype available at that time. Three were from Iran and two were of unknown origin. Further genetic studies and inheritance of resistance among resistant/resistant crosses and crosses with *H13*, the only known *Ae. tauschii*-derived source of resistance in bread wheat, showed that resistance in each accession was controlled by a single dominant gene that was different from all others (Hatchett and Gill, 1983). This documented tremendous genetic diversity for resistance to Hessian fly in *Ae. tauschii* and several of these new genes were transferred to bread wheat (Cox and Hatchett, 1994; Gill and Raupp, 1987) to develop germplasms WGRC1, WGRC3, WGRC4, WGRC6, and WGRC26 (Table III). Next, monosomic mapping was used to determine the chromosomal location of *H13* on 6D, the first gene transferred from *Ae. tauschii* to wheat (Gill *et al.*, 1987), followed by designation and monosomic mapping of other Hessian fly-resistance genes in WGRC1 (*H22* on 1D), WGRC3 (*H23* on 6D; genetic analysis was used to show that this gene is different from *H13* also located on 6D), and WGRC6 (*H24* on 3D). Later, Cox and Hatchett (1994) mapped an additional gene, *H26*, on chromosome 4D

**Table V**  
**Alien Transfers Derived from *Haynaldia villosa* and *Secale cereale* (for Description of Abbreviations, see Footnote to Table IV)**

Alien species	Germplasm	Alien target gene(s)	Description	Size of alien translocation	Size of missing segment	FL of break point	Mode of transfer <sup>a</sup>	Type <sup>b</sup>	Agricultural contribution <sup>c</sup>	Reference
<i>H. villosa</i>	KS04WGRC48	<i>Pm21/Cmc</i>	T6AL·6V#1S	6VS	6AS	0	1	C	+	Chen <i>et al.</i> , 1995, 1996; Liu <i>et al.</i> , 1999; Qi <i>et al.</i> , 1996
<i>S. cereale</i>	<i>T. aestivum</i> cultivars Aurora and Kavkaz	<i>Pm8/Sr31/Lr26/Yr9</i>	T1BL·1R#1S	1RS	1BS	0	S	C	++	Bartos and Bares, 1971; Bartos <i>et al.</i> , 1973; Friebe <i>et al.</i> , 1989, 1996b; Lukaszewski, 1993; Mettin <i>et al.</i> , 1973; Ren <i>et al.</i> , 1997; Rogowski <i>et al.</i> , 1993; Schlegel and Korzun, 1997; Zeller, 1973; Zeller <i>et al.</i> , 1982
	<i>T. durum</i> KS91WGRC14 MA1, MA2	<i>Pm8/Sr31/Lr26/Yr9/Gli-B1/Glu-B3</i> (lacking <i>Sec-1</i> )	Ti1R#1S <sub>40;9; 44:38</sub> ·1BL Ti1R#1S <sub>40;9; 44:45</sub> ·1BL	1RS <sup>rec</sup>	1BL	0	HR	C	— —	Friebe <i>et al.</i> , 1987, 1989, 1993a Lukaszewski, 2000

(continued)

Table V (continued)

Alien species	Germplasm	Alien target gene(s)	Description	Size of alien translocation	Size of missing segment	FL of break point	Mode of transfer <sup>a</sup>	Type <sup>b</sup>	Agricultural contribution <sup>c</sup>	Reference
	Amigo	<i>Gb2/Pm17</i> (allelic to <i>Pm8</i> )	T1AL-1R#2S	1RS	1AS	0	I	C	++	Heun <i>et al.</i> , 1990; Hollenhorst and Joppa, 1981; Hsam and Zeller, 1997; Hsam <i>et al.</i> , 1995; Jiang <i>et al.</i> , 1994b; Lowry <i>et al.</i> , 1984; Lukaszewski, 1993; Sebesta and Wood, 1978; Sebesta <i>et al.</i> , 1995b; The <i>et al.</i> , 1992; Zeller and Fuchs, 1983
	GRS 1201	<i>Gb6</i>	T1AL-1R#3S	1RS	1AS	0	I	C	—	Porter <i>et al.</i> , 1991, 1994
	GRS 1204	<i>Gb6</i>	T2AL-2AS-1R#3S T2AS-1R#3S-1RL#3L			0.39 in S 0.27 in L	I	N	—	Friebe <i>et al.</i> , 1995e
	Transec	<i>Dn</i> <i>Lr25/Pm7</i>	T1BL-1R#4S T4BS-4BL-2R#1L	1RS 2.40 μm	1BS 1.03 μm of 4BL	0 0.61	HR I	C N	— —	Marais <i>et al.</i> , 1994 Driscoll and Anderson, 1967; Driscoll and Bielig, 1968; Driscoll and Jensen, 1963, 1964, 1965; Friebe <i>et al.</i> , 1996b; Heun and Friebe, 1990

