Chapter 1
Use of Alien Genetic Variation for Wheat Improvement

P.K. Gupta

Abstract Wheat production and productivity at the global level has witnessed a remarkable improvement during the last five decades, thus helping in providing food security. However, the annual growth rate in wheat production has declined from $\sim 3\ \%$ in earlier decades to 0.5–0.7 % in recent years causing concern. Therefore, major worldwide efforts are being made to improve the yield potential of bread wheat. In this connection, alien genetic variation has been found to be an important source of genetic variation both for qualitative and quantitative traits of agronomic importance. A number of alien species belonging to the tribe Triticeae of the family Poaceae have been utilized for this purpose. These alien species have been utilized through the production of amphiploids, whole chromosome alien addition and substitution lines, whole-arm Robertsonian translocations, and the translocations involving small segments of alien chromosomes. The transfer of small segments carrying desirable alien genes was achieved through several approaches including irradiation, use of mutants, and suppression of diploidizing gene (Ph1). These alien resources along with the details of their successful utilization for wheat improvement have been described in this chapter.

Keywords Bread wheat • Alien species/genes/additions/substitutions • Amphiploids

1.1 Introduction

Wheat yield and production, worldwide and in India, have shown dramatic improvement during the last five decades. According to recent estimates, the mean global wheat yield has increased from 1.2 tonnes per hectare (t/ha) in the year 1961

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P.K. Gupta (✉)
Department of Genetics and Plant Breeding, Chaudhary Charan Singh University,
Meerut, UP, India
e-mail: pkgupta36@gmail.com

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to ~3 t/ha in the year 2014 (in UK, the yield increased from 2.8 t/ha in 1948 to 8 t/ha in 2014). The world wheat production during the same period improved from ~225 million tones (mt) to ~715 mt. However, the annual growth rate in production has gone down from ~3 % during the 1970s and 1980s to 0.5–0.7 % in recent years, which has been a matter of concern. It has also been observed that major advances in wheat yield and production have been due to better management and improved agricultural practices rather than by an improvement in the genetic potential (however, in UK, according to some estimates, the increase has been mainly due to improved genetic potential). A flow of newer varieties that are resistant to emerging new races of pathogens, particularly the three rusts, has also contributed to an improvement in yield and production, although it has been difficult for wheat breeders to sustain this activity. These aspects are being discussed at the global level through a Wheat Initiative launched in the year 2011 and have been more recently discussed during a meeting held as a part of Norman Borlaug Centenary Celebrations. The meeting was appropriately called ‘Wheat for Food Security’ and was held at the International Institute for Wheat and Maize Improvement (CIMMYT) in Mexico. The new ‘International Wheat Yield Partnership’ (IWYP) program, as a part of Wheat Initiative, was also launched during this meeting.

The major limitations in wheat yield and production have been due to biotic and abiotic stresses, which have been regularly addressed in recent years with limited success. It has also been recognized that the genetic variability, being limited within the wheat germplasm (primary gene pool), secondary, and tertiary gene pools can be exploited for additional genetic variability. This useful variability has been described as alien genetic variation, since it is available in taxa, which though lie outside the species delimitations of cultivated wheat, but can be crossed with wheat, even though sometimes using embryo rescue. Considerable information on the use of alien genetic variation for wheat improvement is available in several reviews published in the past (Sears 1981; Sharma and Gill 1983; Knott 1987; Islam and Shepherd 1991, Jiang et al. 1994a, b; Gill et al. 1996; Mujeeb-Kazi and Rajaram 2002). In this chapter, we briefly describe these alien genetic resources and discuss their utility in wheat improvement, with emphasis on relatively recent work, since earlier work has been adequately covered in several reviews published in the past.

1.2 Alien Genetic Resources

The major sources of alien genetic variation for wheat improvement are the taxa belonging to the sub-tribe Triticinae of the tribe Triticeae. These taxa include species from the following old and classical genera: *Triticum*, *Secale*, *Aegilops*, *Agropyron*, and *Haynaldia* (now called *Dasypyrum*). The old classical genus *Agropyron* is now known to include several newly described genera including *Thinopyrum*, *Lophopyrum*, *Elymus*, and *Leymus*. These and other alien genera have been classified in primary, secondary, and tertiary gene pools. The primary gene pool includes species of genera *Triticum* and *Aegilops*, which represent the progenitors of hexaploid wheat; the chromosomes of these species can pair with wheat chromosomes and genes can be transferred by normal recombination process without any aid of induced recombination or irradiation. In other words, the species carrying genomes A, B, or D constitute the primary gene pool. This gene pool contains hexaploid wheat landraces, cultivated tetraploid wheats, the wild tetraploid wheats (*T. turgidum*; syn. *Triticum dicoccoides*), and diploid progenitors of the A, B, and D sub-genomes to durum and bread wheats. Some cross-combinations require embryo rescue, but no cytogenetic manipulation is needed in exploiting this primary gene pool. The secondary gene pool consists of species belonging to the genera *Triticum* and *Aegilops*, which share only one sub-genome with the three sub-genomes of wheat, the other one or more genomes being not shared. Several diploid species of the Sitopsis section are included in this pool, and the F_1 hybrids within this gene pool exhibit reduced chromosome pairing. In such cases, gene transfers have been achieved through direct crosses, breeding protocols, homologous exchange of chromosome segments between the related genomes and through the use of special manipulation strategies. Embryo rescue is a complementary aid for obtaining hybrids. The tertiary gene pool includes diploid and polyploid species of the genera belonging to the tribe Triticeae, which carry genomes other than those present in hexaploid wheat. Homoeologous relationship between the chromosomes of these species and wheat allow alien gene transfers through more complex chromosome manipulations. Special techniques involving irradiation, use of *ph1* mutants or callus culture-mediated induction of translocations are also used. The wild hexaploid wheat landraces and distant relatives of wheat [e.g., *Secale cereale* (rye), *Thinopyrum bessarabicum*] also provide a vast and largely untapped reservoir of genetic variation that is used for improvement of target traits in wheat. Some of the alien species listed in Table 1.1 have been successfully utilized for the development of whole chromosome alien addition/substitution lines and/or translocations carrying each a complete alien chromosome arm or a small alien chromosome segment.

In UK, a major program in the form of WISP (Wheat Improvement Strategic Program) consortium has recently been launched to utilize alien genetic variation for wheat improvement. It is a BBSRC-funded collaborative program, which brings together experts from the following five UK institutions, and will run from 2011 to 2017: (i) John Innes Centre, (ii) National Institute for Agricultural Botany (NIAB), (iii) University of Nottingham, (iv) University of Bristol, and (v) Rothamsted Research Institute. The program will collect and generate new and novel wheat germplasm characterized for traits relevant to academics and breeders. It will also identify gene-based or DNA-based molecular markers for selecting these traits. The program is structured around three complementary ‘pillars’ (landraces, synthetics, and ancestral gene introgression), each of which will broaden the pool of genetic variation in wheat by a different route. Among the three pillars, the last one will deal with new and useful alien genetic variation from related species.

