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BREAD WHEAT

Improvement and Production

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Cytogenetics, phylogeny and evolution of cultivated wheats

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A wealth of data on the genomic structure of cultivated wheats has accumulated after almost a century of research, beginning with the pioneering genetic experiments of NilssonEhle (1909) and the cytological studies of Sakamura (1918) and Sax (1918). The tools for studying genetics have evolved over the years. Beginning in the 1920s, the method of nuclear genome analysis based on chromosome pairing behaviour in interspecific hybrids (Kihara, 1919; Sax, 1922) provided information on genome constitution, phylogeny and the evolution of *Triticum* and *Aegilops* species (summarized in Lilienfield, 1951). In the 1930s, Sears (summarized in Sears, 1954, 1966; Sears and Sears, 1978) began studies with wheat aneuploids that ushered in the era of formal cytogenetic analysis and gene mapping of individual chromosomes and arms in wheat (a catalogue of mapped genes is

published each year, see McIntosh *et al*., 1998 for the latest edition). In the 1970s, modern staining techniques were used to analyse the substructures of cereal chromosomes, and a cytogenetic karyotype of wheat was developed (Gill and Kimber, 1974a; Gill, B.S. *et al*., 1991). Non-isotopic methods of mapping DNA sequences *in situ* (*in situ* hybridization) on chromosomes on a glass slide were used to construct a molecular karyotype of wheat (Rayburn and Gill, 1985; for review see Jiang and Gill, 1994a). These so-called molecular cytogenetic methods of genome analysis have greatly facilitated cytogenetic analysis in wheat and related species, especially the analysis of alien transfers (Friebe *et al*., 1991, 1996a). The technique of DNA restriction fragment length polymorphism (RFLP) analysis and linkage mapping was applied to wheat in the 1980s (Chao *et al*., 1989; Kam-Morgan *et al*., 1989). The genetic linkage maps of common wheat (Liu and Tsunewaki, 1991; Cadalen *et al*., 1997; Devos and Gale, 1993; Van Deynze *et al*., 1995; Nelson *et al*., 1995a, 1995b, 1995c; Marino *et al*., 1996), durum wheat (Blanco *et al*., 1998) and two of the progenitor species have been developed (Gill, K.S. *et al*., 1991; Dubcovsky *et al*., 1996).

The century has ended with the production of powerful deletion stocks (Endo and Gill, 1996) that were used to develop cytologically based physical maps of molecular markers for the 21 chromosomes of wheat (Gill *et al*., 1993, 1996a, 1996b; Delaney *et al*., 1995a, 1995b; Mickelson-Young *et al*., 1995; Werner *et al*., 1992; Hohmann *et al*., 1994). These cytogenetic maps pave the way for targetted mapping and eventual cloning of agronomically significant genes in polyploid wheat. The recently constructed microsatellite map of wheat (Röder *et al*., 1998) is a major milestone that will promote wide application of molecular markers in wheat breeding research. Building upon an earlier review (Morris and Sears, 1967), the last comprehensive review of wheat cyto-genetics appeared in 1987 (Morris, 1987). This chapter will highlight main advances since then, woven in a historical context that is most relevant to wheat crop improvement efforts worldwide.

CULTIVATED WHEATS BELONG TO THREE PLOIDY GROUPS

By the 1920s, it was known that cultivated wheat species of the genus *Triticum* have chromosome numbers of 2n=14, 28 and 42 (Sakamura, 1918). This suggested a basic 1x chromosome number of 7 and the

occurrence of diploid (2n=2x=14), tetraploid (2n=4x=28) and hexaploid (2n=6x=42) wheat species. Numerous studies since then have confirmed that 1x=7 is the basic chromosome number of the tribe Triticeae (or the basic Triticeae genome is organized into seven chromosomes). Furthermore, a specific chromosome or part of a chromosome in a basic genome is genetically related to a specific chromosome or a part of it in all other genomes of the Triticeae species. This is because gene synteny has been conserved throughout genome evolution and speciation of the genera in the Triticeae tribe and Poaceae family (Ahn *et al*., 1993). These genetically related chromosomes in different genomes are called homoeologous as compared to essentially genetically identical homologous pairs of chromosomes in diploid species. Poly-ploid wheat contains homologous as well as homoeologous chromosomes. The whole cytogenetic enterprise rests on the recognition of homoeology and gene content of individual chromosomes in different genomes of the Triticeae species. This information is used to formulate strategies for the manipulation of unique genes in different genomes of diverse species for wheat crop improvement. In addition, this information is useful in studies of the natural phenomenon of genome evolution and speciation that has generated a wondrous species diversity.

TAXONOMIC STATUS OF *TRITICUM* AND *AEGILOPS* SPECIES

The most recent taxonomic treatment of *Triticum* and *Aegilops* (van Slageren, 1994) is followed here with some modifications (Table 4.1, Table 4.2). One major disagreement is the treatment of *Amblyopyrum* (formerly *Ae. mutica*) as a separate genus; in Table 4.2 it is retained in genus *Aegilops* as *Ae. mutica*.

Two valid biological species of *Triticum* exist at each ploidy level (Table 4.1). Among diploid wheats, *T. monococcum* (einkorn wheat) is still cultivated to a limited extent, and its wild form ssp. *aegilopoides* (also known as *T. aegilopoides*) is widely distributed in the Middle East. Hybrids between the two are fully fertile. The second diploid wheat species *T. urartu*, previously thought to be endemic to Armenia, is sympatric with *T. aegilopoides* and wild tetraploid *Triticum* species throughout their range of distribution in the Middle East (Johnson, 1975). Johnson and Dhaliwal (1976) showed that hybrids between *T.*

monococcum and *T. urartu* were fully sterile (although their chromosomes paired as ring bivalents indicating identical genomic constitution) and unequivocally established *T. urartu* as a valid biological species.

