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Review

Cytogenetics and Evolution of *Triticum aestivum* L. em Thell

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ABSTRACT

The need and promise in wheat cytogenetics research lie in the established precise relationships between genes and chromosomes as well as among chromosomes of different genomes. One fundamental approach to unlock the natural mysteries is the exploitation of complete genomes and from gross morphology of chromosomes to each and every nucleotide of the genome. The high degree of interspecific and individual variation of entire genome as well as the genotypic plasticity of some fitness properties, such as, adaptation to extreme climates, resistance to diseases and insects and high yield potential indicate the high selection pressure acting on its genetic system. In this review we summarize current knowledge of interrelationships between the form and function of chromosomes and the evolution pattern of wheat genome development.

Key Words: Cytogenetics; Chromosomal aberrations; Polyploidy; Evolution; *Triticum aestivum* L.

INTRODUCTION

Cytogenetics deals with the evolution of crops by way of the study of their chromosome structure, number, function and movement and numerous variations in theses properties of chromosomes. It is a discipline that deals with the chromosomal basis of Mendalian inheritance and is of fundamental importance to breeding crop plants including wheat. It represents a common constructional concept in the plant development system, the reproductive system, and in the arrangement of genes on the chromosomes. The development of amphiploids as "bridge" species is one of the available procedures to facilitate gene flow between wheat and related species of different ploidy level (Stalker, 1980).

Chromosome behaviour furnishes the mechanism for observed genetic segregation and breeding behaviour. There are striking differences in gross morphology and ploidy levels of chromosomes within and out of species. How these are reflected in the information on genetic maps and breeding behaviour is therefore important to geneticists and breeders. It is therefore to be expected that the architectural properties of chromosomes are related to functional aspects. High variability is demonstrated by the fitness to range of environment and resistance to different biotic stresses. However, the functional background of this variation is not well understood. An improved knowledge of the influence of architectural properties on the various functional behaviour of genetic make up is thus desirable.

In this paper, we summarized current knowledge of the evolution of different chromosome pattern and possible interrelationships between form and function of genetic material in wheat. Since functional aspects of architectural features of different genomes are considered, the review also refers to the topic of individual and interspecific variation, leading towards the evolution. The article attempts to covers the cytogenetics and evolution of wheat under following broad headings:

1. Formal description of wheat cytology
2. Evolution of chromosome number
3. Structural changes in chromosome number
4. DNA, hybridization and gene mapping,
5. Alien chromosome transfer

Formal Description of Wheat Cytology

Genome description. *Triticum aestivum* L. em. Thell (2n = 6x = 42) is an autogamous allohexaploid species (AABBDD) that combines the genomes of three diploid ancestral species (Poehlman and Sleper, 1996). The donors of the A and D genomes, *T. monococcum* (2n = 14, AA) and *Aegilops squarrosa* (2n = 14, DD) were already clearly identified by genomic analysis (Morris & Sears, 1967). However, the donor of the B genome is still controversial and believed to be extinct, much modified or not yet discovered. Many related diploid species studied showed partial homology and chromosome pairing so far but not to the extent observed for the A and D genome donors. *Ae. speltoides* (2n = 14, BB) is the species generally accepted as the probable donor of the B genome (Dvorak, 1972; Miller, 1987; Yan *et al*., 1998). 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). Reassessment of the origin of the polyploid wheats indicates that *Triticum speltoides* cannot be the B genome donor to *T. turgidum* or *T. aestivum* (Kimber, 1974). *T. speltoides* is probably homologous to the G genome of *T. timopheevii* and according to Kimber (1974) the donor of B genome to *T. turgidum* or *T. aestivum* is unrecognized hitherto.