Table 1.1 Some examples of alien species, which have been used for the production of alien–wheat chromosome additions, substitutions, and translocations

Species and genome	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 biuncialis (Mb)	Farkas et al. (2014)
Aegilops peregrina (U^US^U)	Friebe et al. (1996b)
Secale cereale (R)	Gill and Kimber (1974), 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)

1.3 Strategies for Using Alien Genetic Variation

The process for the transfer of target genes from alien species into wheat often involves prior development of amphiploids and the alien addition/substitution lines. This is followed either by irradiation or by induced recombination (facilitated by absence of chromosome 5B or presence of *ph1* mutant) to produce translocations. Different strategies for using alien genetic variation will be briefly discussed in this section.

1.3.1 Amphiploids for Transfer of Alien Chromosome Segments

During the 1950s and 1960s, production of amphiploids used to be the first step for utilization of alien genetic variation for wheat improvement. The production and utilization of amphiploids generally involved the following steps: (i) crossing tetraploid wheat (AABB) or hexaploid wheat (AABBDD) with a diploid or tetraploid alien species to produce F_1 hybrids (sometimes using embryo rescue); (ii) doubling the chromosome number in the F_1 hybrids through colchicine treatment to produce amphiploids; (iii) crossing and backcrossing the amphiploid (some times after irradiation treatment; see next paragraph) with hexaploid wheat to facilitate transfer of either an alien segment or the whole alien chromosome or only one arm of a chromosome to wheat [for details about transfer of a whole chromosome leading to production of alien addition and alien substitution lines, and an arm leading to Robertsonian translocations, see later in this chapter].

As an example of the above procedure, in a recent study, a 10*x* amphiploid ($AABBDDU^bU^bM^bM^b$) was produced by combining hexaploid wheat (AABBDD) and tetraploid *Ae. biuncialis* ($U^bU^bM^bM^b$). This amphiploid was used for irradiation leading to transfer of alien segments, which could be identified using multicolor FISH (McFISH) (Molnar et al. 2009).

In another study conducted in Pakistan, Mujeeb-Kazi and his coworkers utilized *Ae. variabilis* ($2n = 4x = 28$; UUSS) as an alien species for imparting resistance against *Cochliobolus sativus* (spot blotch) and *Tilletia indica* (Karnal bunt). The amphiploids with $2n = 8x = 56$ (AABBUUSS) and $2n = 10x = 70$ (AABBDDUUSS) were obtained using this alien species. The morphology and cytogenetics of these amphiploids were examined with a view to transfer alien chromosome segments carrying genes for resistance against spot blotch and Karnal bunt into the recipient durum and bread wheat germplasm.

Direct use of amphiploids for wheat improvement through the transfer of an alien segment from crested wheatgrass (*Agropyron cristatum* = PP) carrying genes for resistance against leaf rust was also reported recently (Ochoa et al. 2015). The transfer of the alien segment involved crossing and backcrossing of the amphiploid AABBDDPP with hexaploid wheat (AABBDD). The amphiploid (AABBDDPP) itself was earlier obtained by crossing tetraploid wheat (*Triticum turgidum* L. conv. Durum Desf. $2n = 4x = 28$; AABB) with a self-fertile allotetraploid ($2n = 4x = 28$; DDPP) obtained through a cross between diploid wheat (*Aegilops tauschii* Coss.) and crested wheatgrass (*A. cristatum*). After three backcrosses, a fertile stable line (named TH4) was obtained with 42 chromosomes. Fluorescence in situ hybridization (FISH), genomic in situ hybridization (GISH), and use of genome-specific molecular markers confirmed that TH4 carried a compensating Robertsonian translocation involving the long arm of wheat chromosome 1B and the short arm of an unidentified *A. cristatum* chromosome. This TH4 line and similar other lines produced using this approach will certainly be used in future wheat breeding programs, as sources of resistance against a number of biotic and abiotic stresses (see later for details).

1.3.2 Use of Synthetic Hexaploid Wheats (SHWs)

One of the most successful programs for utilization of alien genetic variation for wheat improvement has been the development of a large number of SHWs by combining the genomes of tetraploid wheat (AABB) and *Aegilops tauschii* (DD) (Fig. 1.1). Since late 1980s, these SHWs have been produced in thousands at CIMMYT and are being utilized all over the world for the introgression of alien genetic material from *Ae. tauschii* into modern bread wheat cultivars (Lage et al. 2004; Talbot 2011). It has been shown that the hybrids produced from a cross between SHW and an improved variety exhibit double the genetic diversity relative

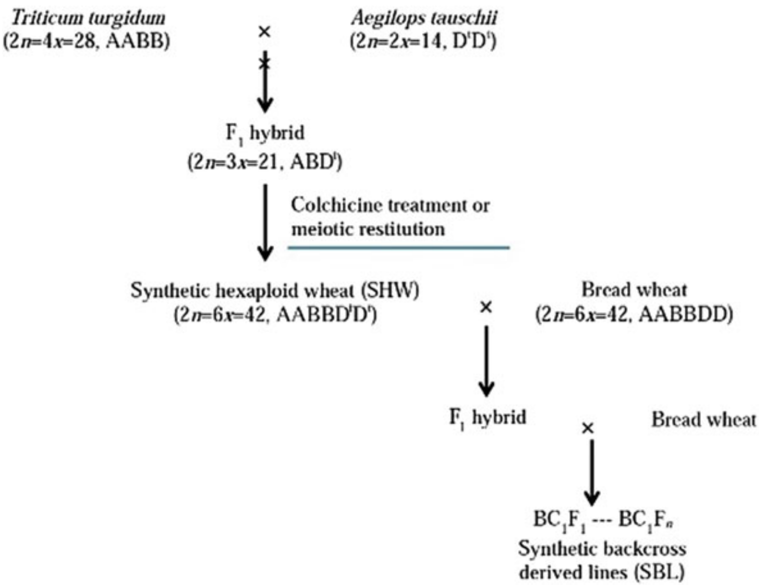


Fig. 1.1 Different steps involved in the transfer of desirable traits from synthetic hexaploid wheat (*SHW*) into elite cultivars in the form of synthetic backcross-derived lines (*SBLs*)

to its parents (Kazi and Van Ginkel 2004). Once created, a SHW (like any other amphiploid, as mentioned above) can be crossed with one or more bread wheat cultivars, followed by repeated backcrosses (Lange and Jochemsen 1992; Trethowan and Mujeeb-Kazi 2008) to produce synthetic backcross-derived lines (SBLs; Fig. 1.1). In actual practice, these SBLs have been subjected to selection, and the selected SBLs exhibited significant yield increases across a diverse range of environments, demonstrating their potential for improving wheat productivity worldwide.

The desirable traits, which could be improved using SHWs include the following: (i) resistance or tolerance to a number of biotic stresses including resistance to leaf blotch, glume blotch, crown rot, yellow leaf spot, leaf blight, powdery mildew, and karnal bunt; they also exhibited resistance to certain insect pests such as Green bugs and Hessian fly (Van Ginkel and Ogbonnaya 2007); (ii) tolerance to a number of abiotic stresses including drought, heat, and salinity; in some cases, the SBLs were shown to have deeper or thicker roots assisting wheat plant in water uptake, which helped the plant to survive under water stress (Schachtman et al. 1991, 1992); (iii) tolerance to preharvest sprouting; (iv) large kernels and heavy spikes; and (v) a higher concentration of both micro- and macronutrients (Fe, Mn, K, and P), relative to that in *T. aestivum* (Calderini and Ortiz-Monasterio 2003). A brief account of activities involving use of SHWs in different countries will be presented in this section.