Both tetraploid species *T. turgidum* and *T. timopheevii* have cultivated as well as wild forms. The hybrids between *T. turgidum* and *T. timopheevii* are sterile, establishing them as valid biological species. The hulled wheat *T. turgidum* ssp. *dicoccum* (emmer wheat) was one of the ancient cultivated wheats. However, it is the free-threshing macaroni or durum wheats that are more widely cultivated now. *Triticum timopheevii* is of little economic importance. The wild forms of both tetraploid wheats *T. turgidum* ssp. *dicoccoides* (also known as *T. dicoccoides*) and *T. timopheevii* ssp. *armeniacum* (also known as *T. armeniacum* or *araraticum*) are widely distributed in the Fertile Crescent. *Triticum dicoccoides* is found exclusively in Israel, Syria and Lebanon, *T. armeniacum* in Azerbaijan and Armenia, and both overlap in Turkey, northern Iraq and possibly Iran.

Both hexaploid species *T. aestivum* and *T. zhukovskyi* are only found in cultivation. *Triticum zhukovskyi* is a botanical curiosity. However, *T. aestivum*, also known as common, bread or dinkel wheat, is of paramount economic importance and, along with rice, is a staple food of humankind.

TABLE 4.1 **Species of genus *Triticum* and their genomic constitution**

Species	Genomic constitution	
	Nuclear	Organellar
Triticum aestivum L. (common or bread wheat)	ABD	B (rel. to S)
Subspecies: *compactum* (Host) MacKey (club wheat); *macha* (Dekapr. & Menabde) MacKey; *spelta* (L) Thell. (large spelt or dinkel wheat); *sphaerococcum* (Percival) MacKey (Indian dwarf wheat)		

Triticum turgidum L. (pollard wheat)	AB	B (rel. to S)
Subspecies: *carthlicum* (Nevski) A. Löve & D. Löve (Persian wheat); *dicoccum* (Schrank) Thell. (emmer wheat); *durum* (Desf.) Husn. (macaroni or durum wheat); *paleocolchicum* (Menabde) A. Löve & D. Löve; *polonicum* (L.) Thell. (Polish wheat); *turanicum* (Jakubz.) A. Löve & D. Löve (Khorassan wheat); *dicoccoides* (Körn. ex Asch. & Graebn.) Thell. (wild emmer)		
Triticum zhukovskyi Menabde & Ericz.	A^tA^mG	A (rel. to S)
Triticum timopheevii (Zhuk.) Zhuk. (cultivated form) Subspecies: *armeniacum* (Jakubz.) van Slageren (wild form)	A^tG	G (rel. to S)
Triticum monococcum L. (einkorn or small spelt wheat) Subspecies: *aegilopoides* (Link) Thell. (wild form)	A^m	A^m
Triticum urartu Tumanian ex Gandilyan (wild form)	A	A

Aegilops is the most closely related genus to *Triticum* and both share annual growth habits (Table 4.2). Two of the three genomes present in bread wheat were donated by two different *Aegilops* species (see below). The genus *Aegilops* is comprised of 11 diploid species and 12 polyploid species, including tetraploids and hexaploids. Seven distinct genomes are present in diploid species genomes, and all, except the T genome of *Ae. mutica*, are also present in polyploid *Aegilops* species.

PHYLOGENY OF POLYPLOID WHEATS

One wild diploid *Triticum* species and two species of the closely related taxon *Aegilops* are involved in the phylogeny of polyploid wheats (Figure 4.1). Kihara (1919) and Sax (1922) presented cytological data on the pairing behaviour of interspecific hybrids between 2x/4x and 4x/6x wheats indicating that *T. monococcum* and *T. turgidum* share one genome in common and *T. turgidum* and *T. aestivum* share two

genomes in common. The cytological data did not discriminate between *T. monococcum* and *T. urartu* genomes (Johnson and Dhaliwal, 1976), but the molecular evidence showed that *T. urartu* actually is the Agenome donor of both polyploid wheats (Dvorak *et al*., 1988, 1993; and references cited therein), erroneously proposed as the Bgenome donor by Johnson (1975).

There has been much controversy regarding the origin of the B and G genomes of poly-ploid wheats since the early proposal of Sarkar and Stebbins (1956) supported by Riley *et al*. (1958) that *Ae. speltoides* was the donor of the second genome of tetraploid wheats. Recent molecular evidence is convincing that the B and G genomes of tetraploid wheats were donated by *Ae. speltoides* (Dvorak and Zhang, 1990). Cytoplasmic genome hetero-geneity within *Ae. speltoides* indicates that it may be the maternal (=cytoplasmic) donor of all polyploid wheats (Wang *et al*., 1997). Jiang and Gill (1994b) reported cytological evidence supporting a diphyletic origin of the two tetraploid wheat species.