Wheat cytology today. Wheat domestication occurred in primitive farms of Southwestern Asia, at the "Fertile Crescent" of Mesopotamia, between 7,000 and 9,000 BC (Bell, 1987). Since the beginning of wheat breeding about 200 years ago, quite impressive improvements in yield, bread making quality, plant architecture, and increased resistance to biotic and abiotic stresses were obtained. The total number of accessions in national and local gene banks around the world has been estimated as about 400,000, although there may be duplications (Poehlman & Sleper, 1996). Several useful cytogenetic strategies were developed to manipulate the chromosomes of part or the whole genome of a species for the improvement of bread wheat. A wealth of data on the genomic structure of cultivated wheat has accumulated after almost a century of research, beginning with the pioneering genetic experiments of Nilsson-Ehle (1909) and the cytological studies of Sakamura (1918) and Sax (1918). 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 (Lilienfield & Kihara, 1951). In the 1930s, Sears (Sears, 1954, 1966; Sears & 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 (McIntosh *et al*., 1998). In the 1970s, modern staining techniques were used to analyze the substructures of cereal chromosomes, and a cytogenetic karyotype of wheat was developed (Gill & Kimber, 1974; Gill, 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 & Gill, 1985; Jiang & Gill, 1994). These so-called molecular cytogenetic methods of genome analysis have greatly facilitated cytogenetic analysis in wheat and related species, especially the analysis of alien chromosome transfers (Friebe & Gill, 1994; Friebe *et al*., 1999). 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 genetic marker on 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, *et al*., 1991) and molecular karyotyping (Pederson & Langridge, 1997). Many useful genes from wild species are available to be used in breeding programmes as source of genes for disease resistance applying different chromosomal engineering techniques involving backcrosses, "bridges" crosses and selection of cytological as well as desired agronomic characteristics (Stalker, 1980; Dhalival *et al*., 1986; Gale & Miller, 1987). The transfer of alien genes depends on the passage of a piece of chromosome from the donor species to the recipient species, which have to be as small as possible in order to avoid the transfer of undesirable characteristics. Obviously the transference will be easier if the donor species have chromosomes fully homologous to bread wheat, allowing the occurrence of crossing over and genetic recombination via chiasmata. Riley and Kimber (1966) reviewed the possibility of transferring genes from related species to bread wheat by evaluating artificial amphiploids and chromosomal addition and substitution lines as well as translocated chromosomal segments.

Evolution of Chromosome Number

Monosomics. Chromosome constitutions of monosomic lines of Chinese Spring and Pb. C591 cultivars were studied over a period of 18 years. Of the 617 plants of Chinese Spring 65.6% were monosomics and 0.5% were double monosomics. Similarly, of the 573 plants of Pb. C591 69.6% were monosomics and 0.5% were double monosomics (Singh & Rajlakshmy, 1994). The monosomic line for chromosome 3A of the wheat cultivar Pb. C591 was used to examine the location of the genes involved in chlorophyll synthesis. The F_2 disomic plants obtained from crosses between the monosomic 3A line of Pb. C 591 with 9 other wheat cultivars produced only green seedlings, while the monosomic plants gave albino with the frequency of 10.5%. This indicated the presence of chlorophyll synthesis gene, allelic to the genes located on the chromosome 3A of Pb. C 591 (Ramana & Singh, 2002). Chromosomal localization and linkage mapping of a powdery mildew resistance gene were conducted in the resistant alien addition line of wheat (*Triticum aestivum*) variety Pova. Monosomic analysis revealed that a major dominant gene controlling disease resistance was located on chromosome 7D (Zeller *et al.,* 2002). Monosomic analyses employing the susceptible set of 21 Chinese Spring monosomic lines revealed that one of the monosomics from 1A, 7A and 2B had increased 1000-grain weight, whereas those from monosomics 4B, 5B, 6B, 1D and 7D had reduced 1000-grain weight (Kaur *et al.,* 2000). Gene, *Yr24* for resistance to stripe rust (*Puccinia striiformis* sp. *tritici*) was transferred from durum (*Triticum turgidum*) wheat to bread wheat (*T. aestivum*) via an amphiploid (synthetic wheat) with *Aegilops tauschii* and *Yr24* was found to be located in chromosome 1B by monosomic analysis (McIntosh & Lagudah, 2000). The monosomic analysis for *Mlar* gene demonstrated that the gene was an allele of the *Pm3* locus (*Pm3g*), which was also appeared to control resistance to powdery mildew (Sourdille *et al*., 1999). Influences of the absence of some chromosomes on characters like number of stomata, distance between stomata in a row, distance between stomatal rows, stomata length and width was investigated. The absence of chromosomes from ms 7A and ms 6D produced the greatest effect on the linear size of stomata (Davydov, 1999). The monosomic hybrids differed from the rest of the hybrids for 42.9% of characters in 3D