1.3.2.1 SHWs in Europe, Asia, and Australia

In several countries including Australia, Argentina, Equador, China, India, and Pakistan, the SBLs have shown 5–40 % increase in yield over local modern check varieties (Ogbonnaya et al. 2007). In Australia (DPI, Victoria), under their ‘Synthetic-Enriched Resources for Genetic Enhancement’ (synERGE) program, 30 % increase was achieved through the use of SHWs. In China also, use of synthetic wheats started in 1995, and four varieties (Chuanmai 38, Chuanmai 42, Chuanmai 43 and Chuanmai 47) were released in Sichuan since 2003; Chuanmai 42—out-yielded commercial check variety by 23 %—and has been grown on >100,000 ha since 2006 (Yang et al. 2009). In Norway also, 448 synthetic wheats from CIMMYT were tested for powdery mildew, and synthetic wheats with partial resistance were crossed with local cultivars (unpublished results).

At the National Institute of Agricultural Botany (NIAB) of Cambridge University, SHWs were used for developing a ‘super wheat’, which had 30 % higher yield than existing wheat cultivars (in 2012) and also carried tolerance against a number of biotic and abiotic stresses. This will be the first commercialized form of synthetic wheat, which is likely to be released by 2019–2022 (http://www.niab.com/ news_and_events/article/281).

In Pakistan, during the two years of yield trials, two varieties derived from SHWs had 20 and 35 % higher yields than the commercial check variety (Kazi and Van Ginkel 2004). In 2003, a CIMMYT synthetic wheat derivative was also registered in Spain under the name Carmona. This is an early maturing variety that provides seed in a shorter period relative to most commercial cultivars and is valuable for those wheat growers, who often plant late in the year in southern Spain. Carmona also has a better grain quality and is suited to zero-tillage systems, where it resists foliar diseases and produces higher yields (Kazi and Van Ginkel 2004).

1.3.2.2 SHW-Derived ‘VOROBEY’ at CIMMYT

The biggest breakthrough in wheat breeding after ‘Veery,’ which carried the 1BL.1RS translocation, was the development of ‘Vorobey’ involving synthetic hexaploid wheats (SHW). Under the CIMMYT’s program of Semiarid Wheat Yield Trial (SAWYT) that was started in 1991 for the development of wheats for the drought-prone areas, as many as 8 % of the lines in 5th SAWYT (1996) represented SHW-derived lines; this proportion increased to 46 % in 15th SAWYT (2006). However, the average coefficient of parentage of SHW in all synthetically derived crosses decreased from 75 to 19 %. Using yield across locations as an index, the average rank of the SHW-derived lines improved during the 5th to 12th SAWYT, so that in SAWYT 11 and 12, SHW-derived line Vorobey was a top-performing line. Vorobey performed well across all environments, giving yields up to 8 t/ha. The use of SHW in wheat breeding for rainfed environments at CIMMYT has increased significantly over the past 10–20 years and the performance and effect of SBLs improved with time. High grain yield also had a positive correlation with

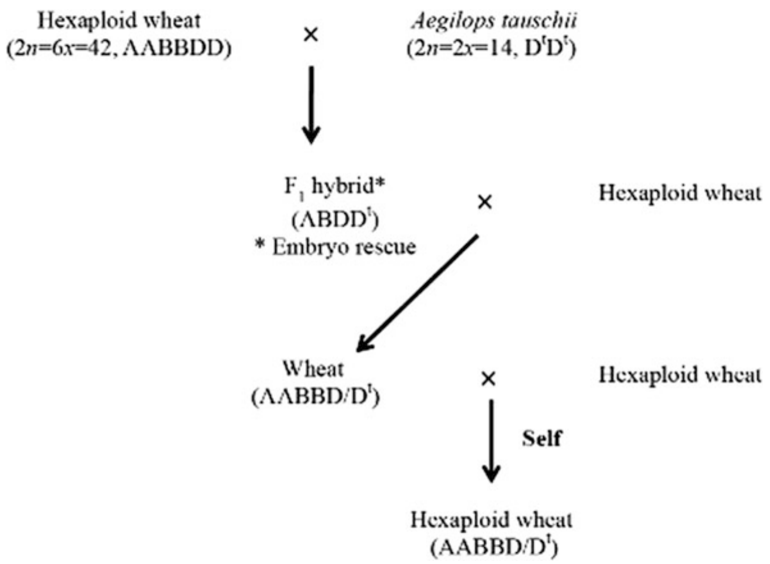


Fig. 1.2 Development of an advanced backcross population for AB-QTL analysis from the cross, wheat (6*x*) × *Ae. tauschii* (2*x*)

improved harvest index, improved grain weight and increased above ground biomass (Rattey et al. 2009, 2011; Shearman et al. 2005). The primary synthetic superior progenies also had larger seed size/weight, improved number of seeds/spike and number of spikes/plant (Cooper 2013; Cooper et al. 2012).

1.3.2.3 SHWs for QTL Mapping

SHWs have also been utilized for developing mapping populations that have been used for QTL interval mapping. A list of these mapping populations has been compiled by Ogbonnaya et al. (2013). SHWs have also been utilized for developing a number of AB-QTL populations, which have been utilized for QTL mapping (Huang et al. 2003, 2004; Moorthy et al. 2006; Naz et al. 2008). Different steps involved in the production of AB-QTL populations in the form of synthetic backcross-derived lines (SBLs) are depicted in Fig. 1.2.

1.3.3 Use of F_1 Hybrids (Wheat × Alien Species) for Alien Gene Transfer

An alternative to the above approach of using amphiploids (including SHWs) involved production and utilization of tetraploid/pentaploid F_1 hybrids ($2n = 28$ or

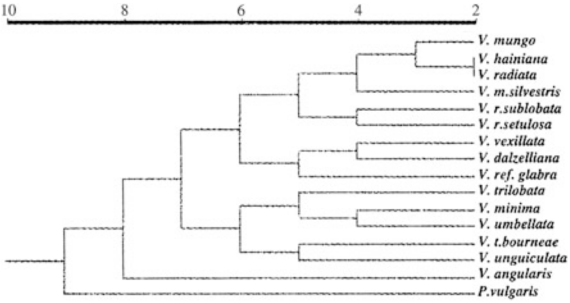


Fig. 1.3 Direct cross for transfer of one or more genes from tetraploid wheat into hexaploid wheat

$2n = 35$) from the cross, wheat ($6x$) × alien species ($2x$ or $4x$). Following steps are involved in this alternative approach: (i) hybridization of wheat with an alien species (Figs. 1.2 and 1.3); (ii) selfing or backcrossing the F_1 hybrids to hexaploid wheat to obtain stable hexaploids ($6x = 42 = 21^{II}$); alternatively, the seed of F_1 hybrids may be irradiated or allowed to undergo induced recombination between the chromosomes of wheat and those of the alien species via suppression of the pairing control gene *Ph1* (see later), and (iii) production and identification of wheat progeny, which contains a small alien chromosome segment carrying the target alien gene, but avoiding the simultaneous transfer of associated deleterious genes.