ST-1	<i>Lr45</i>	T2AS-2R#3S- 2R#3L	1.71 $\mu$ m	1.58 $\mu$ m	0.39	I	C	—	McIntosh <i>et al.</i> , 1995a; Mukade <i>et al.</i> , 1970
WRT238		T3AS-3R#1S	3RS	3AL	0	I	N	—	Acosta, 1962; Friebe <i>et al.</i> , 1996b
90M126-2	<i>Sr27</i>	T3AL-3R#1S	3RS	3AS	0	I	C	—	Friebe <i>et al.</i> , 1996b; Marais and Marais, 1994
90M129-9		T3BL-3R#1S	3RS	3BS	0	I	C	—	
KS93WGRC28	<i>Pm20, rf</i>	T6BS-6R#3L	6RL	6BL	0	S	N	—	Friebe <i>et al.</i> , 1994a, 1995a; Heun and Friebe, 1990; Porter and Tuleen, 1972
KS85HF011 KS89WGRC8 Hamlet	<i>H21</i>	T2BS-2R#2L	2RL	2BL	0	TC	C	—	Friebe <i>et al.</i> , 1990a, 1999b; Lee <i>et al.</i> , 1996; Sears <i>et al.</i> , 1992a; Seo <i>et al.</i> , 1997
88HF16KS92	<i>H25</i>	T6BS-6BL-6R#1L	6.95 $\mu$ m		0.11	I	N	—	Delaney <i>et al.</i> , 1995a; Friebe <i>et al.</i> , 1991a,
WGRC17		T4BS-4BL-6R#1L	3.88 $\mu$ m		0.40	I	N	—	1999b; Mukai
WGRC19		T4BS-4BL-6R#1L	3.88 $\mu$ m		0.40	I	N	—	<i>et al.</i> , 1993;
WGRC20		Ti4BS-4AL-6R#1L- 4AL	0.70 $\mu$ m		0.06, 0.19	I	N	—	Sebesta <i>et al.</i> , 1997

**Table VI**  
**Alien Transfers Derived from *Agropyron* Species (for Description of Abbreviations, see Footnote to Table IV)**

Alien species	Germplasm	Alien target gene(s)	Description	Size of alien translocation	Size of missing segment	FL of break point	Mode of transfer <sup>a</sup>	Type <sup>b</sup>	Agricultural contribution <sup>c</sup>	Reference
<i>A. elongatum</i> ( <i>Thinopyrum ponticum</i> 2n = 10x = 70)	Agatha	<i>Lr19/Sr25</i>	T7DS-7DL-7Ac#1L	2.55 μm	2.62 μm of 7DL	0.32	I	C	+	Dvorak and Knott, 1977; Friebe <i>et al.</i> , 1994b; Knott, 1968; McIntosh <i>et al.</i> , 1977; Sharma and Knott, 1966
	Agatha-28	<i>Lr19/Sr25</i>	T7DS-7DL-7Ac#1L	2.73 μm	2.71 μm of 7DL	0.29	EMS	C	—	Friebe <i>et al.</i> , 1994b; Knott, 1980
	Agatha-235	<i>Lr19</i>	Ti7DS-7DL-7Ac#1L-7DL	1.99 μm	1.29 μm of 7DL	0.31, 0.75	EMS	C	—	Friebe <i>et al.</i> , 1994b; Knott, 1980
	7Ag#11	<i>Lr29</i>	T7DL-7Ac#1L-7Ac#1S				HR	C	—	Friebe <i>et al.</i> , 1996b; McIntosh <i>et al.</i> , 1995b; Procnier <i>et al.</i> , 1995; Sears, 1973, 1978
	Agent	<i>Sr24/Lr24</i>	T3DS-3DL-3Ac#1L	1.26 μm	1.38 μm of 3DL	0.70	S	C	++	Dedryver <i>et al.</i> , 1996; Friebe <i>et al.</i> , 1996b; Jiang <i>et al.</i> , 1994a; McIntosh <i>et al.</i> , 1977; Schachermayr <i>et al.</i> , 1995; Smith <i>et al.</i> , 1968