TABLE 4.2 **Species of genus *Aegilops* and their genomic constitution**

Species	Genomic constitution[a]	
	Nuclear	Organellar
Aegilops speltoides Tausch	S	S,G,G^{2}
Aegilops longissima Schweinf. & Muschl.	S^{1}	S^{12}
Aegilops searsii Feldman & Kislev ex Hammer	S^{s}	s^{v}
Aegilops sharonensis Eig	S^{sh}	S^{1}
Aegilops bicornis (Forssk.) Jaub. & Spach	S^{b}	s^{b}
Aegilops tauschii Coss. var. *tauschii,* var. *strangulata*	D	D
Aegilops uniaristata Vis.	N	N

Aegilops comosa Sm. in Sibth. & Sm. var. *heldreichii*	M	M
Aegilops caudata L.	C	C
Aegilops umbellulata Zhuk.	U	U
Aegilops mutica Boiss.	T	T,T^{2}
Aegilops cylindrica Host	$D^{c}C^{c}$	D
Aegilops ventricosa Tausch	$D^{v}N^{v}$	D
Aegilops crassa Boiss.	$\underline{D}^{c1}\underline{M}^{c}(D^{c1}X^{c})$	D^{2}
var. *glumiaristata*	$\underline{D}^{c1}\underline{D}^{c2}\underline{M}^{c}(D^{c1}D^{c2}X^{c})$	.
Aegilops juvenalis (Thell.) Eig	$\underline{DMU}$ $(D^{c}X^{c}U^{j})$	D^{2}
Aegilops vavilovii (Zhuk.) Chennav.	$\underline{DMS}$ $(D^{c}X^{c}S^{v})$	D^{2}
Aegilops triuncialis L.	$U\underline{C}^{t}$	U,C^{2}
Aegilops columnaris Zhuk.	$U\underline{M}$ (UX^{CO})	U^{2}
Aegilops neglecta Req. ex Bertol. (syn. *Ae. triaristata)*	$U\underline{M}$ (UX^{n})	U
var. *recta* (Zhuk.) Hammer	$\underline{UMN}$ $(UX^{t}N)$	U
Aegilops geniculata Roth (syn. *Ae. ovata)*	$U\underline{M}$ (UM^{0})	M°
Aegilops biuncialis Vis.	$U\underline{M}$ (UM^{0})	U
Aegilops kotschyi Boiss.	$U\underline{S}$ (US^{1})	s^{v}
Aegilops peregrina (Hack. in J. Fraser) Maire & Weiller (syn. *Ae. variabilis)*	$U\underline{S}$ (US^{1})	s^{v}

[a]Underlined genomes are modified at the polyploid level and those in brackets were deduced from DNA analysis. *Source:* Modified from Dvorak, 1998, based on chromosome pairing and DNA analysis.

Whereas the tetraploid wheats are of ancient origin, as evident from their wide distribution in nature, both hexaploid wheats are of recent origin under cultivation. McFadden and Sears (1944, 1946) and Kihara (1944) demonstrated that *Ae. tauschii* was the D-genome donor of bread wheat, which arose from a hybridization of *T. turgidum* and *Ae. tauschii* ssp. *strangulata*, about 7 000 years ago (see Dvorak *et al*., 1998 for latest review). *Triticum zhukovskyi* arose from the hybridization of *T. timopheevii* with *T. monococcum* (Upadhya and Swaminathan, 1963).

DOMESTICATION OF CULTIVATED WHEATS

The Fertile Crescent is considered the birth-place of cultivated wheats about 8 000 to 10 000 years ago. Pure stands of wild diploid einkorn and wild tetraploid emmer are found there and may have been harvested and cultivated as such. Recent genetic evidence indicates that einkorn wheat (*T. monococcum*) may have been domesticated from wild einkorn (*T. monococcum* ssp. *aegilopoides)* in the region of the Karacadag mountains in southeast Turkey (Heun *et al*., 1997). Both wild and cultivated einkorn seed remains have been excavated in the nearby archaeological sites dating from 7500 to 6200 BC.

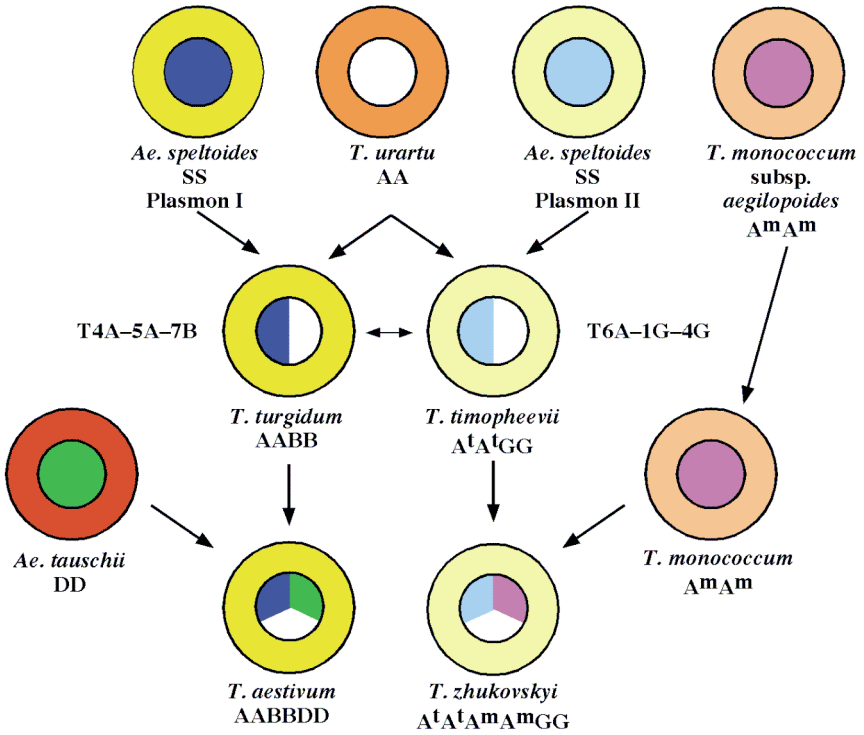

FIGURE 4.1 Phylogeny of polyploid wheats

The remains of cultivated emmer (*T. turgidum* ssp. *dicoccum*) have been discovered at several archaeological sites in Syria dating to 7500 BC (Zohary and Hopf, 1993). The free-threshing forms arose by mutation from primitive emmer wheats.