1.3.4 Alien Addition and Substitution Lines in Hexaploid Wheat

Starting in the 1950s and 1960s, additions and substitutions of whole individual alien chromosomes from a number of alien species to hexaploid wheat genome were successfully achieved (Evans and Jenkins 1960; Riley 1960; Islam et al. 1981; Friebe et al. 1998). Generally, disomic alien chromosome substitutions could be obtained only for the corresponding homoeologous wheat chromosomes. For instance, 1R rye chromosome could be substituted only for 1A, 1B, and 1D chromosomes, so that for any diploid alien species with $2n = 14$, only 21 disomic compensating substitutions were possible. This production of disomic alien additions/substitutions was initially attempted with the hope that these alien additions and substitutions may give birth to new cultivated species that may prove to be superior to cultivated hexaploid wheat (*T. aestivum*); this hope was never materialized, partly due to an instability of these lines and partly due to lack of their superiority over best wheat cultivars. Some of the alien species used for this purpose include the following (Gupta 1995): *Secale cereale*, *Aegilops comosa*, *Ae. geniculata*, *Ae. longissima*, *Ae. bicornis*, *Ae. biuncialis*,

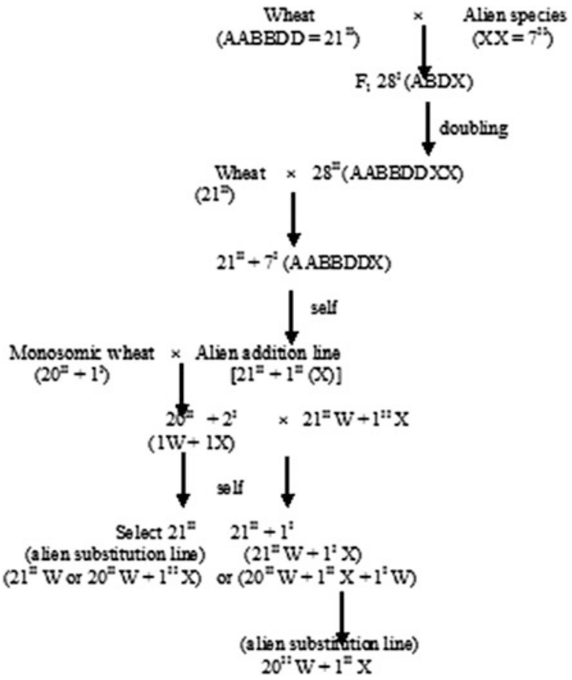


Fig. 1.4 Different steps involved in the production of whole chromosome alien addition and alien substitution lines in hexaploid wheat

Agropyron junceum, *Ag. intermedium*, *Ag. elongatum*, *Dasypyrum villosum,* and *Hordeum vulgare* (note that some of the *Agropyron* species listed here are now known to belong to new genera like *Thinopyrum*).

Alien addition lines have largely been produced and utilized for gene transfer using the following steps (Fig. 1.4): (i) hybridization between wheat and the alien species followed by colchicine doubling of chromosome number to produce an amphiploid (e.g., $8x$ = AABBDDUU in case of alien species *Aegilops umbellulata*); (ii) crossing of the amphiploid with hexaploid wheat to get a heptaploid hybrid ($7x$ = AABBDDU), which will form 21^{II}W + 7^{I}U at meiosis; (iii) selfing this hybrid followed by selection of monosomic/disomic addition lines (21^{II}W + 1^{I}U; 21^{II}W + 1^{II}U); (iv) crossing of these addition lines with wheat monosomics to get alien substitution lines (20^{II}W + 1^{II}U); (v) use of the alien addition/substitution lines for irradiation or induced recombination to produce translocations including those involving whole-arm substitutions (centric fusion).

The alien addition and substitution lines carried a large number of desirable traits including resistance against a variety of diseases. Therefore, these addition/substitution lines have been used for systematic transfer of these traits to elite and high yielding wheat cultivars. In a recent study, *Aegilops biuncialis* chromosome $3M^{b}$ addition and substitution [$3M^{b}$(4B)] or translocation ($3M^{b}$.4BS centric fusion) have been obtained with a view to improve the grain micronutrient (Fe, Zn, Mn, K) contents in the grain (Farkas et al. 2014).

1.3.5 Alien Substitution/Translocation Lines in Tetraploid Wheat

At USDA-ARS Cereal Crops Research Unit, Fargo, ND (USA), alien substitution/translocation stocks were also produced in tetraploid wheat cultivar ‘Langdon.’ As listed by Joppa (1993), these stocks included the following: (i) 39 Langdon-*T. dicoccoides* substitution lines; (ii) 14 Langdon D-genome substitution lines; (iii) 4 translocation lines representing 1AS-1AL.1DL translocations. The details of these stocks are also available at GrainGenes.

More recently, at the same station at Fargo (USA), the alien species *Thinopyrum bessarbicun* ($2n = 14$) was utilized to produce at least 14 alien addition lines in tetraploid wheat. These addition lines were studied using mcFISH and molecular markers (Jauhar and Peterson 2013).

1.3.6 Reconstitution of New Genomes Involving Alien Species

Efforts were also made to reconstitute entirely new genomes, by combining variable number of chromosomes from two different genomes (Evans 1964). In this study, an amphiploid (AABBEE), derived by combining tetraploid wheat and a diploid alien species (*Agropyron elongatum* = EE), was crossed with bread wheat. The F_1 hybrid plants (AABBDE) exhibiting $14^{II} + 14^{I}$ at meiosis were selfed, and in the progeny, plants exhibiting 21^{II} at meiosis were selected. The hexaploids were backcrossed again with wheat to identify the number of D and E chromosomes in the reconstituted genome, through a study of meiosis in the F_1 hybrids (Fig. 1.5).

1.3.7 Whole Alien Chromosome Arm Translocations

One of the most promising approach for alien gene transfer for wheat improvement has been to produce Robertsonian translocations, each involving a whole chromosome arm from an alien species (Fig. 1.6). The most important of these translocations is the 1BL.1RS translocation found in the ‘Veery’ series of wheat cultivars. The 1RS arm from rye (*Secale cereale*) carries a battery of resistance genes specifying resistance to leaf rust (*Lr26*), stem rust (*Sr31*), stripe rust (*Yr9*), and powdery mildew (*Pm8*) (Friebe et al. 1996a, b), and genes for adaptation to abiotic stresses, including a robust drought-tolerant root system (Sharma et al. 2011). Because of tight linkage of these genes on the chromosome arm 1RS, the genes are inherited as a single linkage block.