	Teewon	<i>Sr24/Lr24</i>	T1BL-1BS-3Ae#1L		0.50 in the satellite of 1BS	I	N	—	Friebe <i>et al.</i> , 1996b; Jiang <i>et al.</i> , 1994b; Sebesta <i>et al.</i> , 1995a; The <i>et al.</i> , 1992	
	K2046	<i>Sr26</i>	T6AS-6AL-6Ae#1L	2.48 $\mu$ m	3.63 $\mu$ m of 6AL	0.09	I	C	++	Dundas and Shepherd, 1998; Friebe <i>et al.</i> , 1994b; Knott, 1961, 1968
	CI15322	<i>Wsm</i>	T4DS-4DL-1Ae#1L	1.31 $\mu$ m	0.73 $\mu$ m of 4DL	0.67	I	N	—	Friebe <i>et al.</i> , 1996b; Jiang <i>et al.</i> , 1993b; Martin <i>et al.</i> , 1976; Pfannenstiel and Niblett, 1978; Sebesta and Bellingham, 1963; Sebesta <i>et al.</i> , 1972
	875-94-2	<i>Cmc2</i>	T5BL-6Ae#2S	6Ae#2S	5BS	0	S	C	—	Friebe <i>et al.</i> , 1996b; Kim <i>et al.</i> , 1992; Whelan and Hart, 1988; Whelan <i>et al.</i> , 1983
<i>A. inter- medium</i>	KS93WGRC27	<i>Wsm1</i>	T4DL-4Ai#2S	4Ai#2S	4DS	0	I	C	—	Friebe <i>et al.</i> , 1991b; Gill <i>et al.</i> , 1995; Talbert <i>et al.</i> , 1996; Wells <i>et al.</i> , 1973, 1982
	CI17883	<i>Wsm1</i>	T6AL-4Ai#2S T6AS-4Ai#2L	4Ai#2S 4Ai#2L	6AS 6AL	0 0	I	N	—	Friebe <i>et al.</i> , 1991b; Wells <i>et al.</i> , 1973, 1982

(continued)

Table VI (continued)

Alien species	Germplasm	Alien target gene(s)	Description	Size of alien translocation	Size of missing segment	FL of break point	Mode of transfer <sup>a</sup>	Type <sup>b</sup>	Agricultural contribution <sup>c</sup>	Reference
	A29-13-3	<i>Wsm1</i>	T4AL-4Ai#2S	4Ai#2S	4AS	0	HR	N	—	Chen <i>et al.</i> , 1998; Liang <i>et al.</i> , 1979; Wang and Liang, 1977; Wang and Zhang, 1996; Wang <i>et al.</i> , 1977; Wells <i>et al.</i> , 1982
	T4	<i>Lr38</i>	T3DL-3DS-7Ai#2L	2.78 $\mu\text{m}$	0.67 $\mu\text{m}$ of 3DS	0.46	I	N	—	Friebe <i>et al.</i> , 1992d, 1993b; Wienhues, 1960, 1966, 1967, 1971, 1973, 1979
	T7	<i>Lr38</i>	T6DS-6DL-7Ai#2L	4.19 $\mu\text{m}$	1.45 $\mu\text{m}$ of 6DL	0.32	I	N	—	
	T24	<i>Lr38</i>	T5AL-5AS-7Ai#2L	4.20 $\mu\text{m}$	0.88 $\mu\text{m}$ of 5AS	0.35	I	N	—	
	T25	<i>Lr38</i>	T1DS-1DL-7Ai#2L	2.55 $\mu\text{m}$	0.82 $\mu\text{m}$ of 1DL	0.59	I	N	—	
	T33	<i>Lr38</i>	T2AS-2AL-7Ai#2L	2.42 $\mu\text{m}$	1.40 $\mu\text{m}$ of 2AL	0.62	I	N	—	