monosomics (heading date, ear length, spikelet number per ear) and 71.4% in 5B monosomics (heading date, common and productive tillering, last internode length and ear length); euploid hybrids differed for 85.7% of the characters (Kussovska *et al.*, 1999). Monosomic lines of common wheat were used in studies of the effects of the *Ph1* gene on types and rates of centromere division of univalents at meiosis. The results suggested that *Ph1* is a trans -acting gene affecting centromere-microtubules interaction (Vega & Feldman, 1998a). Monosomic and substitution analysis showed that at least 10 of the 21 pairs of chromosomes were involved in the control of frost resistance. Chromosomes 5A and 5D were found to have the largest effect on frost hardiness (Sutka *et al.*, 1997). To introduce barley genes for early heading on chromosome 5H into wheat, wheat-barley 5H recombinant lines were produced. Chinese Spring (CS) monosomic 5B was pollinated with the wheat-barley 5H addition line (Murai *et al.*, 1997). Two alien monosomic addition lines and one alien translocation line of Chinese Spring were used to induce chromosome breakage, resulting in the occurrence of deletion chromosomes (Endo, 1995). F_2 monosomic analysis and screening of a series of 19 CS compensating nullitetrasomic and two ditelosomic lines (2AS and 5BL) indicated that the resistance gene was located on chromosome arm 5BL (Stock *et al.*, 1996). The disomic was not sensitive to radiation, but some monosomic lines which showed increased resistance after irradiation were judged to be radiosensitive. Yield-related traits such as tiller number, heading date, plant height, flag leaf length and number of spikelets/ear did not change greatly in the monosomics, except in monosomic 4A, which was judged more radiosensitive on this basis (Yuanwu & Yujun, 1995). The monosomic and disomic addition lines of 4R and 6R in WL711 also maintained resistance against a particular isolate of Karnal bunt during backcrossing whereas their euploid segregants were as susceptible as the recurrent parent (Datta *et al.*, 1995). Monosomic analysis of the wheat line PI294994, carrying the gene *Dn5* for resistance to Russian wheat aphid (*Diuraphis noxia*), indicated that *Dn5* is located on chromosome 7D (Toit *et al.*, 1995). Monosomic analysis showed that the large spikelet number of Branch 1 was controlled by genes on chromosomes 1D (recessive) and 5B (dominant) (Peng *et al.*, 1998a). Chromosomal location of the genes for the supernumerary spikelet (SS) character in the bread wheat line Yupi Branching was determined using monosomic lines of the normal-spiked Chinese Spring. The chromosomes 2D, 4A, 4B and 5A of bread wheat were found to carry genes for SS character (*bh* (branched head) genes). Comparison of disomic and monosomic plants in 2D, 4A, 4B and 5A F_2 populations revealed that the *bh* genes were hemizygous-effective and dosage-independent. The F_1 monosomic analysis showed that the *bh* genes of Yupi Branching were recessive (Peng *et al.*, 1998b).