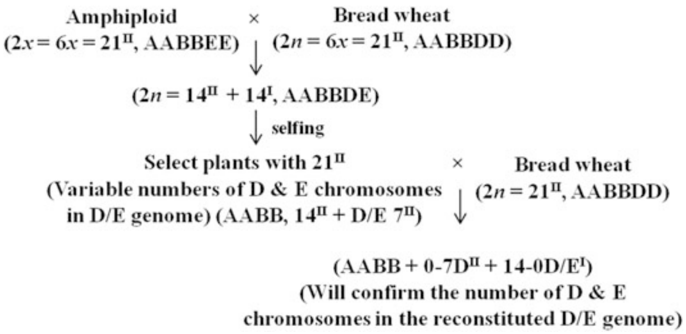
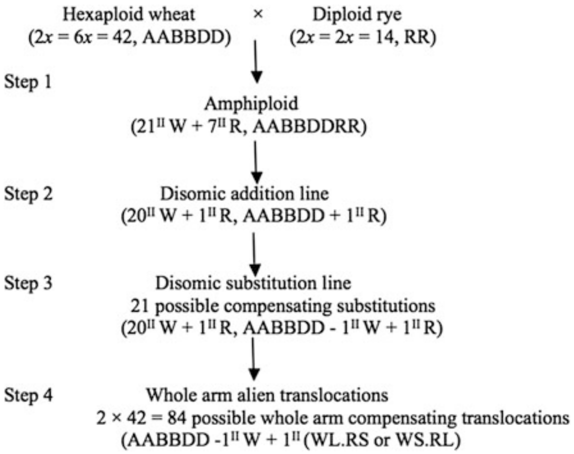


Fig. 1.5 Steps involved in the reconstitution of a new genome utilizing chromosomes from the D-genome of wheat and E genome of *Agropyron elongatum*

Fig. 1.6 Different steps involved in the production of alien introgression lines in wheat, where a complete arm of alien chromosome is substituted for a homoeologous wheat chromosome arm



The second example of the transfer of a whole arm of an alien chromosome is T6AL.6VS, where the 6AS arm of wheat was replaced by the 6VS arm from *Dasypyrum villosum* (syn. *Haynalidia villosa*). The alien chromosome arm 6VS carries genes for resistance against (i) all known races of powdery mildew; (ii) wheat curl mite, (ii) stripe rust, (iv) Fusarium head scab, and (v) soilborne mosaic virus. In the plants heterozygous for *Pm21*, the chromosome T6AL·6VS does not pair with the normal 6AL·6AS in their short chromosome arms during meiosis. Thus, all of the genes on the 6VS arm are inherited as a single linkage block. In another recent study, *Ae. biuncialis* chromosome $3M^b$ addition and substitution [$3M^b$(4B)] and translocation ($3M^b$L.4BS, a centric fusion) were obtained with a view to improve the grain micronutrient (Fe, Zan, Mn, K) contents in the grain. Some examples of whole-arm substitutions (including the above two examples) are listed in Table 1.2.

Table 1.2 Some examples of the transfer of alien chromosome arms for wheat improvement

Donor species	Target gene	Translocation	Method of transfer
Ae. umbellulata	*Lr9*	T6BS.6BL-6UL	Irradiation
Ae. biuncialis	Genes for K, Zn, Mn	T4B.3Mb	Induced recombination
Secale cereale	*Pm8*, *Sr31*, *Lr26*	T1BL.1RS	Spontaneous
	Yr9, *Pm17*, *Gb2*	T1AL.1RS	Irradiation
Ag. 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

Many of the above whole-arm translocations could be easily identified with the help of FISH. For instance, 1BL/1RS translocation in Indian wheat cultivars were identified by Kumar et al. (2003), and those in Pakistani wheats were identified by Tahir et al. (2014).

1.3.8 Transfer of Alien Segments: Translocation Lines

Transfer of alien chromosome segments (each representing part of a chromosome arm) was achieved using either of the following two major approaches: (i) seed of an alien addition/substitution line carrying the gene of interest on the alien chromosome was irradiated, plants raised from irradiated seed backcrossed to a wheat cultivar, and selection exercised in segregating backcross population for desirable translocations; (ii) mutants for *Ph1* locus (*ph1* mutants) were used to facilitate meiotic pairing between the alien chromosome and its wheat homoeologue. Spontaneous translocations, following crosses made between wheat and an alien species, have also been reported.

1.3.8.1 Translocations Due to Irradiation

A large number of lines with translocations between wheat and alien chromosomes were produced through irradiation of seed for alien addition/substitution lines. These translocation lines carried each a small chromosome segment from an alien species and are largely listed in earlier reviews on the subject (for list of reviews, see above). Some of the examples of these translocations produced during the 1950s and 1960s included the following: (i) a translocation (called '*Transfer*') with an *Aegilops umbellulata* chromosome segment carrying a gene for leaf rust resistance (Sears 1956); this was the first example of useful transfer of an alien chromosome segment for improvement of wheat; (ii) a translocation (called '*Translocation-4*') with an *Agropyron elongatum* chromosome segment carrying a gene for leaf rust resistance (Sharma and Knot 1966); (iii) a 6A-6E translocation with a segment from *Ag. elongatum* chromosome 6E carrying stem rust resistance gene *Sr26*; this stock carrying alien segment was used extensively for the development of several Australian wheat cultivars (see Knott 1971, for a review); (iv) a 4A-2R translocation (called '*Transec*') carrying resistance against leaf rust and powdery mildew (Driscoll and Jensen 1964); this stock had low yields perhaps due to non-homoeologous nature of the translocation and due to loss of some essential genes from wheat.

One of the recent examples of translocations involving alien chromosome segments involved the use of an amphiploid, which combined the genomes of hexaploid wheat (AABBDD) and tetraploid alien species, *Ae. biuncialis* ($U^bU^bM^bM^b$). The 10*x* amphiploid ($AABBDDU^bU^bM^bM^b$) was irradiated, and translocations were identified in M_0 and M_1 generations using multicolor FISH (McFISH) (Molnar et al. 2009). Translocations obtained in this and similar other studies will prove useful for wheat improvement.

Majority of the above translocations, however, were long terminal or long proximal in nature, except 'Transfer,' which carried an intercalary translocation. Such long translocations would carry substantial linkage drag, if the gene of interest (GOI) in the alien chromosome is located farther away from the telomere/centromere, at an interstitial position. Sears (1981) suggested that interstitial transfers can be obtained by intercrossing either the two translocations each carrying the GOI (one carrying a proximal translocation and the other carrying a distal translocation), or between the translocation line (carrying the GOI in a terminal alien chromosome segment) and the recipient wheat cultivar. This would allow recombination to produce a translocation line carrying a small interstitial segment (for details, see Islam and Shepherd 1991).

1.3.8.2 Translocations Due to Induced Meiotic Recombination

In addition to the above translocations, which were introduced following irradiation, strategies were also developed for utilizing induced homoeologous pairing between one or more wheat chromosomes and their corresponding alien homoeologues available within an alien addition or an alien substitution line. (i) use of nullisomy for chromosome 5B carrying *Ph1*; (ii) use of 5B/5D nullisomic-tetrasomic line devoid of 5B chromosome; (iii) use of a *ph1* mutant, which does not suppress, but instead allows homoeologous pairing; (iv) suppression of the diploidizing effect of *Ph1* locus by the genome of a specific strain of *Ae. speltoides*/*Ae. mutica*.

(i) *Use of 5B nullisomy*. Nullisomy for 5B can be achieved through different strategies, involving either the use of nullisomic/monosomic for 5B, mono-5B wheat (carrying a disomic alien substitution of choice) or by using 'nullisomic-5B tetrasomic-5D.' Each of these cytogenetic stocks could be used as a female parent in a cross with either an alien species or with an alien addition/substitution line. Monosmics for 5B were used by Riley (1966) for transfer of alien genetic variation from *Ae. bicornis*, and by Joshi and Singh for transfer of alien genetic variation from rye (*Secale cereale*). Later, Sears (1972, 1973) utilized nulli-5B tetra-5D for crosses with alien substitution lines, each carrying an alien chromosome from *Ag. elongatum*, and successfully transferred two leaf rust resistance genes (*Lr 19*, *Lr24*) from this alien species. These lines carrying alien chromosome segments were later shown to be 3D-3Ag and 7D-7Ag translocations.