86-187	<i>Sr44</i>	T7DS- 7Ai#1L·7Ai#1S		HR	N	—	Cauderon, 1966; Cauderon <i>et al.</i> , 1973; Friebe <i>et al.</i> , 1996b; McIntosh, 1991
TC6	<i>Bdv</i>	T7DS-7Ai#1S· 7Ai#1L	0.33	TC	C	—	Banks <i>et al.</i> , 1995; Cauderon, 1966; Cauderon <i>et al.</i> , 1973; Friebe <i>et al.</i> , 1996b; Hohmann <i>et al.</i> , 1996
TC7	<i>Bdv</i>	T1BS-7Ai#1S· 7Ai#1L	0.37	TC	N	—	
TC14	<i>Bdv</i>	T7DS-7DL-7Ai#1L	0.56	TC	C	—	Ayala <i>et al.</i> , 2001; Banks <i>et al.</i> , 1995; Cauderon, 1966; Cauderon <i>et al.</i> , 1973; Friebe <i>et al.</i> , 1996b; Hohmann <i>et al.</i> , 1996
<i>Th. distichum</i>	Indis	<i>Lr19/Sr25</i> T7DS-7DL-7Ae#1L		S	C	+	Friebe <i>et al.</i> , 1996b; Marais and Marais, 1990; Marias <i>et al.</i> , 1988; Prins <i>et al.</i> , 1996

in WGRC26. [Ma \*et al.\* \(1993\)](#) identified molecular markers linked to both genes and confirmed chromosome mapping results for *H23* and *H24*. [Liu \*et al.\* \(2005a\)](#) have identified a microsatellite marker cosegregating with *H13* at the distal end of 6D short arm (6DS), a result contrary to the previous reported location on 6D long arm based on telosomic mapping ([Gill \*et al.\*, 1987](#)). A reexamination of the pedigree results showed that a wrong telosomic stock was used in the arm mapping experiment. These data also call for reevaluation of the relationship between *H13* and *H23* for which molecular marker data now show that both are located in the distal region of 6DS. [Liu \*et al.\* \(2006\)](#) have identified a molecular marker at the tip of chromosome 1AS cosegregating with a new Hessian fly gene transferred from dicoccum in WGRC42. The same marker also is tightly linked with genes *H9*, *H10*, and *H11*, indicating that they all map on chromosome 1A and not on 5A as reported previously ([Liu \*et al.\*, 2005b](#)).

Unlike Hessian fly, genetic analysis of leaf rust resistance in *Ae. tauschii* showed widespread occurrence of *Lr21* alleles in Iran ([Miller, 1991](#)). The molecular analysis showed that the *Lr40* gene in WGRC7 (derived from *Ae. tauschii* accession TA1649, collected in Iran) was allelic to *Lr21* (derived from TA1599, also collected in Iran, see [Rowland and Kerber, 1974](#)), and molecular cloning has confirmed this ([Huang and Gill, 2001](#); [Huang \*et al.\*, 2003](#)). A mistake was discovered in the released WGRC2 line, as it was identical to WGRC7 ([Huang and Gill, 2001](#)). Since then, original seed of WGRC2 has been evaluated, and it contains *Lr39* derived from TA1675 and is located on 2DS ([Raupp \*et al.\*, 2001](#)). In addition, it has been discovered that *Lr41* in WGRC10 previously located on 1D by monosomic mapping ([Cox \*et al.\*, 1994b](#)) is allelic to *Lr39* in 2DS arm ([Singh \*et al.\*, 2003](#)). WGRC16 was reported to have a gene designated *Lr43* located on 7D by monosomic mapping ([Hussein \*et al.\*, 1997](#)). Segregation analysis and evaluation with markers for *Lr21* and *Lr39* indicated that in fact, WGRC16 carries the gene combination *Lr21* and *Lr39* (Brown-Guedira, unpublished data). These analyses indicate that *Lr39* also may be widespread in *Ae. tauschii* since this gene appears to have been transferred from multiple accessions. The *T. turgidum* subsp. *armeniicum*-derived gene *Lr50* in wheat germplasm WGRC36 was mapped to 2B long arm and is the first leaf rust-resistance gene located on that chromosome arm ([Brown-Guedira \*et al.\*, 2003](#)). *Lr50* was also transferred to wheat from several different accessions of *T. turgidum* subsp. *armeniicum*. The molecular mapping is ongoing for all the remaining leaf rust-resistant WGRC lines and a clearer picture of diversity of leaf rust-resistance genes should emerge in the near future.