Bread wheat arose farther northwest, away from the Fertile Crescent, in the corridor extending from Armenia in Transcaucasia to the southwest coastal areas of the Caspian Sea in Iran (Dvorak *et al*., 1998). In this region, *Ae. tauschii* var. *strangulata* is predominant, which evidently hybridized with cultivated emmer to produce *T. aestivum*. Perhaps several independent hybridization events occurred that constitute the gene pool of bread wheat (Talbert *et al*., 1998). The first bread wheats may have looked similar to *T. aestivum* ssp. *spelta* found growing in Iran from which free-threshing types were derived by mutation (McFadden and Sears, 1946). The European spelt wheats may have been derived secondarily from a hybridization involving *T. compactum* and emmer wheat (Ohtsuka, 1998).

CYTOGENETIC STRUCTURE OF CULTIVATED WHEATS

Triticum aestivum

Bread wheat has a genome size of 16 billion base pairs (bp) of DNA organized into 21 pairs of chromosomes, seven pairs belonging to each of the genomes A, B and D (Sears, 1954; Okamoto, 1962). Sears (1954) identified individual chromosomes of wheat by monosomy and made some observations on their gross morphology, although most chromosomes were cytologically indistinguishable. Sears and Sears (1978) isolated marker telocentric chromosomes to expedite their identification. Chinese Spring aneuploid stocks have been converted to locally adapted varieties by numerous cytogeneticists (Law, 1993) for the mapping of phenotypic traits. Wheat chromosomes are most efficiently identified based on their unique heterochromatic banding (C-banding) patterns (Gill, B.S. *et al*., 1991) (Plate 2) and molecular karyotyping (Pederson and Langridge, 1997). In Plate 2, the C-banding patterns of each of the 21 chromosomes of wheat is unique as shown

for each chromosome at somatic metaphase (left) or meiotic metaphase (univalent) (right) stages. The C-banding technique reveals the location of two classes of chromatin, namely heterochromatin (dark-staining regions) and euchromatin (light-staining regions), along the chromosome axis. The rapid identification of somatic chromosomes from readily available root meristems has revolutionized cytogenetic research in wheat. Genomic affinity of individual chromosomes is determined by meiotic pairing analysis (Naranjo *et al*., 1987; Gill and Chen, 1987) or by sequential banding and genomic *in situ* hybridization (Jiang and Gill, 1993, 1994b).

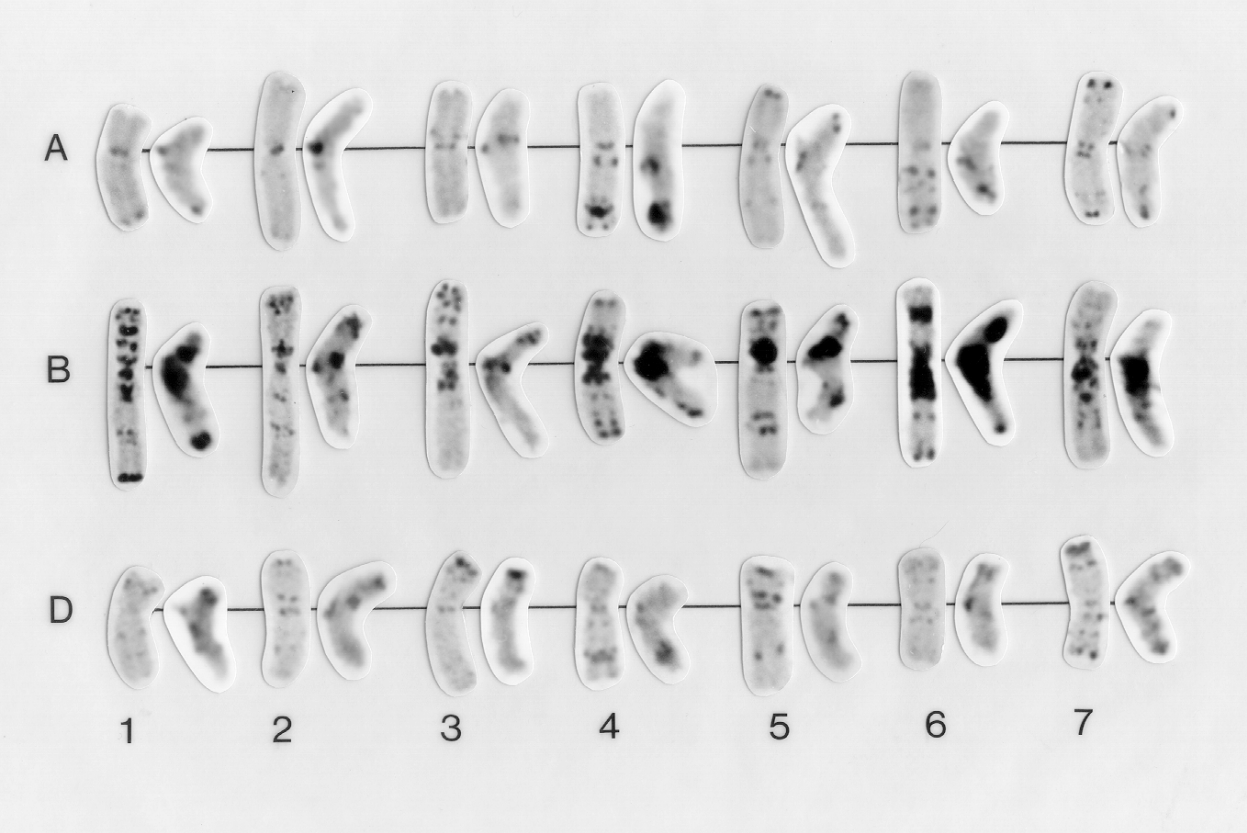

PLATE 2 The C-banded karyotype of Triticum aestivum cv. Chinese Spring wheat

Although gross chromosome homologies are conserved, structural changes involving chromosomes 4A, 5A and 7B are apparently present in all hexaploid and tetraploid wheats (Naranjo *et al*., 1987; Naranjo,

