Chapter 2
Genome Structure and Chromosome Function

Khwaja G. Hossain, Scott A. Jackson, and Shahryar F. Kianian

Abstract Aneuploidy refers to the loss or gain of individual chromosomes or loss of a portion of an individual chromosome from the normal chromosome set. The resulting gene-dosage imbalance may or may not noticeably affect phenotype. Although its phenotypic manifestations are usually apparent, information about the underlying alterations in structure, expression, and interphase organization of unbalanced chromosome sets is still sparse. Aneuploidy is the most common chromosomal aberration in plants, and aneuploids are valuable for the study of chromosome evolution, phenotypic manifestation of chromosome loss or gain, and mapping genes and genome. Breeding programs intended to transfer desirable genes from one species to another produce addition lines as intermediate crossing products. Such aneuploids can be used for further introgression, but their abnormal recombination and segregation interfere with production of stable introgression lines. They can have specific morphological characteristics, but more often additional confirmation is needed. Their genetic and cytogenetic properties make them powerful tools for fundamental research on regulation of homeologous recombination, distribution of chromosome-specific markers and repetitive DNA sequences, and regulation of heterologous gene expression. Recent advancements and availability of genomic resources have widened the scope for their use. They make possible assignment of individual linkage groups to specific chromosomes and can improve identification of quantitative trait loci (QTLs) and underlying DNA components/sequences.

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Abbreviations

CIMMYT	International Maize and Wheat Improvement Center
CSSLs	Chromosome segment substitution lines
DSB	Double-strand breakage
GISH	Genomic in situ hybridization
LDN	Langdon
NILs	Near isogenic lines
QTL	Quantitative trait locus
RCSLs	Recombinant chromosome substitution lines
RDA	Representation difference analysis
RH	Radiation hybrid

Contents

2.1 Plant Chromosome Addition

The normal or disomic condition of two gene doses per chromosome in a somatic cell is usually the basic state in an organism, but meiotic irregularities, chromosome aberrations, aging, or environmental stresses may result in deviation from the basic chromosome number in the genome. This deviation is termed aneuploidy and can occur in any eukaryotic organism. Aneuploids are represented symbolically by the somatic chromosome number because their gametic chromosome numbers vary. The deviation can consist of additions or subtractions of individual chromosomes, either of which has severe effects in mammals and is often lethal early in the life cycle. In plants, especially with higher ploidy levels, such changes in chromosome numbers are readily tolerated, but if the doses of several chromosomes are changed, the imbalance in gene interactions cannot be tolerated even in polyploid plants or their gametes.

2.2 Native Addition Lines

The addition of a single extra chromosome of a species to the normal somatic complement (2n) is termed trisomy, and in a diploid species it implies that one chromosome exists in three copies in each somatic cell, whereas all other

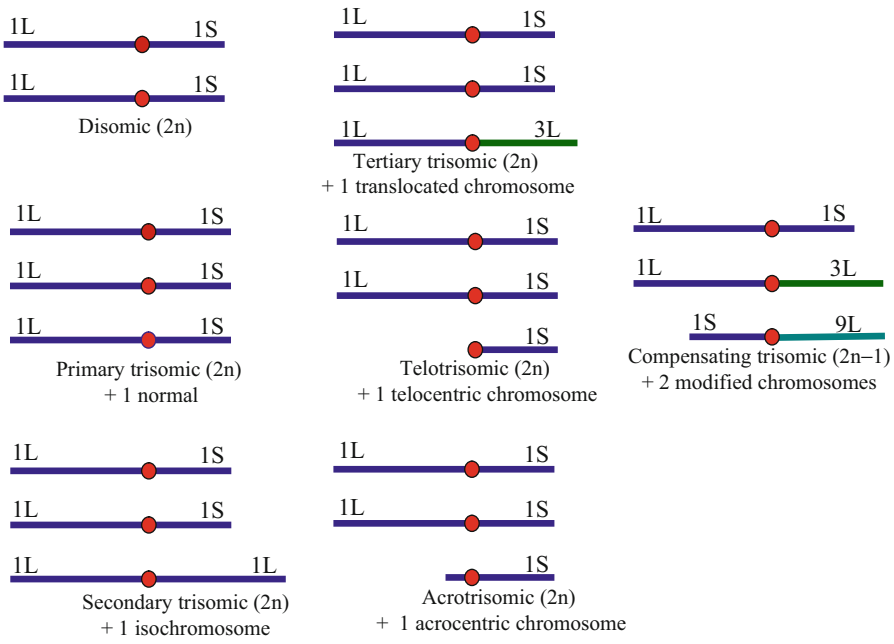

Fig. 2.1 Terms and diagrams illustrating the disomic and various trisomic states in diploid species

chromosomes exist in the normal two. In plants, depending on the composition of the extra chromosomes, trisomic states have been classified into different types that can be distinguished cytologically at meiosis (Fig. 2.1). Tetrasomy (2n + 2) is the state in which two extra copies of a chromosome is present, such that the cell has four doses of one chromosome but only two of other chromosomes. Double trisomics carry an extra copy of each of two nonhomologous chromosomes, i.e., three doses of each of two different chromosomes. The various terms and diagrams illustrating the disomic and other aneuploid states are presented in Fig. 2.1.