In molecular analysis of other germplasm, dominant male sterility gene *Ms3* (in KS87UP9) has been tagged with molecular markers located

in the proximal region of 5AS (Qi and Gill, 2001). Wheat curl mite resistance gene *Cmc4* in WGRC40 has been located in 6DS and tagged with a molecular marker (Malik *et al.*, 2003a). Genes on alien segments transferred by intergenomic manipulation have been characterized only as to the identity of chromosome segments involved as analyzed by C-banding and *in situ* hybridization (see Tables IV–VI), but their molecular analysis is more problematic. How this kind of analysis must be undertaken is illustrated by molecular mapping of *H25* transferred from rye and tagged with a molecular marker located 1.7 cM from the gene (Delaney *et al.*, 1995a).

## VI. GERMPLASM FOR WHEAT-BREEDING PROGRAMS

A primary goal of the WGRC, from its earliest days, has been to develop new germplasm from interspecific and intergeneric crosses and release it in a genetic background that will encourage its use by public and private wheat breeders. The WGRC has made germplasm available in two ways: (i) through formal release by the Kansas State University Agricultural Experiment Station, cooperating experiment stations, and/or the USDA–ARS and (ii) through submission of entries in the USDA–ARS Regional Germplasm Observation Nursery (RGON).

From 1985 through 2004, the WGRC issued 48 germplasm releases (Table III). Most of these lines were registered in the journal *Crop Science* and deposited with the National Plant Germplasm System. Release notices were sent to research and breeding organizations in the United States and around the world.

In all, but three of the germplasm lines, the primary traits were resistances to pathogens, insects, or mites. Nine carried chromosomal translocations involving alien segments; most of the remainders were derived from hybridization with *Aegilops* and *Triticum* species, followed by homologous recombination. Because the WGRC's intention is to expand the gene pool of wheat with useful genetic diversity not previously available, much effort has been focused on determining the genetic basis of the traits expressed by these germplasm lines. Allelism studies, monosomic analysis, linked markers, molecular cytogenetics, and other methods have provided information on the locations of genes in most of the released lines (Tables IV–VI).

The WGRC has not only concentrated on problems of economic importance in the US hard winter wheat region (e.g., leaf rust, Hessian fly, virus diseases, wheat curl mite, Septoria leaf and glume blotch, tan spot, Russian wheat aphid, and heat stress) but also has released germplasm

that addressed problems of greater relevance in other regions (e.g., powdery mildew and *Fusarium* head blight). For recurrent parents, researchers generally used hard winter wheat cultivars or experimental lines adapted to the central and southern Great Plains. However, two of the releases were durum wheats with unique chromosomal segments from rye (Table III).

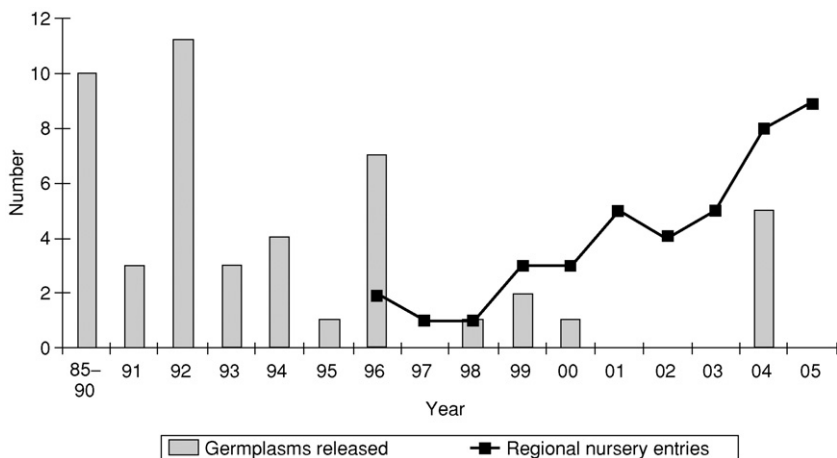
The second route of germplasm dissemination has been through the RGON, to which breeders and geneticists throughout the hard winter wheat region submit early-generation lines for evaluation and observation. Lines are evaluated for at least eight traits, with testing for each trait done by cooperators at one or more appropriate sites in the region. The RGON is coordinated by the USDA–ARS Wheat, Sorghum, and Forage Unit at Lincoln, Nebraska, which distributes the data to all interested members of the wheat research community. WGRC scientists entered approximately 80 lines in the RGON from 1996 to 2004 and distributed seed in response to any subsequent requests.