1990). Furthermore, chromosome 4A has undergone complex structural rearrangements (Mickelson-Young *et al*., 1995) and fails to pair with its ancestral 4A of diploid wheat or 4A of *T. timopheevii* (Gill and Chen, 1987). Such a chromosomal restructuring event coinciding with the origin of polyploid species is called a species-specific translocation, and it is postulated to restore fertility in the raw amphiploid (Gill, 1991). Chromosome 4B has undergone an inversion in Chinese Spring and other wheats but not in winter wheats (Endo and Gill, 1984; Mickelson-Young *et al*., 1995). In addition, some translocation polymorphisms have been documented in different wheat cultivars (Friebe and Gill, 1994).

Although polyploid, wheat shows disomic inheritance due to diploid-like pairing regulated by two major pairing homoeologous genes *Ph1* (Riley and Chapman, 1958) and *Ph2* (Mello-Sampayo, 1971) and some minor genes (see Sears, 1976 for review). Mutants of *Ph* genes have been produced (Sears, 1977) and genes epistatic to *Ph* genes (*Phl*) have been identified in related diploid species and transferred to common wheat (Chen *et al*., 1994). *Phl*, as well as *Ph* gene mutants, can be used in alien gene transfers by induced homoeologous pairing (Koebner and Shepherd, 1986; Sears, 1993).

As mentioned earlier, cytogenetically based physical maps have been constructed for all 21 chromosomes of wheat. In Figure 4.2, the physical map (left) shows an ideogram of C-banded chromosome 5D. The position of deletion breakpoints is indicated on the left. Thus, 5DS-2 (top left) is a deletion stock with breakpoint at 78 percent of fraction length from the centromere in the short arm. The molecular markers mapped in deletion intervals are indicated on the right. The 5D genetic map shows centimorgan (cM) distances on the left and the position of molecular markers on the right. The group 5 consensus physical map is an integrated map based on deletion mapping data of chromosomes 5A, 5B and 5D of wheat (see Gill *et al*., 1996a for details). Common markers joining the genetic and physical maps are indicated. The integrated map clearly shows that recombination is suppressed in the proximal centromeric regions of wheat chromosomes. The consensus physical map also shows the paucity of markers in the centromeric region. The approximate position of some major genes including *Ha* (hardness gene), *Vrn* (vernalization response), *Lr1* (leaf rust

resistance), *Fr1* (frost resistance) and others are indicated on the map (see Boyko *et al*., 1999).

The cytogenetic maps show that molecular markers, most of which are cDNA (copy DNA of actively transcribing genes), are non-randomly distributed in clusters in the distal regions of the chromosomes. Recombination is also mostly restricted to gene cluster regions. The gene density and bp/cM ratio in cluster regions may vary from 55 to 120 kilo-bases (Kb) of DNA. Moreover, agronomically important genes are also mostly located in gene cluster regions and may be amenable to map-based cloning using targetted mapping strategies (Gill *et al*., 1996a, 1996b).

Triticum turgidum

Durum wheat has a genome size of 10 billion bp of DNA organized into 14 pairs of chromosomes. The structure of A- and B-genome chromosomes of durum wheat is essentially identical to the corresponding homologues in bread wheat. Durum wheat is far less tolerant of aneuploidy than bread wheat, and monosomic analysis was difficult due to poor fertility of the monosomics. However, the development of D-genome chromosome substitution lines and double ditelocentric stocks have greatly expedited chromosome and arm mapping of genes (Joppa, 1987). A *Ph1* gene deletion mutant (Giorgi and Cuozzo, 1980) and a DS5B(5D) stock (Joppa, 1987) are useful stocks for alien gene transfers in durum wheat. Wild *T. dicoccoides* shows extensive chromosome polymorphism, in addition to the primitive chromosome arrangement similar to Chinese Spring in some accessions (Kawahara, 1988).

Triticum timopheevii

The individual chromosomes of *T. timopheevii* were cytogenetically identified by banding analysis of meiotic pairing configurations of *T. timopheevii*/*T. turgidum* hybrids (Gill and Chen, 1987) and substitution lines of *T. timopheevii* chromosomes in common wheat (Brown-Guedira *et al*., 1996). There has been some differentiation of the A genome of *T. timopheevii* as compared to the A genome of diploid and polyploid wheats. Badaeva *et al*. (1994) have presented extensive data on

chromosome polymorphisms in wild populations of *T. timopheevii*. A species-specific founder translocation involving chromosomes 6At, 1G and 4G (Jiang and Gill, 1994b) distinguishes *T. timopheevii* from *T. turgidum*, which contains a founder translocation involving chromosomes 4A, 5A and 7B (Naranjo, 1990). *Triticum timopheevii* and *T. turgidum* have a common origin from the same diploid progenitor species, share the *Ph1* gene (Dhaliwal, 1977) and their B and G genomes share more homology with each other than with any other genome of the Triticeae (Gill and Chen, 1987). The cytogenetic data indicate that genes can be transferred from *T. timopheevii* into wheat by direct crosses and recombination.