In the plant kingdom, trisomy is very common and was first discovered in jimsonweed, *Datura stramonium*, by Blakeslee (1921). Diploids usually tolerate the primary trisomic state, and depending on identity of the extra chromosome, vigor of the plant varies. Complete sets of primary trisomics exist in a number of diploid crop species, including barley (*Hordeum vulgare* L.; Tsuchiya 1958, 1961), maize (*Zea mays* L.; McClintock 1929; McClintock and Hill 1931), tomato (*Solanum lycopersicum* L.; Lesley 1932), and rye (*Secale cereale,* Kamanoi and Jenkins 1962). The modified trisomics (secondary, tertiary, etc.) are only viable in a few diploids, and extra effort is required to obtain them (Mattingly and Collins 1974).

The first detailed morphological description of a complete series of 12 primary trisomics was documented in *Datura* (Blakeslee 1934). Morphological distinctions of primary trisomy have now been described in *Avena* (oats; Azael 1973; Rajhathy 1975), *Pennisetum* (Manga 1976), and many other species (Khush 1973). In many species, the morphological distinctions are not large enough for identification of

primary trisomics, but the series of primary trisomics mentioned above and trisomics of many other species can be distinguished cytologically.

In plants, the phenotypic effects of trisomy are clearest in diploids; in polyploid species genome multiplication often masks the dosage effects of an extra chromosome. The trisomics of a series within a species are more easily differentiated from diploids and from each other when they are all in the same homozygous genetic background.

Trisomy affects many aspects of development and differentiation throughout the plant life cycle. In species with a range in chromosome length, extra copies of longer chromosomes can have more pronounced effects (including greater reduction in fertility, as was documented in rice (*Oryza sativa* L.) by Khush et al. 1984) than extras of shorter ones. Certain trisomic conditions modify different plant organs in the same direction. In tomato, for example, trisomies 3 and 4 increase the lengths of leaves, stems, inflorescences, fruits, and seeds; trisomies 7 and 10 decrease the lengths of most of these plant parts (Rick and Barton 1954). Trisomies are identified by key features, such as seedling traits in spinach, leaf traits in tomato, panicle types in sorghum, and seed-capsule size and shape in *Datura* (Weber 1983). In cases where chromosome morphology or phenotypic effects are not applicable, trisomies can be identified by chromosome banding and in situ hybridization, techniques applied to distinguish different primary trisomics in diploid wheat (*Triticum monococcum* L.) (Friebe et al. 1991).

Since the classical studies of *Datura* trisomics by Blakeslee (1921), primary trisomics have been used extensively to associate marker genes with a particular chromosome, to associate a genetic linkage group with the individual chromosome, and to test the independence of linkage groups (Singh 2003). The cytogenetic maps in maize (Rhoades and McClintock 1935), tomato (Rick and Barton 1954), barley (Tsuchiya 1967), and rice (Khush et al. 1984) have been established by the primary-trisomic method. A set of primary trisomics has been identified in soybean (*Glycine max* L. Merr.; Xu et al. 2000) and has been used to associate morphological mutants and SSR markers to their respective chromosomes (Zou et al. 2003).

2.3 Alien Addition Line

Addition of an alien chromosome (i.e., one from another species) to the somatic complement of a species is termed monosomic addition; it can arise in the progenies of interspecific hybrids and polyploids. Plant geneticists and breeders have gained interest in extending genetic variation of crop plants using germ plasm from related species. In a long-term crossing program, known as introgressive hybridization, economically or otherwise important genes are being incorporated into the recipient parent by sexual or somatic hybridization between related species or genera, followed by consecutive backcrossing with the recipient parent. In the offspring families, lines are selected in which only a single alien chromosomes has been added. Monosomic additions were first described by Leighty and Taylor (1924), but their use and potential were better demonstrated in a study by O'Mara (1940). Khush (1973) and Sybenga (1992) provide full overviews of alien additions in

Table 2.1 The complete sets of chromosome additions with their parental species, karyotype analysis, and references

Donor species	Recipient species	No. of alien addition sets	Cytogenetics	References
Aegilops speltoides	*Triticum aestivum* (wheat)	7	C-banding, FISH with repeat probes	Friebe et al. (2000)
Allium cepa (onion)	*Allium fistulosum*	8	Karyotype analysis	Shigyo et al. (1996)
Beta webbiana	*Beta vulgaris* (beet)	9	Karyotype analysis	Reamon-Ramos and Wricke (1992)
Beta patellaris	*Beta vulgaris* (beet)	9	Karyotype analysis	Mesbah et al. (1997)
Beta procumbens	*Beta vulgaris* (beet)	9	Karyotype analysis	Van Geyt et al. (1988)
Lycopersicon esculentum (tomato)	*Solanum tuberosum* (potato)	12	GISH	Ali et al. (2001)
Oryza officinalis	*Oryza sativa* (rice)	12	Karyotype analysis	Jena and Khush (1989)
Solanum lycopersicum	*Lycopersicon esculentum* (tomato)	12	Karyotype analysis	Chetelat et al. (1998)
Wheat	Various species	20	Karyotype analysis	Shepherd et al. (1988)
Zea mays (maize)	*Avena sativa* (oat)	10	Karyotype analysis	Kynast et al. (2001)
Barley	Wheat	7	karyotype analysis	Islam and Shepherd (2000)

relation to other aneuploids in plant genetics. Table 2.1 presents a list of monosomic addition lines in different plant species with their parental species, means of selection, and references.