(ii) *Use of ph1 mutants*. In the second approach, one may use a homozygous *ph1* mutant line and cross it to either an alien species (Fig. 1.7) or to a mono-5B, alien substitution line (Fig. 1.8), so that in the F_1 hybrid, mutant *ph1* allele will be in hemizygous condition and will induce recombination between alien chromosomes and their wheat homoeologues to allow transfer of alien segments (Figs. 1.7 and 1.8). Once alien transfer is achieved in disomic condition, one may use this stock in the normal backcrossing program to transfer the alien segment to a high yielding elite genotype.

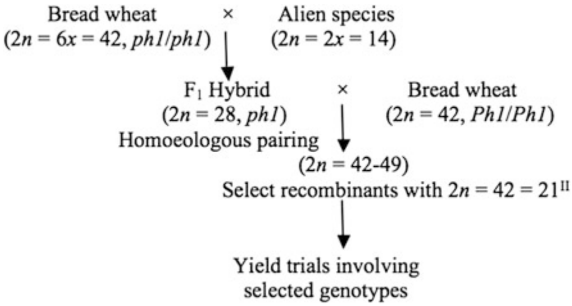


Fig. 1.7 Steps involved in the transfer of an alien segment through a cross between a homozygous *ph1/ph1* mutant and a diploid alien species

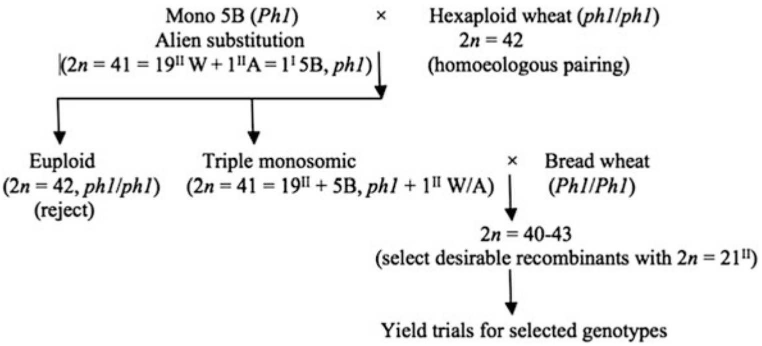


Fig. 1.8 Steps involved in the use of *ph1* mutant/deletion for transfer of alien segment to wheat genome through recombination

In a recent study, crossing of wheat—*Ae. biuncialis* disomic addition lines with *CSph1b* (Chinese Spring wheat mutant for *ph1b*) led to an increased frequency of pairing between wheat and *Aegilops* chromosomes in the F_1 hybrids (Schneider et al. 2005; Molnár and Molnár-Láng (2010).

(iii) *Suppression of Ph1 activity*. It is known that certain strains of *Ae. speltoides* or *Ae. mutica* suppress the effect of *Ph1* locus in F_1 hybrids obtained through a cross between wheat and one such strain. Although this feature can be directly utilized for transfer of desirable alien genes from these two alien species, the system can also be utilized for transfer of alien genes from other alien species. For instance, Riley et al. (1968) successfully utilized this system for transfer of stripe rust resistance (*Yr8*) associated with an alien segment from *Ae. comosa.* In this study, an alien addition line carrying relevant chromosome from *Ae. comosa* was crossed to an *Ae. speltoides* strain that was known for suppression of *Ph1* effect. The F_1 hybrids were crossed and backcrossed to a specific elite wheat cultivar, and desirable recombinants were selected in each segregating backcross generation.

1.3.8.3 Use of DNA-Based Molecular Markers for Alien Gene Transfer

Protein and DNA-based molecular markers have also been used for the detection of alien segments transferred to wheat using the approaches described above. These markers also facilitated selection of plants carrying small interstitial segments derived through recombination between two translocations that each carried a long terminal or proximal segment. For instance, Koebner and Shepherd (1986) and Sears (1981) induced recombination (using *ph1b* mutant, or nulli 5B-tetra 5D line) between wheat and rye chromosome segments involving the translocations 1DL.1RS and 1BL.1RS. Following markers were utilized for identification of recombinants, each carrying a desirable small alien segment: (i) protein markers, Tri-1 and Gli-D1 encoded by genes located on 1DS, and (ii) the gene encoding protein Sec-1 (a storage protein), and the gene *Sr31* for stem rust resistance, both located on rye chromosome arm 1RS. In another study, a number of isozymes (Aco-1, Est-2, Got-2, and Acph-3) encoded by genes carried by one or more *Agropyron* chromosomes were also used for tracking the presence of a small desirable alien chromosome segment in a translocation line (Nichols 1983; Jenkin et al. 1984).

DNA-based molecular markers were also utilized for following the transfer of alien chromosome segments in the translocation lines. These molecular markers included SCAR, PLUG, SSR, and SNP markers. FISH, mcFISH, and GISH were also used for ascertaining the identity of the transferred alien chromosome segments in improved wheat cultivars. A summary of some of the studies involving transfer of alien chromosome segments using DNA-based molecular markers and FISH/mcFISH/GISH is presented in Table 1.4. Some details of the studies involving improved wheat cultivars for ascertaining the presence/absence of alien chromosome segments are briefly described in the next section.

1.4 Molecular Dissection of Alien Segments in Improved Wheat Cultivars

The alien segments that are present in a large number of improved wheat cultivars have been identified following several approaches including physical mapping through FISH, McFISH, GISH, and genetic mapping using DNA-based molecular markers. These are briefly described.

1.4.1 Use of FISH and GISH for Detection and Physical Mapping of Alien Segments

Fluorescence in situ hybridization (FISH) and genomic in situ hybridization (GISH) have been extensively used to identify alien chromosome segments in wheat genome. The first such attempts were made during the 1990s, when segments of rye and *Aegilops tauschii* chromosomes could be identified using FISH, GISH (Friebe et al. 1995a, b, c), and multicolor FISH (McFISH; Mukai and Yamamoto 1998). As early as 1992, GISH was also used to identify alien chromatin from several alien species (*Leymus multicaulis*, *Thinopyrum bessarabicum*, *Hordeum chilense*, *H. vulgare* L., and *Secale cereale*) in wheat chromosomes (Schwarzacher et al. 1992). Research work on detection of *Thinopyrum* alien segments in wheat using GISH were also reviewed by Chen (2005). Recently, a wheat-*Ae. biuncialis* $3M^b(4B)$ disomic substitution and a $3M^b.4BS$ centric fusion in the F_3 progenies were identified using in situ hybridization with genomic DNA probes (FISH and GISH) and SSR markers (Farkas et al. 2014).