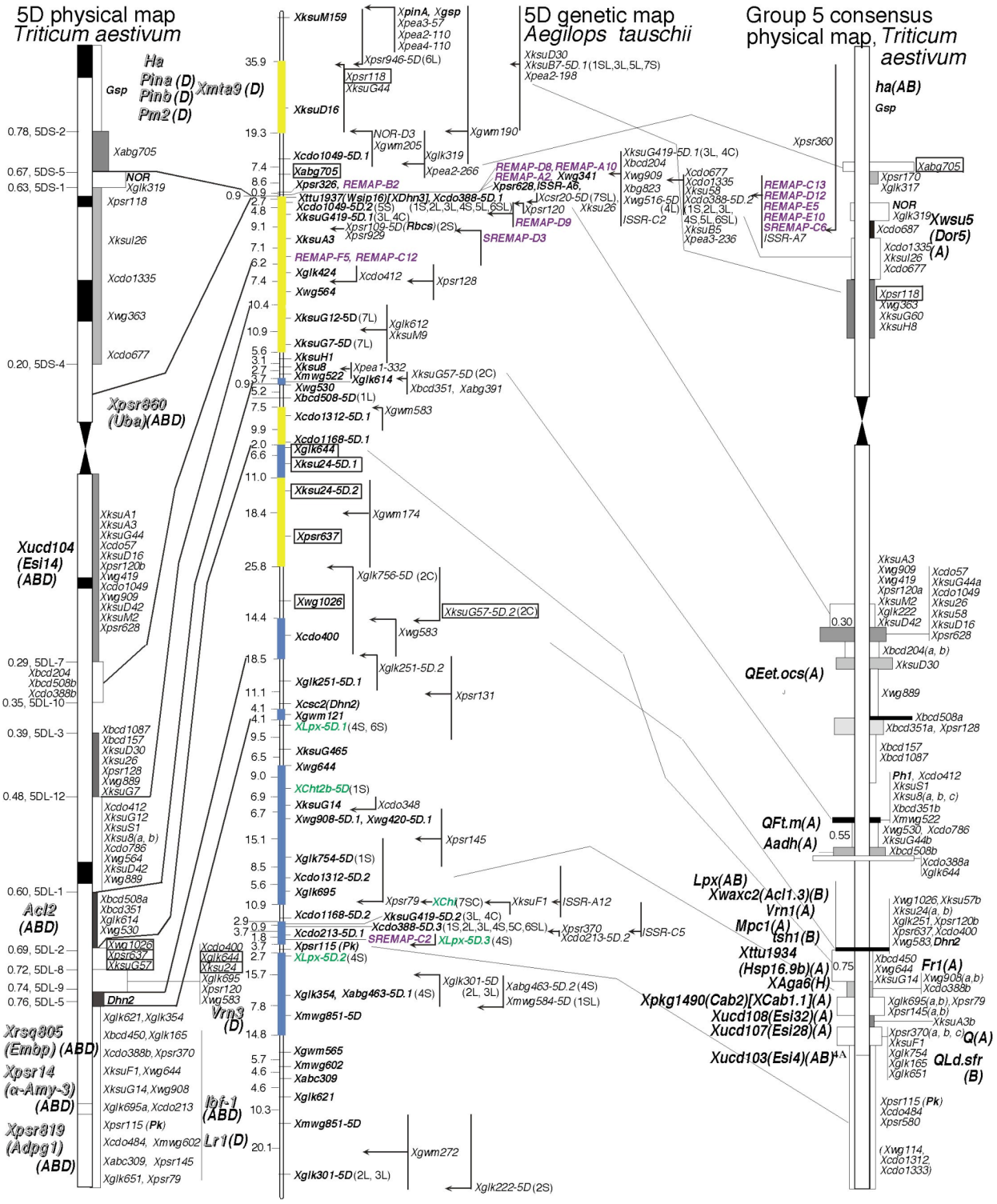

FIGURE 4.2 Integrated physical and genetic map for the group-5 chromosomes of wheat

Triticum monococcum

The A genome of diploid wheat consists of 5 billion bp of DNA organized into seven pairs of chromosomes. Kuspira and his colleagues (see Friebe *et al*., 1990) carried out cytogenetical studies and developed a primary trisomic series that proved to be of limited value due to its high sterility. Friebe *et al*. (1990) constructed the standard karyotype, and all chromosomes were individually identified. In addition to cytological polymorphism associated with different geographical populations, both *T. monococcum* and *T. urartu* contain a translocation involving chromosomes 4A and 5A (Dubcovsky *et al*., 1996). There has been some differentiation between the A genome of diploid and polyploid wheats as evidenced from the reduced level of pairing, or absence of pairing in the case of chromosome 4A (Gill and Chen, 1987), in the amount of C-heterochromatin (Friebe and Gill, 1996) and other structural features (Jiang and Gill, 1994c). Genetic transfers are feasible from diploid to polyploid wheats by bridging crosses or direct crosses (Cox *et al*., 1991). However, because of genome differentiation, linkage drag is likely, and methods to enhance recombination may need to be deployed (Dubcovsky *et al*., 1995). Those who wanted to improve *T. monococcum* by crosses with 4x and 6x wheats were disappointed as such transfers are impossible (Sharma and Waines, 1981).

STANDARD KARYOTYPES OF *AEGILOPS* AND OTHER TRITICEAE SPECIES

Because wild species are excellent sources of useful genes, interspecific hybridization and cytogenetic identification of individual chromosomes of wild species is a necessary first step in the exploitation of wild species in wheat improvement. Based on cytogenetic analysis, each analysed chromosome must be individually identified (by banding or molecular karyotyping), assigned to one of the seven basic homoeologous groups of the Triticeae and assigned as to its genomic affinity. The cytogenetic identification of chromosomes of progenitor species is straightforward and is based on comparative banding analysis using the standard karyotype of bread wheat (see Friebe and Gill, 1996 for review).