Monosomic additions can be selected on the basis of specific alien traits, like disease resistance, aberrant plant phenotype, species-specific molecular markers, and karyotypic analysis. Morphological traits can be binary traits, like the *liguleless* leaves of the maize chromosome 3 monosomic addition in oat (Muehlbauer et al. 2000) and dominant resistance genes, or quantitative traits, such as plant size and spike morphology. The phenotypes of monosomic-addition-derived hybrids between genetically related parents often resemble those of the corresponding primary trisomic (Chetelat et al. 1998). Alien chromosomes are sometimes distinguished by karyotype analysis; examples are four monosomic additions to beet (*Beta* sp.) containing alien chromosomes from *Beta procumbens* C. Sm. or *B. patellaris* Moq. that confer nematode resistance (de Jong et al. 1986).

The most important tool for visualization of alien chromosome is genomic in situ hybridization (GISH). Reports establishing the number of alien chromosomes in intergeneric backcross families are numerous (Raina and Rani 2001); examples are tomato to potato (Jacobsen et al. 1995), maize to oat (Riera-Lizarazu et al. 1996),

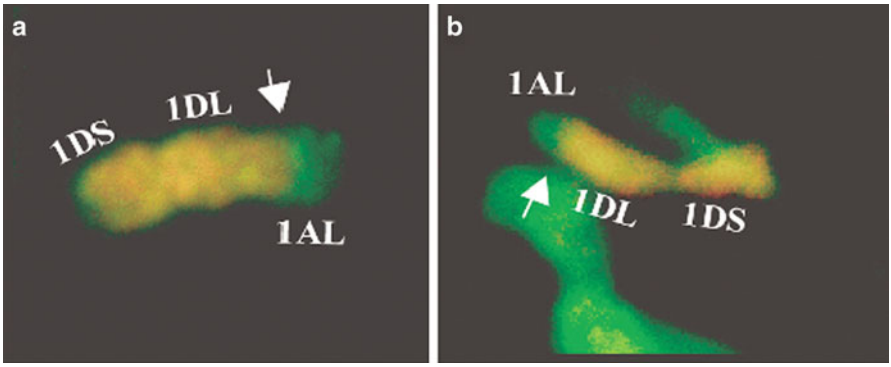

Fig. 2.2 GISH analysis of two putative 1DS. 1DL–1AL chromosomes in (**a**) (lo) durum *scs*^{ae}/LDN-dDt1A and (**b**) (lo) durum *scs*^{ae}/LDN 16. Fluorescein- (*yellow-green*) and rodamine-labeled (*red*) LDN-16 and *Aegilops tauschii* genomic DNA, respectively, were used in GISH analysis. The pattern of chromosome labeling suggests the presence of the short arm of chromosome 1D (1DS), the proximal region of the long arm of chromosome 1D (1DL), and a terminal segment that probably originated from a homoeologous distal region of chromosome 1A (1AL). *White arrows* mark the putative homoeologous recombination points (picture from Hossain et al. 2004b)

Beta corolliflora Zosimovic ex Buttler to beet (Gao et al. 2000), and S-genome chromosome to wheat (Belyayev et al. 2001).

The potential of alien chromosome addition for breeding programs depends largely on the genetic distance between the parental species, which is critical to the possibility of recombination between alien chromosomes and their homeologous counterparts in the recipient species. In parents that can be combined in sexual crosses, such as wheat and rye, maize and *Pennisetum*, and *Festuca* and *Lolium*, crossovers between homeologous chromosomes are not rare and may reveal recombinant chromosomes, even in the first backcross generations.

The extent of crossover recombination between the homeologs in monosomic additions depends primarily on the genetic relation between the parent species but is also influenced by difference in the alien chromosomes and their genetic background. In some cases, unequal crossovers between homeologs and alien chromosomes result in heteromorphic chromosome addition – for example, introgression and mapping of the species cytoplasm specific (*scs*) gene located on chromosome 1D in an alloplasmic durum wheat (*Triticum turgidum* L.; AABB) line to overcome incompatibility (Maan 1992, Hossain et al. 2004b). In this line, the portion of the *T. aestivum* L. chromosome 1D carrying the *scs* gene has been introgressed (Fig. 2.2). The lack of meiotic recombination of this 1D portion in the durum background made it suitable for physical mapping. By means of gamma-ray irradiation, the *scs* gene and the 1D chromosome have been physically mapped in wheat (Hossain et al. 2004b; Kalavacharla et al. 2006). The development of radiation hybrid (RH) lines from oat-maize somatic additions has allowed mapping of molecular markers on a subchromosome level of the maize genome (Riera-Lizarazu et al. 2000; Okagaki et al. 2001).