Disomics. The plants with disomic genetic constitution are also important for the evolutionary perspectives as the disomic individuals are missing with complete sets of homologous chromosomes as opposed to monosomic (6x-1) or nullisomic (6x-2) etc. A wheat (*Triticum aestivum*) disomic addition line $2n = 6x$ with 44 chromosomes controlling blue aleurone colour was crossed with a short-statured spring wheat 'Sonora 64'. Isoline pairs of blue-disomic addition lines and non-blue euploid lines were produced by selecting plants segregating for blue aleurone for 12 generations. Nineteen of 20 blue aleurone lines were $2n = 44$ addition lines, and one had $2n = 42$ chromosomes. Several lines of evidence showed that this line had a spontaneous translocation in which the ß arm of wheat chromosome *4A* was replaced by an Elytrigia chromosome arm carrying the blue aleurone gene (Jan *et al.*, 1981). During the development of disomic additions of rye (*Secale cereale* L.) chromosomes to wheat (*Triticum aestivum* L.), two reverse tandem duplications on wheat chromosomes 3D and 4A were isolated. By virtue of their meiotic pairing, the reverse tandem duplications initiated the chromatid type of the breakage-fusion-bridge (BFB) cycle. This BFB cycle continued through pollen mitosis and in the early endosperm divisions, but no clear evidence of its presence in embryo mitoses was found **(**Lukaszewski, 1995). Thirteen disomic and one monosomic wheat-*Aegilops geniculata* chromosome additions were identified. Furthermore, two mono-telosomic (MtA7U^gL, MtA7M^gL) and nine di-telosomic (DtA1U^gS, DtA1U^gL, DtA2U^gS, DtA1M^gL, DtA2M^gL, DtA3M^gS, DtA5M^gS, DtA6M^gL, DtA7M^gS) wheat *A. geniculata* additions were recovered. C-banding and meiotic pairing analyses revealed that all added U^g and M^g genome chromosomes were structurally unaltered compared to the *A. geniculata* parent accession. Chromosome 4M^g has a strong gametocidal gene that, when transferred to wheat, causes extensive chromosome anomalies (Friebe *et al.*, 1999). The progeny of wheat-rye di-monosomics 5R-5A and 5A-5D of *Triticum aestivum* cv. Saratovskaya 29 and *Secale cereale* cv. Onokhoiskaya, differing in the dosage of the gene *P* (*Edu*), the promoter of the equational division of univalents, located on rye chromosome 5R were studied. Different dosages of these genes were responsible for the level of equational division of non-homologous univalent chromosomes and the frequency of their transmission via gametes (Shchapova *et al*., 1998). Examination of Chinese spring mutant ph 1B by the nullisomic 5B, tetrasomic 5D and disomic substitution 5B lines with Rye indicated that Krl and ph 1 were at separate loci (Fan *et al.*, 1988).

Structural Changes in Chromosome Numbers

Telosomics. Telosomic analysis showed that the gene is located on the short arm of chromosome 7B with a distance of 14.3% from the centromere (Taketa *et al.*, 2002*).* Chinese Spring telosomic lines were crossed with substitution lines in which single chromosomes of the cultivars were substituted for their Chinese Spring homologues. The telosomic lines were also crossed with Chinese Spring the reduced pairing in the intercultivar hybrids was caused

primarily by chromosome differentiation, rather than by specific genes. Because the differentiation involved a large part of the chromosome complement in each hybrid, it was concluded that it could not be caused by structural changes such as inversions or translocations (Dvořák *et al.,* 1981). The short arm of homeologous group 1 chromosomes is known to contain many agronomically important genes. Using ditelocentric lines of wheat cv. Chinese Spring (CS, nondormant & ABA insensitive), F_2 seeds between monosomic lines of CS and a wheat line Kitakei-1354 (dormant, ABA sensitive) and deletion lines of CS chromosome 4A, germinability of seeds and embryo-half seeds incubated in water and ABA (abscisic acid) were examined. The results indicated that the long arm of chromosome 4A carried major gene(s) for the embryo sensitivity to ABA and dormancy (Noda *et al.,* 2002).

Inversions. A massive restructuring of chromosomes was observed during the production of a substitution of chromosome 6B(s) from *Triticum speltoides* for chromosome 6B of Chinese Spring wheat (*Triticum aestivum* L.). Deletions, translocations, ring chromosomes, dicentric chromosomes and a paracentric inversion were observed. Chromosome rearrangements occurred in both euchromatic and heterochromatic regions (Kota & Dvorak, 1988). Pericentric inversions occur in chromosome 4B at early tetraploid stage (Naranjo *et al.*, 1988).