The cytogenetic analysis of non-progenitor species that carry a different genome than those of bread wheat is more time-consuming. The classical cytogenetic approach is illustrated in Figure 4.3. A synthetic amphiploid is used to isolate all alien chromosomes as single chromosome additions in wheat. The genetic identity (homoeology grouping) of individual chromosomes is determined by molecular markers, especially RFLPs. Gametophytic and sporophytic compensation experiments may follow, leading to the production of a set of individual alien chromosome substitution lines.

In the second approach, the cytogenetic identity and homology of an unknown alien chromosome is determined from its pairing behaviour with a wheat chromosome of known homology. The alien chromosome is induced to pair with a wheat chromosome by manipulating the *Ph*-gene system. The paired chromosomes in meiotic configurations at metaphase I of meiosis (MI) are identified by banding analysis (Naranjo *et al*., 1987; Gill and Chen, 1987). This approach was used to detect some of the species-specific translocations in wheat and has also been used to construct standard cytogenetic karyotypes and detect structural changes in the genomes of several alien species. Using this approach, one can also determine the relative feasibility of genetic transfer between specific wheat and alien chromosomes.

The third approach, which is not fully developed but individual pieces are in place, allows rapid molecular cytogenetic identification of individual chromosomes *in situ* (on a glass slide). Technical advances in DNA probe labelling, *in situ* hybridization and microscopy allow repeated hybridization, mapping and processing of chromosome images for multiprobe mapping on a single metaphase figure. A sequential banding/*in situ* hybridization procedure also can be used to determine the genetic and/or genomic affinity of cytologically identifiable individual chromosomes of a species using appropriate probes (Jiang and Gill, 1993, 1994b). A procedure for rapid cytogenetic mapping and assigning of genomic affinity of individual chromosomes of polyploid *Ae. cylindrica* using the tools and techniques of wheat cytogenetic analysis are demonstrated in Plate 3. The metaphase cell (Plate 3a) was processed for *in situ* hybridization, and ribosomal genes were mapped as indicated (Plate 3b-c). The probe was stripped and hybridized with repetitive DNA probes as indicated (Plate 3d-e).

Repetitive DNA probe pAs1 is D-genome specific (Rayburn and Gill, 1986), and it distinguished the D-genome chromosomes from the C-genome chromosomes. Plate 3f is an overlay that depicts the physical location of all the mapped DNA sequences. All D-genome chromosomes and some C-genome chromosomes and their genomic affinities (and phylogenetic origin) were cytogenetically identified in a experiment in a few days.

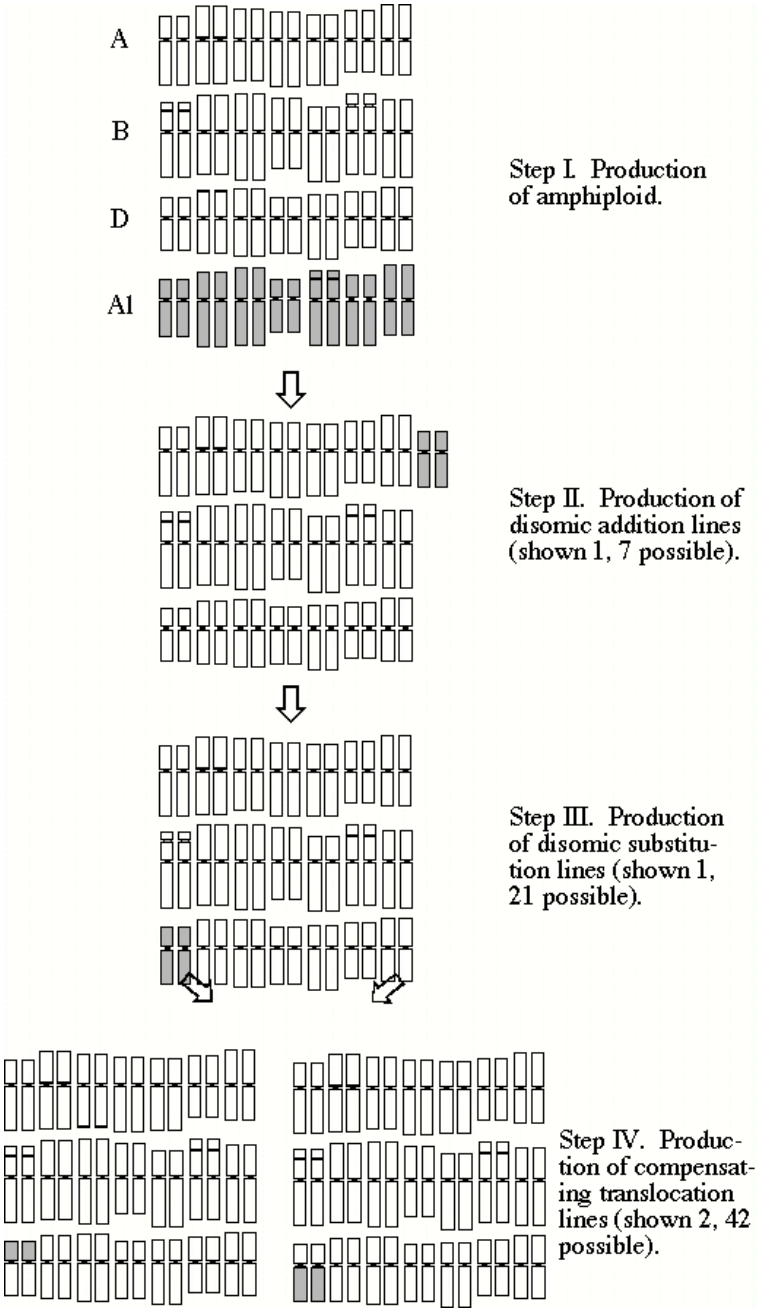

FIGURE 4.3 Scheme for systematic cytogenetic analysis of alien species and introgression of alien genetic variation into wheat