Monosomic alien addition lines have been used in genetic studies of genome organization and plant breeding in crops such as tomato, wheat, and sugi (*Cryptomeria* sp.; Kam-Morgan et al. 1989; Suyama et al. 1996; Chetelat et al. 1998). The series of individual *Allium cepa* L. chromosomes added to the diploid genome of *A. fistulosum* L. constitutes a unique resource for examining the genetic map of *A. cepa* and its genome organization (Barthes and Ricroch 2001). Complete sets of alien monosomic addition lines are valuable tools in genetic studies of plant genome organization (McGrath et al. 1990; Singh 1993). In wheat, tomato, and sugi, alien monosomic addition lines and other aneuploid lines have been used to assign linkage groups to chromosomes (Chetelat et al. 1998; Kam-Morgan et al. 1989; Suyama et al. 1996). Other uses of monosomic addition lines include deletion mapping (Werner et al. 1992b) and the transfer of important genes of wild species by means of translocation (Heijbroek et al. 1988; Jung et al. 1992). Alien-chromosome-addition lines are usually generated to transfer agronomically important gene(s) from wild relatives into cultivated crops, a cost-effective means of fostering germ-plasm use. In addition, these lines have been used for localization of genes for valuable traits on specific chromosomes (Kindiger et al. 1996; Yildirim et al. 1998; Ma et al. 1999), construction of DNA libraries for specific chromosomes after microdissection (Jung et al. 1992), isolation of chromosome-specific DNA sequences (Clarke et al. 1995; Delaney et al. 1995), selective isolation and/or chromosome mapping of cDNAs (Korzun et al. 1996; Li et al. 1996; Biyashev et al. 1997), research on genome composition and chromosome structure (Ananiev et al. 1998; Zhang et al. 1996), and assignment of DNA markers to specific chromosomes (Liu et al. 1996; Suen et al. 1997; Gallego et al. 1998; van Heusden et al. 2000). In recent years, disomic or monosomic addition lines have also been used to study nuclear architecture (Abranches et al. 1998), for analysis of meiotic chromosome behavior (Bass et al. 2000), and to clone specific DNA sequences with the help of representation difference analysis (RDA) techniques (Delaney et al. 1995; Chen et al. 1998). A set of seven disomic addition lines of wheat with *Thinopyrum bessarabicum* Savul. and Rayss chromosomes was produced at the International Maize and Wheat Improvement Center (CIMMYT).

Wheat (*Triticum aestivum* L.)–barley disomic chromosome addition lines have been developed through wide hybridization between the hexaploid ($2n = 6\times = 42$) wheat cultivar Chinese Spring and the diploid ($2n = 2\times = 14$) barley cultivar Betzes (Islam et al. 1975). Each addition line contains the full complement of wheat chromosomes and a single homeologous chromosome pair from barley. Wheat–barley disomic addition lines for six of the seven barley chromosomes, including 1(7H), 2(2H), 3(3H), 4(4H), 6(6H), and 7(5H), and ditelosomic addition lines harboring 13 of the 14 barley chromosome arms have been generated (Islam et al. 1981; Islam 1983; Islam and Shepherd 1990, 2000). Chromosome addition lines have been used often to map genes to donor chromosomes on the basis of the presence or absence of the genes on the chromosomes added to the recipient genome. By means of wheat–barley chromosome-addition lines, isozymes and DNA markers have been physically mapped to chromosomes and chromosome arms (Islam and Shepherd 1990; Garvin et al. 1998).

Wheat–barley chromosome addition lines are useful genetic resources for a variety of studies. Transcript accumulation patterns in Betzes barley, Chinese Spring wheat, and Chinese Spring–Betzes chromosome-addition lines were examined with the Barley1 Affymetrix GeneChip probe array. Of the 4,014 transcripts detected in Betzes but not in Chinese Spring, 365, 271, 265, 323, 194, and 369 were detected in wheat–barley disomic chromosome-addition lines 2(2H), 3(3H), 4(4H), 7(5H), 6(6H), and 1(7H), respectively. Thus, 1,787 barley transcripts were detected in a wheat genetic background and, by virtue of the addition line in which they were detected, were physically mapped to barley chromosomes.

Specific proteins/isozymes and GISH were used to detect the presence of *T. bessarabicum* chromosomes in the advanced backcross derivatives of *T. aestivum* and to establish tentatively the homeology of these added chromosomes (William and Mujeeb-Kazi 1995). Single chromosomes of wild species of *Beta* section IV (*B. procumbens*, *B. webbiana* Moq., *B. patellaris*) (Loptien 1984) were used to transfer resistance to beet cyst nematode into *B. vulgaris* (cultivated beet), and resistant diploids were obtained (Jung and Wricke 1987). Later, a full set of monosomic addition lines in *B. vulgaris* from *B. procumbens* was described morphologically (Lange et al. 1988) and characterized by isozyme markers (Van Geyt et al. 1988). Nine different monosomic addition lines carrying alien chromosomes from *B. webbiana* were differentiated by isozyme markers and morphological characters (Reamon-Ramos and Wricke 1992). A more refined method for identification of alien chromosome additions relies on sequences specific to wild beets that, when used as probes, yield characteristic banding patterns (DNA fingerprints).

2.4 Substitution Line

In aneuploids, replacement of a chromosome by its homeolog is called chromosome substitution and can be easily brought about in the backcross families of the interspecific hybrids and monosomic additions. The development of substitution lines involves the replacement of a pair of chromosomes in one variety or species, the recipient, by the homologous pair from another variety or species, the donor. The heteromorphic (homeologous) bivalents in such monosomic substitutions generally demonstrate higher levels of crossover recombination between the alien chromosome and its homeologous counterpart than those in the corresponding monosomic addition and are therefore more appropriate for producing recombinant chromosomes (Ji and Chetelat 2003). A set of monosomics (a monosomic, a $2n-1$ individual, has lost one chromosome from the 2n complement) and/or their derivatives such as nullisomics (which have lost both homologs and are $2n-2$) and monotelosomics (which are $2n-1$ pair $+1$ telosome) must be available to supply $n-1$ gametes for the crosses and backcrosses. Reciprocal substitutions, in which homologous chromosomes are exchanged, can also be established between two varieties with monosomic sets.