1.4.2 Use of Molecular Markers for Detection of Alien Segments

Molecular markers have also been utilized to locate and map alien segments on wheat chromosomes. In a recent study, Olson et al. (2013) transferred an *Ae. tauschii* alien segment carrying resistance against African stem rust fungus race TTKSK (Ug99) to an elite hard winter wheat line, KS05HW14. In BC_2 mapping populations, bulked segregant analysis (BSA) allowed identification of marker loci on 6DS and 7DS linked to stem rust resistance genes transferred from *Ae. tauschii* accessions TA10187 and TA10171, respectively. Linkage maps were developed for both genes and closely linked markers were identified, which can be used for selection and pyramiding with other Ug99-effective stem rust resistance genes. The *Ae. tauschii*-derived resistance genes were temporarily designated *SrTA10187* (associated with SSR loci *Xcfd49* and *Xbarc173*) and *SrTA10171* (associated with SSR loci *Xgdm88* and *Xwmc827*). These genes will serve as valuable resources for stem rust resistance breeding. In another recent study, alien segments carrying genes *Lr57*, *Yr40,* and *Sr53* earlier transferred from chromosome $5M^g$ of *Ae. geniculata* to chromosome 5D of wheat (Kuraparthy et al. 2007a, b, c; Liu et al. 2011) were recently mapped using SNPs (Tiwari et al. 2014). These examples illustrate that molecular markers can be effectively used for mapping and transfer of alien segments across wheat genotypes.

1.4.3 Radiation Hybrids for Identification of Alien Genes

Efforts have also been made to decipher the genetic architecture of alien segments available in wheat cultivars. Such an analysis was often difficult due to lack of pairing between the alien segment with the corresponding wheat segment, thus eliminating the possibility of obtaining recombinants for genetic analysis. An alternative approach was followed in a recent study, where Cao et al. (2011) localized the *Pm21* gene to a segment using radiation hybrid mapping and also used microarray analysis to identify candidate genes induced on infection of this cultivar with powdery mildew pathogen, *Bipolaris graminis* f. sp. *tritici* (*Bgt*).

1.5 Limitations in Alien Gene Transfer

In the past, there have been two major factors that have reduced the effectiveness of wheat/alien gene transfer. These are briefly discussed in this section.

1.5.1 Insufficient Number of Markers

The first limitation of alien gene transfer has been the availability of insufficient number of markers to screen large populations of wheat for the presence of alien chromosome segments. However, by combining comparative mapping with next generation sequencing (NGS) technology, it is now possible to develop an unlimited number of markers for any part of the genome. These markers are now being used to screen large populations for specific introgressions in monocot species (Tiwari et al. 2014).

1.5.2 Linkage Drag in Alien Gene Transfer

The second limitation in alien gene transfer is that an alien segment introgressed into wheat is often associated with some deleterious genes resulting in reduction in yield and/or fitness. Unfortunately, it is often very difficult to reduce the chromosome segment further, even by additional suppression of pairing control genes like *Ph1*. An alternative approach to reduce the size of a chromosome segment involved intercrossing of two lines with different but overlapping alien chromosome segments that carry the same target gene. As a result of recombination between the two overlapping alien segments, in the presence of pairing control genes, some of the progeny produced will carry a reduced alien chromosome segment that would carry the target gene but not the deleterious genes. However, this approach described by Sears for two *Aegilops umbellulata* chromosome segments carrying a gene for stem rust resistance (*Sr* genes) required identification of lines possessing overlapping alien chromosome segments in the first place (see Islam and Shepherd for a review). This strategy has rarely been followed due to lack of markers available to identify individuals carrying overlapping alien chromosome segments. However, the sequencing of the model genomes and the development of NGS technology provide means by which markers would be available for the whole genome of an alien species to allow selection of individuals with overlapping alien segments carrying the target gene(s).

1.6 Taxonomy of Alien Species and Wheat

The taxonomy of the grasses belonging to the tribe Triticeae has also been a subject of discussion for the last more than five decades. Two important and unfortunate revisions involved the following: (i) During the late 1950s and early 1960s, all species of the genus *Aegilops* were merged within the genus *Triticum* on the ground that two of the three sub-genomes of hexaploid wheat (A, B, and D sub-genomes), namely B and D sub-genomes are derived from the genus *Aegilops* (*Ae. speltoides* and *Ae. tauschii*). It was argued that progenitors of two of the three sub-genomes of bread wheat belonging to the genus *Triticum* cannot come from another genus, *Aegilops*. The revised classification with new names for all species of *Aegilops* within the genus *Triticum* proposed by Bowden (1959) was used by scientists in the North America and elsewhere for almost two decades (1965–1985), till Gupta and Baum (1986) questioned this classification. Later, van Slageren (1994) also recognized *Triticum* and *Aegilops* as two independent valid genera, with the result that during the last more than two decades now, once again *Aegilops* has been recognized as valid genus and the use of new names of *Aegilops* species within the genus *Triticum* was discontinued. This old classification has been followed in listing alien species in Tables 1.3 and 1.4). One major disagreement is the treatment of *Amblyopyrum* (formerly *Ae. mutica*) as a separate genus (van Slageren 1994); in

Table 1.3 Some examples of alien species and the genes that were successfully utilized for wheat improvement

Alien species	Wheat cultivar	Gene/chromosome	Reference
Th. ponticum		*Sr43* (7el/7DL)	Kim et al. (1993)
Th. intermedium	L693 KSUD27, MWG684 SFR1	YrL693 (–/1B)	
	T4 (TA5504)	*Lr38*, 7a [7Ai#2L (7D)]	Friebe et al. (1993, 1996a, b)
Th. elongatum	Agatha	*Lr19*, 7D (T7DS_7DL-7Ae#1L)	
	Agent, Sears' translocations P83-171.1-12 (TA3475); P84-171.5-7 (TA3476); P73-231.1b-2, P75-231-1 (TA3506)	*Lr24*, 3D, PSR1203	McIntosh et al. (1977), Jiang et al. (1994a, b)
	Sears' translocation P75-271.3-2 (TA3494)	*Lr29*, 7D (T7DL-7Ae#1L_7Ae#1S)	Friebe et al. (1996a, b)
E. trachycaulus (TA12052)	WGRC45	Undesignated, 1B (T1B_1HtS)	Friebe et al. (2005)
Ae. umbellulata	Transfer	*Lr9*, 6BL (T6BS_6BL-6U#1L)	Sears (1956, 1961), Schachermayr et al. (1994), Autrique et al. (1995), Friebe et al. (1996a, b)
Ae. ventricosa	VPM1	*Lr37*, 2AS	Bariana and McIntosh (1993)
Ae. kotschyi	Line S14	*Lr54/Yr37*, 2D	Marais et al. (2005)
Ae. sharonensis	Line 0352-4	*Lr56/Yr38*, 6A	Marais et al. (2006)
Ae. geniculata PAU-T756 (TA10437)	TA5602 [DS WL711 5M^g(5D)]	*Lr57*, 5DS (T5DL_5DS-5M^{g}S)	Kuraparthy et al. (2007a)
Ae. triuncialis (TA10438)	TA5605 (WL711*4/TA10438)	*Lr58*, 2BL (T2BS_2BL-2tL)	Kuraparthy et al. (2007b)
Ae. peregrina	Line 0306	*Lr59*	G. F. Marais, unpublished
Ae. speltoides	CS 2A/2M#4/2, RL6079	*Lr28*, 4A (T4AS_4AL-7S#2S), OPJ-02378	McIntosh et al. (1982), Friebe et al. (1996a, b), Naik et al. (1998)
Ae. speltoides/T. monococcum amphiploid	RL5711	*Lr35*, 2B (T2B/2S#2)	Kerber and Dyck (1990), Friebe et al. (1996a, b)