For germplasm, one indicator of relevance is its frequency in pedigrees of advanced lines and cultivars. Breeders in the central and southern US hard winter wheat region enter some of their most advanced lines in the Southern Regional Performance Nursery (SRPN). The 2005 SRPN, sown in 2004, had 44 experimental entries. The numbers of entries that have had WGRC germplasm lines or RGON entries as direct parents (i.e., in the final cross before selection) have risen steadily from one or two in 1996–1998 to nine in 2005 (Fig. 4). Those lines were derived from WGRC parents distributed in the late 1980s and throughout the 1990s (Fig. 4).

Of course, germplasm has a practical impact on agriculture only when it is used to develop cultivars. The lag time between release of a germplasm line and the release of a cultivar descended from that line is longer than the lag time for breeding lines that was evident in Fig. 4. By 2004, WGRC parents had appeared in the pedigrees of three hard winter wheat cultivars, “Overley,” Agripro “Thunderbolt,” and Agripro “Fannin,” and the soft red winter wheat “Rachael.” WGRC10 is one of the parents of the Croatian cultivar “Talija.” WGRC parents have been used frequently by the wheat-breeding program at CIMMYT (van Ginkel, M., personal communication).

## VII. THE NEXT 25 YEARS

It is worth projecting what the WGRC will look like in the next 25 years. The WGRC was a dream that became a reality and had tremendous growth during the last 25 years, far outpacing the infrastructure, staff needs, and the



**Figure 4** Numbers of germplasm releases by the WGRC from 1985 through 2004 (bars) and numbers of entries in the Southern and Northern Regional Performance Nurseries from 1996 through 2005 in which at least one immediate parent was developed by the WGRC.

operating budget. Yet the challenge for the next 25 years to the year 2030 is even greater. Population growth and economic development are putting a huge stress on the natural range of the wild wheat species and relatives that are the wellspring of genetic diversity, the capital for crop improvement programs. The concept that we could sample the natural genetic diversity and conserve it in our gene banks is only partially true. We know now that stress resistance genes against environmental assault are fast evolving and for these we must have sufficiently large populations over diverse geographic regions so that such evolutionary processes can go on in nature in response to the ever changing and man-made environmental conditions. Thus, we must pay attention to *in situ* conservation. For rational decisions on the areas to be conserved and collections to be made, we must understand the structure and distribution of genetic diversity of our crop plant relatives. We must survey what we have in our gene banks, after eliminating duplicated collections, and analyze collections from areas of genetic diversity for further collections and *in situ* conservation. For harnessing the natural genetic variation for crop improvement, we must have extensive and intensive knowledge of crop plant morphology, physiology, and especially the genomic knowledge at the level of chromosomes structure and behavior, and down to the DNA sequence. This will require a huge investment in genetic and genomic tools, resources, and infrastructure. To reflect this and to meet this challenge, we have redefined the mission of the WGRC to the

Wheat Genetics and Genomic Resources Center (WGGRC). The WGGRC will strive its best to serve the wheat genetics community in this new environment. The WGGRC will promote and conduct collaborative research on the following objectives:

1. Collect, maintain, evaluate, document, and conserve regions of high and useful genetic diversity and distribute wheat genetic and molecular resources.
2. Develop and distribute improved germplasm using traditional and novel genetic technologies for enhancing and sustaining crop production and productivity.
3. Develop and distribute genetic stocks especially to facilitate functional analysis of the wheat genome.
4. Conduct wheat genome mapping and sequencing of genes and allele mining to facilitate marker-assisted breeding and value-added trait development.
5. Conduct training and outreach.

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