Some alien substitutions occur spontaneously after wide crosses and may not be noticed until some generations later, as happened in the development of some European wheat varieties. The wheat breeders unconsciously retained homeologous

a rye-wheat substitution (the wheat chromosome 1B pair replaced by rye chromosome 1R) during selection for several disease resistances from crosses between triticale (a hybrid of wheat and rye) and wheat (Zeller 1973). Another example of a spontaneous substitution occurred during transfer of a dominant gene for resistance to tobacco mosaic virus from a diploid species (*Nicotiana glutinosa* L.) to tetraploid tobacco (*N. tabacum* L.). The hexaploid amphiploid from the interspecific cross was backcrossed to *N. tabacum*. After a second backcross followed by selfing, a line was obtained with the same chromosome number of as *N. tabacum* that was homozygous for resistance (Gerstel 1943).

Substitution lines are available in many species, but their development may differ according to ploidy level. For example, in wheat the process of developing substitution lines in tetraploid wheat (*T. turgidum*) is different from that in hexaploid wheat (*T. aestivum*) because the vigor, fertility, and n – 1 gametic transmission rates of tetraploid monosomics are low (Sears 1966; Mochizuki 1968).

A considerable amount of genetic information can be obtained from substitution lines without further crosses. One-way or reciprocal substitutions, with duplicate lines, and their two parental varieties, can be grown in statistically designed arrangements, with several replications and preferably several environments over locations and years. The significant differences of quantitative traits in any of the substitution lines and the recipient variety can be attributed to the introgressed chromosome. If duplicates of a substitution line differ significantly in the same direction from the recipient variety, the interpretation is that one or more genes on the substituted chromosome have enough effect to be distinguished from their alleles on the recipient chromosome.

King et al. (2002) produced a large series of substitution lines from interspecific hybrids of *Festuca pratensis* Huds. and *Lolium perenne* L. The range of substitution lines, each with different recombinant chromosomes, provided excellent material for physical mapping of the introgressed *F. pratensis* chromosome segments and for comparing genetic and physical maps for the molecular markers on this chromosome.

In polyploids, some gametes with the euploid chromosome number are generated by unequal but numerically compensating divisions during meiosis, which in turn generate chromosomally unbalanced sporophytes. For example, in an autotetraploid species, the four homologs (or homeologs) of a chromosome may split 3–1 during anaphase I in a micro- or megaspore mother cell, whereas the homologs (homeologs) of another chromosome may split 1–3 (i.e., double-opposed nondisjunction). If other chromosomes separate equally, the resulting gametes will be monosomic for one chromosome and trisomic for another.

Chromosome substitution in allopolyploids can occur through nonhomologous/nonhomeologous substitution, as well as through homeologous substitution, i.e., replacement of a chromosome from one progenitor diploid species with a homeolog from another progenitor. Homeolog substitution can occur through compensating but unequal divisions of univalents and multivalents, and also through bivalent pairing of homeologs. Poole (1932) screened the progeny of a spontaneous cross between *Crepis rubra* L. and *C. foetida* L. for homeologous substitution of a single chromosome that was differentiated by a morphological marker.

An important advance in understanding of the genetics of polyploid wheat was the discovery that specific chromosomes in each of the genomes compensate for the