Translocations. The glutamate oxaloacetate transaminase (GOT) zymogram phenotypes of a series of 15 translocation lines, a chromosome addition line and a chromosome substitution line were determined. In each of the translocation lines a segment of the long arm of *Triticum aestivum* chromosome 3D has been replaced by a portion of an *Agropyron elongatum* homoeologue. It was obtained that the products of the *T. aestivum* GOT-3 triplicate structural gene set randomly dimerize with the product of the homoeologous *A. elongatum* gene. Each translocation chromosome was found to carry either *Got-D3* or *Got-Ag3* **(**Gary *et al.*, 1976). Positive performance is reported for centric translocations of chromosome 1 of rye (*Secale cereale* L.) in bread wheat (*Triticum aestivum* L.). The 1RS translocations in Pavon delayed maturity, reduced plant height in some cases, and increased root biomass. These results encouraged the development and use of the 1RS.1AL and 1RS.1DL translocations in wheat breeding programmes (Ehdaie, 2003). In hexaploid wheat (*Triticum aestivum* L.) disease resistance genes transferred from alien sources are often associated with undesirable traits. Replicated trials using near-isogenic lines of spring wheat 'Seri 82' were conducted for 2 yr under non-moisture stress and simulated moisture stress conditions to determine the effects of the 7DL.7Ag and 1BL.1RS translocations (from *Agropyron elongatum* and *Secale cereale* L., respectively) on grain yield and related traits. Several yield-related traits of the near-isogenic genotypes varied significantly. Presence of each translocation caused lateness and, when present together, the 1BL.1RS and 7DL.7Ag translocations delayed heading and maturity by 7 and 5 D, respectively. The genetic background of the recipient wheat can affect the utility of a translocation (Singh *et al.*, 1998). Centric translocations of the short arm of rye (*Secale cereale* L.) chromosome 1R are useful in wheat (*Triticum aestivum* L.) breeding because they confer resistance to several pests and diseases and improve yield. Their major disadvantage is in reduced bread making quality. To remedy this defect, rye chromosome arm 1RS in translocations 1RS.1BL and 1RS.1DL was induced by the *ph1b* mutation to recombine with the short arms of wheat group-1 chromosomes. Translocated lines were identical to that of normal wheat; it was concluded that these manipulations could eliminate the quality defect associated with the 1RS.1BL translocation (Lukaszewski, 2000).

Additions, substitutions and deletions. Four deletion mutants of rye chromosome 6R were identified in the progeny of wheat (*Triticum aestivum* L.) lines of *ph1bph1b* genotype and monosomic for chromosome 6R. The rye chromosome carried a resistance gene against the cereal cyst nematode (CCN) (*Heterodera avenae*) and this chromosome originated in triticale line T-701 (Triticosecale) (Dundas *et al.*, 2001*).* The 4Ag (4D) chromosome substitutions of wheat are a source of blue aleurone, with the blue aleurone trait being conferred by a chromosome of homoeologous group 4 from *Agropyron elongatum*. Two blue-grained wheat accessions, TRI2401, a disomic 4A ($4A^a$) substitution that is close or identical to Blaukorn Weihenstephan, and TRI10365, a disomic 4A (4B) substitution that is identical to Blaukorn Moskau, were chosen from the Gatersleben gene bank because of some impurity of blue grain colour (Ceoloni & Worland, 1998). By the substitution lines the involvement of chromosomes of group 4 and also chromosome 5B in the accumulation of hydroxamic acids in wheat seedlings was proved (Niemeyer & Jerez, 1997). Testcrosses of the deletion chromosome with telocentrics and nullisomic-tetrasomic combinations suggested that the deletion involved the long arm of chromosome 5D. Studies of chromosome morphology indicated that the deletion chromosome was metacentric, and the length of the long arm was reduced by approximately 60% (Atkinson *et al.*, 1995).The transfer and identification of *Aegilops ovata* chromosomes into the hexaploid wheat genome as additions and substitutions are reported. An *A. ovata* ($2n = 4x = 28$) accession involved in the production of an amphiploid by crossing with Chinese Spring ditelo 5AL wheat line was used for chromosome N-banding analysis (Landjeva & Ganeva, 1998).

DNA Hybridization and Gene Mapping

***In situ* Hybridization.** Genomic *in situ* hybridization (GISH) could be used to determine differences in the genomes of wheat (AABBDD) and jointed goat grass (CCDD) of the BC_1 generation (Wang *et al.,* 2002). By the combination of cytological analysis and using genomic *in situ* hybridization technique to identify an alien chromosome in wheat-*Haynaldia villosa* monosomic

addition lines, the meiotic behaviour of the alien chromosome. The results indicated that the frequency of bivalent pairing was lower than the value expected in PMCs of two monosomic addition lines, the frequency of wheat chromosomes un-pairing increased, and the wheat homologous chromosome pairing was interfered with by the added chromosome (Ruifen *et al.,* 2002*).*