(continued)

Table 1.3 (continued)

Alien species	Wheat cultivar	Gene/chromosome	Reference
Pop. No. 2’	Line 2-9-2	*Lr36*, 6BS (T6BL_6BS-6BS#2S)	Dvorak and Knott (1990)
	CI17882, CI17884, CI17885, KS90H450	*Lr47*, 7A (Ti7AS-7S#1S-7AS_7AL)	Friebe et al. (1991)
TA1836	WGRC47	Unknown	Brown-Guedira et al. (2003)
Ae. tauschii	Uruguay	*Lr1*, 5DL, PSR567 GLK621	McIntosh et al. (1965), Ling et al. (2004)
	Festiguay, Kenya W1483	*Lr2, Lr15*, 2DS	Luig and McIntosh (1968)
RL5289 (TA1599), TA1649, TA1670, TA1691, TA2378, TA2468, TA2470, TA2472, TA2527, TA2528, TA2529, TA2530	RL5406, WGRC7, WGRC16	*Lr21*, 1DS, KSUD14 (*Lr40* is identical to Lr21)	Kerber and Dyck (1969), Huang and Gill (2001)
RL5271	RL5404	*Lr22a*, 2DS	Dyck and Kerber (1970)
RL5497-1	RL5713	*Lr32*, 3DS, BCD1278 CDO395	Kerber (1987), Autrique et al. (1995)
Not found in *Ae. Tauschii*	RL6058, PI58548	*Lr34/Yr18*/Bdv1, 7DS, SWM10	Dyck (1977), Bossolini et al. (2006), Lagudah et al. (2006)
TA1675, TA2460, TA2470, TTCC295 (*Ae. cylindrica*)	WGRC2, WGRC10, WGRC16, WX930249-4-1	*Lr39*, 2DS, GDM35 (*Lr41* is identical to *Lr39*)	Raupp et al. (2001), Singh et al. (2003)
	WGRC11	*Lr42*, 1DS	Cox et al. (1994a, b)
	WGRC16	*Lr43, Lr21, Lr39*	G.L. Brown-Guedira, unpublished
RL5683, RL5686, RL5688, RL5689, RL5778, RL5688; RL5662, RL5764, RL5766, RL5767, RL5781-1,RL5782-1 RL5766, RL5767 RL5662	RL5865 (TC/RL5766), RL5866 (TC/RL5767), RL5867 (TC/RL5662), RL5869, RL5868	*LrA*, 2DS (not allelic to *Lr39*) *LrB*, 5D; LrC (not allelic to *Lr39*, suppressed at the hexaploid level); LrD (not allelic to *Lr39*, suppressed at the hexaploid level); ALrA ALrB ALrC	Innes and Kerber (1994)
TA2541, TA1661, TA1683, TA1585, TA1583, TA1672, TA1665, TA1667, TA1677, TA2482	WGRC12	ALrD ALrE ALrF ALrG ALrH ALrI ALrJ ALrK ALrL	Miller (1991)

(continued)

Table 1.3 (continued)

Alien species	Wheat cultivar	Gene/chromosome	Reference
Triticum timopheevii	FTF, Sabikei 12, Timvera W1308, PI170925 (Red Egyptian type)	*Lr18*, T5BS_5BL-5G#1L	McIntosh (1983), Yamamori (1994), Friebe et al. (1996a, b)
TA145, TA870, TA874, TA895, TA1520	WGRC36	*Lr50*, 2BL, GWM382	Brown-Guedira et al. (1999, 2003)
TA28, TA913, TA1538	WGRC35	Unknown	Brown-Guedira et al. (1999)
TA30		Unknown	Brown-Guedira et al. (1999)

Table 1.4 Examples of using FISH, GISH, and DNA-based molecular markers for mapping alien segments in derived lines of wheat

Alien species/genome	Wheat cultivar	Alien gene/chromosome	FISH/GISH/marker type used	Reference
Ae. tauschii (KB) *Ae. tauschii* (Lr21)	PBW343	1D, 2D, 4D, 6D, 1D	SSR SNP	Chhuneja et al. (2008), Neelam et al. (2013)
Th. ponticum	Jinan177		FISH pSc119.2, pAs1, GISH	Wang et al. (2005)
Th. intermedium	Z-148; MY11	1St-1D	PLUG; SCAR	Hu et al. (2012)
Ag. elongatum (*Lr19* + *Yp*); Ae. *longissima (Pm13)*	4*x* wheat	7Ag-7A 3S-3B	FISH, GISH	Ceoloni et al. (2000)
Ag. elongatum (*Lr29*)	RL6080	7Ag-7D	SCAR	Procunier et al. (1995)
Secale cereale (*Lr25*)	RL6084	2R-4A	SCAR	Procunier et al. (1995)
Ae. speltoides (*Sr39*)		2S-2B		Niu et al. (2011)
Th. intermedium				
Ae. geniculata (*Lr57, Yr40*)	TA5601 TA5602	$5M^{g}S$-5DL	SNP	Tiwari et al. (2014)
Ae. caudata (*LrAC* = *Lr57*)	T291-2 (PBW343)	5C-5D	SSR	Riar et al. (2012)

Table 1.4, it is retained within the genus *Aegilops* as *Ae. mutica*. (ii) Another important and unfortunate proposal made by Dewey (1984) and Love (1984) was the genomic system of classification, where no two taxa with the same genomic constitution could belong to the same genus. As a consequence, a large number of new genera were created, where *Aegilops–Triticum* group was split into as many as

16 genera (5 genera from *Triticum* and 11 genera from *Aegilops*). Consequently, diploid, tetraploid, and hexaploid wheats were assigned to different and independent genera based on their genomic constitutions. This classification was also criticized by us (Baum et al. 1987) and was never put to usage by geneticists and plant breeders.

1.7 Summary and Future Perspectives

Cytogenetic manipulation in polyploid wheats has been relatively easier due to the presence of homoeologous chromosomes carrying duplicate or triplicate genes, so that loss of one copy is tolerated due to compensating effect of the other inserted chromosomes, segments, or genes. It is also for this reason that the genetic variation from the primary, secondary, and tertiary gene pools has been extensively utilized for wheat improvement with remarkable success. The work involving this activity has been adequately covered in several earlier reviews, so that most of this earlier work has not been included in this chapter. Readers may like to consult these earlier reviews for details about the earlier work. However, a summary of this earlier work and some of the recent work on this subject has been covered in this chapter. In recent years, some of the limitations in the transfer of alien chromosome segments carrying desirable segments have now been overcome with the availability of gene targeting approaches and the DNA-based molecular markers; these have been briefly described.

With the availability of the newer approaches including those of gene targeting (not covered in this chapter) and the use of DNA-based molecular markers, a renewed interest in the transfer of alien genetic variation for wheat improvement and in the study of wheat cultivars or genetic stocks carrying alien genetic variation has been witnessed in recent years. More such studies will be conducted in future. For instance, the BBSRC-funded WISP (Wheat Improvement Strategic Program) consortium has been launched in UK with major emphasis on the use of alien genetic variation for wheat improvement. It has been recognized that the alien species carry wealth of genetic resource, which has only been marginally utilized so far. Major part of this genetic resource remains still unexploited and will be the subject of future research in the field of molecular cytogenetics and molecular-/genomics-based plant breeding.

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