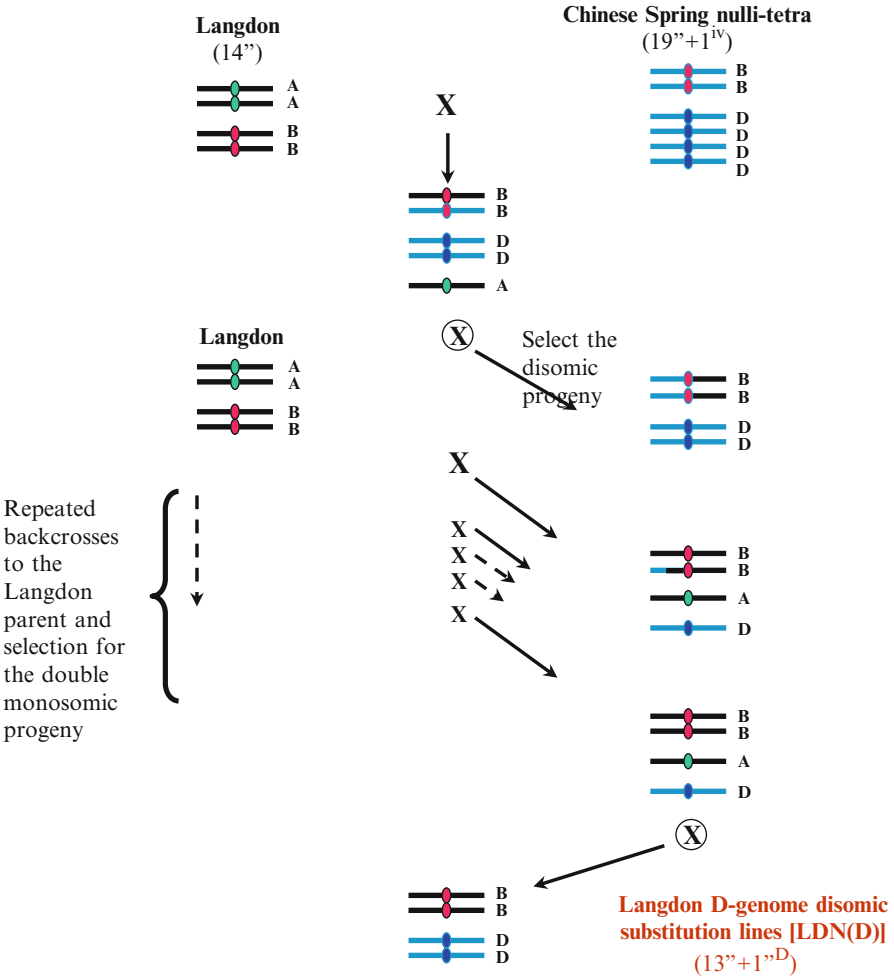

Fig. 2.3 Illustration of the process used by Joppa and Williams (1988) to generate the Langdon D-genome disomic substitution lines in tetraploid wheat. Only the critical chromosomes are shown in this illustration. The homoeologous chromosomes from different genomes do not pair with each other in the presence of *Ph* (pairing homoeologous) gene on 5BL. The hexaploid Chinese Spring chromosomes are represented in blue, the Langdon chromosomes in black, the recombined chromosomes in recombined colors, and the different genomes by colored centromeres

loss of other specific chromosomes in the other genomes. Sears's (1966) classic study of the compensating nullisomic-tetrasomic of Chinese Spring clearly demonstrated this principle. After that study, series of D-genome chromosome substitution lines in tetraploid durum wheat were developed by replacement of a chromosome from the A or B genome by its homeolog from the D-genome chromosome (e.g. see Fig. 2.3) (Joppa and Williams 1977). The procedures for localizing genes on chromosome are similar to those used in analysis of monosomics in hexaploid wheat, as

exemplified by the identification of chromosomal location of stem-rust resistance in Langdon (LDN) durum by means of monosomic substitution lines (Salazar and Joppa 1981). In the progeny of monosomic substitution, some plants disomic for the D-genome chromosome and nullisomic for the A- or B-genome chromosome were observed, and eventually Joppa and Williams (1988) developed complete sets of D-genome disomic substitution lines in tetraploid wheat (LDN-D substitutions). These substitution lines have been used to locate genes by simple observation of their presence or absence in the different aneuploids (du Cros et al. 1983; Joppa et al. 1983) or by crosses between aneuploids and a mutant line (Konzak and Joppa 1988). The LDN D-genome disomic-substitution lines have been used to produce sets of intervarietal chromosome substitution lines such as *Triticum dicoccoides* Koern. substitution lines (LDN-DIC) (Fig. 2.4). LDN-DIC substitutions have been analyzed for several important characters such as genes on the substituted chromosome that affect protein content of the grain (Joppa and Cantrell 1990) or confer higher yield (Cantrell and Joppa 1991). Joppa (1993) later used these LDN-DIC substitutions and the corresponding LDN D-genome disomic substitutions in an elegant crossing scheme to develop recombinant inbred chromosome lines in two generations. These lines have been extensively used to locate genes and quantitative trait loci to their chromosomes.

The availability of a set of *T. aestivum* Chinese Spring/*Aegilops tauschii* Coss. chromosomal substitution lines provided the opportunity to use the method of advanced backcross quantitative trait locus (QTL) analysis for the study of QTLs specific for individual chromosomes (Pestsova et al. 2001). New wheat introgression lines were developed by backcrossing of the chromosomal substitution lines with Chinese Spring wheat to produce different segments of individual chromosomes of *A. tauschii* in the common wheat background. The development of the lines was accompanied and confirmed by microsatellite-marker analysis (Pestsova et al. 2001).

In searching genetic variability in barley, Matus et al. (2003) developed a population of recombinant chromosome substitution lines (RCSLs) by crossing *H. spontaneum* (accession Caesarea 26–24, from Israel) and *H. vulgare* cultivar Harrington (North American malting quality standard). In a preliminary assessment of RCSLs, they noted that *H. spontaneum* ancestral genome introgression, in many cases, caused loss of acceptable phenotype in the cultivated progenitor, but in some cases that ancestral genome was a source of favorable alleles for some important agronomic traits and malting quality (Matus et al. 2003). RCSLs represent a useful source of genetic diversity that can be used as a model for physiological and genetic research. In rice, a relatively large segment of a particular chromosome from the donor parent is substituted in the recurrent parental background to form chromosome segment substitution lines (CSSLs), whereas a very small chromosomal segment containing the target QTLs or genes of a donor line is substituted (Yano 2001). Secondary mapping populations, such as CSSLs or near-isogenic lines, are required to facilitate a more comprehensive analysis of target QTLs. To facilitate the genetic analysis of quantitative traits and the use of marker-assisted breeding in rice, Ebitani et al. (2005) developed a novel mapping population consisting of 39 CSSLs.