TABLE 4.3 **Some examples of species for which standard cytogenetic karyotypes have, been constructed and a large number of alien-wheat chromosome additions, substitutions and translocation lines have been isolated**

Species	Reference
Aegilops tauschii(D)	Joppa, 1987; Friebe *et al.,* 1992a
Aegilops speltoides (S)	Friebe *et al.,* 2000
Aegilops longissima (S^l)	Friebe *et al.,* 1993
Aegilops searsii (S^s)	Friebe *et al.,* 1995a
Aegilops umbellulata (U)	Friebe *et al.,* 1995b
Aegilops caudata (C)	Friebe *et al.,* 1992b
Aegilops peregrina (U^US^U)	Friebe *et al.,* 1996b
Secale cereale (R)	Gill & Kimber, 1974b; Mukai *et al.,* 1992
Thinopyrum intermedium (E1E2X)	Friebe *et al.,* 1992c
Leymus racemosus (JN)	Qi *et al.,* 1997
Elymus trachycaulus (SH)	Jiang *et al.,* 1994a
Hordeum chilense (H^{ch})	Cabrera *et al.,* 1995

Some of the species of *Aegilops* and other genera for which standard

karyotypes have been constructed and a large number of wheat-alien addition, substitution and translocation lines have been isolated are listed in Table 4.3. As an example, all seven chromosomes of *Ae. longissima* have been isolated as addition and substitution lines (Friebe *et al*., 1993). The next urgent task is the isolation of individual arms as compensating translocation lines (Figure 4.3) (Friebe *et al*., 1994a, 1994b). All wheat and alien chromosomes where gene synteny is conserved are candidates for the production of translocations. Structurally modified wheat chromosomes, such as 4A, 4B and arms 5AL, 7BS and others where fertility and other pivotal genes are located, should not be used in such manipulations. In general, all D-genome chromosomes are good candidates for the production of compensating translocations as they are the least modified among the three genomes of wheat.

The compensating translocation lines then need to be evaluated for biotic and abiotic stress factors and physiological, agronomic and other desirable traits in greenhouse and field experiments. The donor species accessions can be screened, and useful genetic factors transferred to wheat using compensation translocations in bridging crosses (Friebe *et al*., 1994a, 1994b). Thus, once a complete set of compensating translocation stocks incorporating the entire donor species genome have been isolated, any genetic variation in that species can be accessed for wheat improvement via bridging crosses.

TABLE 4.4 **Alien transfer in production agriculture**

Donor species	Target gene	Translocation	Method of transfer
Aegilops umbellulata	*Lr9*	T6BS.6BL-6UL	Irradiation
Secale cereale	*Pm8, Sr31, Lr26*	T1BL.1RS	Spontaneous
	Yr9, Pm 17, Gb2	T1AL.1RS	Irradiation
Agropyron elongatum	*Lr24, Sr24*	T3DS.3DL-3Ae#1L	Spontaneous

	Lr24, Sr24	T3DS.3DL-3Ae#1L	Induced recombination
	Sr26	T6AS.6AL-6Ae#1L	Irradiation
	Lr19, Sr25	T7DS.7DL-7Ae#1L	Irradiation

CHROMOSOME ENGINEERING

Because of polyploidy, the wheat genome is highly buffered, and the transfer of chromosome segments or large linkage blocks is more important than single genes. In general, compensating translocations involving exchanges of short arms may be agronomically desirable as is the case of transfers of the short arm of rye chromosome 1R substituting for short arms of wheat chromosomes 1A or 1B (Table 4.4). For translocations involving large alien chromosome arms, the unwanted chromatin in the translocation lines must be removed by chromosome engineering.

Already, there are spectacular examples of alien chromosome segments transferred to wheat, either by physical means (irradiation) or by genetic manipulation that have immensely improved the productivity of the wheat crop (Table 4.4). Sears (1993) has suggested some refinements in both induced homoeologous pairing and irradiation treatments to enhance the recovery of desirable transfers. Jiang *et al*. (1994b) have discussed strategies for the production and identification of desirable alien transfer segments.

C-banding is used to identify the alien chromosome with the target gene, the recipient wheat chromosome and the translocated chromosome. Genomic *in situ* hybridization using labelled alien DNA in excess of unlabelled wheat DNA is used to determine the size of the transferred alien segment and the size of the wheat segment that it replaced. A typical example of cytogenetic analysis for an alien transfer is shown in Plate 4. The C-banding pattern of a donor chromosome 4Ai#2 from *Thinopyrum intermedium* is shown on top. Gene *Wsm1*,

which conditions resistance to wheat streak mosaic virus (WSMV), a devastating disease of wheat for which wheat lacks resistance, is located on the short arm of 4Ai#2. A subterminal C-band is diagnostic for the identification of the short arm. Three different transfer lines involving wheat chromosomes 6A, 4A and 4D were analysed. Translocations involving 6A (left) and 4A (a highly rearranged chromosome) (middle) were non-compensating and agronomically undesirable. However, T4DL.4Ai#2S is a whole arm compensating translocation as donor DNA painting assay shows (right bottom). This germplasm is being used in many breeding programmes to develop WSMV-resistant wheat cultivars.

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