Mapping the genes. Gene mapping is an important era for wheat cytogenetic studies. Number of genes have been identified and located on the chromosomes by using elegant laboratory techniques. The molecular cloning of *Lr21* was facilitated by diploid/polyploid shuttle mapping strategy (Huang *et al*., 2003). Meiotic chromosome pairing in *Triticum aestivum* is controlled by genetic systems promoting and reducing pairing. The cytologically diploid-like meiotic behavior of hexaploid wheat (*i.e.*, exclusive bivalent pairing of homologues) is largely controlled by the pairing homoeologous gene *Ph1*. The pairing of homoeologous chromosomes (partially homologous) is prevented principally by the activity of a single locus (*Ph*) distantly located on the long arm of chromosome 5B (Riley, 1974). This gene suppresses pairing between homoeologous chromosomes of the three closely related genomes that compose the hexaploid wheat complement. Telocentrics for the ß arm of chromosome 4A and the long arm of 6B were used as cytological markers for the determination of chiasma frequency (Fu & Sears, 1973).Genetic male sterility (GMS) genes have been mapped in hexaploid wheat (*Triticum aestivum*) by Klindworth *et al*. (2002). They crossed four mutant GMS genes (FS2, FS3, FS20 & FS24) with a cultivar which has *msc1* allele, to determine the allelic relationship. In the monosomic analysis of the mutated FS20 gene, half of the monosomic 3A plants were male sterile. Therefore, the mutated gene in FS20 was located in chromosome 3A. The incorporation of leaf rust resistance gene *Lr34* into 'Thatcher' is known to enhance stem rust resistance. The effect of this gene in a 'Canthatch' background and its relationship with the 7DL suppressor were determined by replacing chromosome 7D of 'Canthatch' with 7D of 'Chinese Spring', which possesses *Lr34* on the short arm. Stem rust (Puccinia graminis f.sp. tritici) is due to a suppressor gene on chromosome 7DL that inhibits the expression of the relevant resistance gene(s) (Kerber & Aung, 1999). Chromosomes 3A, 3D, 4D, 7A and 7B of Sel26 were considered to carry recessive awn-promoters, whereas chromosome 6D has a gene or genes for awn-inhibition (Sharma *et al.,* 1995). In a study the monosomic and disomic addition lines of 4R and 6R in WL711 also maintained resistance against a particular isolate of Karnal bunt during backcrossing whereas their euploid segregants were as susceptible as the recurrent parent (Datta *et al.*, 1995). Monosomic analysis of the wheat line PI294994, carrying the gene *Dn5* for resistance to Russian wheat aphid (*Diuraphis noxia*), indicated that *Dn5* is located on chromosome 7D (Toit, 1995). Genes for powdery mildew (caused by *Eryphis graminis*.f.sp. *tritici*) resistance were mapped in *T.aestivum* at het seedling stage. A recessive gene on chromosome 7B and are dominant gene on chromosome 5D werer suspected to control the disease resistance in the line Siyan 94-1-2 (Peusha *et al.,* 2002; XiuQiang *et al.*, 2002). Progeny analysis indicated that the brittle rachis (barrel type) of the Tibetan weedy landrace (*Triticum aestivum* var. *tibetanum*) was found to be governed by a single dominant gene on the short arm of chromosome 3D, which has been designated *Br1* (Qingfu *et al.*, 1998). The large number of total florets per spike of 10A is controlled by genes on chromosomes 5A, 7A, 1B, 2B, 2D and 6D, while genes on chromosomes 1B, 2B, 2D and 6D controlled mainly the number of sterile florets per spike (Zheng *et al.,* 1993). Monosomic analysis revealed that the gene for pubescence is located on chromosome 7B. Telosomic analysis showed that the gene is located on the short arm of chromosome 7B with a distance of 14.3% from the centromere (Taketa *et al.,* 2002). *Mlar* was located by monosomic analysis on the short arm of the chromosome 1A, in the vicinity of the locus *XGli-A5* coding for storage proteins in wheat (Sourdille *et al.,* 1999). Frost resistance genes were evaluated in monosomic lines of Cheyenne, Mironovskaya 808 and Rannyaya 12, grown under controlled environment conditions. For all there cultivars, a reduction in the degree of frost resistance were observed when chromosomes 5A, 3B, 3A, 5B or 7A were missing (Veisz & Sutka, 1998). Monosomics were used to locate the genes controlling kernal colour, kernal groove shape and the shape of the upper margin of the glume. Two dominant genes controlling kernal colours, R1 and R3, dark being dominent to light, were found on chromosomes 3D and 3B respectively. Two dominant genes controlling the inheritence of sharp margin of the kernal groove were located on chromosomes 3A and 5A. Chromosome 7D of Chinese spring variety had greatest effect on the plant height, it appears that a recessive gene for semi dwarfness which reduces straw length about 18 cm (Zhirov *et al.,* 1973). The long arm of chromosomes 1B, 1D and 4D contain genes coding the 5 largest glutenin sub units of Chinese spring. Same chromosome contributes to the gluten composition of other hexaploid wheat varieties. Nulisomic, trisomic and di-telocentric lines were used to locate these chromosomes (Bietz *et al.,* 1975).