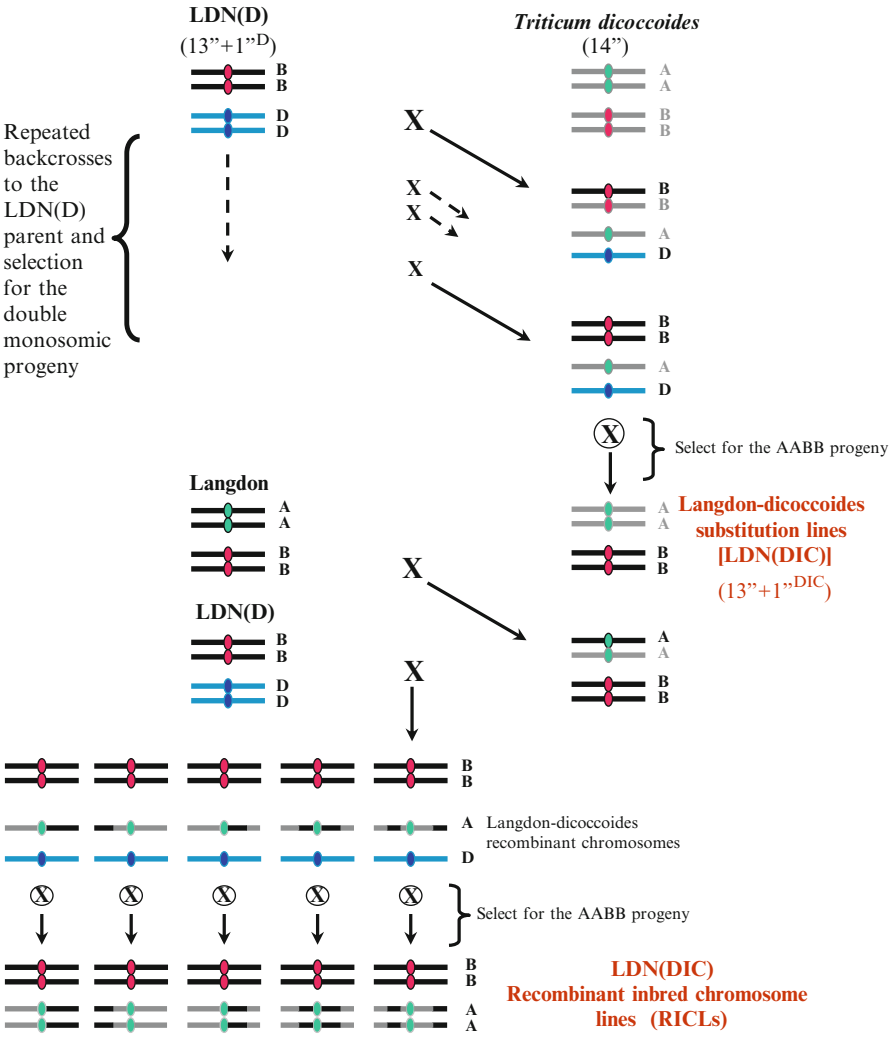

Fig. 2.4 Illustration of the process used by Joppa and Cantrell (1990) to generate the Langdon-*dicoccoides* substitution lines and that used by Joppa (1993) to develop homozygous recombinant inbred chromosome lines. Only the critical chromosomes are shown in this illustration. The homoeologous chromosomes from different genomes do not pair with each other in the presence of the *Ph* (pairing homoeologous) gene on 5BL. The *Triticum dicoccoides* chromosomes are represented in gray, the Langdon chromosomes in black, the D-genome chromosomes in blue, the recombined chromosomes in recombined colors, and the different genomes by colored centromeres

In each line, a different chromosomal segment of the *O. indica* cultivar Kasalath was substituted in the genetic background of the *O. japonica* cultivar Koshihikari (Japanese elite cultivar). The substituted chromosome segments in the 39 CSSLs covered most of the genome, except for small regions at the distal end of the short

arm of chromosome 8 and at the distal end of the long arm of chromosome 12. To verify the potential advantages of QTL detection in these CSSLs, they used the CSSLs to locate QTLs for heading date. Their results clearly demonstrated that the use of CSSLs permitted identification of a larger number of QTLs than did a BC_1F_3 population derived from the same cross combinations. Kubo et al. (1999) produced IR24 CSSLs with Asominori genetic background by repeated backcrossing and marker-assisted selections. The CSSLs carrying an IR24 homozygous segment at the middle region of chromosome 2 showed spotted, drooping, and somewhat yellowish green leaves at seedling stage under natural conditions.

2.5 Deletion Line

Chromosomal deletions are most commonly induced by ionizing radiation, which causes random breakages in double-stranded DNA. Depending on the type of break, repair of these breakages can occur through one of two general sets of mechanisms. The first, collectively called homologous recombination, occurs when the broken DNA strand uses a homologous template to prime repair DNA synthesis (van den Bosch et al. 2002; West 2003). In most cases of homologous recombination, the choice of an appropriate template results in conservation of the original DNA sequence at the break site. Alternatively, a double-strand breakage can be repaired by nonhomologous end joining, in which the broken chromosome is sealed without consultation of external homologies (Lieber et al. 2003) and results in the loss or addition of nucleotides. An alternative approach is to use transposons and site-specific recombination – an idea first proposed by van Harren and Ow (1993). According to this method, a T-DNA site is produced bearing a transposon and two copies of the target site for a site-specific recombinase. The transposon and one target site jump together and reinsert themselves into the chromosome at a location close to the T-DNA site. Recombination between the two specific sites, catalyzed by the recombinase, results in inversion or deletion of a large fragment of genome, depending on the alignment of the two specific sites.

Endo (1988) reported a unique genetic mechanism (gametocidal chromosomes) for the systematic production of even more powerful novel aneuploid stocks, namely, deletion stocks with terminal deletions of various sizes in individual chromosome arms, useful for subarm localization of genes. When a certain chromosome from *Aegilops cylindrica* is present in Chinese Spring in the monosomic condition, chromosomal breaks occur in the gametes that lack the *A. cylindrica* chromosome and generate various chromosome aberrations, including deletions. The broken chromosome ends, if not fused to other broken ends, are stabilized by the rapid gain of telomere structure (Werner et al. 1992a). Such deletions in plants without the *A. cylindrica* chromosome are transmitted regularly to the offspring. The breakpoints of deletion chromosomes carry telomere repetitive sequences (Werner et al. 1992a; Tsujimoto 1993), so deletion chromosomes are stable and transmitted to the offspring without further structural changes. This stability is also proved by the sequences of the breakpoints (Endo and Gill 1996; Tsujimoto et al. 1999). Thus, a

series of deletion lines on a chromosome can indicate specific chromosomal regions and can be used to isolate genes located in a specific chromosomal region (Kojima et al. 2000).

By this gametocidal technique, about 436 deletion lines have been developed in wheat. These stocks are immensely useful for localization of genes on chromosomes and chromosomes arms (Endo and Gill 1996; Lazo et al. 2004; McIntosh 1988). As the genome of common wheat is so large (2n = 6× = 42, AABBDD; 17,300 Mb), sequencing and mapping of the expressed portion is a logical first step for gene discovery. In a set of the deletion stocks, 7,104 expressed-sequence-tag unigenes have been localized on homeologous chromosomes of wheat (Conley et al. 2004; Hossain et al. 2004a; Lazo et al. 2004; Linkiewicz et al. 2004; Miftahudin et al. 2004; Munkvold et al. 2004; Peng et al. 2004; Qi et al. 2004; Randhawa et al. 2004).

In barley, a reliable, fast, and inexpensive approach has been developed by deletion mapping (Schubert et al. 1998). Diploid species like barley do not tolerate deletions, but deletion lines of barley can be obtained from wheat lines with single chromosomes 2C of *Aegilops cylindrica* and a pair of individual barley chromosome that have been developed (Shi and Endo 1997) in the genome background of Chinese Spring. Deletions and translocations of barley chromosomes in wheat lines have been identified that are monosomic for the *A. cylindrica* chromosome 2C (Schubert et al. 1998).

Chromosome deletions are useful tools for analyzing and manipulating plant genomes. Not only do they allow individual genes to be identified and mapped by classical and subtractive techniques, but also they can be used to eliminate a whole chromosome region, thus allowing analysis of chromatin structure and function (Gill et al. 1996; Cecchini et al. 1998; Visir and Mulligan 1999). In some plant species with large genomes and low gene density, genome deletion should provide the most efficient method for mutagenesis and gene mapping. The availability of detailed deletion libraries for plant species of agricultural and scientific importance is therefore highly desirable, but well-characterized deletions are difficult to generate.

RH mapping is based on radiation-induced chromosome breakage and analysis of chromosome-segment retention or loss with molecular markers. A high-resolution (100-kb) contiguous map of human chromosomes with 20,000 human genes has been constructed by means of the RH mapping approach and human-mouse cell hybrid lines (Hudson et al. 1995; Stewart et al. 1997; Deloukas et al. 1998). Since the success of RH mapping in human, this approach has been used in other animal genomes such as mouse (McCarthy et al. 1997), pig (Hawken et al. 1999), dog (Vignaux et al. 1999), zebrafish (Kwok et al. 1999), cat (Murphy et al. 2000), and rat (Watanabe et al. 1999). The duplicated and rearranged nature of plant genomes frequently complicates identification, chromosomal assignment, and eventual manipulation of DNA segments. Separating an individual chromosome or a portion of it from the full complement by its addition to an alien genetic background and subsequent mapping of radiation-induced deletions provide a powerful approach for analyses of these genomes. This potential has been realized in maize for mapping of duplicated sequences, gene families, and molecular markers to chromosome segments and for functional-genomics analyses using oat-maize chromosome-addition

lines (Riera-Lizarazu et al. 2000; Kynast et al. 2002). Extensive use of RH mapping in plant genomes is limited by the difficulty of identifying materials that contain different portions of the chromosome of interest. In durum wheat, an alloplasmic durum line, (lo) durum, has been identified with chromosome 1D of *T. aestivum* carrying the species-cytoplasm-specific (*scs*) gene. The chromosome 1D of this line segregates as a whole without recombination, precluding the use of conventional genome mapping. An RH mapping population was developed from a hemizygous (lo) *scs* line by means of 35-krad gamma rays. The analysis of 87 individuals of this population with 39 molecular markers mapped on chromosome 1D revealed 88 radiation-induced breaks in this chromosome. Analysis of molecular-marker retention allowed the localization of the *scs* gene and eight linked markers on the long arm of chromosome 1D (Hossain et al. 2004b). Physical mapping methods that do not rely on meiotic recombination are necessary for complex polyploid genomes such as wheat, because of the uneven distribution of recombination and significant variation in genetic-to-physical distance ratios, and RH mapping has proven valuable. A high-resolution RH map of wheat chromosome 1D (D genome) has been developed in a tetraploid durum-wheat (AB genomes) background that detected 2,312 chromosome breaks. The mapping resolution was estimated to be ~199 kb/break and provided the starting point for BAC contig alignment (Kalavacharla et al. 2006). To date, this resolution is the highest that has been obtained by plant RH mapping and serves as a first step for the development of RH resources in wheat. Analyzing 2,400 irradiated plants, Catanach et al. (2006) identified two major genomic regions in *Hieracium caespitosum* that collectively control apomixis, one at the level of the avoidance of meiosis and the other at the level of avoidance of fertilization. In conjunction with a BAC library, the deletion mapped is now being used to isolate sequences corresponding to the *LOA* and *LOP* loci. Radiation-induced deletion mapping has installed apomixis in target species and has therefore advanced us toward the goal of using this technology for the improvement of crop species to increase global welfare.

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