Isochromosome. Vega and Feldman (1998b) used an isochromosome system to determine the processes associated with chromosome pairing which was affected by the *Ph1* gene of common wheat. It was concluded that *Ph1* mainly reduced the frequency of interchromosome pairing without affecting intrachromosome pairing. On the other hand, intrachromosomal pairing was reduced in the absence of synaptic gene *Syn-B1*. Premeiotic colchicine treatment, drastically decreased pairing of conventional chromosomes, reducing interchromosome but not intrachromosome pairing. They suggested that *Ph1* acts on premeiotic alignment of homologues and homoeologues as a means of ensuring diploid- like meiotic behavior in polyploidy wheat.

The isochromosomes deficient for different terminal segments in the two arms were used to determine the segments of chromosome arm responsible for the initiation of chiasmata pairing in meiosis (Lukaszewski, 1997). The deficient segments of asymmetrical isochromosomes paired with a frequency similar to that of normal arms, indicating that the deficient arms retained normal capacity for pairing. Pairing of arms of different length was prevented not by the deficiency itself, but rather, by the heterozygosity for the deficiency.

Alien chromosome transfer. To introduce barley genes for early heading, present on chromosome 5H, into wheat, wheat-barley 5H recombinant lines were produced. Chinese Spring (CS) monosomic 5B was pollinated with the wheat-barley 5H addition line followed by the pollination of CS (nullisomic-5B tetrasomic-5H) with double monosomic for 5B and 5H from the selected progeny. By using molecular markers after different crossed and selfed progenies the recombinant plants homozygous for wheat-barley chromosomes were isolated (Murai, *et al.*, 1997). The I chromosome of *Ae. triuncilis* was transferred by Endo and Tsunewaki (1975) to *T. aestivum* through the cytoplasm substitution lines, the presence of this I chromosome causes the non-viability of the gametes (McIntosh & Lagudah, 2000). Chromosome V2 (carrying gene for resistance of powdery mildew) is transferred to *T. aestivum* and analyzed by disomic addition and substitution lines (Liu *et al.*, 1988).

Chromosome breakage occurs in a hexaploid wheat (*Triticum aestivum* L.) variety Chinese Spring carrying a single gametocidal chromosome 2C, from *Aegilops cylindrical.* In an attempt to generate deletions in barley chromosomes, the 2C chromosome was introduced into six wheat-barley addition lines. Plants disomic for each of the barley chromosomes and monosomic for 2C were identified using C-banding and meiotic analysis (Fang & Endo, 1997). Chromosome pairing was studied by C- banding in wheat into rye hybrids and it suggested that chromosome 4A belongs to B genome and also purposed that chromosome 4B originated from the A genome.

Concluding remarks. Mapping the wheat chromosomes is not only important for fundamental cytogenetic information, but also for efficient manipulation of germplasm in wheat. Because of the pioneering studies on the development of identified aneuploids and methods involving them, a number of genes have been assigned to chromosomes. It would be desirable to get gene marker for specific monosomes, particularly those which are difficult to identify by chromosome morphology or phenotypic effects. Some suitable genes will be available in the course of gene assignments to chromosomes; additional ones may have to be sought in mutation studies. Any destructive features of chromosome structure may be useful in chromosome identification work, if they can be transferred to the material under investigation. Groups of desirable chromosomes can be combined to reconstitute the architecture of wheat plant in a more elite template. However, it is not unrealistic to speculate that direct, physical transfers of chromosomes from one wheat plant to another by micromanipulation may become an eventuality.

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